

# Are Subitizing and Counting Implemented as Separate or Functionally Overlapping Processes?

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**Enumeration of small groups of four or fewer objects is very fast and accurate (often called “subitizing”), but gets slower and more error prone for more than four items (“counting”). Many theories have been proposed to account for this dichotomy, most suggesting that “subitizing” and “counting” are two qualitatively different and separable processes. Others, in contrast, have proposed that the two operations reflect two different levels along a continuum of complexity. In this paper we present a PET study that attempts to characterize subitizing and counting at a neural level in order to investigate whether they are implemented as separate or functionally overlapping processes. Subjects performed an enumeration task on visual arrays of dots that varied in numerosity (1–4 and 6–9 dots) and spatial arrangement (canonical and random). The results demonstrated a common network for subitizing and counting that comprises extrastriate middle occipital and intraparietal areas. The intensity and spatial extent of this network were modulated by the number of dots and their spatial arrangement: activation increased as the number of items in the visual array increased, reaching maximum peak and extent for counting 6–9 randomly arranged items. Direct comparison between subitizing and counting showed that counting, relative to subitizing, was correlated with increased activity in this occipitoparietal network, while subitizing did not show areas of increased activation with respect to counting. Results speak against the idea of the two processes being implemented in separable neural systems.** © 2002 Elsevier Science

**Key Words:** PET; subitizing; counting; number processing; attentional shifts; parietal cortex; pattern recognition.

## INTRODUCTION

Visual object enumeration is very rapid and accurate for four or fewer items, but slow and error prone for over four items. Many theories have been proposed to account for this dichotomy, most suggesting that “subitizing” (the ability to enumerate a small group of four or fewer objects fast and accurately) and “counting” (the error prone and slow process of serially counting more than five objects) are two processes of a radically different cognitive and neural nature (Kaufman *et al.*, 1949; Mandler and Shebo, 1982; Trick and Pylyshyn, 1993; Peterson and Simon, 2000). A very different position on the issue of the separability of the two processes is taken by those who propose that the two operations are not different in nature, but simply reflect two different levels along a continuum of difficulty (Balakrishnan and Ashby, 1991, 1992). To date, the question of separability of the two processes, both at the cognitive and at the neural level, remains open.

In this paper, we first review previous studies of enumeration processes, and then we present a functional imaging study that attempts to address unanswered questions. In particular, the aim of this study was to characterize enumeration and counting at a neural level in order to investigate whether they are implemented as separate or functionally overlapping processes.

Suggestions that the processes underlying subitizing and counting are different in nature come from both behavioral and neuropsychological studies. The earliest source of evidence for the existence of two separate processes comes from latencies of enumeration as a function of the numerosity: typical findings show that enumeration time increases slowly from one to three to four items (50–80 ms/item) and then starts increasing sharply and linearly (by about 200 ms/item) (Akin and Chase, 1978; Mandler and Shebo, 1982; Trick and Pylyshyn, 1993; Simon *et al.*, 1998). Mandler and Shebo’s (1982) explanation for the low reaction times (RTs) in the subitizing range (1–4) was that the dots in the displays always form a familiar

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shape: a line from two dots, a triangle from three dots, and a quadrilateral from four dots. Subitizing may therefore consist of the recognition of a familiar pattern and therefore rely on a separate mechanism that is not involved in counting. Another theory of the subitizing-counting dichotomy has been proposed by Trick and Pylyshyn (1993). According to these authors subitizing is based on a limited capacity preattentive visual process that is capable of individuating a maximum of four items in parallel, while counting requires serial shifts in spatial attention. Along the same line, others have suggested that the discontinuity in enumeration performance reflects a capacity-limited short-term memory system (Cowan, 2001).

Behavioral data also show that counting, but not subitizing, requires both ocular movements to locate and mark objects (or groups of objects) in space (Atkinson *et al.*, 1976a,b; Klahr and Wallace, 1976; Oyama *et al.*, 1981; Simon and Vaishnavi, 1996), and verbal working memory, specifically the subvocalization component (Logie and Baddeley, 1987). Moreover, counting is influenced by the spatial arrangement of objects (facilitated by perceptual groupability of items and by the geometry of the array) while subitizing is not (Atkinson *et al.*, 1976a,b; Mandler and Shebo, 1982; van Oeffelen and Vos, 1983).

Nevertheless, although behavioral data show a set of experimental manipulations that affect counting but not subitizing, the only experimental manipulation that has been shown to affect subitizing but not counting is one that prevents perceptual "pop-out" of the targets to be enumerated. Typically this is affected by using targets that differ from distractors by a combination of two features (as used in displays for conjunction search). With this manipulation, enumeration RTs increase linearly, with no apparent discontinuity, suggesting that under those conditions subitizing is prevented, and one only mechanism (serial counting) is deployed. This is the evidence that made Trick and Pylyshyn conclude that subitizing is based on the preattentive ability to apprehend up to four items in parallel (by means of assigning four attentional indexes in parallel, which they call FINST, as for Fingers of INSTantiation) (Trick and Pylyshyn, 1993, 1994). Even if this account is seductive in its simplicity, as a parallel model of subitizing it remains problematic, since it cannot accommodate the fact that RTs increase even in the subitizing range. In fact they attribute the subitizing slope to a response choice stage. They claim this stage consists in matching each FINSTed items with number names in a serial fashion. Therefore, there is still the possibility that subitizing and counting simply reflect two different levels along a continuum of difficulty. This point has been made by Balakrishnan and Ashby (1991, 1992), who analyzed a large set of behavioral enumeration data with refined statistical tests

and showed no statistical evidence of discontinuity in the reaction times between subitizing and counting. In contrast, their analysis showed that the "mental effort" (measured in terms of RTs) required to enumerate increased with each additional element in the display, both within and beyond the putative subitizing range. Neuropsychological data are thus particularly valuable: the presence of a double dissociation between counting and subitizing in brain-damaged patients would be strong evidence for the existence of two distinct processes, even if the two processes could, in principle, be working in complete synergy in normal adults (Shallice, 1988). However, the evidence for a double dissociation is unconvincing. One dissociation is revealed in a study of a group of patients with simultanagnosia (following lesions to the right parietal hemisphere). These patients showed intact subitizing (even if in some cases the subitizing range was limited to two items) but impaired counting (Dehaene, 1994). In the opposite direction two cases have been reported, but they do not present compelling evidence for the impaired subitizing vs intact counting dissociation. One patient, a developmental dyscalculic, Charles, when presented with sets of dots for unlimited time, was able to count to arbitrary limits, but showed an increasing monotonic function of 200 ms per dot from a single dot, suggesting that he was counting even in the normal subitizing range (Butterworth, 1999). Nevertheless, recent investigations on this patient showed that, when dots were presented very briefly (100 ms), his reaction time slope showed the typical discontinuous pattern around four (while he remained overall slower than normal controls) (M. Piazza and B. Butterworth, unpublished). This result suggests that this patient had a problem of lack of self-confidence in such enumeration task that led him to adopt a slow counting strategy even in the subitizing range. This was probably a consequence of his weakness in the domain of number cognition, more than a truly impaired subitizing mechanism. The other case was a patient with severe acquired acalculia who could not, on command, say how many dots were in an array unless she was permitted to count them aloud and use finger pointing (Cipolotti *et al.*, 1991). However, in this study, the investigators were not able to use computer-controlled presentation of dots, and the patient's counting limit was four, since she could not recall numbers above 4. These data are not conclusive with respect to the dissociability of subitizing and counting processes. Other neuropsychological data suggest that subitizing does not depend on awareness of an object's locality in egocentric space. For instance, three patients with neglect (following a lesion in the right parietal lobe) were able to report the total number of objects presented but showed extinction (the inability to consciously perceive objects in the contralesional space when the ipsilesional space is concurrently stimulated) when the task

was to locate the same objects in space (Vuilleumier and Rafal, 1999). This study only showed a number of objects in the subitizing range (up to four), and therefore the relation between the awareness of object's location in space and counting remains unclear. Overall, the neuropsychological literature suggests a crucial role for parietal areas in controlling voluntary shifts of attention that may also be required for counting. However, it does not provide a very good characterization of the neural substrates of subitizing and counting. Functional brain imaging may be able to fill this gap.

To date there are two functional imaging studies (using PET and fMRI) that examine enumeration processes (Sathian *et al.*, 1999; Fink *et al.*, 2001). Sathian *et al.* (1999) investigated the subitizing–counting dichotomy in light of the preattentive–attentive mechanisms first proposed by Trick and Pylyshyn (1993, 1994). These investigators presented subjects with a visual search type of display, consisting of 16 bars, containing 1 (pop-out), 1–4 (subitizing), and 6–9 (counting) vertical bars in a variable number of horizontal bars. The task consisted of counting vertical bars. The results showed that counting, relative to subitizing, activated a widespread network of brain regions comprising bilateral middle occipital and superior parietal and right frontal regions. On the other hand, subitizing, relative to single target detection, activated foci only in the middle occipital extrastriate cortex. This was interpreted as supporting the idea that subitizing is a preattentive process, while counting is a serial process that involves shifting visual attention. However, interpretation of the results is not straightforward for three reasons: first, counting and visual search operations were confounded, because the type of search paradigm used explicitly forced subjects to make serial search through the set in order to single out the relevant elements, and therefore the brain activation found in the counting range could be attributed to the visual search operations rather than to a counting process itself. Second, since the total number of elements in the display was constant (16), the ratio between targets and distractors increased with the number of targets to be counted. This means that the probability that one vertical item (target) was surrounded by horizontal items (distractors) was much higher in the subitizing range than in the counting range. Therefore, the perceptual salience of the targets was not matched in the subitizing (1–4) and counting (6–9) conditions, and so the attentive effort to isolate targets from the background may have led to brain activation that could not be strictly related to enumeration processes. Finally, the rate and duration of presentation varied between the subitizing and the counting conditions, because the display remained on the screen until the subjects gave their answer. This may have created artifacts (Price and Friston, 1997).

In the other neuroimaging study of numerosity (Fink *et al.*, 2001), subjects were presented with visual arrays of 3 to 5 dots on which they performed two types of matching tasks: a numerosity matching task comparing the numerosity of the array to 4 and a shape matching task comparing the shape of the array to a square. Results show that shape matching activated temporoparietal, cingulate, and dorsolateral prefrontal cortices, relative to numerosity matching, while the reverse contrast (numerosity vs shape), revealed striate, extrastriate, and inferior frontal activations. The author's interpretation is again in favor of the numerosity task relying on preattentive parallel processing. However, although this study is interesting, it is not really tapping into enumeration strategies. In fact, it is clear that a matching task can in principle be performed on the basis of information that is perceptual rather than numerical. Subjects could have deployed strategies such as matching the sets in terms of brightness, density, and occupancy, which were not controlled in the display. This would explain the higher involvement of visual areas and no involvement of parietal areas for the numerical task with respect to the shape task. Also, it does not contribute to the debate we are directly interested in, about whether subitizing and counting are separable. Therefore, the issue of separability requires further investigation.

The current experiment makes use of PET to investigate the question of separability of subitizing and counting processes and to investigate further the neural basis of enumeration processes in general. It also attempts to investigate the validity of one specific model to account for subitizing that links subitizing to pattern recognition (Mandler and Shebo, 1982). If the two processes are separable, they may rely on two distinct neural systems. If a pattern recognition is involved in subitizing, it should activate brain areas typically found in object recognition (i.e., occipitotemporal and fusiform areas) (Ungerleider and Minshkin, 1982; Moore and Price, 1999; Malack *et al.*, 1995, Grill-Spector *et al.*, 1998), while counting should involve a wider network that may not involve strong activation of the areas related to subitizing.

To ensure that the outcomes could be interpreted straightforwardly in terms of the normal behavioral results, the stimuli used were those standardly used in enumeration tasks—black dots on a white background.

## METHODS

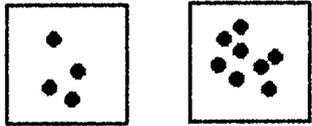
### Subjects

Nine right-handed English-speaking male volunteers (mean age 29 years, range 22–45 years) with no history of neurological disorders gave informed consent to participate in 12 consecutive measurements of rCBF using PET. One subject suffered cramps during the

### Canonically arranged dots



### Randomly arranged dots



**FIG. 1.** Examples of canonical and random arrangements of dots presented for quantification, for numerosity 4 and 8.

acquisition of the 7th scan, and only 6 scans (of 12) were included in the analysis. The study was approved by the local hospital ethics committee and the Administration of Radioactive Substances Advisory Committee (UK) (ARSAC).

### Design and Task

The experiment comprised a  $2 \times 2$  factorial design with two baseline conditions. The variables manipulated were: (i) numerosity of dots that had two levels—subitizing range (1–4 dots) and counting range (6–9 dots); and (ii) spatial arrangement of dots that had two levels—canonical and random. For canonical arrangements, an easily recognizable and geometrical arrangement of dots was assigned to each numerosity, while for random arrangement, a sparse distribution of dots was assigned to each numerosity (see Fig. 1). The task was to say aloud, as quickly and accurately as possible, the number of dots presented. Responses were recorded using a microphone and used to measure RTs and accuracy.

The baseline conditions comprised one baseline for the subitizing range and one for the counting range. The former consisted of the presentation of one single dot, to which subjects were asked to respond with the word “one.” The latter consisted of a combination of two different scans: in the first the stimulus always consisted of the same display of six dots, and the subjects were asked to simply respond with the word “six” without performing any counting; in the second baseline scan the stimulus was always a display of nine dots, and subjects were instructed to respond with the word “nine” without counting. These baseline conditions were included in order to control for the visual stimulation on the two numerosity ranges (1–4 and 6–9) and

for verbal production and auditory processing, even though the visual stimulation was not completely controlled in the case of the 1–4 range. Instructions were given prior to each scan.

### Stimuli and Procedures

Stimuli in all conditions consisted of black dots ( $0.36^\circ$ ) on a white background, arranged on a virtual 32-space matrix that subtended a visual angle of  $2^\circ$  and were presented at the center of a 13-in. video monitor of a Macintosh computer 7200/90. For each subject, 12 scans were acquired, 8 for the experimental tasks and 4 for the baseline tasks in a pseudorandom order.

During each scan, 32 different stimuli were presented for 2500 ms each, at a rate of one every 4 s, preceded by a fixation point that lasted for 500 ms and followed by 1000 ms of blank screen. Within each experimental scan, the same stimulus was presented four times. Therefore, within the experiment, random and canonical conditions were controlled within subjects so that any repetition priming effects would be equivalent in each condition. In order to facilitate a pattern recognition strategy for the canonical arrangement of dots, the subjects were familiarized with the canonical patterns being presented with each numerosity four times prior to the scanning session. In order not to trivialize the task, but also to maximize occurrence of crucial trials for each scan (Corbetta *et al.*, 1993), we manipulated the probability of occurrence of each stimulus within each experimental scan. During the 45 s of data acquisition period, the probability of appearance of the crucial stimuli (e.g., 1–4 dots for the subitizing range condition) was 100%, but decreased to 30% in the period preceding and following it. Noncrucial stimuli (e.g., 6–9 dots for the subitizing range condition) were randomly chosen from the other noncrucial conditions. For the baseline conditions, no noncrucial trial was presented and therefore the probability of occurrence of the crucial stimuli was 100% through the whole scan.

### PET Scanning

The 12 PET scans were obtained using a Siemens/CPS ECAT EXACT HR+ (Model 962) PET scanner (Siemens/CTI, Knoxville, TN). Participants received a 20-s intravenous bolus of  $H_2^{15}O$  at a concentration of 55 Mbq  $ml^{-1}$  and at a flow rate of 10  $ml\ min^{-1}$  through a forearm cannula. Images were reconstructed by filtered back projection into a  $128 \times 128 \times 63$  image matrix (voxel size  $2.1 \times 2.1 \times 2.4$  mm) using measured attenuation correction. For each subject, a T1-weighted structural magnetic resonance (MR) image was obtained with a 2-T Magnetom Vision scanner (Siemens, Erlangen, Germany).

## Data Analysis

The data were analyzed with statistical parametric mapping (SPM99; Wellcome Department of Cognitive Neurology, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>) implemented in Matlab (Mathworks Inc., Sherborn, MA) using standardized procedures (Friston, 1995a,b). Head movements that occurred between scans were corrected by realigning the time series with the first scan. The realigned images were normalized into a standard stereotaxic space (Talairach and Tournoux, 1988) to allow for intersubject averaging and then smoothed using a Gaussian filter (full-width at half-maximum) of  $16 \times 16 \times 16$  mm to accommodate intersubject differences in anatomy and to increase signal-to-noise ratio. Conditions were estimated in a fixed effect fashion according to the general linear model at each voxel. In this experiment, we were interested in the effects of quantifying a set of dots compared to a low-level baseline and in the effect of number of dots (subitizing range (1–4) vs counting range (6–9) and in the effects of arrangement (canonical vs random) that were specific or common to the two numerosities (1–4 and 6–9). The contrasts were as follows:

## Main Effects

### *Effect of Task: The Quantification System*

Areas more activated during a quantification task (enumeration), irrespective of numerosity and arrangement of dots, were identified with a contrast of all the experimental conditions (1–4 canonically arranged dots, 6–9 canonically arranged dots, 1–4 randomly arranged dots, 6–9 randomly arranged dots) versus the baselines conditions (a single dot, and 6 dots, or 9 dots). In these areas, we report  $Z$  values for all the simple effects separately.

### *Effects of Numerosity on Quantification*

*Activation for enumerating 6–9 dots versus 1–4 dots, irrespective of arrangement.* Areas more activate for enumerating 6–9 dots irrespective of arrangement were identified with a conjunction (Price and Friston, 1997) of two contrasts: 6–9 randomly arranged dots > 1–4 randomly arranged dots and 6–9 canonically arranged dots > 1–4 canonically arranged dots. In addition, to control for visual input, we used the inclusive masking option in SPM to mask the conjunction with contrasts 6–9 random > 6–9 baseline and 6–9 canonical > 6–9 baseline.

*Activation for enumerating 1–4 dots versus 6–9 dots, irrespective of arrangement.* The same procedure was used to identify areas more activate in enumerating 1–4 dots than 6–9 dots, irrespective of arrangement. Contrasts 1–4 random > 6–9 random and 1–4 canon-

ical > 6–9 canonical were combined using conjunction analysis masking with contrasts (1–4 random > 1–4 baseline) and (1–4 canonical > 1–4 baseline).

### *Effects of Spatial Arrangement on Quantification*

*Activation for canonical versus random arrangement, irrespective of numerosity.* Areas more active in the canonical arrangement irrespective of numerosity were identified with a conjunction of contrasts (1–4 canonical > 1–4 random) and (6–9 canonical > 6–9 random). In addition, to ensure that the areas identified corresponded to an increase in activity in the quantification tasks rather than a decrease in activity for the baseline conditions, we excluded any regions that were not more active for canonical than the baseline ( $P < 0.01$ ). This was achieved using the inclusive masking option in SPM and masking the conjunction with contrasts 1–4 canonical > 1–4 baseline and 6–9 canonical > 6–9 baseline.

*Activation for random versus canonical arrangement, irrespective of numerosity.* The same procedure was used to identify areas more activate for the random arrangement than the canonical irrespective of number of dots. Contrasts 1–4 random > 1–4 canonical and 6–9 random > 6–9 canonical were combined using the conjunction analysis and the result was masked with contrasts 1–4 random > 1–4 baseline and 6–9 random > 6–9 baseline.

## Specific Effect

### *Effects Specific for 6–9 Dots Randomly Arranged (Counting)*

The inclusive masking option was used to identify the areas that were more active for 6–9 randomly arranged relative to 6–9 canonical (at  $P < 0.05$  corrected), masked (at  $P < 0.001$  uncorrected) with 6–9 randomly arranged relative to (i) 6–9 baseline; (ii) 1–4 random; and (iii) the numerosity by arrangement interaction.

### *Effects Specific for 6–9 Dots Canonically Arranged*

Six to 9 canonically arranged were contrasted with 6–9 randomly arranged (at  $P < 0.05$  corrected) and masked (at  $P < 0.001$  uncorrected) with 6–9 canonically arranged relative to (i) 6–9 baseline; (ii) 1–4 canonical; and (iii) the numerosity by arrangement interaction.

### *Effects Specific for 1–4 Dots Randomly Arranged*

One to 4 randomly arranged relative to 1–4 canonical (at  $P < 0.05$  corrected) was masked (at  $P < 0.001$  uncorrected) with 1–4 randomly arranged relative to (i) 1–4 baseline; (ii) 1–4 canonical; and (iii) the numerosity by arrangement interaction.

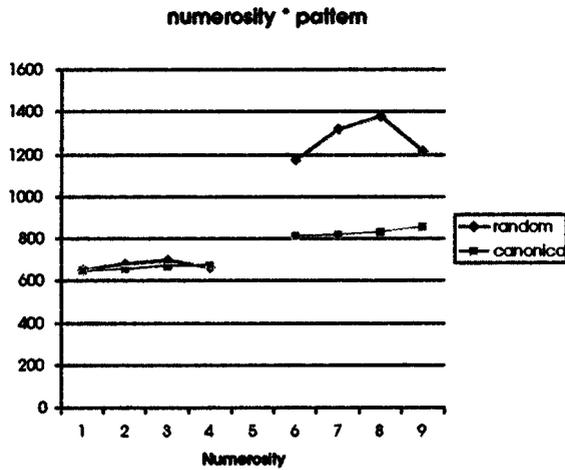


FIG. 2. Median reaction times averaged across subjects, in the quantification task.

### Effects Specific for 1–4 Dots Canonically Arranged

One to 4 canonically arranged relative to 1–4 random (at  $P < 0.05$  corrected) was masked (at  $P < 0.001$  uncorrected) with 1–4 canonically arranged relative to (i) 1–4 baseline; (ii) 1–4 random; and (iii) the numerosity by arrangement interaction.

For each of the above effects we discuss activation that reached significance at  $P < 0.05$  corrected for multiple comparisons. A level of significance of  $P < 0.001$  will be accepted for the discussion only for specific regions of interest defined by previous neuroimaging and neuropsychological data. The *a priori* areas of interest were parietal regions that have previously been activated in neuroimaging studies of shifts of attention in space and of attentional modulation of visual inputs. Interestingly, the same regions have been shown to play a crucial role in the manipulation of numbers (typically in number comparison and calculation) both in imaging and in neuropsychological studies (Cipolotti *et al.*, 1991; Dehaene and Cohen, 1994, 1995; Dehaene *et al.*, 1998; Thioux *et al.*, 1999; Vuilleumier and Rafal, 1999; Rickard *et al.*, 2000; Pesenti *et al.*, 2000). A second region of interest is extrastriate occipitotemporal cortex that has previously been activated in studies of pattern recognition and naming (Kanwisher *et al.*, 1996; Rolls and Booth, 1998; Moore and Price, 1999; Murtha *et al.*, 1999) and may be one of the areas in which activity is strongly influenced by top-down attentional modulatory input from parietal cortex (Friston and Büchel, 2000; Chawla *et al.*, 1999).

## RESULTS

### Behavioral Data

Overall, accuracy of performance was close to 100% for all four conditions, and therefore no further analy-

sis of errors was performed. Figure 2 shows RTs as a function of number of dots and of arrangement. Subjects showed the expected subitizing–counting performance with the random arrangement, resulting in the discontinuity of the slopes in the subitizing range and in the counting range. The drop in RTs for nine dots was interpreted as due to a “guessing end effect” (Sathian *et al.*, 1999; Simon *et al.*, 1998) and therefore was excluded from further behavioral analysis. Slopes for the canonical arrangement were approximately 8 ms for the subitizing range and 13 ms for the counting range. For the random arrangement, they were 20 ms per item for the subitizing range and 105 ms per item for the counting range. This last value was lower than usually found in counting experiments (see Trick and Pylyshyn, 1993, for a review), probably because each random pattern was repeated throughout the experiment, leading subjects to “within experiment learning.” Nevertheless, the RT data indicate the effect of subitizing and counting range for the random arrangement. The behavioral data also show that subjects were better at quantifying the sets with a canonical spatial arrangement in the counting range. This facilitation of the canonical arrangement over the random arrangement did not appear in the subitizing range. This is in agreement with what has previously been observed (Mandler and Shebo, 1982; Dehaene and Cohen, 1994). These effects were tested by entering reaction times on correct trials only into a  $2 \times 2$  repeated measure analysis of variance, with number of dots [subitizing range (1–4 dots) and counting range (6–9 dots)] and spatial arrangement of dots (canonical and random) as between subject factors. The analysis showed a significant main effect of number of dots [ $F(1,8) = 46.3$ ,  $P < 0.0001$ ], with counting being much slower than subitizing (670 and 1112 ms); a significant main effect of spatial arrangement [ $F(1,8) = 21.39$ ,  $P < 0.005$ ], with random arrangements enumerated much slower than canonical arrangements; and finally, a significant number of dots  $\times$  arrangement interaction [ $F(1,8) = 16.07$ ,  $P < 0.005$ ]. Planned comparison showed that the effect of number of dots was modulated by their spatial arrangement: for the random arrangement, counting was significantly slower than subitizing [ $F(1,8) = 61.327$ ,  $P < 0.001$ ], while for the canonical arrangement the difference between subitizing and counting did not quite reach significance [ $F(1,8) = 4.672$ ,  $P = 0.062$ ]. Moreover, planned comparisons also showed that in the counting range, the dots arranged in a random display were enumerated slower than when arranged in a canonical way [ $F(1,8) = 35.057$ ,  $P < 0.0005$ ], while in the subitizing range there was no difference between the two arrangements.

**TABLE 1**  
The Quantification System

Areas		Talairach coordinates			Cluster size (No. of voxels)	Z scores					Other effects <sup>a</sup>
		x	y	z		All > baseline	6–9 Ran > baseline	6–9 Can > baseline	1–4 Ran > baseline	1–4 Can > baseline	
Middle occipital	R	36	–76	–12	}4713	5.8	5.1	3.6	4.4	2.9	N
		36	–60	–14		<b>4.7</b>	<b>4.9</b>	3.4	4.4	n.s.	
	L	–32	–90	0	}2523	<b>5.2</b>	4.7	3.5	3.2	3.0	N, C
		–48	–78	–14		<b>4.9</b>	<b>4.9</b>	3.4	2.9	n.s.	
		–10	–92	–8		<b>4.5</b>	4.6	3.5	3.3	n.s.	
Intraparietal	R	30	–70	44	<sup>b</sup>	<b>5.2</b>	<b>5.9</b>	3.9	2.7	2.9	C
	L	–28	–70	38	83	3.4	3.7	2.5	n.s.	n.s.	N
Midbrain		–2	–34	–10	449	<b>4.5</b>	3.9	<b>4.8</b>	n.s.	n.s.	n.s.
Middle frontal	R	54	32	36	37	3.6	4.2	n.s.	n.s.	n.s.	n.s.
Cerebellum	L	–36	–40	–32	236	3.8	3.7	3.4	2.6	2.9	n.s.

*Note.* Regions that show increased activation during quantification tasks for all numerosities and arrangements relative to the baseline tasks and relative Z scores. Can, canonical arrangement; Ran, random arrangement. In bold type, Z scores corrected for multiple comparisons, at  $P < 0.05$ , and related regions. In the column “other effects” regions that show increased activation as the number of dots increases, irrespective of arrangement (N), and regions that showed increased activation specifically in counting 6–9 randomly arranged dots (C) are indicated.

<sup>a</sup> Areas that are affected by other variables: N, numerosity; C, counting.

<sup>b</sup> This cluster is included in the right middle occipital one.

## Neuroimaging Data

### Main Effects

*Effect of task: The quantification system (see Table 1).* At a corrected level of significance, when subjects performed a quantification task, areas of enhanced brain activity were found in the middle/inferior occipital extrastriate cortex bilaterally, in the posterior bank of the right intraparietal sulcus, and in the midbrain. Decomposition of the main effect of task into simple effects for each condition relative to baseline showed that the significance of the main effect of task is modulated by the number of dots: it increases as the numerosity increases. Individual contrasts relative to baseline show that the activation both in extrastriate and in parietal areas is more significant for 6–9 dots than 1–4 dots irrespective of arrangement (see effect of numerosity below). At an uncorrected level, activation was also found in the left intraparietal sulcus, which was an *a priori* region of interest, in the right middle frontal gyrus, and in the left cerebellar hemisphere.

*Effects of numerosity on quantification (see Table 2).* Activation for enumerating 6–9 dots versus 1–4 dots, irrespective of arrangement: At a corrected level of significance, activation in the middle/inferior occipital extrastriate cortex bilaterally was enhanced for enumerating 6–9 dots compared with 1–4 dots, irrespective of spatial arrangement.

At an uncorrected level, there was also enhanced activation in the left posterior intraparietal sulcus and the right cerebellum. Only the former was an *a priori* region of interest.

Activation for enumerating 1–4 dots versus 6–9 dots, irrespective of arrangement:

There were no brain regions that were more active for enumerating 1–4 dots than 6–9 dots.

*Effects of spatial arrangement on quantification.* Irrespective of numerosity, there were no areas that were more active for either random or canonical arrangements.

### Specific Effect

The only specific effects were observed for (a) 6–9 dots randomly arranged (counting) which, relative to all the other conditions, enhanced activation in the left middle–inferior occipital areas and right superior parietal cortex (see Table 3).

There were no effects specific for (b) 6–9 dots canonically; (c) 1–4 dots randomly arranged; or (d) 1–4 dots canonically arranged.

## DISCUSSION

This study tested two main hypotheses:

1. That counting and subitizing are dissociable at the neural level; and
2. That quantifying familiar patterns of dots (canonically arranged arrays) relies on neural circuits linked to pattern recognition.

1. In relation to the dissociability of brain areas underlying counting and subitizing we found little evidence for subitizing or counting specific regions de-

**TABLE 2**  
Effects of Numerosity on Quantification

Area		Talairach coordinates			Cluster size (No. of voxels)	Z scores		
		x	y	z		All 6–9 > all 1–4	6–9 Ran > 1–4 Ran	6–9 Can > 1–4 Can
Inf./mid. occipital	R	30	–92	–4	}433	<b>5.1</b>	4.5	3.6
		44	–88	–4		4.0	3.4	4.0
		40	–88	10		3.9	3.4	4.0
	L	62	–56	–26	54	3.9	n.s.	n.s.
		–36	–86	–2	}291	<b>4.9</b>	<b>6.1</b>	3.4
Intraparietal Cerebellum	L	–8	–100	–10	18	4.4	3.4	3.4
	R	–28	–66	40	201	4.1	4.2	n.s.
		10	–72	–30		3.7	n.s.	n.s.

*Note.* Regions that show increased activation as the number of dots increases during quantification, irrespective of spatial arrangement scores (6–9 > 1–4, common to random and canonical arrangement). In bold type, Z scores corrected for multiple comparisons, at  $P < 0.05$ , and related regions.

spite 18 scans per condition (9 subjects  $\times$  2). Subitizing does not seem to rely on a separate dedicated neural mechanism that is not also involved in counting. In contrast, the results reveal a pattern of activation in bilateral middle occipital and parietal areas (see Table 2 and Fig. 3), where intensity and spatial extent is modulated by the number of dots and their spatial arrangement. Activation increases as the number of items on the visual array increases, reaching a maximum peak and extent when counting 6–9 randomly arranged items is required. This modulation mirrors behavioral data, in that RTs are higher for quantifying arrays of 6–9 than for 1–4 dots, and within the 6–9 range, they are higher for counting randomly arranged than canonically arranged dots.

2. In relation to pattern recognition strategy in the quantification tasks, we found that areas linked with object recognition in the bilateral occipitotemporal cor-

tex were activated for quantification irrespective of arrangement, and we did not find any effect specific to canonical spatial arrangement. It therefore appears likely that pattern recognition was evoked by all conditions, but when the configuration was not canonical (i.e., for random 6–9), there was additional contribution from the right superior parietal lobe.

In summary, this experiment identifies a network of areas comprising extrastriate middle occipital and posterior intraparietal areas that is more active for counting than for subitizing and also for subitizing than for the baseline (see Table 1).

The *middle occipital areas* are extrastriate visual areas that have been linked to object recognition even when visual input is controlled (Grill-Spector *et al.*, 1998; Moore and Price, 1999). Activation in the middle occipital regions during quantification, even when no

**TABLE 3**  
Effects Specific to Counting

Area		Talairach coordinates			Cluster size (No. of voxels)	Z scores			
		x	y	z		>6–9 Can	Interact ion <sup>a</sup>	>6–9 baseline	>1–4 Ran
Superior parietal	R	28	–68	50	462	<b>5.0</b>	3.6	<b>5.9</b>	<b>4.9</b>
Inf./mid. occipital	L	–22	–86	–14	}648	<b>4.8</b>	4.3	<b>4.6</b>	<b>6.1</b>
		–16	–88	–26		4.3	3.7	4.6	n.s.
	–42	–86	–14	22	3.4	n.s.	4.4	4.5	
	–40	–92	12	100	4.4	3.6	4.5	4.0	
	Anterior insula	R	38	18	–4	60	3.5	3.4	4.0

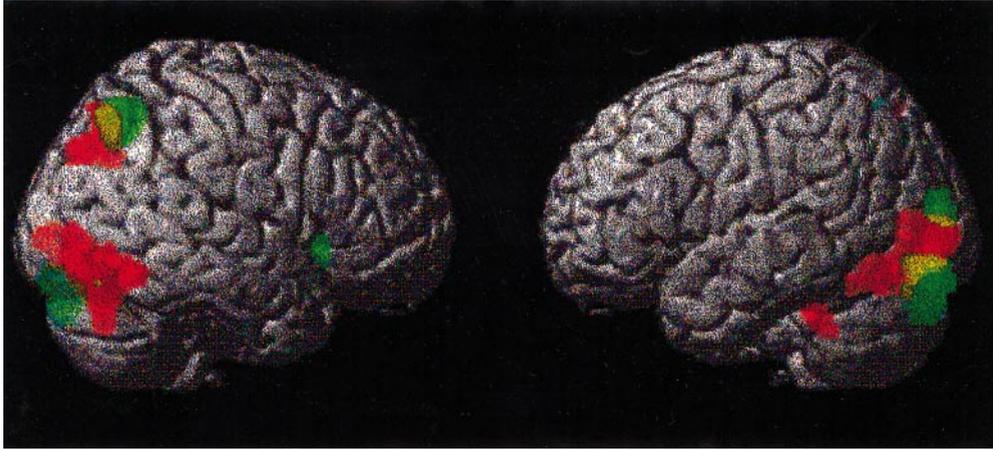
*Note.* Regions that show increased activation that is characteristic for quantification of 6–9 randomly arranged dots (counting), with respect to 6–9 canonically arranged dots, and to all other conditions. In bold type, Z scores corrected for multiple comparisons, at  $P < 0.05$ , and related regions.

<sup>a</sup> Numerosity  $\times$  Arrangement interaction.

recognizable shape was present (in the counting random configuration condition), suggests that subjects may have tried in all conditions to deconstruct the array into patterns in order to count by groups. Previous studies have shown that subjects deploy this grouping strategy for counting, when they can (Atkinson *et al.*, 1976; Mandler and Shebo, 1982; van Oeffelen and Vos, 1983). Our dots were not controlled for spatial proximity, in that some were closer than others (see one example in Fig. 2), and proximity is a very well known grouping principle. In fact it has been shown that subjects, when facilitated by grouping cues like spatial proximity, always adopt the strategy of counting by adding subclusters of dots (Atkinson *et al.* 1976b; van Oeffelen and Vos, 1983). Therefore, subjects are very likely to have applied this strategy in our study. In other words, when quantification was required, there was a top-down attentional effect on the visual input in order to perform sequential grouping. Other studies have also associated activation in middle occipital gyri with top-down attentional modulation of visual processing (Mangun *et al.*, 1998). For example, these areas are active in tasks that required covert and overt shifts of visual attention in response to a cue, compared with detecting the cue (LaBar *et al.*, 1999; Luck *et al.*, 1997), quantifying sets of five or more targets among distractors, compared with sets with four or fewer targets, and quantifying sets of four or fewer targets among distractors compared with simply detecting a target (Sathian *et al.*, 1999). In the two latter cases, from the paper by Sathian *et al.* discussed earlier, the activation in middle occipital areas was tentatively attributed to a form-discrimination process and linked to the fact that subjects had to select and count vertical among horizontal bars. However, this interpretation does not hold for our study, because no particular form discrimination was necessary in order to isolate the objects to be counted.

The *intraparietal areas* have previously been associated with number processing, and their role in the circuit controlling finger movements has suggested an intimate involvement with counting (Butterworth, 1999). Supported by experimental and clinical evidence, Dehaene and colleagues have proposed a neuro-anatomical model of number representation: this model implies that areas within the intraparietal sulci bilaterally are the “cerebral localisation of a category-specific internal representation of numbers” (Chochon *et al.*, 1999, page 625), that is involved in calculation, as well as in *quantification* operations, and in comparison of numerical magnitudes (Dehaene and Changeux, 1993; Dehaene *et al.*, 1998). Furthermore, the model proposed that right and left inferior parietal areas give differential contributions to number processing: the right hemisphere supports the *analogue* representation of numerical quantities (as, for exam-

ple, in estimation processes), while the *left* parietal region connects the quantity representation with the linguistic code. Our study is consistent with this hypothesis because we show that left-lateralized parietal activation is modulated by numerosity and is *not* involved in subitizing 1–4 dots (Table 1). In other words, the left parietal area may relate to the internal subvocalization of the verbal number sequence or some other kind of linguistic sequences, such as sequential additions of small numbers, as would occur when counting by groups (van Oeffelen and Vos, 1983; Logie and Baddeley, 1987). In contrast, the right-lateralized parietal activation, which is present for subitizing but most extensive for counting randomly arranged dots, could reflect the access to domain specific representation of quantities and numbers (Chochon *et al.*, 1999). Nevertheless, even if this account of parietal activation in our quantification task is interesting, it is not the only possible, and not even the most plausible, explanation of our data. In fact, parietal cortices play a well-known role in visuospatial operations such as shifting attention in space and visuospatial working memory, and this account would very well fit with behavioral data that show that counting, more than subitizing, requires ocular movements to locate and mark objects (or groups of objects) in space (Atkinson *et al.*, 1976a,b; Klahr and Wallace, 1976). Data from lesion studies (see De Renzi, 1982, for a review), and from functional imaging studies, indicate that the superior parietal cortex, especially in the right hemisphere, is often engaged in tasks that require shifts of spatial attention, with and without eye movement (Anderson *et al.*, 1994; Nobre *et al.*, 2000; Corbetta *et al.*, 1993, 1998; Ashbridge *et al.*, 1997), and visuospatial working memory (Carlson, 1998; LaBar *et al.*, 1999; Mecklinger *et al.*, 2000). These data support the involvement of shifts of attention among objects to locate them in space and visuospatial WM to keep track of already counted objects during counting, but to a lesser extent subitizing and pattern recognition for 6–9 canonically arranged dots, as implied by behavioral studies of enumeration (Trick and Pylyshyn, 1993, 1994; Simon and Vaishnavi, 1996). The neuroimaging study of counting and subitizing processes by Sathian *et al.* (1999) also found activation in this same right parietal region for counting with respect to subitizing, but not for subitizing with respect to single target detection. This pattern of data was interpreted as supporting the idea that subitizing is based on a preattentive process that does not involve attentional shifts, while counting is a serial process that does involve attentional shifts. In contrast, in the present study, activation could be detected in parietal areas even for subitizing relative to the baseline condition. There are two possible explanations for this incongruity between the two studies:



**FIG. 3.** Counting and the quantification system. In red, the occipitoparietal circuit activated during quantification tasks for all numerosities relative to baseline. In green, areas of increased activation specific for counting (6–9 randomly arranged dots). In yellow, the overlap.

1. The threshold applied to the statistics: ours was lower, and it might have allowed us to detect smaller activations; or

2. The nature of the baselines: in our study subjects did not have to deploy any spatial attention during the baseline task, since they only had to look at a single dot, while in the Sathian *et al.* experiment, subjects had to search for a single target in an array of distractors, and therefore the attentional requirement was much higher than in our case. This might have cancelled out the small supplementary activation in parietal areas for the subitizing range in their study. Moreover, neither our study nor that of Sathian *et al.* measured ocular movements. It is highly possible that in unlimited (as in Sathian *et al.*) or limited but long (as in the present study) stimulus presentation, the amount of eye movement differed between the subitizing and the counting condition, and this could well account for the higher parietal activation in counting than in subitizing.

What seems quite clear from our data is that subitizing does not rely on a dedicated circuit that is *not* involved in counting. In contrast, both extrastriate and parietal areas get recruited along a continuum in relation to the numerosity and the spatial arrangement of the array. These data (i) suggest that subitizing and counting are not dissociable at the neural level, being implemented in a network where recruitment is modulated by the number of objects, and (ii) present complementary evidence to behavioral and neuropsychological evidence on the subitizing–counting issue. Interpreting subitizing and counting as lying on a continuum may appear to conflict with the behavioral data that show a dramatic increase in RTs between subitizing (1–4 dots) and counting (6–9 randomly arranged dots). However, we believe that our behavioral result is exaggerated (especially for the very small slope in the

subitizing range) due to the block presentation that we were forced to use by the PET design. In fact, when numerosity 1–4 and 6–9 are presented as mixed trials, RTs are not always so dramatically dichotomously distributed, even if the difference in slopes for subitizing and counting seems to be present (Oyama *et al.*, 1981; Frick, 1987; Trick and Pylyshyn, 1993, 1994; Dehaene and Cohen, 1994; Simon and Vaishnavi, 1996). However, there is still no definitive account of behavioral data from enumeration experiments, and the debate on how to interpret the apparent dichotomy in RT distribution remains open.

It is possible that operations like attentional shifts, eye movements, and online maintenance of visuospatial information, that are supported by the same occipitoparietal networks (or by separate subregions that are not dissociable with the present imaging techniques), are all engaged, in different proportions and intensities, in subitizing, counting, and pattern recognition. Clearly more work is needed to investigate the precise relation between activation and increasing numerosity, but this can only be addressed with an event-related design in fMRI.

## CONCLUSION

The aim of this study was to characterize subitizing and counting at a neural level in order to investigate whether they are implemented as separate or functionally overlapping processes. Our data suggest that no brain area is specific for subitizing or counting. In contrast, results reveal a pattern of activation in bilateral middle occipital and parietal areas for both quantification tasks (subitizing and counting) and that this activation increases as the number of items in the visual array increases, reaching maximum peak and extent when counting 6–9 randomly arranged items

(i.e., not facilitated by canonical configuration) is required. In relation to pattern recognition, we found that areas linked with object recognition in the bilateral occipitotemporal cortex were activated for quantification irrespective of arrangement, and we did not find any effect specific to canonical spatial arrangement. It therefore appears likely that some form of pattern recognition was evoked by all conditions. Overall, these results do not confirm the existence of a dedicated neural system for subitizing that is not involved in counting. The previous hypothesis that subitizing and counting are two qualitatively different mechanisms based on two separate networks does not receive confirmation from the present study.

## REFERENCES

- Akin, O., and Chase, W. 1978. Quantification of three-dimensional structures. *J. Exp. Psychol. Hum. Percept. Perform.* **4**(3): 397–410.
- Anderson, T., Jenkins, I., Brooks, D. J., Hawken, M. B., Frackowiak, R. S., and Kennard, C. 1994. Cortical control of saccades and fixation in man. A PET study. *Brain* **117**(5): 1073–1084.
- Ashbridge, E., Walsh, V., and Cowey, A. 1997. Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia* **35**(8): 1121–1131.
- Atkinson, J., Campbell, F., and Francis, M. R. 1976a. The magic number  $4 \pm 0$ : A new look at visual numerosity judgements. *Perception* **5**: 327–334.
- Atkinson, J., Francis, M. R., and Campbell, F. 1976b. The dependence of the visual numerosity limit on orientation, colour, and grouping in the stimulus. *Perception* **5**: 335–342.
- Balakrishnan, J. D., and Ashby, F. G. 1991. Is subitizing a unique numerical ability? *Percept. Psychophys.* **50**(6):555–564.
- Balakrishnan, J. D., and Ashby, F. G. 1992. Subitizing: Magical numbers or mere superstition? *Psychol. Rev.* **54**: 80–90.
- Butterworth, B. 1999. *The Mathematical Brain*. Macmillan, London.
- Carlson, S., Martin Kaupp, S., Rama, P., Salli, E., Korvenoja, A., Aronen, H. J. 1998. Distribution of cortical activation during visuospatial n-back tasks as revealed by functional magnetic resonance imaging. *Cereb. Cortex* **8**(8): 743–752.
- Chawla, D., Rees, G., and Friston, K. J. 1999. The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neurosci.* **2**(7):671–676.
- Chochon, F., Cohen, L., van de Moortele, P. F., and Dehaene, S. 1999. Differential contributions of the left and right inferior parietal lobules to number processing. *J. Cogn. Neurosci.* **11**(6):617–630.
- Cipolotti, L., Butterworth, B., and Denes, G. 1991. A specific deficit for numbers in a case of dense acalculia. *Brain* **114**: 2619–2637.
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., Linenweber, M. R., Petersen, S. E., Raichle, M. E., Van Essen, D. C., and Shulman, G. L. 1998. A common network of functional areas for attention and eye movements. *Neuron* **21**(4): 761–773.
- Corbetta, M., Miezin, F. M., Shulman, G. L., and Petersen S. E. 1993. A pet study of visuospatial attention. *J. Neurosci.* **13**(3): 1202–1226.
- Cowan, N. 2001. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behav. Brain Sci.* **26**(1): 87–116.
- De Renzi, E. 1982. *Disorder of Space Exploration*. Wiley, New York.
- Dehaene, S., and Changeux, J.-P. 1993. Development of elementary numerical abilities: A neuronal model. *J. Cogn. Neurosci.* **5**: 390–407.
- Dehaene, S., and Cohen, L. 1995. Towards an anatomical and functional model of number processing. *Math. Cogn.* **1**: 83–120.
- Dehaene, S., Dehaene-Lambertz, G., and Cohen, L. 1998. Abstract representations of numbers in the animal and human brain. *Trends Neurosci.* **21**(8):355–361.
- Dehaene, S., and Cohen, L. 1994. Dissociable mechanisms of subitizing and counting: Neuropsychological evidence from simultaneous agnosic patients. *J. Exp. Psychol. Hum. Percept. Perform.* **29**(5): 958–975.
- Fink, G. R., Marshall, J. C., Gurd, J., Weiss, P. H., Zafiris, O., Shah, N. J., and Zilles, K. 2001. Deriving numerosity and shape from identical visual display. *NeuroImage* **13**: 46–55.
- Frick, R. W. 1987. The homogeneity effect in counting. *Percept. Psychophys.* **41**(1):8–16.
- Friston, K. J., Holmes, A., et al. 1995a. Spatial realignment and normalization of images. *Human Brain Mapping* **2**: 165–189.
- Friston, K. J., Holmes, A., Worsley, K. J., Poline, J. B., Frith, C. D., and Frackowiak, R. S. J. 1995b. Statistical parametric maps in functional imaging: A general linear approach. *Hum. Brain Mapp.* **2**: 189–210.
- Friston, K. J., and Büchel, C. 2000. Attentional modulation of effective connectivity from V2 to V5/MT in humans. *Proc. Natl. Acad. Sci. USA* **97**(13):7591–7596.
- Gallistel, C. R., and Gelman, R. 2000. Non-verbal numerical cognition: from reals to integers. *Trends Cogn. Sci.* **4**(2): 59–65.
- Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzhak, Y., and Malach R. 1998. A sequence of object-processing stages revealed by fMRI in the human occipital lobe. *Hum. Brain Mapp.* **6**(4): 316–328.
- Kanwisher, N., Chun, M. M., McDermott, J., and Ledden, P. J. 1996. Functional imaging of human visual recognition. *Cogn. Brain Res.* **5**(1–2): 55–67.
- Kaufman, E. L., Lord, M. W., Reese, T., and Volkman, J. 1949. The discrimination of visual number. *Am. J. Psychol.* **62**: 498–525.
- Klahr, D., and Wallace, J. G. 1976. *Cognitive Development*. Erlbaum, Hillsdale, NJ.
- LaBar, K. S., Gitelman, D. R., Parrish, T. B., and Mesulam, M. 1999. Neuroanatomic overlap of working memory and spatial attention networks: A functional MRI comparison within subjects. *NeuroImage* **10**(6): 695–704.
- Logie, R. H., and Baddeley, A. D. 1987. Cognitive processes in counting. *J. Exp. Psychol. Learning, Memory, Cognition* **13**(2): 310–326.
- Luck, S. J., Girelli, M., McDermott, M. T., and Ford, M. A. 1997. Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cogn. Psychol.* **33**(1): 64–87.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., and Tootell, R. B. 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc. Natl. Acad. Sci. USA* **92**(18): 8135–8139.
- Mandler, G., and Shebo, B. J. 1982. Subitizing: An analysis of its component processes. *J. Exp. Psychol. Gen.* **11**: 1–22.
- Mangun, G. R., Buonocore, M. H., Girelli, M., and Jha, A. P. 1998. ERP and fMRI measures of visual spatial selective attention. *Hum. Brain Mapp.* **6**(5–6): 383–389.
- Mecklinger, A., Bosch, V., Grunewald, C., Bentin, S., and von Cramon, D. Y. 2000. What have Klingon letters and face in com-

- mon? An fMRI study on content-specific working memory system. *Hum. Brain Mapp.* **11**(3): 146–161.
- Moore, C. J., and Price, C. J. 1999. Three distinct ventral occipito-temporal regions for reading and object naming. *NeuroImage* **10**(2): 181–192.
- Murtha, S., Chertkow, H., Beauregard, M., and Evans, A. 1999. The neural substrate of picture naming. *J. Cogn. Neurosci.* **11**(4): 399–423.
- Nobre, A., Gitelman, D., Dias, E. C., and Mesulam, M. M. 2000. Covert visual spatial orienting and saccades: Overlapping neural systems. *NeuroImage* **11**(3): 210–216.
- Oyama, T., Kikuchi, T., and Ichihara, S. 1981. Span of Attention, backward masking, and reaction time. *Percept. Psychophys.* **29**: 106–112.
- Pesenti, M., Thioux, M., Seron, X., and De Volder, A. 2000. Neuro-anatomical substrates of arabic number processing, numerical comparison, and simple addition: a PET study. *J. Cogn. Neurosci.* **12**(3): 461–479.
- Peterson, S., and Simon, T. J. 2000. Computational evidence for the subitizing phenomenon as an emergent property of the human cognitive architecture. *Cogn. Sci.* **24**(1): 93–122.
- Price, C. J., and Friston, K. J. 1997. Cognitive Conjunction: a new approach to brain activation experiments. *NeuroImage* **5**: 261–270.
- Price, C. J., Moore, C. J., and Frackowiak, R. S. J. 1996. The effect of varying stimulus rate and duration on brain activity during reading. *NeuroImage* **3**(1): 40–52.
- Rickard, T. C., Romero, S. G., Basso, G., Wharton, C., Flitman, S., and Grafman, J. 2000. The calculating brain: An fMRI study. *Neuropsychologia* **38**(3): 325–335.
- Rolls, E. T., and Booth, M. C. A 1998. View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. *Cereb. Cortex* **8**(6): 510–523.
- Sathian, K., Simon, T. J., Peterson S, Patel, G. A., Hoffman, J. M., and Grafton, S. T. 1999. Neural evidence linking visual object enumeration and attention. *J. Cogn. Neurosci.* **11**(1): 36–51.
- Shallice, T. 1988. *From Neuropsychology to Mental Structure*. Cambridge Univ. Press, Cambridge, MA.
- Simon, T., and Vaishnavi, S. 1996. Subitizing and counting depend on different attentional mechanisms: Evidence from visual enumeration in afterimages. *Percept. Psychophys.* **58**(6): 915–926.
- Simon, T. J., Peterson, S. Patel, G., and Sathian, K. 1998. Do the magnocellular and parvocellular visual pathways contribute differentially to subitizing and counting? *Percept. Psychophys.* **60**(3): 451–464.
- Talairach, J., and Tournoux, P. 1988. *Co-planar Stereotaxic Atlas of the Human Brain*. Thieme, Stuttgart.
- Thioux, M., Seron, X., and Pesenti, M. 1999. Functional neuroanatomy of the semantic system: The case for numerals. *Brain Lang.* **69**(3): 488–490.
- Trick, L. M., and Phylyshyn, Z. W. 1994. Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychol. Rev.* **101**(1): 80–102.
- Trick, L. M., and Pylyshyn, Z. W. 1993. What enumeration studies can show us about spatial attention: Evidence for limited capacity preattentive processes. *J. Exp. Psychol. Hum. Percept. Perform.* **19**(2): 331–351.
- Ungerleider, L. G., and Minshkin M. 1982. *Two Cortical Visual Systems: Analysis of Visual Behaviour* (J. Jingle, M. A. Goodale, and R. J. W. Mansfield, Eds.). MIT Press, Cambridge, MA.
- van Oeffelen, M. P., and Vos, P. G. 1983. Configurational effects on the enumeration of dots: Counting by groups. *Mem. Cogn.* **10**(4): 396–404.
- Vuilleumier, P., and Rafal, R. 1999. “Both” means more than “two”: Localizing and counting in patients with visuospatial neglect. *Nature Neurosci.* **2**(9): 783–784.