Neural Evidence Linking Visual Object Enumeration and Attention

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Abstract

■ Visual object enumeration is rapid and accurate for four or fewer items but slow and error-prone for over four items. This dichotomy has recently been linked to visual attentional phenomena by findings suggesting that "subitizing" of small sets of objects is preattentive whereas "counting" of over four items demands spatial shifts of attention. We evaluated this link at a neural level, using $H_2^{15}O$ positron emission tomography to measure changes in regional cerebral blood flow while subjects enumerated the number of target vertical bars that "popped out" of a 16-bar visual display consisting of both horizontal and vertical bars. Relative to a condition with a single target, subi-

tizing (one to four targets) activated foci in the occipital extrastriate cortex, consistent with involvement of early, preattentive visual processes. Relative to subitizing, counting (five to eight targets) activated a widespread network of brain regions, including multiple foci implicated in shifting visual attention—large regions of the superior parietal cortex bilaterally and a focus in the right inferior frontal cortex. These results offer the first direct neural support for mapping the subitizing-counting dichotomy onto separable processes mediating preattentive vision and shifts of visual attention. ■

INTRODUCTION

When humans are asked to enumerate the items in a visual display, their performance shows a clear discontinuity around four items (Trick & Pylyshyn, 1994). Performance below this limit is highly accurate, rapid, and apparently effortless, with typical reaction time (RT) increases of about 50 msec per item. The term *subitizing* was introduced to designate this phenomenon (Kaufman, Lord, Reese, & Volkmann, 1949). In contrast, enumeration of over four items is more error-prone, much slower, and appears to be effortful, with RT increasing by as much as 300 msec per item. This dichotomy has been recognized for over a century (Jevons, 1871) and is widely interpreted as evidence for distinct processes: subitizing of small sets of objects and the operation of *counting* for over four objects. It is interesting to note that, throughout the history of number notation systems, rarely are more than four repetitions of a particular symbol encountered (Zhang & Norman, 1995). This is probably no coincidence because the purpose of such notation is to convey quantitative information efficiently, minimizing the need for a counting-like process.

Numerous studies have explored the efficiency of visual search for a target item in a multielement visual display. These studies led to the concept of a dichotomy in visual search analogous to that in object enumeration. Certain combinations of target and distractor items result in rapid and efficient search, where the target "pops out" of the display and RT is essentially invariant with increasing display size. For instance, a bar oriented orthogonally to the other bars in a display pops out (Treisman, 1988). Other displays yield relatively inefficient search, where RT increases as a function of the number of items (Treisman, 1988). An example is search for a conjunction of features, where the target is a bar of a given orientation and color among distractors differing from the target on one of these two dimensions. Treisman and her colleagues suggested that a search for a unique target feature is "preattentive" (Neisser, 1967) and occurs in parallel over the display without requiring spatially focussed attention, whereas a search for feature conjunctions involves serial shifts of attention (Treisman, 1988).

Although varying theoretical formulations of the mechanisms underlying visual search have been offered (Duncan & Humphreys, 1989; Enns & Rensink, 1990; He & Nakayama, 1992; Joseph, Chun, & Nakayama, 1997;

Julesz, 1984; Treisman, 1988; Wolfe, Cave, & Franzel, 1989), the dichotomy in performance is apparently closely related to that in object enumeration. As Julesz (1984) noted, subitizing appears to be a preattentive process. Subjects can subitize under conditions associated with feature popout, for example, when enumerating the number of green vertical lines among green horizontal lines (Trick & Pylyshyn, 1993). However, when popout is eliminated, as in a conjunction search task calling for enumeration of white vertical lines among green vertical and white horizontal lines, RT increases smoothly as a function of increasing target number without the usual discontinuity (Trick & Pylyshyn, 1993). Based on the failure of subitizing under such conditions, it was proposed that object individuation occurs preattentively and in parallel across the display up to the limit of four items, accounting for the speed of subitizing, whereas the slower process of counting demands serial shifts of attention (Trick & Pylyshyn, 1993, 1994). Consistent with this proposal, it appears that the automatic capture of visual attention by multiple abrupt onsets also has an upper bound of four (Yantis, 1996). Further, when subjects enumerate stimuli presented in retinal after-images, subitizing is unaffected, but counting is compromised, presumably due to inability to scan the after-image using eye movements or perhaps even covert attentional shifts (Simon & Vaishnavi, 1996).

One way to evaluate the relationship of visual enumeration to attentional mechanisms is at the neural level. However, the neural substrate for the subitizing-counting dichotomy remains unclear. Assuming that preattentive and attentive processing are distinct, the evidence cited above leads to the prediction that subitizing and counting should activate different sets of brain regions that are involved, respectively, in these two kinds of processes. Preattentive processing is believed to occur relatively early in the visual hierarchy (Treisman, 1988), whereas attentional effects tend to be more prominent in higher-order visual areas (Colby, 1991). Although there has been relatively little study of the neural mechanisms underlying preattentive phenomena, neuronal responses in the primary visual cortex to a bar are enhanced when there is "orientation contrast" between this bar and surrounding bars (Knierim & Van Essen, 1992), a condition that leads to popout. Lesions of V4, a higher-order visual area where attentional effects are prominent (Desimone & Duncan, 1995) have no effect on detection of salient targets that typically pop out during visual search but impair detection of nonsalient targets (Schiller & Lee, 1991). Evidence from neurophysiology (Robinson, Bowman, & Kertzman 1995), studies of patients with brain lesions (Posner, Walker, Friedrich, & Rafal, 1984) and PET scanning (Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta, Shulman, Miezin, & Petersen, 1995; Nobre et al., 1997) implicate the parietal cortex in the processes mediating serial shifts of attention.

Patients with simultanagnosia (inability to perceive a complex scene despite being able to perceive its parts) due to parietal lobe dysfunction have difficulty enumerating four or more objects but not fewer, suggesting that the mechanisms involved in counting, but not subitizing, depend on processing in the parietal lobe (Dehaene & Cohen, 1994). This is consistent with mediation of attentional shifts by parietal cortical areas. In the present article, we report an investigation of the neural basis of visual object enumeration using $H_2^{15}O$ positron emission tomographic (PET) scanning to measure changes in regional cerebral blood flow (rCBF) while subjects viewed 16-bar displays consisting of both horizontal and vertical bars and enumerated the number of vertical targets (Figure 1). In four distinct experimental conditions, the number of targets was zero (target-absent), one (single target), one to four (subitizing) or five to eight (counting). The total number of bars in the display was kept constant to avoid differences due purely to stimulus intensity.

Based on the evidence reviewed above, we predicted that the processes mediating the preattentive phenomena of popout and subitizing would be localized in areas of the occipital cortex concerned with relatively low-level visual processing and that the parietal cortex would be the locus of operations mediating counting. Alternatively, if "preattentive" processing represents simply one end of a difficulty continuum (Duncan & Humphreys, 1989), one might expect to find similar brain regions activated in both subitizing and counting, with quantitatively greater activation due to counting. A preliminary report of our findings has been presented (Patel et al., 1997).
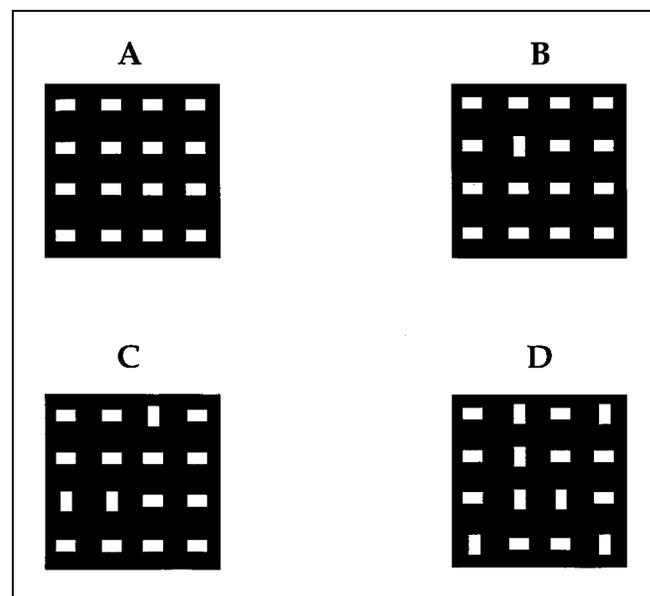
Figure 1. Examples of visual displays, which consisted of 16 bright green bars on a red background. A: Vertical target absent. B: Single vertical target present. C: Subitizing condition with one to four vertical targets. D: Counting condition with five to eight vertical targets.

Figure 2. Median reaction time (RT, msec, symbols), averaged across subjects and mean error rates (bars) as a function of the number of vertical targets. (A) Prescanning session. (B) Scanning session.
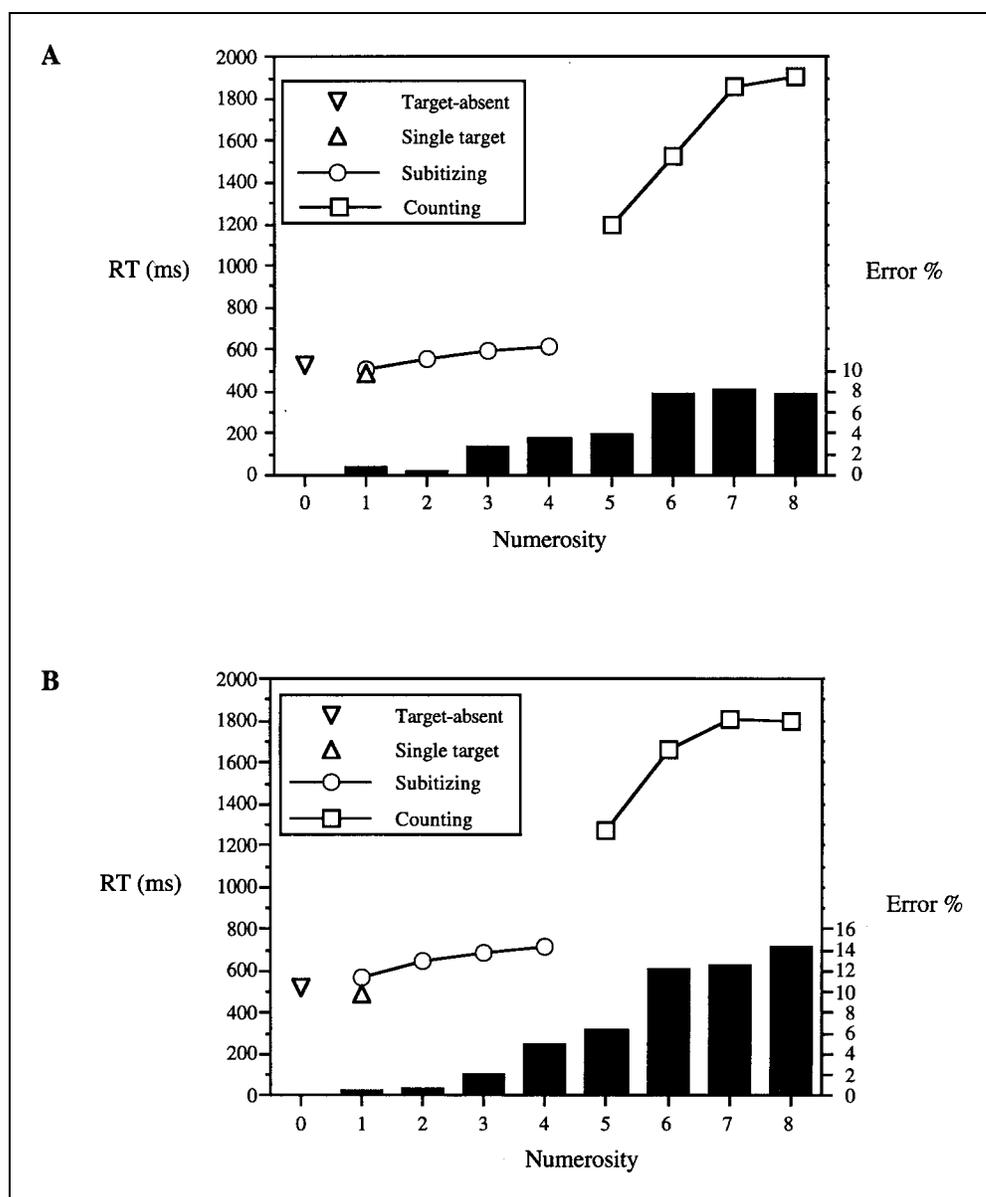
RESULTS AND DISCUSSION

Performance Data

We acquired performance data in a separate session prior to scanning. Figure 2A shows RTs and error rates as a function of the number of vertical targets in this session. It is clear that subjects showed the expected subitizing-counting performance discontinuity between four and five targets. That subjects were subitizing for one to four targets was confirmed by the lack of a quadratic trend (one-way analysis of variance, or ANOVA; $F(1, 28) = 0.067; p = 0.94$) for RTs in this range (Chi & Klahr, 1975). Linear regression slopes were approximately 38 msec per item for the subitizing range and 329 msec per item for the counting range (five to seven targets). [For the regressions, data for $n = 0$ and $n = 8$

were excluded because 0 is not usually considered part of the subitizing range and RTs tend to be falsely short for the highest n due to a guessing "end-effect" (Simon, Peterson, Patel, & Sathian, 1998) that is apparent in Figure 2.] These values are typical of those usually obtained (Simon et al., 1998; Trick & Pylyshyn, 1993).

Performance data were also collected during scanning. Although the total number of trials for each condition was less than half the number in the prescanning session, the pattern of results was essentially similar (Figure 2B), with linear regression slopes of approximately 48 msec per item for subitizing and 272 msec per item for counting. Within-subject comparisons using ANOVAs (RTs) and t tests (error rates) showed no significant differences between sessions for any of the numerosities studied ($\alpha = 0.05$).

Table 1. Locations of activations significant at $p < 0.005$ (uncorrected), along with t values, uncorrected p values, and percentage changes in rCBF. Rows in boldface indicate activations surviving correction for multiple comparisons (see Methods); their locations are shown in Figures 3 and 4. x, y, z: Talairach coordinates (Talairach & Tournoux, 1988); BA: Brodmann's areas.

Locus #	x	y	z	t	p	% rCBF change (mean ± SD)	Location	BA
					Single Target – Target-Absent			
PA1	33	−38	−1	3.98	0.00037	3.53 ± 1.87	R caudate tail	
PA2	40	−78	6	3.91	0.00045	3.68 ± 1.52	R middle/inferior occipital gyrus	19
PA3	18	−69	29	3.46	0.0015	2.92 ± 2.74	R parieto-occipital fissure	18/19
PA4	−32	−45	44	4.03	0.00032	4.37 ± 2.60	L superior parietal gyrus/intraparietal sulcus	7
					Subitizing – Single Target			
SP1	7	−60	−27	4.59	0.000065	3.13 ± 2.21	R cerebellum	
SP2	−31	−81	−16	3.67	0.00087	2.96 ± 1.56	L inferior occipital/fusiform gyrus	18/19
SP3	**28**	**−87**	**4**	**6.01**	**0.0000011**	**3.64 ± 2.15**	R middle/inferior occipital gyrus	**18/19**
SP4	−38	−79	9	4.50	0.000085	2.02 ± 2.20	L middle occipital gyrus	18/19
					Counting – Subitizing			
CS1	−5	−67	−24	3.51	0.0014	2.87 ± 3.82	Cerebellar vermis	
CS2	−30	−53	−5	3.44	0.0016	3.40 ± 1.87	L collateral sulcus	19/37
CS3	−35	−70	−2	3.60	0.0011	2.82 ± 1.85	L lingual gyrus	18/19
CS4	**−24**	**−84**	**14**	**5.30**	**0.0000083**	**3.67 ± 3.12**	L superior/middle occipital gyrus	**18/19**
CS5	**48**	**−61**	**−3**	**6.01**	**0.0000011**	**4.26 ± 2.29**	R middle temporal gyrus	**19/37**
CS6	**37**	**−70**	**−4**	**5.13**	**0.000013**	**4.24 ± 1.84**	R middle occipital gyrus	**19**
CS7	19	−94	0	4.62	0.00006	2.94 ± 2.87	R gyrus descendens	17/18
CS8	**31**	**−78**	**21**	**6.01**	**0.0000011**	**4.62 ± 1.81**	R middle occipital gyrus	**18/19**
CS9	**31**	**−57**	**43**	**6.01**	**0.0000011**	**6.61 ± 3.38**	R superior parietal gyrus/intraparietal sulcus	**7/40**
CS10	**51**	**8**	**31**	**5.98**	**0.0000011**	**3.54 ± 2.37**	R inferior frontal gyrus	**44**
CS11	40	29	36	4.40	0.00011	3.54 ± 2.22	R middle frontal gyrus	8/9/46
CS12	**−28**	**−56**	**43**	**6.01**	**0.0000011**	**3.74 ± 1.92**	L superior parietal gyrus/intraparietal sulcus	**7/40**
CS13	3	7	48	3.89	0.00048	2.57 ± 1.20	R anterior cingulate	24/32
CS14	25	−7	58	4.81	0.000035	4.43 ± 2.96	R middle/superior frontal gyrus	6

Changes in rCBF

Table 1 shows significant activations where rCBF values in the index condition exceeded those in the appropriate control condition, and Table 2 shows the corresponding significant deactivations (rCBF decreases). Changes in rCBF that remained significant after correction for multiple comparisons (see Methods) are shown in boldface in the tables; their locations are illustrated in Figures 3 through 5. Figure 6 graphically displays rCBF values in each condition at each of the sites in Tables 1 and 2, grouped according to location. Loci of rCBF changes that survived correction for multiple comparisons can be accepted with a high degree of confidence. The remain-

Table 2. Locations of deactivations; those surviving correction for multiple comparisons (boldface rows) are shown in Figure 5. Other details as in Table 1.

Locus #	x	y	z	t	p	% rCBF change (mean ± SD)	Location	BA
					Target-Absent − Single Target			
AP1	8	−65	−26	4.24	0.00018	2.24 ± 1.35	R cerebellum	
AP2	−11	−30	−27	4.07	0.00028	4.14 ± 3.31	L upper pons	
AP3	9	41	3	4.36	0.00013	2.68 ± 2.95	R anterior cingulate	32
AP4	−26	−47	3	3.60	0.0011	3.52 ± 2.75	L hippocampus	
AP5	−56	−60	15	3.44	0.0016	2.94 ± 2.45	L middle temporal gyrus	39
AP6	−2	−23	16	3.75	0.00071	2.38 ± 3.12	Bilateral thalamus	
AP7	−4	−62	37	3.96	0.00039	2.60 ± 3.41	L precuneus	7
AP8	−48	−61.5	27	3.25	0.0027	1.71 ± 3.01	L superior temporal sulcus	39
					Single Target − Subitizing			
PS1	48	−61	13	4.33	0.00014	2.80 ± 2.29	R middle temporal gyrus	39
PS2	53	13	27	3.91	0.00045	2.33 ± 2.12	R middle/inferior frontal gyrus	44
PS3	−65	−33	23	3.49	0.0014	3.75 ± 1.37	L supramarginal gyrus	40
PS4	55	−45	36	4.45	0.000097	2.21 ± 2.31	R intraparietal sulcus	40
PS5	33	−3	36	4.00	0.0035	3.08 ± 1.83	R middle frontal gyrus	6
PS6	−54	−51	−16.5	3.13	0.0037	2.81 ± 3.89	L inferior temporal gyrus	37
					Subitizing − Counting			
SC1	**27**	**−79**	**−25**	**6.01**	**0.0000011**	**4.59 ± 2.74**	R cerebellum	
SC2	−26	−78	−27	4.55	0.000074	4.80 ± 3.76	L cerebellum	
SC3	**−42**	**−12**	**−11**	**5.70**	**0.0000026**	**2.59 ± 2.64**	L middle temporal gyrus	**21**
SC4	47	−17	1	4.40	0.00011	2.29 ± 1.61	R superior temporal gyrus	21/22
SC5	**−6**	**39**	**29**	**6.01**	**0.0000018**	**3.25 ± 2.56**	Bilateral superior frontal gyrus	**9**
SC6	−48	−63	27	5.18	0.000012	4.15 ± 3.37	L superior temporal gyrus/inferior parietal cortex	39
SC7	**47**	**−63**	**26**	**5.84**	**0.0000017**	**4.23 ± 2.06**	R superior temporal gyrus/inferior parietal cortex	**39**
SC8	**−3**	**−59**	**30**	**6.01**	**0.0000011**	**5.09 ± 2.31**	Bilateral precuneus	**7**
SC9	−57	−21	26	4.78	0.000038	2.41 ± 2.92	L supramarginal gyrus	40
SC10	−40	−24	40	4.83	0.000033	3.32 ± 3.71	L postcentral gyrus	1/2
SC11	3	−28	44	3.56	0.0012	2.10 ± 1.97	R posterior cingulate	31

ing localizations in the tables are considered tentative; however, the availability of converging data from other studies tends to increase confidence in such localizations. The ability to spatially compare foci between independent studies is limited. According to Haxby and coworkers (Haxby et al., 1994), up to 9-mm differences in localization may be obtained between different groups of 6 to 10 subjects performing the same task, whereas foci centered over 20 mm apart are probably distinct. Table 3 lists loci, identified in other studies, that are potentially related to those in the present study with center-to-center distances of 20 mm or less. Foci cen-

Figure 3. Subitizing – single target. Location of the activation that achieved significance after correction for multiple comparisons (see Table 1), displayed on a horizontal slice (identified by *z* Talairach coordinate) through the "average" MRI. Display threshold is $p < 0.005$ ($t > 3.02$, uncorrected).
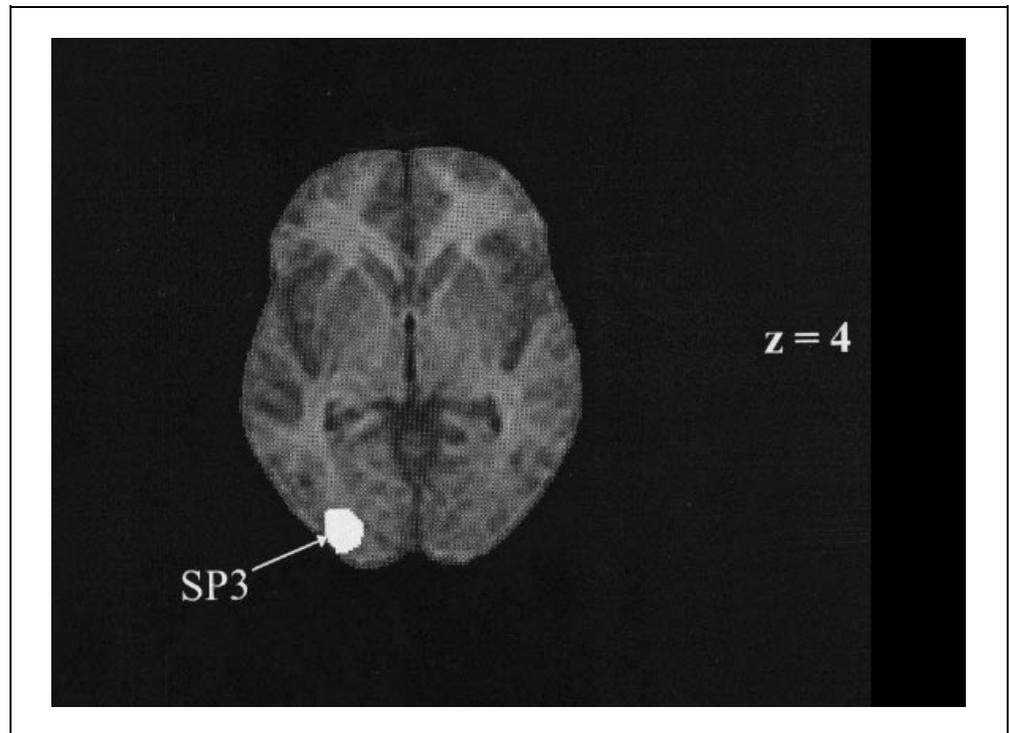
tered less than 10 mm apart are likely to represent a single site; the identity of foci centered 10 to 20 mm apart is more speculative.

Localization of Cerebral Cortical Processes Involved in Subitizing

Compared to the single-target condition, rCBF increases in the subitizing condition were found at sites in occipital extrastriate cortex bilaterally (Table 1). Of these, the site in the right middle/inferior occipital gyrus (SP3, Figure 3) remained significant after correction for multiple comparisons. These rCBF differences point to mechanisms involved in subitizing over and above those involved in segregating a single target from nontargets. The occipital activations on this comparison are consistent with our a priori prediction that the underlying preattentive processes occur at relatively early stages of the visual processing hierarchy. It is of interest that one of these sites (SP3) was centered about 15 mm from a locus (PA2) activated by popout. This proximity could reflect the operation of common preattentive processes such as object individuation that are believed to be crucial to the phenomena of popout and subitizing (Trick & Pylyshyn, 1993, 1994). The cortical sites activated by subitizing were also close to sites (Table 3) recruited when form discriminations were required in tasks shifting the spatial locus of attention (Heinze et al., 1994; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Woldorff et al., 1997). Activations in these studies could reflect attentional modulation of visual processing as a result of interaction with an attention control

mechanism (Corbetta, 1998). Figure 6A shows that at the three occipital loci activated on the subitizing – single-target subtraction (SP2–4), rCBF during counting was similar to or greater than that during subitizing. This suggests that enumeration necessarily recruits processing at these loci. As discussed later, a subcortical focus (SP1) was also active in the case of subitizing, whereas counting recruited a number of additional cortical and subcortical loci.

Localization of Cerebral Cortical Processes Mediating Counting

Relative to subitizing, counting activated sites in multiple cortical regions, including the extrastriate visual cortex bilaterally, right frontal cortex, and right anterior cingulate cortex (Table 1). Importantly, rCBF at all these loci (CS2–14) during counting systematically exceeded that during the other three conditions (Figure 6A through D), with small (if any) differences between these three conditions, indicating that counting recruits *specific* processes that are not required in the other three conditions. Especially notable were large activations in the superior parietal lobule/intraparietal sulcus bilaterally. These, along with the activations in the right inferior frontal gyrus, right middle temporal gyrus, and some of the occipital activations remained significant after correction for multiple comparisons (Figure 4). The parietal sites (CS9 and CS12) and the right inferior frontal site (CS10) were close to activations (Table 3) reported in tasks thought to depend on spatial shifts of attention (Corbetta et al., 1993, 1995; Nobre et al., 1997), strongly

Figure 4. Counting − subitizing; foci identified by labels in Table 1; details as in Figure 3.
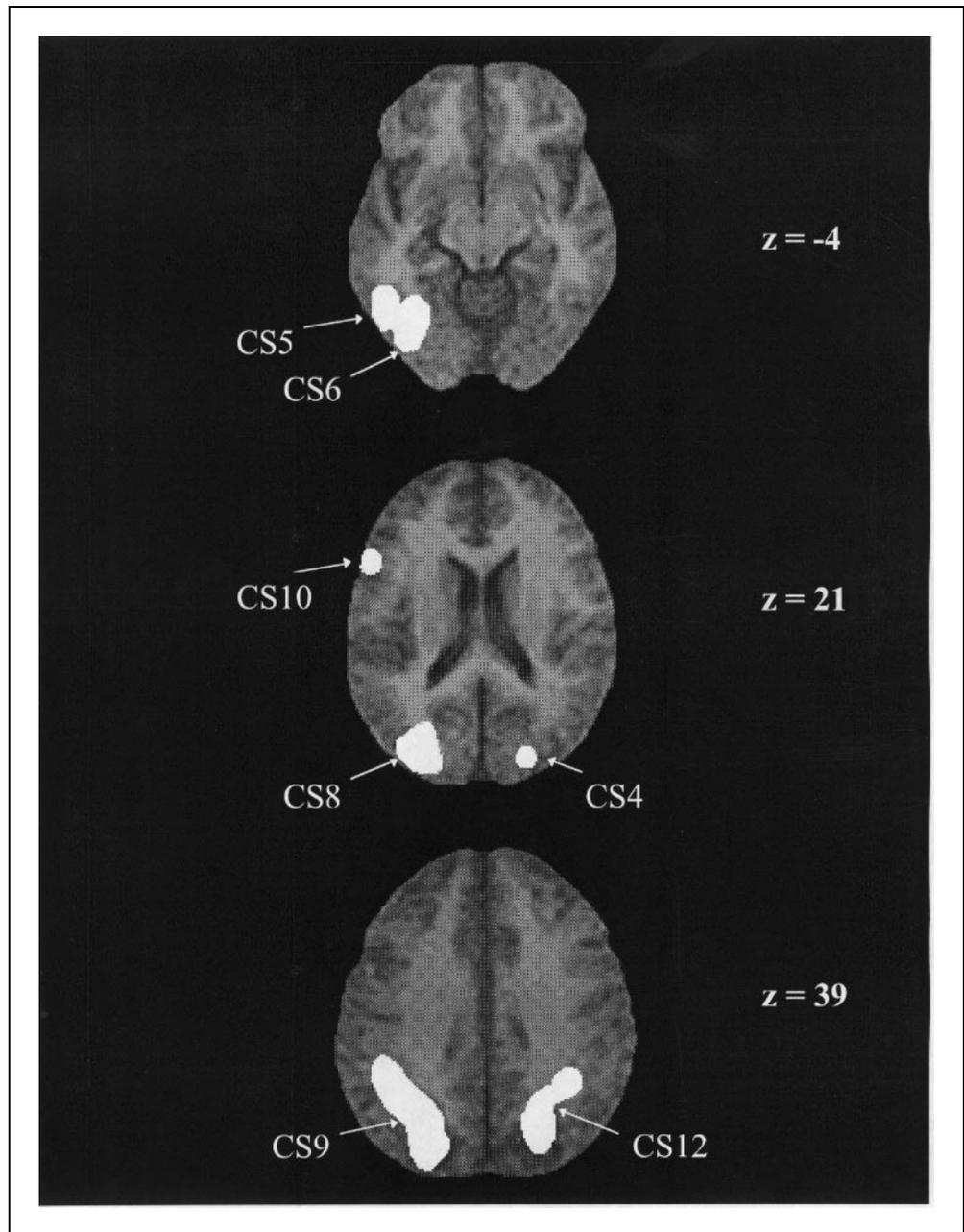
supporting the proposal that spatial attentional shifts are involved in counting but not subitizing (Simon & Vaishnavi, 1996; Trick & Pylyshyn, 1993, 1994). These cortical regions may represent a distributed neural system that controls the spatial allocation of attention, whereas the occipito-temporal activations could reflect greater attentional modulation of visual processing during counting as compared to subitizing (Corbetta, 1998). Eye movements could in theory have contributed to some of these activations. However, their amplitude was probably quite small given that our displays were presented foveally (maximum eccentricity about 1°) and were preceded by a fixation symbol. In any case, eye movements and covert spatial attentional shifts activate essentially identical cor-

tical regions (Corbetta, 1998), implying that similar results would be expected even if eye movements had been prohibited.

Consistent with a role of the anterior cingulate cortex in attentionally demanding tasks, our activation in this region (CS13) was close to sites (Table 3) active during spatial attentional shifts (Corbetta et al., 1993; Heinze et al., 1994; Nobre et al., 1997). One of our occipital activations (CS6) was near a focus (Table 3) recruited in a spatial attentional task involving form discrimination (Heinze et al., 1994), whereas discrimination of grating orientation relative to grating detection (Orban, Dupont, Vogels, Bormans, & Mortelmans 1997; Vandenberghe et al., 1996) activated multiple foci (Table 3) close to CS6

Figure 5. Subitizing − counting; foci identified by labels in Table 2; other details as in Figure 3. Site SC6 is included despite its failure to survive correction for multiple comparisons.
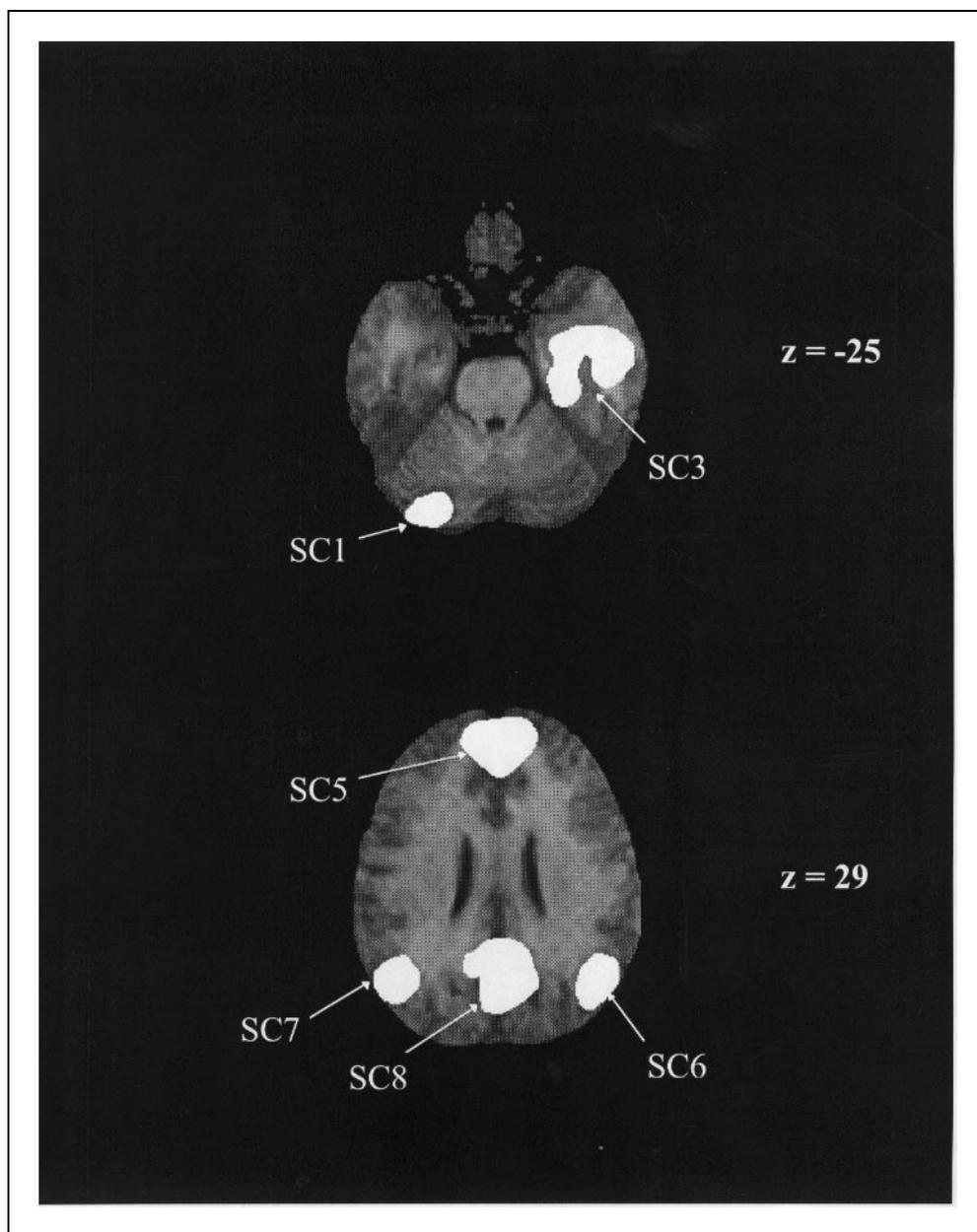
(right occipital), CS10 (right inferior frontal), and CS13 (anterior cingulate), possibly reflecting similar processes in attention-demanding tasks involving orientation/form discrimination. The preponderance of right-sided activations due to counting is consistent with the well-known dominance of the right hemisphere for spatial attentional operations (Corbetta et al., 1993; Heilman, Watson, Valenstein, & Goldberg, 1987; Nobre et al., 1997; Whitehead, 1991).

Localization of Orientation Popout in Cerebral Cortex

Because vertical bars pop out of a field of horizontal bars (Treisman, 1988), it is important to note changes in rCBF attributable to popout alone to evaluate those due to the processes of enumeration in our tasks. Moreover, very little is known of the neural substrate of feature popout, so localization of the neural processes involved in orientation popout is of considerable interest in its own right. Relative to the target-absent condition, the single-target condition evoked rCBF increases in the left superior parietal cortex and two distinct sites within the right extrastriate cortex (Table 1). At all three cortical sites (PA2–4), rCBF values during subitizing and counting were comparable to those in the single-target condition, consistent with target detection via orientation popout in these three conditions (Figure 6A,B). These activations are attributable to the neural processes mediating orientation popout and are, to our knowledge, the first data that speak to their possible neural localization.

The activation in the right parieto-occipital fissure

Sathian et al. 43

B: PARIETAL

C: FRONTAL / ANTERIOR CINGULATE

D: TEMPORAL

E: SUBCORTICAL
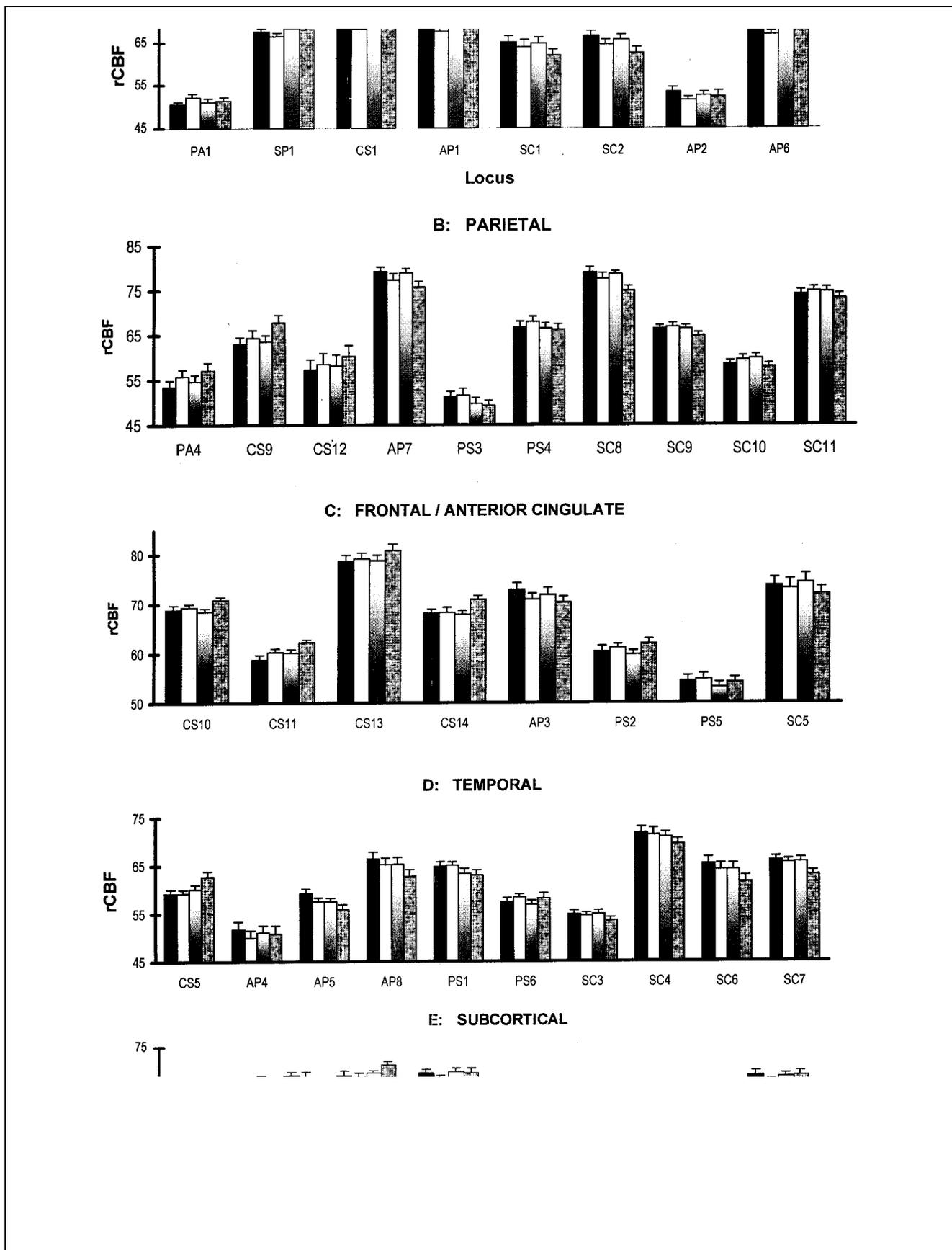
Figure 6. Mean rCBF (ml/100 g/min) for each condition at all loci listed in Tables 1 and 2. Bars: SEM; TA: target-absent; ST: single target; Sub: subitizing; C: counting.

Table 3. Relationship of loci (identified by locus # of Tables 1 and 2) of rCBF change in present study to identified activations/deactivations (Talairach coordinates: *x, y, z*) in other studies. Distance (D) is center-to-center separation between referenced site and given locus # in present study.

Locus #	Reference	*x*	*y*	*z*	*D (mm)*	*Task*
Occipital						
SP2	Heinze et al., 1994	−27	−77	−14	6	Attend right to identify object − passive viewing
SP2	Mangun et al., 1997	−20	−78	−16	11	Attend right to identify object − attend left
SP3	Woldorff et al., 1997	18	−91	12	13	Attend left to identify object − attend right
SP4	Mangun et al., 1997	−44	−74	0	12	Attend right to identify object − attend left
PA3	Sergent et al., 1992	15	−82	30	13	Grating orientation discrimination − fixation
CS6	Mangun et al., 1997	48	−62	−4	14	Attend left to identify object − attend right
CS6	Vandenberghe et al., 1996	30	−70	−4	7	Grating orientation discrimination − grating detection
Parietal						
CS9	Nobre et al., 1997	34	−60	36	8	Luminance-cued target detection − passive viewing of background display
CS12	Corbetta et al., 1995	−31	−53	44	4	Search for conjunction of motion/color − passive viewing of similar displays
PS4	Shulman et al., 1997c	49	−55	40	12	Passive viewing − active visual tasks (meta-analysis)
SC8		−7	−53	34	8	
SC9		−57	−35	40	20	
SC10	Haxby et al., 1994	−46	−22	48	10	Passive viewing − face/location matching
SC11		2	−44	36	16	
Frontal / Anterior Cingulate						
CS10	Nobre et al., 1997	46	10	36	8	Luminance-cued target detection − passive viewing of background display
CS10	Orban et al., 1997	50	4	24	8	Grating orientation discrimination − grating detection
CS13	Heinze et al., 1994	3	14	34	16	Attend left to identify object − passive viewing
CS13	Nobre et al., 1997	8	16	44	10	Luminance-cued target detection − passive viewing of background display
CS13	Vandenberghe et al., 1996	−8	0	48	13	Grating orientation discrimination − grating detection
CS13	Corbetta et al., 1993	7	5	34	15	Passive viewing − fixation point
AP3	Haxby et al. 1994	4	40	8	7	Passive viewing − face matching
SC5	Shulman et al., 1997c	−9	43	42	14	Passive viewing − active visual tasks (meta-analysis)
Temporal						
SC3	Shulman et al., 1997c	−47	−23	−16	13	Passive viewing − active visual tasks (meta-analysis)
SC4	Shulman et al., 1997a	39	−11	12	15	
SC6	Shulman et al., 1997c	−43	−69	36	12	
Subcortical						
CS1	Shulman et al., 1997b	−5	−75	−10	16	Active visual tasks − passive viewing (meta-analysis)
AP6		−7	−17	8	11	
AP6		11	−15	8	17	
AP6	Heinze et al., 1994	1	−18	0	17	Attend right to identify object − passive viewing

(PA3) was close to a site (Table 3) that was exclusively activated during visual discrimination of grating orientation in a PET study examining responses to a variety of visual stimuli (Sergent, Ohta, & MacDonald, 1992). Although the definition of the homologous area of the macaque cerebral cortex is not clear, it is relevant that an area in the anterior bank of the parieto-occipital fissure in macaque monkeys (termed V6 or PO) contains an especially large proportion of orientation-selective neurons (Galletti, Battaglini, & Fattori, 1991). Thus, this region of the extrastriate visual cortex may be critical for visual discrimination of orientation.

The proximity of the activation in the right middle/inferior occipital gyrus (PA2) to an active site on the subitizing – single-target subtraction (SP3) has been discussed above. The focus in the left superior parietal lobule (PA4) was within the large activation in this region on the counting-subitizing subtraction. Further, the center of this larger region also showed a mean rCBF increase of 2.21% (SD 1.82%) in the single-target condition compared to the target-absent condition, which is in the lower part of the range of values in Tables 1 and 2. We argue above that this cortical region is involved in attention-shifting. Hence, the activation at this focus could reflect the capture of visual attention by the salient target.

These relationships suggest that the activations found on the single-target condition, despite failing to survive correction for multiple comparisons, are nonaccidental and deserving of further study. Some of these activations, such as the one in the right parieto-occipital fissure (PA3), may be related to the specific orientation discrimination called for in the present study; others could reflect a process, such as automatic capture of attention, that characterizes visual popout regardless of the dimension along which it occurs. Studies where popout is achieved by employing different stimulus characteristics will be necessary to resolve these possibilities. Our study does not directly address the issue of whether popout represents a process that is distinct from attentive visual search (Treisman, 1988) or merely one extreme along a continuum (Duncan & Humphreys, 1989).

Deactivations in Cerebral Cortex

There were many cortical sites where rCBF values during subitizing exceeded those during counting (Table 2), including loci in the right superior temporal gyrus, left supramarginal gyrus, left postcentral gyrus, right posterior cingulate cortex and bilaterally in the superior frontal gyri, precuneus, and superior temporal/inferior parietal cortex. A number of these survived correction for multiple comparisons (Figure 5); all (SC3–11) had lower rCBF values in the counting condition than in any of the other three conditions (Figure 6B through D), implying that these sites were specifically deactivated by counting. As Table 3 shows, most of these deactivations

(SC3–6, SC8–11) were close to deactivated loci in other studies (Haxby et al., 1994; Shulman et al., 1997a; Shulman et al., 1997c).

Many investigators have reported decreases in rCBF elicited by various tasks (Haxby et al., 1994; Kawashima, O'Sullivan, & Roland, 1995; Shulman et al., 1997a; Shulman et al., 1997c). For a particular experimental-control task pair, such decreases may represent either active suppression generated by processes in the experimental task or greater activity in the control task (Shulman et al., 1997c). In their meta-analysis of blood flow changes in a number of active visual tasks relative to passive viewing of similar stimuli, Shulman and co-workers (1997c) suggested that candidate processes for active task-related suppression are those involved in irrelevant sensory modalities (in nonvisual sensory areas) or automatic response systems (in the ventromedial frontal cortex), whereas control tasks could have been associated with unconstrained verbal thought processes (in language-related areas of the left hemisphere) or heightened monitoring of the external environment (in precuneus, posterior cingulate cortex, and other parieto-occipital areas), body image (in the inferior parietal cortex), or emotional state (in the ventromedial frontal cortex, amygdala, and somatosensory association areas). To this might be added unconstrained visual imagery during certain control tasks (Kosslyn, Thompson, Kim, & Alpert, 1995). In the present context, this possibility is pertinent in the case of the precuneus, a cortical region active during memory-related imagery (Fletcher et al., 1995) and one where we and Shulman et al. (1997c) found deactivation at neighboring sites (Table 3).

It is interesting that none of our deactivations due to counting were in the occipital cortex, although some of them were in areas processing sensory information in nonvisual modalities: the left primary somatosensory cortex (SC10) and bilateral auditory association cortex of the superior temporal gyrus (SC3 and SC4) but not the primary auditory cortex. The somatosensory cortical deactivation was centered 6 mm from a focus activated by stimulation of the right index finger (Drevets et al., 1995). Haxby et al. (1994) reported a deactivation site nearby (Table 3) and also found deactivations in primary and association areas of the auditory cortex. Shulman and colleagues (1997a), in their overview of visual tasks, reported consistent deactivations of the primary somatosensory and auditory association areas but not of primary somatosensory or primary auditory cortex. It has been argued that directing attention to one sensory modality results in rCBF decreases in cortical areas processing input from other sensory modalities (Haxby et al., 1994; Kawashima et al., 1995). Further evidence for this was recently found when attention was focussed on a particular modality to select a motor response to a stimulus that could be auditory, somatosensory, or visual (Grossenbacher, Weeks, & Hallett, 1997).

At a number of cortical loci, rCBF was greater in the

single-target condition than for subitizing. As Table 2 shows, these deactivations were in the cortex of the right middle temporal gyrus, left inferior temporal gyrus, left supramarginal gyrus, and right intraparietal sulcus and at two distinct sites in the right frontal cortex. Of these locations, two showed comparable rCBF decreases in both subitizing and counting conditions relative to the single-target and target-absent conditions (PS1, Figure 6D; PS3, Figure 6B), suggesting that these foci in the right temporal and left parietal cortex were deactivated by a common enumeration process. Further reinforcing this, the parietal site (PS3) was centered about 14 mm from a deactivation due to counting (SC9). At two other sites, rCBF was at least as great during counting as in the single target condition but was lower in target-absent and subitizing conditions (PS2, Figure 6C; PS6, Figure 6D). These sites, in the right frontal and left temporal cortex, might have been activated by shifts or capture of attention associated with the counting and single-target conditions, respectively. Alternatively, they could represent deactivations by a process common to the target-absent and subitizing conditions, such as perceptual grouping. A right parietal site was most active in the single-target condition relative to the other three conditions (PS4, Figure 6B), suggesting that its activation depended on a process unique to this condition (in contrast to the three sites showing greater rCBF in all target-present conditions relative to the target-absent condition; PA2–4, see above); this site was close to a deactivation in the Shulman et al. (1997c) meta-analysis (Table 3). Finally, a right frontal locus appeared to be specifically deactivated by subitizing because rCBF was lower in this condition than in the other three (PS5, Figure 6C).

Cortical foci where rCBF was greater in the target-absent than in the single-target condition were found in the left hippocampal region, right anterior cingulate cortex, left precuneus, left middle temporal gyrus, and left superior temporal sulcus (Table 2). Among these foci, the left hippocampal site appeared to be specifically deactivated by the single target because rCBF in this condition was lower than in the other three (AP4, Figure 6D). At two medial foci, rCBF was comparable in counting and single-target conditions and higher in target-absent and subitizing conditions (AP3, Figure 6C; AP7, Figure 6B), reciprocal to PS2 and PS6 discussed in the previous paragraph. These flow changes may thus represent either attentional deactivation or grouping-related activation. The anterior cingulate locus (AP3) was close to a deactivation (Table 3) in the Haxby et al. (1994) study; the precuneus locus (AP7) was about 7.5 mm from our precuneus deactivation due to counting (SC9). At two foci in the left temporal lobe, rCBF was comparable during subitizing and the single-target condition but substantially lower during counting (AP5&8, Figure 6D), suggesting progressive deactivation with increasing stimulus complexity.

Overall, then, these findings lend weight to the notion that processing in many visual tasks is accompanied by rCBF decreases in particular cortical areas. Although the proximity of many deactivated foci in different studies suggests that a common factor or set of factors (whose nature remains unclear) may be operative in causing these flow decreases, especially in the precuneus and in nonvisual sensory processing areas, the differences between studies in the localization of deactivations and the particular patterns we found imply that certain rCBF decreases may be task-specific.

Involvement of Structures Outside Cerebral Cortex

We found rCBF changes in the cerebellum on a number of subtractions. Two foci 5 mm apart were identified in the medial part of the right cerebellar hemisphere, one on the subitizing – single-target subtraction (SP1, Table 1) and the other on the target-absent – single-target subtraction (AP1, Table 2). Both these foci and one in the pons (AP2) showed rCBF values that were lower in the single-target condition than in the other three conditions (Figure 6E). A common feature of these three conditions was that RT was longer than in the single-target condition (Figure 2), although the difference between target-absent and single-target conditions was small. Cerebellar activation has been found in a number of visual tasks (Shulman et al., 1997b). The common denominator among these tasks is not clear but may involve processes related to response selection (Shulman et al., 1997b; Thach, 1996). Despite the distance of our foci from reported cerebellar activations in other visual tasks (Shulman et al., 1997b), recruitment of the medial right cerebellum (and the pontine locus) may be related to the additional load imposed by the other conditions compared to simple-target detection, especially with respect to the larger set of possible responses in subitizing and counting.

Relative to subitizing, counting activated a focus (CS1, Table 1) in the cerebellar vermis and deactivated sites more laterally in both cerebellar hemispheres (SC1 and SC2, Table 2). These sites can be considered specific activations/deactivations because rCBF values were, respectively, greater than or less than those in the other three conditions (Figure 6E). SC1 in the right cerebellum was the only cerebellar focus to survive correction for multiple comparisons (Figure 5). The focus in the vermis was close to a site (Table 3) where Shulman et al. (1997b) reported activation common to a number of visual tasks relative to passive control tasks: They favored response selection as the common factor. Interestingly, children with cerebellar hemispheric damage associated with surgical resection of tumors are impaired at rapidly shifting attention between the color and form of visual stimuli at the same location (Akshoomoff & Courchesne, 1994) as well as between visual and auditory stimuli (Akshoomoff & Courchesne, 1992). Given that counting

requires spatial shifts of attention, our data add weight to the idea that the cerebellum plays a role in attention-shifting of various kinds.

A focus in the tail of the caudate nucleus was more active in the single-target condition than in the target-absent condition (PA1, Table 1); rCBF values due to subitizing and counting were intermediate (Figure 6E). This activation may be related to the occurrence of visually responsive neurons in this region in monkeys (Brown, Mishkin, & Desimone, 1993); the reported involvement of these neurons in selective attention (Shuvaev & Shefer, 1997) may relate to attentional capture by the salient target(s).

Finally, a thalamic locus that was more active in the target-absent than in the single-target condition (AP6, Table 2) was close to thalamic sites (Table 3) in the meta-analysis of Shulman et al. (1997b) and in the study of Heinze et al. (1994). Because rCBF values at our thalamic focus were least for the single-target condition as compared to the other three conditions (Figure 6E), its recruitment could have been related to longer RTs (and greater task complexity) in these three conditions (as in the case of the medial right cerebellum and the pontine focus, see above), analogous to other right thalamic activations attributable to increased attentional demand (Heinze et al., 1994; Shulman et al., 1997b).

Conclusions

Numerous brain regions and various patterns of task-related rCBF change are involved in visual popout and object enumeration. Orientation popout is characterized by activation of foci in the tail of the right caudate nucleus, right occipital cortex, and bilateral parietal cortex, with these sites showing varying degrees of selectivity for single versus multiple targets. It is also associated with specific deactivation of nonneocortical foci located in the medial right cerebellum, pons, thalamus, and left hippocampus. The operation of subitizing activates a small number of foci in the right and left occipital extrastriate cortex, all of which are also active during counting, while specifically deactivating a right frontal focus. Both subitizing and counting deactivate foci in the right temporal and left parietal cortex. Compared to subitizing, counting specifically activates and deactivates a much wider network of brain regions, consistent with the notion that distinct neural processes are involved in these two kinds of visual object enumeration. The localization of these neural processes in the occipital cortex for subitizing and (among other regions) in the superior parietal and right inferior frontal cortices for counting supports the mapping of the subitizing-counting dichotomy in visual object enumeration onto distinguishable neural systems responsible for preattentive vision and serial shifts of attention. Further work is required to establish the extent to which the neural operations underlying other preattentive and attention-demanding tasks are segregated.

METHODS

Subjects

Eight healthy males aged 18 to 26 years (mean age, 21) were studied after obtaining informed consent. All were strongly right-handed according to the 14 items of the Edinburgh handedness inventory with the highest validity (Raczkowski, Kalat, & Nebes, 1974). The procedures were approved by the Human Investigations Committees of Emory University and Georgia Institute of Technology and the Radiation Safety Committee of Emory University.

PET Scanning

PET scans were acquired in two-dimensional mode using a Siemens ECAT 951 scanner that collected 31 contiguous planes covering a 105-mm field of view, with nominal isotropic resolution of 5 mm at full width half maximum (FWHM). Subjects lay supine in the scanner with the head restrained using a thermoplastic mold. Scan acquisition began 10 sec after intravenous injection of a bolus of $H_2^{15}O$ (35 mCi) and continued for 90 sec. Task performance began 30 sec prior to injection and continued for about 170 sec. For each task, the probability of the index condition was 75% overall but was increased to 90% during the 90-sec scan period. On the remaining trials, the target was absent, except in the target-absent condition, for which there were one to four targets on these trials. These probability manipulations maximized occurrence of the condition of interest for each scan without trivializing the task (Corbetta et al., 1993). About 50 trials were performed during each scan period for all tasks except the counting task, for which approximately 40 trials occurred during scanning. A series of scans was performed, comprising three repetitions of each of the four tasks in a pseudorandom order.

Visual Displays and Tasks

As described previously (Simon et al., 1998), displays were presented on a Macintosh IIfx computer with a 13-in. video monitor (resolution, 640 × 480 pixels) and viewed at a distance of approximately 60 cm. Display presentation and acquisition of performance data were controlled using the Superlab package (Cedrus Corp., Phoenix, AZ). In each trial, the actual display was preceded by presentation of a fixation (+) symbol for 1 sec. The bars were bright green rectangles, measuring 0.25° × 0.14°, on a red background square of side 2°. The locations of the vertical target bars were randomized. In the prescanning session, the four conditions were presented in blocks of 320 trials with rest periods after each

set of 40 trials. The probability of the index condition was 75%, with presentations on the remaining 25% of trials being as in the scanning session. Trials were randomized within blocks in both sessions. Subjects were asked to verbally report the number of vertical lines in the display as rapidly as possible without sacrificing accuracy. Responses were recorded using a microphone and were used to measure RT. In the prescanning session, subjects then made a numeric keypad response that was used to measure accuracy (Simon et al., 1998). In the scanning session, accuracy measurements were based on manual records of the verbal responses, verified by reference to an audio cassette recording. Prior to data analysis, trials with an inaccurate response or with an RT exceeding 2.5 standard deviations (for the particular subject and condition) were excluded (Simon et al., 1998).

Image Analysis

PET images were reconstructed and analyzed as described elsewhere (Sathian, Zangaladze, Hoffman, & Grafton, 1997). Briefly, this involved within-subject coregistration (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998), followed by mapping of PET images into Talairach coordinate space to allow between-subject averaging (Woods, Grafton, Watson, Sicotte, & Mazziotta, 1998), smoothing with a three-dimensional Gaussian filter to a final isotropic resolution of 14.8 mm FWHM and subsequent normalization for changes in global blood flow. Differences in rCBF between tasks were investigated using repeated-measures analysis of variance for various task pairs (Neter, Wasserman, & Kutner, 1990), calculating the variance independently at each pixel. Linear contrasts between task means were used to generate subtraction images consisting of a pixel-by-pixel map of the t statistic, with an uncorrected threshold of $p < 0.005$. Sites showing rCBF changes were localized with respect to Talairach coordinates (Talairach & Tournoux, 1998). To aid visualization in relation to cortical anatomy, they were superimposed on an "average" magnetic resonance image derived from a separate population of 18 subjects.

Correction for Multiple Comparisons

Given our *a priori* expectations for activations, we confined our principal volume of interest to the occipital and parietal cortex bilaterally, using the occipito-temporal incisure and the central sulcus as guides to limit its anterior extent. To minimize Type I error, the critical t value of 5.01 was obtained by correcting for the number of independent resolving elements within the search space (Worsley, Evans, Marrett, & Neelin, 1992). We also attempted to minimize Type II error by surveying the entire gray matter with a correction for the number of independent resolving elements in this volume (Worsley

et al., 1992), resulting in a critical t value of 5.41 for this survey. For deactivations, the entire gray matter was surveyed using the critical t value of 5.41.

REFERENCES

Akshoomoff, N. A., & Courchesne, E. (1992). A new role for the cerebellum in cognitive operations. *Behavioral Neuroscience, 106,* 731–738.

Akshoomoff, N. A., & Courchesne, E. (1994). ERP evidence for a shifting attention deficit in patients with damage to the cerebellum. *Journal of Cognitive Neuroscience, 6,* 388–399.

Brown, V. J., Mishkin, M., & Desimone, R. (1993). Responses of neurons in the tail of the caudate nucleus of the macaque during the performance of a visual discrimination task. *Society for Neuroscience Abstracts, 19,* 13.11.

Chi, M. T. H., & Klahr, D. (1975). Span and rate of apprehension in children and adults. *Journal of Experimental Child Psychology, 19,* 434–439.

Colby, C. L. (1991). The neuroanatomy and neurophysiology of attention. *Journal of Child Neurology, 6,* S88–S116.

Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent or overlapping neural systems? *Proceedings of the National Academy of Sciences, USA, 95,* 831–838.

Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1993). A PET study of visuospatial attention. *Journal of Neuroscience, 13,* 1202–1226.

Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science, 270,* 802–805.

Dehaene, S., & Cohen, L. (1994). Dissociable mechanisms of subitizing and counting: Neuropsychological evidence from simultanagnosic patients. *Journal of Experimental Psychology: Human Perception and Performance, 20,* 958–975.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18,* 193–222.

Drevets, W. C., Burton, H., Videen, T., Snyder, A. Z., Simpson, J. R., & Raichle, M. E. (1995). Blood flow changes in human somatosensory cortex during anticipated stimulation. *Nature, 373,* 249–252.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review, 96,* 433–458.

Enns, J. T., & Rensink, R. A. (1990). Influence of scene-based properties on visual search. *Science, 247,* 721–723.

Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S. J., & Dolan, R. J. (1995). The mind's eye—pre-

cuneus activation in memory-related imagery. *NeuroImage, 2,* 195–200.

Galletti, C., Battaglini, P. P., & Fattori, P. (1991). Functional properties of neurons in the anterior bank of the parieto-occipital sulcus of the macaque monkey. *European Journal of Neuroscience, 3,* 452–461.

Grossenbacher, P. G., Weeks, R. A., & Hallett, M. (1997). Attention for action focused on auditory, tactile or visual stimuli results in crossmodal suppression of blood flow. *Society for Neuroscience Abstracts, 23,* 121.11.

Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. *Journal of Neuroscience, 14,* 6336–6353.

He, Z. H., & Nakayama, K. (1992). Surfaces versus features in visual search. *Nature, 359,* 231–233.

Heilman, K. M., Watson, R. T., Valenstein, E., & Goldberg, M. E. (1987). Attention: Behavior and neural mechanisms. In F. Plum (Ed.), *Higher functions of the brain* (pp. 461–481). Bethesda, MD: American Physiological Society.

Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Münte, T. F., Gös, A., Scherg, M., Johannes, S., Hundeshagen, H., Gazzaniga, M. S., & Hillyard, S. A. (1994). Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature, 372,* 543–546.

Jevons, W. S. (1871). The power of numerical discrimination. *Nature, 3,* 281–282.

Joseph, J. S., Chun, M. M., & Nakayama, K. (1997). Attentional requirements in a 'preattentive' feature search task. *Nature, 387,* 805–807.

Julesz, B. (1984). Towards an axiomatic theory of preattentive vision. In G. M. Edelman, W. E. Gall, & W. M. Cowan (Eds.), *Dynamic aspects of neocortical function* (pp. 585–612). New York: Wiley.

Kaufman, E., Lord, M., Reese, T., & Volkmann, J. (1949). The discrimination of visual number. *American Journal of Psychology, 62,* 498–525.

Kawashima, R., O'Sullivan, B. T., & Roland, P. E. (1995). Positron-emission tomography studies of cross-modality inhibition in selective attentional tasks: Closing the "mind's eye." *Proceedings of the National Academy of Sciences, USA, 92,* 5969–5972.

Knierim, J. J., & Van Essen, D. C. (1992). Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. *Journal of Neurophysiology, 67,* 961–980.

Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature, 378,* 496–498.

Mangun, G. R., Hopfinger, J. B., Kussmaul, C. L., Fletcher, E. M., & Heinze, H.-J. (1997). Covariations in ERP and PET measures of spatial selective attention in human extrastriate visual cortex. *Human Brain Mapping, 5,* 273–279.

Neisser, U. (1967). *Cognitive psychology.* Englewood Cliffs, NJ: Prentice-Hall.

Neter, J., Wasserman, W., & Kutner, M. H. (1990). *Applied linear statistical models.* Boston: Irwin.

Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S. J., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain, 120,* 515–533.

Orban, G. A., Dupont, P., Vogels, R., Bormans, G., & Mortelmans, L. (1997). Human brain activity related to orientation discrimination tasks. *European Journal of Neuroscience, 9,* 246–259.

Patel, G. A., Simon, T. J., Peterson, S., Hoffman, J. M., Grafton,

S. T., & Sathian, K. (1997). PET activations during visual popout and object enumeration. *Society for Neuroscience Abstracts, 23,* 619.2.

Posner, M. I., Walker, J. A., Friedrich, F. A., & Rafal, R. D. (1984). Effects of parietal injury on covert orienting of visual attention. *Journal of Neuroscience, 4,* 1863–1874.

Raczkowski, D., Kalat, J. W., & Nebes, R. (1974). Reliability and validity of some handedness questionnaire items. *Neuropsychologia, 12,* 43–47.

Robinson, D. L., Bowman, E. M., & Kertzman, C. (1995). Covert orienting of attention in macaques. II. Contributions of parietal cortex. *Journal of Neurophysiology, 74,* 698–712.

Sathian, K., Zangaladze, A., Hoffman, J. M., & Grafton, S. T. (1997). Feeling with the mind's eye. *NeuroReport, 8,* 3877–3881.

Schiller, P. H., & Lee, K. (1991). The role of the primate extrastriate area V4 in vision. *Science, 251,* 1251–1253.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain, 115,* 15–36.

Shulman, G. L., Corbetta, M., Buckner, R. L., Raichle, M. E., Fiez, J. A., Miezin, F. M., & Petersen, S. E. (1997a). Top-down modulation of early sensory cortex. *Cerebral Cortex, 7,* 193–206.

Shulman, G. L., Corbetta, M., Buckner, R. L., Fiez, J. A., Miezin, F. M., Raichle, M. E., & Petersen, S. E. (1997b). Common blood flow changes across visual tasks: I. Increases in subcortical structures and cerebellum but not in nonvisual cortex. *Journal of Cognitive Neuroscience, 9,* 624–647.

Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E., & Petersen, S. E. (1997c). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience, 9,* 648–663.

Shuvaev, V. T., & Shefer, V. I. (1997). The neurons of the monkey caudate nucleus are involved in the process of spatial selective attention. *Society for Neuroscience Abstracts, 23,* 620.4.

Simon, T. J., Peterson, S., Patel, G., & Sathian, K. (1998). Do the magnocellular and parvocellular visual pathways contribute differentially to subitizing and counting? *Perception and Psychophysics, 60,* 451–464.

Simon, T. J., & Vaishnavi, S. (1996). Subitizing & counting depend on different attentional mechanisms: Evidence from visual enumeration in afterimages. *Perception and Psychophysics, 58,* 915–926.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the brain.* New York: Thieme.

Thach, W. T. (1996). On the specific role of the cerebellum in motor learning and cognition: Clues from PET activation and lesion studies in man. *Behavioral and Brain Sciences, 19,* 411–431.

Treisman, A. (1988). Features and objects: The fourteenth Bartlett Memorial lecture. *Quarterly Journal of Experimental Psychology, 40A,* 201–237.

Trick, L. M., & Pylyshyn, Z. W. (1993). What enumeration studies can show us about spatial attention. Evidence for limited capacity preattentive processing. *Journal of Experimental Psychology: Human Perception and Performance ,19,* 331–351.

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

Vandenberghe, R., Dupont, B., De Bruyn, B., Bormans, G., Michiels, J., Mortelmans, L., & Orban, G. A. (1996). The influence of stimulus location on the brain activation pat-

tern in detection and orientation discrimination: A PET study of visual attention. *Brain, 119,* 1263–1276.

Whitehead, R. (1991). Right hemisphere processing superiority during sustained visual attention. *Journal of Cognitive Neuroscience, 3,* 329–334.

Woldorff, M. G., Fox, P. T., Matzke, M., Lancaster, J. L., Veeraswamy, S., Zamarripa, F., Seabolt, M., Glass, T., Gao, J. H., Martin, C. C., & Jerabek, P. (1997). Retinotopic organization of early visual spatial attention effects as revealed by PET and ERPs. *Human Brain Mapping, 5,* 280–286.

Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance, 15,* 419–433.

Woods, R. P., Grafton, S. T., Holmes, C. J., Cherry, S. R., & Mazziotta, J. C. (1998). Automated image registration: I. General methods and intrasubject validation. *Journal of Computer Assisted Tomography, 22,* 139–152.

Woods, R. P., Grafton, S. T., Watson, J. D. G., Sicotte, N. L., & Mazziotta, J. C. (1998). Automated image registration: II. Intersubject validation of linear and nonlinear models. *Journal of Computer Assisted Tomography, 22,* 153–165.

Worsley, K. J., Evans, A. C., Marrett, S., & Neelin, P. (1992). A three-dimensional statistical analysis for CBF activation studies in human brain. *Journal of Cerebral Blood Flow Metabolism, 12,* 900–918.

Yantis, S. (1996). Attentional capture in vision. In A. F. Kramer, M. G. H. Coles, & G. D. Logan (Eds.), *Converging operations in the study of visual selective attention* (pp. 45–76). Washington, DC: American Psychological Association.

Zhang, J., & Norman, D. A. (1995). A representational analysis of numeration systems. *Cognition, 57,* 271–295.