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# Deriving Numerosity and Shape from Identical Visual Displays

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**We presented identical displays of three to five dots in a functional magnetic resonance imaging (fMRI) experiment with normal volunteers. Two distinct directed attention tasks were performed on these displays: In one condition, subjects assessed the numerosity of the display; in the other condition, they assessed the shape of the display. Decisions based on numerosity activated differentially striate and extrastriate visual processing areas as well as left inferior frontal cortex. Decisions based on shape derived from arrangement activated differentially temporoparietal cortex bilaterally, medial posterior cingulate cortex, and left dorsolateral prefrontal cortex. These divergent neural activations in response to identical stimuli suggest that attentional mechanisms are deployed in very different ways in rapid enumeration of visual objects and in linking spatially discrete elements to one form.** 

*Key Words:* **serial/parallel processing; fMRI; attentional modulation; subitizing; spatial binding; directed attention task.**

## INTRODUCTION

Of each stimulus display shown in Fig. 1, one can ask (and unambiguously answer) the questions: Does the configuration of the dots form a square? Are there exactly four dots in the display? Early stimulus processing and final motor response will be held in common by the two tasks and should hence activate the same brain regions. But the mental operations required to perform enumeration and shape assignment will diverge and should thus be associated with distinct neural activations, despite identical input. Only by keeping the displays constant can we isolate in relatively pure form these different processes performed upon the stimulus representations.

With respect to assessing shape from arrangement, the dots may first be grouped together such that the individual (local) dots are seen to form a (global) figure. Linking such spatially discrete elements to one form demands significant attentional resources when the separation between the elements of the display is greater than twice the size of the element (Kovács and Julesz, 1994; Kovács, 1996; Singer, 1998; Treisman, 1988). Lesion studies (Robertson and Lamb, 1991) suggest that temporoparietal cortex is implicated in these figural operations, with local processing mediated by the left and global processing by the right hemisphere. Once grouped (by the simplest closed contour), the shape can then be compared with the target shape (square) drawn from stored visual representations. Finally, an explicit decision is required as to whether the stimulus configuration does indeed form a square. Prefrontal cortex may be implicated in such decision making (Sakagami and Tsutsui, 1999).

By contrast, the enumeration task could rely on either of two distinct mechanisms that have been postulated for deriving the numerosity of small sets of visual objects (i.e., subitizing): (a) the process may involve a fast, parallel mechanism that does not involve sequential counting of each element in the display (Butterworth, 1999; Dehaene, 1997). According to this model, subitizing is primarily a parallel preattentional process (Sathian *et al.*, 1999), although neither reaction time data (Mandler and Shebo, 1982), nor the results of functional neuroimaging studies (Sathian *et al.*, 1999) unambiguously support this claim; (b) the process may involve a serial, albeit preverbal, counting mechanism that can even be used by animals. In the human case, the output of this device can then be mapped onto a particular digit (Gallistel and Gelman, 1992). In this model, it is the preverbal nature of the counting process itself that accounts for the speed with which small numbers of items can be (reliably) enumerated. Since subitizing is serial in this model, spatial attention will be required to localize the elements of the display.

Irrespective of which of these mechanisms is employed, our experiment required that an explicit decision is taken as to whether the cardinality of the display is four: unlike the design of conventional subitizing experiments, we required a two-choice man-



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| Stimulus exemplars | Task | | mean RT (ms, ± sdev) | | mean Error Rate (%, ± sdev) | |
|---|---|---|---|---|---|---|
| | "Square"? | "4"? | "Square"? | "4"? | "Square"? | "4"? |
|  | ✔ | ✔ | L 569 ± 169<br>R 562 ± 138<br>L+R 566 ± 155 | L 600 ± 158<br>R 598 ± 135<br>L+R 599 ± 146 | L 2 ± 1<br>R 1.8 ± 1<br>L+R 1.9 ± 0.7 | L 2.2 ± 1.6<br>R 2.3 ± 1.6<br>L+R 2.2 ± 1.1 |
|  | ✔ | ✘ | L 600 ± 207<br>R 603 ± 176<br>L+R 601 ± 192 | L 758 ± 208<br>R 728 ± 195<br>L+R 741 ± 202 | L 3.4 ± 0.7<br>R 1.7 ± 0.5<br>L+R 2.6 ± 0.5 | L 8.0 ± 2.0<br>R 8.0 ± 2.0<br>L+R 8.0 ± 1.0 |
|  | ✘ | ✔ | L 678 ± 205<br>R 671 ± 225<br>L+R 674 ± 215 | L 671 ± 174<br>R 694 ± 193<br>L+R 683 ± 183 | L 5.0 ± 1.3<br>R 2.3 ± 0.8<br>L+R 3.7 ± 0.8 | L 4.7 ± 0.8<br>R 3.3 ± 0.7<br>L+R 4.0 ± 0.5 |
|  | ✘ | ✘ | L 703 ± 173<br>R 653 ± 195<br>L+R 677 ± 187 | L 809 ± 215<br>R 745 ± 189<br>L+R 781 ± 206 | L 2.6 ± 1.8<br>R 3.5 ± 2.0<br>L+R 3.0 ± 1.4 | L 5.4 ± 2.0<br>R 3.4 ± 1.9<br>L+R 4.4 ± 1.5 |
|  | ✘ | ✘ | L 592 ± 171<br>R 576 ± 161<br>L+R 584 ± 166 | L 661 ± 172<br>R 636 ± 185<br>L+R 648 ± 180 | L 1.3 ± 0.6<br>R 0.5 ± 0.4<br>L+R 0.9 ± 0.3 | L 1.8 ± 0.6<br>R 3.5 ± 0.8<br>L+R 2.6 ± 0.5 |

**FIG. 1.** Examples of the stimuli used for deriving numerosity or shape. 3, 4, or 5 dots were displayed. In one task subjects judged whether the dots had or had not a cardinality of 4 (numerosity). In the other task subjects judged whether the dots did or did not form a square (shape). Note that all stimuli were identical across conditions. For the numerosity and shape conditions performed inside the MR scanner the figure also shows the mean reaction times (RT, in ms) ± SD, and the error rates (in %) ± SD for the different stimulus configurations employed in both tasks.

ual response, indicating yes or no to the question of whether the display contains exactly four dots. The verbal encoding of such number facts (for use in exact calculation) implicates left inferior frontal cortex (Butterworth, 1999; Dehaene and Cohen, 1994; Dehaene and Cohen, 1995; Dehaene *et al.*, 1999). It is not known whether simple decisions about numerosity also involve this area, although the fact that a numerical decision must eventually be taken may predispose subjects to employ the fast serial counting procedure (Gallistel and Gelman, 1992) rather than the parallel preattentive procedure (Sathian *et al.*, 1999).

The design of the experiment accordingly implicates directed attention to each of two cognitive tasks performed with respect to the identical stimuli. Differential activations observed can thus be attributed to the distinct cognitive operations performed rather than the initial perceptual processing of the display.

## METHODS

*Subjects.* Nine healthy, right-handed volunteers (1 female, 8 males; aged 31–37) with no history of neurological or psychiatric illness gave informed consent. The study was approved by the local ethics committee of the University Hospital, Heinrich-Heine-Universität (Düsseldorf, Germany).

*Stimuli, tasks, and study design.* In all conditions, stimuli consisted of three, four, or five dots. Each dot, corresponding to a visual angle of 3.4°, appeared pseudorandomly in a subset of nine positions on an imaginary square grid (see Fig. 1). The stimuli subtended a maximum horizontal and vertical visual angle of 21°. The dots were arranged in such a way that the stimuli represented both familiar symmetrical ("canonical") patterns and less familiar asymmetrical patterns in order to reduce interference effects from pattern recognition processes (Mandler and Shebo, 1982).

Stimuli were presented in black on a white background during the fMRI BOLD contrast EPI measurements in the center of a 29-cm screen (horizontal visual angle of 60°, vertical visual angle of 30°) for 300 ms (stimulus on-time) with an interstimulus interval of 1330 ms using MEL (MEL Professional, Psychology Software Tools, Inc., Pittsburgh, PA). Subjects viewed the display from a distance of 25 cm (14-cm screen to mirror, 11-cm mirror to subjects' eyes; the mirror reflected the stimulus display). The stimuli either contained three (25% of trials), four (50% of trials), or five (25% of trials) dots, which when grouped together either formed a square (50% of trials) or other figures (50% of trials). In a block of trials a total of 18 stimuli were shown, hence each condition lasted 30 s. Between conditions a "baseline" (lasting 30 s) was introduced. The "baseline" allowed a 5-s presentation of task instructions (using MEL system font 08 enlarged to a font size of 16) for the task (numerosity or shape, left or right hand for response) that the subjects had to perform. Since hand of response did not interact with either experimental condition all data were subsequently collapsed with respect to hand. The instructions were followed by a white screen with a black

circle (diameter of 20°) presented in the center of the screen for 15 s. In this way, we prevented an overlap of neural activity specific to the different experimental conditions and hence allowed the haemodynamic responses of the different conditions to be separated. The experimental stimuli appeared in a quasirandom sequence such that the same stimulus was never displayed more than twice in a row.

In the numerosity condition, subjects were instructed to judge whether or not the number of dots displayed was equal to four. Subjects pressed a button with their index finger if the number of dots displayed equaled four and another button with their middle finger if the number of dots was not four. In the shape condition, subjects judged whether or not the presented stimulus was a square. Once the decision was made, the motor responses were made in the same way as in the numerosity condition. Reaction times of the button presses (measured from stimulus-onset) and error rates were recorded as measures of task difficulty. Prior to scanning, all subjects were given practice (both outside and inside the scanner) on one block of 20 trials for both the numerosity and shape conditions.

All tasks were performed in free vision for the following reason: We have previously demonstrated that there is a strong interaction between the neural activity resulting from an object-centered visuospatial information processing task and allowing/disallowing eye movements (Fink *et al.*, 1997a). It is therefore likely that allowing/disallowing eye movements during deriving numerosity or shape would interact with the neural activations resulting from performing the task. In principle, this could have been incorporated into the study design. However, we did not want to reduce statistical power by halving the number of repeats per condition. Also, we wished not to introduce a further local component to the stimulus display by adding a fixation aid.

*Eye movement study.* To test for putative differential eye movements between the experimental conditions, we conducted an eye movement study (using an infra-red on-line monitoring video-based eye tracking device) on all subjects after the imaging study: We did not want subjects to be overly practiced before scanning commenced. Eye position was analyzed using the normalized x- and y-coordinates of the subject's gaze on the screen. We compared the length of the total scan path in the experimental conditions by *t* test.

*Functional magnetic resonance imaging and scanning paradigm.* Functional MR images were acquired on a Siemens Vision 1.5T whole-body scanner with echo planar imaging (EPI) capability and using standard imaging procedures (Gradient-echo EPI, TE = 66 ms, TR = 5 s, flip angle = 90°, 30 slices of 4.00 mm thickness each, interslice gap 0.4 mm, FOV = 200 mm, in-plane resolution = 3.125 mm × 3.125 mm) as described previously (Fink *et al.*, 2000). Thirty slices were deemed sufficient for whole brain coverage. Using a midsagittal scout image, the slices were oriented in the plane of the anterior-posterior commissure (AC–PC). Additional high-resolution anatomical images were acquired for all subjects using the 3-D MP-RAGE (magnetization-prepared, rapid acquisition gradient echo) sequence with the following parameters: TE = 4.4 ms, TR 11.4. ms, flip angle = 15°, inversion time (TI) = 300 ms, matrix = 200 × 256, FOV = 20 cm, 128 sagittal slices, slice thickness = 1.33 mm. The fMRI paradigm consisted of a total of 100 scans per experimental run: three dummy acquisitions were followed by eight repetitions of a baseline period of 30-s (6 × TR) followed by eight repetitions of a cycle with a 30-s activation period (6 × TR) followed by one dummy acquisition. Each of these time series was repeated five times per subject. The experimental conditions were presented in a counterbalanced order within each time series, between time series, and between subjects. For example, this led to the following scanning sequence (taken from run 1 from subject 1): 3 dummy acquisitions – B (Baseline) – N (Numerosity) – B – S (Shape) – B – S –B – N – B – S –B – N – B– N – B – S – 1 dummy acquistion.

*Image processing.* All calculations and image manipulations were performed on SPARC 20 workstations (SUN Microsystems Computers) using MATLAB (The Mathworks Inc., Natick, MA) and SPM97d (Statistical Parametric Mapping software, SPM; Wellcome Department of Cognitive Neurology, London, UK; http: www.fil.ion.ucl.ac.uk). SPM was used for image realignment, image normalization, smoothing, and to create statistical maps of significant relative regional BOLD response changes (Friston *et al.*, 1995a,b).

The first three images of each time-series, during which the MR signal reaches a steady-state, were discarded. The remaining 96-volume images of each time-series were automatically realigned to the first image (corresponding to the 4th acquired image of the time series) to correct for head movement between scans. Image sets of the conditions and the baseline were then co-registered to the 3-D anatomical data set using MPItool (MPItool, University of Cologne), the AC and PC points identified, and transformed into a standard stereotactic space (Talairach and Tournoux, 1988), using the intercommissural line as the reference plane for the transformation. This spatial transformation uses linear proportions and a non-linear sampling algorithm (Friston *et al.*, 1995a). Data were thereafter expressed in terms of standard stereotactic coordinates in the x-, y-, and z-axes (as defined in Table 1). The resulting pixel size in standard stereotactic space was 4 × 4 mm with an interplane distance of 4 mm. Transformed functional data sets from each subject were smoothed with a Gaussian kernel of 6 mm, for single-subject analysis, and of 10 mm (full width half maximum) for the group analysis to meet the statistical

requirements of the "General Linear Model" and to compensate for normal variation in individual brain size, shape and sulcal/gyral anatomy across subjects. Voxels that had values greater than 0.8 of the volume mean in all the images were selected to restrict analysis to intracranial regions.

*Statistical analysis.* Following stereotactic normalization and smoothing, statistical analysis was performed. Low frequency cosine waves modeled and removed subject-specific low frequency drifts in signal, and the global means were normalized by proportional scaling. Data were analyzed modeling the different conditions as reference waveforms (i.e., box car functions convolved with a haemodynamic response function (Friston *et al.*, 1995c) in the context of the General Linear Model employed by SPM97d (Wellcome Department of Cognitive Neurology, London; http:/www.fil.ion.ucl.ac.uk)). We accordingly defined a design matrix comprising contrasts modeling the alternating periods of "baseline" and "activation" using a delayed box-car reference vector that accounted for the delayed cerebral haemodynamic response function after stimulus presentation.

*Conjunction analysis.* The data were first analyzed for neural activations common to the experimental conditions relative to the baseline (Price and Friston, 1997). Accordingly, this analysis revealed neural activations that were significantly activated by both experimental tasks when directly comparing each of the experimental tasks with the nonvisuospatial baseline (i.e., Numerosity > Baseline *and* Shape > Baseline). The level of significance was now raised to $P < 0.001$, corrected for multiple comparisons, with an extent threshold of 100 voxels as this analysis compared the experimental conditions to the baseline that did not involve visuospatial analysis.

*Specific effects.* Thereafter, specific effects were tested by applying appropriate linear contrasts to the parameter estimates for each condition, resulting in a *t* statistic for each and every voxel. These *t* statistics (transformed to *Z* statistics) constitute a statistical parametric map (SPM). These SPMs were then interpreted by referring to the probabilistic behavior of Gaussian random fields. Voxels were identified as significant only if they passed a height threshold of $Z = 4.5$ ($P < 0.05$, corrected for multiple comparisons) and belonged to a cluster of at least 100 activated voxels (Friston *et al.*, 1995b). Hemispheric asymmetries were tested for significance by assessing hemisphere × condition interactions using SPM. This procedure was employed when the regional activation in one hemisphere reached the significance level of $P < 0.05$, corrected, and the homologous activation in the other hemisphere just failed to meet that threshold.

*Random effects model.* For the group analysis, repeated measures (scans) were collapsed within subject (after having adjusted for both global blood flow by using proportional scaling, and low-frequency physiological drifts by using a high-pass filter of 120 s, see above) to give one scan per condition per subject. These conditions were then compared between subjects, thereby effecting a random effects model, allowing inference to the general population.

*Localization of activations.* The stereotactic coordinates of the pixels of local maximum significant activation were determined within areas of significant relative activity change associated with the tasks. The anatomical localization of these local maxima was assessed by reference to the standard stereotactic atlas (Talairach and Tournoux, 1988), and validation of this method of localization was obtained by superimposition of the $SPM_{\{Z\}}$-maps on the group mean MR image calculated after each individual's MR image had been stereotactically transformed into the same standard stereotactic space (Friston *et al.*, 1995a).

## RESULTS

### *Neural Activations*

*Activations common to both numerosity and shape judgements.* Significant increases in neural activity ($P < 0.001$, corrected for multiple comparisons) *common* to all conditions relative to baseline (Price and Friston, 1997) were observed in networks concerned with visual processing (temporo-occipital cortex), visuospatial localization (superior and inferior parietal cortex along the intraparietal sulcus), and response execution (primary motor cortex, supplementary motor area, anterior cingulate, ventral premotor cortex, striatum, and cerebellum). Table 1 summarizes the local maxima and the *Z* scores within these regions; Fig. 2 provides a pictorial representation of the neural activations by showing the SPM of the respective conjunction analysis.

*Differential activations caused by numerosity judgements.* Significant increases in neural activity associated with numerosity (*N*) judgements relative to shape (*S*) judgements ($N > S$; $P < 0.05$ corrected) were observed in occipital cortex bilaterally and left lingual gyrus, corresponding to early visual processing areas (Amunts *et al.*, 2000; Sereno *et al.*, 1995; Shipp *et al.*, 1995), and the left inferior frontal gyrus. The hemispheric difference in the lingual gyrus was not significant, suggesting that this region was activated in both hemispheres. No significant increases were observed in either the superior or inferior parietal cortex. The areas activated differentially with numerosity judgements are displayed in Fig. 3; the local maxima and *Z* scores are summarized in Table 2A.

*Differential activations caused by shape judgements.* Increased neural activity associated with shape (*S*) judgements relative to numerosity (*N*) judgements ($S > N$; $P < 0.05$, corrected) were observed in right posterior cingulate cortex, left temporoparietal cortex,

**TABLE 1**

Relative Increases in Brain Activity Common to Deriving Number and Shape from Scattered Dots, Irrespective of the Hand Used for Response

| Region | Side | *x* | *y* | *z* | *Z* score |
|---|---|---|---|---|---|
| Conjunction analysis of experimental conditions relative to baseline | | | | | |
| Temporo-occipital cortex | L | −44 | −68 | +2 | 8.5 |
| | R | 48 | −62 | −14 | 8.4 |
| Primary motor cortex | L | −36 | −8 | +50 | 6.6 |
| | R | 46 | −4 | +50 | 7.9 |
| Striatum | L | −24 | +4 | 0 | 7.6 |
| | R | +24 | +6 | −2 | 7.9 |
| Ventral premotor cortex | L | −58 | +4 | +30 | 7.2 |
| | R | +44 | +10 | +22 | 7.8 |
| Lateral cerebellum | L | −26 | −58 | −24 | 7.3 |
| | R | +30 | −58 | −30 | 7.7 |
| Supplementary motor area | | | | | |
| | R | +6 | 0 | +58 | 7.5 |
| Anterior cingulate | L | −8 | +14 | +38 | 6.5 |
| | R | +10 | +16 | +30 | 7.3 |
| Inferior parietal cortex | L | −42 | −38 | +38 | 7.5 |
| | R | +48 | −40 | +52 | 7.5 |
| Superior posterior parietal cortex | L | −40 | −46 | +54 | 7.1 |
| | R | +28 | −64 | +58 | 7.1 |

*Note.* Coordinates are in standard stereotactic space (Talairach and Tournoux, 1988) and refer to maximally activated foci as indicated by the highest *Z* score within an area of activation associated with all task conditions relative to baseline (i.e., irrespective of whether numerosity or shape were derived and the hand used for reply). *x* is the distance in millimeters to the right (+) or left (−) of the midsagittal (interhemispheric) line; *y* is the distance anterior (+) or posterior (−) to the vertical plane through the anterior commissure; and *z* is the distance above (+) or below (−) the intercommissural line. R, right; L, left. All activations are significant at $P < 0.001$, corrected for multiple comparisons.

and left dorsolateral prefrontal cortex. The hemispheric differences in temporoparietal cortex and dorsolateral prefrontal cortex were not significant suggesting that these areas were activated in both hemispheres (Table 2B). The areas activated differentially with shape judgements are depicted in Fig. 4; the local maxima and *Z* scores are summarized in Table 2B.

### *Behavioral Data*

*Eye movement data.* There were no significant differences in eye movements across tasks and conditions (as assessed outside the MR scanner with the same volunteers). The mean scan path (*N:* 3281 (mean) ± 1244 (SD); *S:* 3257 ± 1505) was not significantly different between the numerosity (*N*) judgement task and the shape (*S*) judgement task.

*Reaction time data.* Reaction times (RT, *N:* 697 ms (mean) ± 124 ms (SD); *S:* 628 ms ± 134 ms) taken outside the MR scanner during the eye movement study differed significantly [$F(1,180) = 25.6$, $P < 0.001$] between conditions while error rates (*N:* 4% (mean) ± 0.9% (SD); *S:* 4% ± 0.7%) did not. RTs and error rates taken inside the scanner *during* the fMRI study are shown in Fig. 1. The differences in RT between conditions were significant [$F(1,180) = 21.2$, $P < 0.001$]. In addition, we calculated the statistical significance of a theoretically crucial subset of comparisons concerning the number of stimulus items in the displays and the canonicity of their arrangement. Since the data were not normally distributed for these restricted subsets, we performed Mann–Whitney Rank Sum Tests on the reaction times. With respect to the square task, there was a significant difference in RT between "yes" responses to squares made of four versus five dots ($P = 0.005$); for the comparison of three dot versus five dot nonsquares, there was a significant difference between "no" responses to nonsquares of three versus five dots ($P < 0.001$). With respect to the numerosity task, the RT differences between "no" responses to three versus five dots was likewise significant ($P < 0.001$). In all comparisons, reaction times were longer to the stimulus displays containing more dots. We also calculated the effect of canonical versus noncanonical shapes for "yes" responses to four dots in the numerosity task. Canonical shapes were responded to more quickly than noncanonical shapes ($P < 0.001$).

## DISCUSSION

That temporo-occipital cortex is implicated in both the numerosity and the shape task (relative to baseline, as assessed by the conjunction analysis) suggests that, whenever possible, subjects made some use of

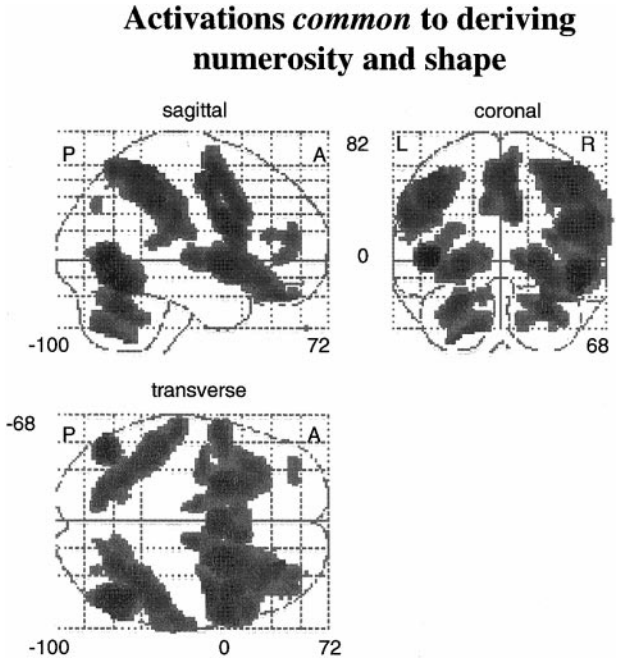


**FIG. 2.** Relative increases in neural activity (for the 9 subjects) associated with both experimental conditions, i.e., deriving numerosity and deriving shape from identical displays relative to the nonvisuospatial baseline, as assessed by the SPM conjunction analysis (see Methods). Areas of significant relative increase in neural activity ($P < 0.001$, corrected multiple comparisons) are shown as through-projections onto representations of standard stereotactic space. Sagittal, side view; coronal, view from the back; transverse, view from above. The exact coordinates of the local maxima within the areas of activation and their $Z$ statistics are given in Table 1. R, right; L, left; A, anterior; P, posterior. The numbers on the axes refer to coordinates of standard stereotactic space.

visual pattern recognition routines in both tasks (Kanwisher *et al.*, 1997; Köhler *et al.*, 1995; Schacter *et al.*, 1995). This is hardly surprising in a task that explicitly calls for the derivation of shape from arrangement. That shape recognition may also have been employed (to some extent) when deriving numerosity is predicted from studies showing that canonical dot patterns (e.g., three dots arranged as an equilateral triangle, four dots as a square) can be quantified faster than random dot patterns (Dehaene and Cohen, 1994; Mandler and Shebo, 1982). The clearest demonstration of canonicity in our experiment comes from the significantly faster reaction time to make the judgement "4" when the dots form a square rather than merely a (nonsquare) quadrilateral (see Fig. 1 and the Results section). Many of the configurations we used are closer to the canonical rather than the random stimuli used in previous experiments (Butterworth, 1999; Dehaene and Cohen, 1994).

The involvement of anterior cingulate (in both tasks) suggests not only that the correct response must be activated but also that incorrect responses must be inhibited (Bush *et al.*, 1998). Such inhibition is perhaps particularly necessary when the stimuli include two types of arrangements that require a different response (positive or negative) consequent upon which task is being performed (see Fig. 1). Parietal cortex activation (both superior and inferior) along the intraparietal sulcus may indicate that both tasks demand the implicit or explicit localization of objects in space (Corbetta *et al.*, 1993; Fink *et al.*, 1997a). The remaining areas of activation common to all task conditions, including primary motor cortex, supplementary motor area, ventral premotor cortex, and lateral cerebellum, reflect the involvement of the motor system in response organization and execution.

In addition to the common areas discussed above, the results clearly show that other brain regions are differentially implicated in making numerosity versus shape judgements. These findings were obtained in an experiment in which the stimulus displays for numerosity and shape conditions were identical, as were the final (two-choice) responses with which subjects indicated their judgements. The differential activations are unlikely to be due to general difficulty differences between the tasks, although the reaction time data (see Fig. 1) does indeed indicate that the numerical task takes significantly longer to perform than the shape task. If generalized difficulty was the sole variable accounting for our results, one would expect that the comparison of numerosity greater than shape ($N > S$) would show no significant activations. In so far as the construct of task difficulty is associated with specific brain regions, one would expect dorsolateral prefrontal cortex to be also associated with the more difficult task (Barch *et al.*, 1997). Our results show that dorsolateral prefrontal cortex is associated with the shape derivation task, not the numerosity task, despite the fact that the reaction time data shows the numerosity task to be the more difficult task.

With respect to numerosity, the reaction time results for stimuli with 3, 4, and 5 dots suggest that a fast serial may have been used (Trick and Pylyshyn, 1994). The reaction times and error rates depicted in Fig. 1 (and analyzed in the Results section) show an increase of 100–130 ms as set size increased from 3 to 5 dots. In conventional enumeration experiments with random stimuli, where the response measure is naming time, responses based on subitizing increase within the range of 20 to 100 ms per item, whereas when subvocal counting is employed the slope increases to 250–350 ms/item with a concomitant increase in error rate to 20% and beyond (Dehaene and Cohen, 1994; Mandler and Shebo, 1982; Trick and Pylyshyn, 1994). Our reaction time results are more similar to those seen when subitizing canonical arrangements (Butterworth, 1999; Dehaene and Cohen, 1994), where the increase between 3 and 5 dot displays is typically no more than 100 ms.

It must, however, be noted that our task differed somewhat from standard experiments on the enumeration of small sets. Our subjects were not asked to state

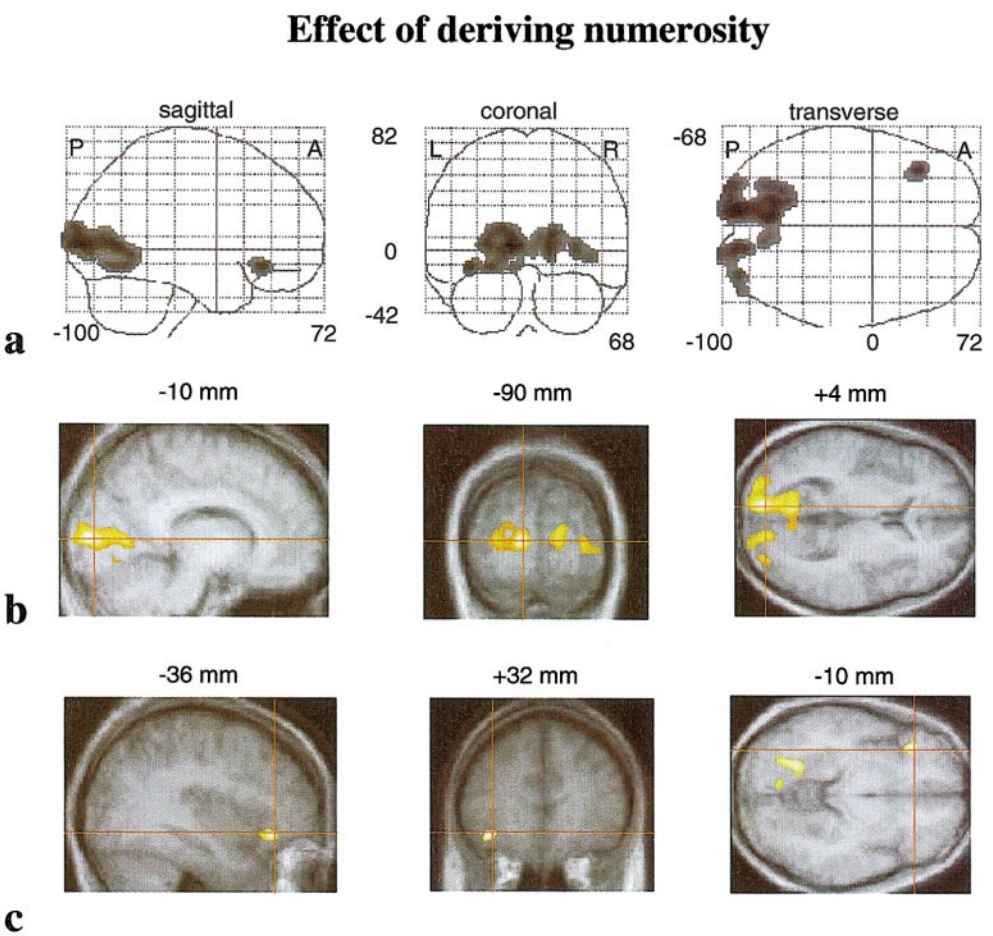


**FIG. 3.** Relative increases in neural activity (for the 9 subjects) associated with deriving numerosity. Areas of significant relative increase in neural activity ($P < 0.05$ corrected) are shown as through-projections (a) onto representations of standard stereotactic space. Sagittal, side view; coronal, view from the back; transverse, view from above. The local maxima of the areas of significant relative increase in neural activity are displayed superimposed on transverse MR sections to detail the functional anatomy of the activations and their relationship to underlying structural anatomy. There is bilateral striate and prestriate (b) as well as left inferior frontal (c) activation with deriving numerosity. The exact coordinates of the local maxima within the areas of activation and their *Z* statistics are given in Table 2A. R, right; L, left; A, anterior; P, posterior.

how many objects each display contained, but rather to indicate whether or not the number of dots was four. It would nonetheless appear that our variant task too can be performed very quickly (between 600 and 800 ms from stimulus onset to response) for small visual numerosities. Consistent with the reaction time data, it

**TABLE 2**

Relative Increases in Brain Activity Associated with Deriving Numerosity or Shape from the Stimuli

| Region | Side | *x* | *y* | *z* | *Z* score |
|---|---|---|---|---|---|
| (A) Effect of deriving numerosity | | | | | |
| Occipital cortex | L | −10 | −90 | +4 | 5.5 |
| | R | +18 | −92 | +12 | 4.6 |
| Lingual gyrus | L | −8 | −68 | +4 | 4.8 |
| | R | +10 | −72 | 10 | 3.9* |
| Inferior frontal gyrus | L | −36 | +32 | −10 | 4.5 |
| (B) Effect of deriving shape | | | | | |
| Posterior cingulate cortex | R | +6 | −34 | +42 | 5.2 |
| Temporoparietal cortex | L | −56 | −58 | +20 | 4.5 |
| | R | +54 | −54 | +20 | 4.1* |
| Dorsolateral prefrontal cortex | L | −32 | +24 | +36 | 5.0 |
| | R | +20 | +46 | +30 | 4.4* |

*Note.* For abbreviations see Table 1. All activations significant at $P < 0.05$, corrected for multiple comparisons; except for starred *Z* scores, where $P < 0.001$, uncorrected. The latter regions are included because there was no significant side-to-side difference, which implies bilateral activation of these regions.

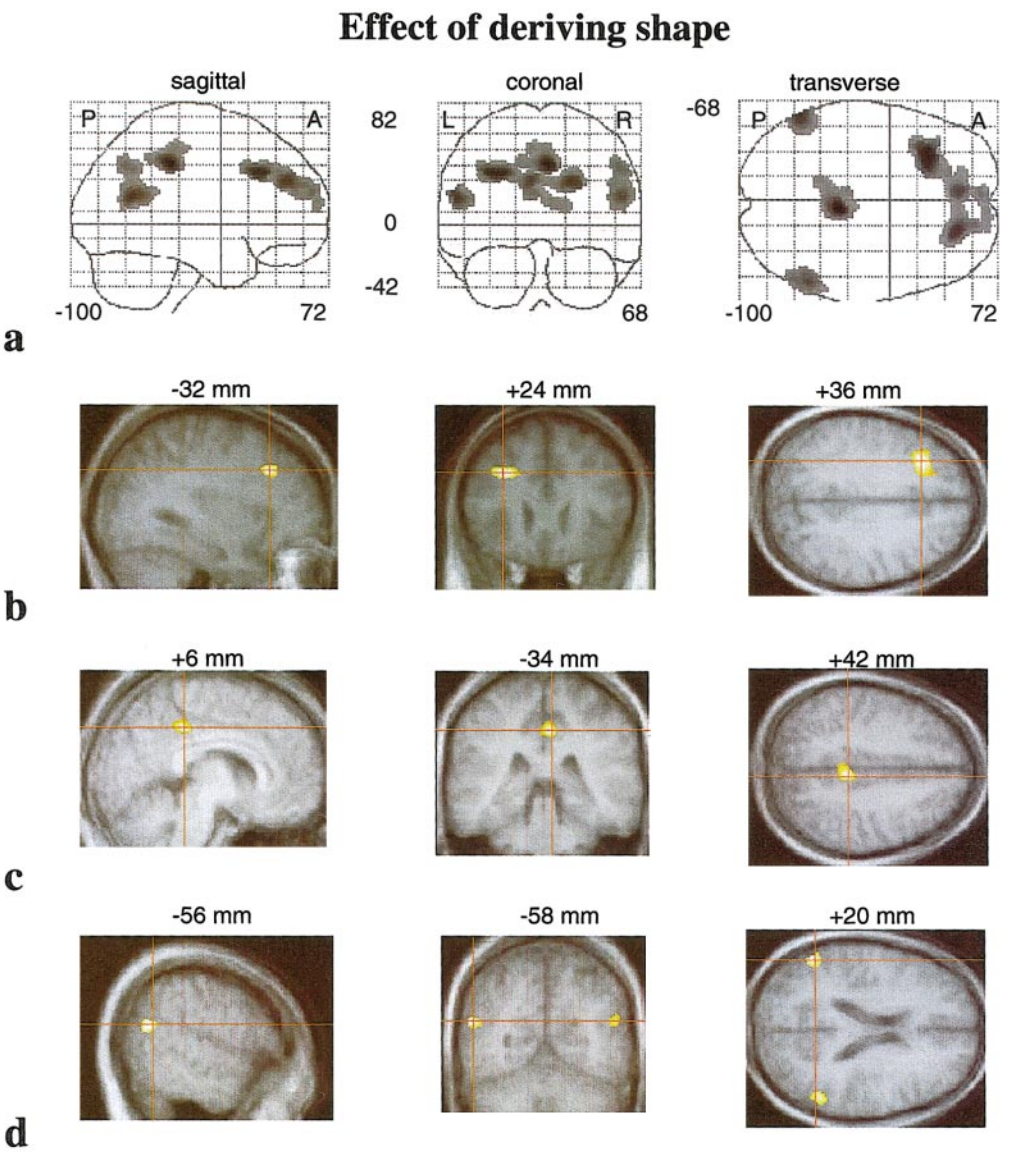


**FIG. 4.** Relative increases in neural activity (for the 9 subjects) associated with deriving shape. Areas of significant relative increase in neural activity ($P < 0.05$ corrected) are shown as through-projections (a) onto representations of standard stereotactic space. Sagittal, side view; coronal, view from the back; transverse, view from above. The local maxima of the areas of significant relative increase in neural activity are displayed superimposed on transverse MR sections to detail the functional anatomy of the activations and their relationship to underlying structural anatomy. There is increased neural activity in dorsolateral prefrontal (b), posterior cingulate (c), and temporoparietal cortex (d). The exact coordinates of the local maxima within the areas of activation and their *Z* statistics are given in Table 2B. R, right; L, left; A, anterior; P, posterior.

further seems that one aspect of our numerosity task draws strongly upon striate and extrastriate areas that have been associated with preattentional parallel processing (Dehaene and Cohen, 1994; Ffytche and Zeki, 1996; Hirsch *et al.*, 1995; Sathian *et al.*, 1999). The initial assignment of numerosity to the display may be the source of those activations in early visual processing areas.

Equally plausibly, it may be that these early visual areas are activated by attentional processes. There is a wealth of evidence from functional neuroimaging (Chawla *et al.*, 1999; Corbetta *et al.*, 1991; Shulman *et al.*, 1997) and single-cell neurophysiology (Desimone, 1998; Luck and Hillyard, 1994) that top-down influences can modulate neural activity in extrastriate visual cortex and perhaps even in striate cortex (Somers *et al.*, 1999). The conjunction analysis (Table 1) shows substantial activation of inferior and superior parietal cortex that could be one source of this modulation. A previous study using PET (Sathian *et al.*, 1999) has shown that when subitizing (in the range 1 to 4 targets) is contrasted with the enumeration of five to eight targets, subitizing does implicate activation of temporoparietal cortex. We accordingly suggest that this

region does not reveal itself in our comparison of numerosity with shape because there is an equal call upon the resources of temporoparietal cortex when deriving shape from scattered objects.

The actual decision that must then be made (Is 4 the numerosity of the display?) is an explicit, exact numerical judgement. Extending the results of lesion studies (Butterworth, 1999) and other neuroimaging experiments that have required subjects to deploy number facts for use in precise numerical calculations (Dehaene *et al.*, 1999), we find that left inferior frontal cortex is also implicated even in our simple numerosity task. That the final decision may be verbally (albeit subvocally) mediated could account for why overall reaction times for this task are slower than for the shape task. Alternatively, even without verbal mediation, the decision component in our numerosity task may be intrinsically more difficult than the decision component in our shape task.

Because the stimulus displays consisted of fairly widely separated dots, our shape judgement task could not be performed by recognition routines based directly upon contour, physical or illusory (Ffytche and Zeki, 1996; Hirsch *et al.*, 1995; Kovács and Julesz, 1994; Kovács, 1996). We accordingly did not expect to find strong activation of inferior temporal regions concerned with shape and object recognition by contour analysis (Price *et al.*, 1996; Schacter *et al.*, 1995; Warrington and Taylor, 1978). Rather, we argued that the global shape on which the judgement depended (Does the display form a square or not?) must be constructed from the sets of distinct local dots by processes that place significant demands upon visual attention. Psychophysical evidence has shown that grouping in the service of shape formation is a serial attentional process (Trick and Enns, 1997). Our reaction time data (see Results section) likewise show that displays with more dots take significantly longer to respond to. Consistent with this analysis, we find bilateral temporoparietal activation centered on the temporoparietal junction in areas previously associated with switching attention between the local and the global aspects of hierarchically organized visual stimuli (Fink *et al.*, 1996, 1997b).

The activation seen in the posterior cingulate cortex may reflect the dual role that this area plays with respect to both the maintenance of attention (Mesulam, 1990) and memory for spatial layouts (Maguire *et al.*, 1998). The final decision (affirmative or negative) then implicates dorsolateral prefrontal cortex, which may also be involved in the attentional modulation of visual processing in extrastriate cortex (Barceló *et al.*, 2000; Kastner *et al.*, 1999).

Finally, we emphasize that core aspects of these two tasks seem to be accomplished by different neural mechanisms when deriving the numerosity of small sets versus the assignment of shape from arrangement. This result was found when the stimulus arrays presented (and their exposure duration) were absolutely identical across the two tasks. Our experimental design thus contrasts with previous functional imaging studies in which subitizing 1 to 4 targets is compared with counting 5 to 8 targets (Sathian *et al.*, 1999). In that design, the process of subitizing is necessarily confounded with the number of items in the display. Having avoided this confound by contrasting subitizing not with subvocal counting but rather with the derivation of shape, we nonetheless find that the assignment of numerosity to small sets draws heavily on striate and extrastriate cortex, albeit modulated perhaps by top-down attentional mechanism in temporoparietal cortex. Nonetheless, deriving shape from scattered objects draws even more strongly upon temporoparietal cortex, due most likely to the fact that task performance involves shifting between local and global representations (Fink *et al.*, 1997b; Robertson and Lamb, 1991).

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