Single-trial classification of parallel pre-attentive and serial attentive processes using functional magnetic resonance imaging

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Theories of perception have proposed a basic distinction between parallel pre-attentive and serial attentive modes of processing. However, chronometric measures are often ambiguous in separating parallel and serial processes. We have used the activity of attention-related regions of the human brain, measured with functional magnetic resonance imaging, to separate parallel from serial processes at the single-trial level in a visual quantification task. In this task, some have suggested the deployment of two qualitatively different processes, a fast parallel 'subitizing' for sets of one, two or three objects and a slow serial counting for larger sets. Our results indicate that attention-related regions of the posterior parietal and frontal cortices show a sudden increase in activity only from numerosity four onwards, confirming the parallel–serial dichotomy of subitizing and counting. Moreover, using the presence or absence of attentional shifts, as inferred from the activation of posterior parietal regions, we successfully predict whether, on a given trial, subjects deployed a serial exploration of the display or a parallel apprehension. Beyond the subitizing/counting debate, this approach may prove useful to probe the attentional demands of other cognitive tasks.

Keywords: attention; parietal; subitizing; counting; functional magnetic resonance imaging

1. INTRODUCTION

Theories of perception have proposed that human perception operates in two modes (Treisman & Gelade 1980; Eriksen & Yeh 1985). The first is assumed to be pre-attentive and parallel, in the sense that it can process different bits of information at the same time and before the deployment of focal attention. The second is assumed to be serial and attentive, in the sense that only the stimuli within the current focus of attention can be processed, so that multiple stimuli can only be processed by successively deploying attention towards each of them. In order to determine the experimental conditions under which pre-attentive parallel processes are sufficient to carry out a given task, reaction time (RT) measures have classically been used. However, chronometric measures are often ambiguous in separating serial and parallel models (Snodgrass & Townsend 1980). For instance, resource-limited parallel processes can mimic the linear increase in RT typically associated with serial processing. Moreover, subjects' reliance on a parallel, pre-attentive strategy versus a serial attentive strategy can be probabilistic rather than deterministic, and this variability might mask the existing dichotomy between parallel and serial processes in certain cases. Finally, the very distinction between those modes of processing has been debated, and alternative models have been proposed (Duncan & Humphreys 1989).

In order to have a sharper picture of the attentional requirements of a given process, and therefore to more easily separate serial from parallel processes, a more specific measure of the deployment of attention at the single-trial level is needed. The functional magnetic resonance imaging (fMRI) signal from cerebral regions supporting attention orienting can provide us with such measure. Posterior parietal cortex, in particular, is systematically activated during internal shifts of attention and is thought to be the source of attentional amplification effects in distant areas (Wojciulik & Kanwisher 1999; Corbetta *et al.* 2000; Friston & Buchel 2000). Here, we propose to use single-trial measures of parietal activation to measure directly whether attentive processes have been deployed in a cognitive task. If subjects sequentially orient their attention towards each stimulus, then the activation of the parietal attention system should be elevated and proportional to the number of attention shifts. In particular, both parietal activation and RT should increase with the number of stimuli. If, however, the increase in RT is due only to parallel processing of increasing difficulty, but without serial attention orienting, then parietal activation should not be modulated by the number of items.

Because fMRI activation can be measured on single trials, it can be used even when the data consist of a mixture of serial and parallel trials. The logic of going from brain activity to the cognitive processes, reversing the usual direction of functional imaging experiments, was previously applied to infer motor behaviour using fMRI signals from the motor cortex (Dehaene *et al.* 1998) or to

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separate trials where subjects imagined a face or a house using fMRI signals from the fusiform face area and the parahippocampal place area (O'Craven & Kanwisher 2000). Here, we similarly show that single-trial parietal activation can be used to sort out trials with or without serial attentive processing, and that this can capture some of the otherwise unexplained inter-subject and inter-trial variability in behaviour.

We apply this approach to separate pre-attentive parallel and serial processes in a quantification task, where subjects attempt to name, as accurately as they can, the number of items presented in a visual array. In this task, performance varies importantly with the number of items presented. Up to three or four items, RTs are fast, increasing very little (less than 50 ms) with every item, and performance is flawless. Above three or four items, RTs show a sudden increase of up to 200 ms per item, and errors occur. Although this performance pattern has been known for a century (Cattell 1886; Warren 1897), its interpretation still remains controversial. The classical view is that it reflects a dissociation of two processes. Above three or four items, subjects count serially using covert attention or overt eye movements. Below this limit, an ill-understood parallel process called 'subitizing' enables subjects to assess numerosity in parallel (Kaufman *et al.* 1949; Trick & Pylyshyn 1994). Fine analyses of the behavioural evidence, however, show a smooth transition rather than a sharp discontinuity in performance at three or four items. Thus, some have claimed that quantification performance can be accounted for by a single serial process (Balakrishnan & Ashby 1991, 1992).

Previous studies using positron emission tomography have shown that a set of parietal, occipital and frontal regions show greater activation during counting than during subitizing (Sathian *et al.* 1999; Piazza *et al.* 2002). This might reflect a parallel–serial dichotomy of the two processes. However, the activity evoked by different numerosities was measured in only two distinct blocks, one collapsing over all numbers below four, and another collapsing across numbers from four to nine. This did not allow us to investigate if the regions more active in counting showed a sudden, discontinuous engagement at a specific numerosity or if their activity increased linearly with each added item, even within the subitizing range. Moreover, it was not possible to obtain a trial-by-trial measure of the brain activity, which could be crucial if subjects' reliance on a parallel pre-attentive process (subitizing) versus a serial one (counting) is probabilistic rather than deterministic.

In the present study, we used an event-related fMRI design to acquire functional images while subjects performed a quantification task on visual arrays of items. By using a silent fMRI period and a magnetic-resonance-compatible microphone, we were able to measure vocal responses in the magnet and to correlate them with brain activation patterns. Our goals were to test the predicted presence of a sudden activation of attentional networks for numbers beyond the subitizing range, and to attempt to detect, on a single-trial basis, whether subjects deployed a serial exploration of the display or a parallel pre-attentive apprehension of numerosity.

2. METHODS

(a) *Subjects*

Ten right-handed, healthy volunteers (five males and five females; age range of 21–29 years) gave written consent to participate in the study. The subjects' right handedness was confirmed by means of the Edinburgh inventory. All had normal or corrected-to-normal sight.

(b) *Procedure*

Cerebral activation was acquired for two experimental tasks: quantification and colour naming. Tasks were presented in sessions of alternating blocks of trials. There were four overall sessions in which one quantification block of 28 trials (four times the numerosity one to seven) was preceded and followed by a colour naming block of four trials. A single word presented on the screen before each block reminded subjects of the forthcoming task. For the quantification task, stimuli consisted of a set comprising between one and seven white squares presented visually on the black background of a computer screen. The squares varied randomly in dimension (subtending between $0.12°$ and $0.24°$ of visual angle). They were presented at random locations within a $100 \, mm \times 125 \, mm$ rectangular area, centred on the screen, the contour of which was visible, and varied from trial to trial between seven different colours (see figure 1 for sample stimuli). The locations of the squares were assigned randomly with the constraint that the borders of any two squares were at least 4 mm apart. Subjects were instructed to say aloud, as fast and accurately as they could, the number of items in the set. To measure response reaction times, a microphone was installed in the coil, and was connected to a voice key, triggered by the response onset. Responses were also tape recorded to measure accuracy.

For the colour naming task, stimuli consisted of empty rectangular areas identical in shape, position and colours, to the ones presented during the quantification task. Subjects were instructed to name aloud the colour of the rectangle. All stimuli were projected on a translucent screen 165 cm from the subject, subtending a visual angle of $5°$. The experiment was programed using EXPE6 software (see http://www.ehess.fr/centres/lscp/expe/). Trials were presented at a slow rate of one every 12 s (corresponding to five fMRI volumes acquisition period). Stimuli and responses occurred during the first fMRI acquisition, where the read-out gradient was disabled, which greatly decreased the scanner noise, and allowed us to detect and record subjects' vocal response. During the inter-trial period, a fixation cross was present in the centre of the screen. In order to alert subjects of the upcoming stimuli, 1000 ms before the presentation of the stimuli, the fixation cross thickened, then disappeared after 500 ms. Stimuli remained on the screen for 200 ms.

(c) *Imaging parameters*

The experiment was performed on a 3T MRI system (Bruker, Germany). Functional images sensitive to blood-oxygen level dependent contrast were obtained with a T2*-weighted gradient echo-planar imaging sequence (TR (repetition time), 2.4 s; TE (echo time), 40 ms; angle, $90°$; FOV (field of view), $192 \, mm \times 256 \, mm$; matrix, 64×64). The whole brain was acquired in 26 slices with a slice thickness of 4.5 mm. Synchronized with the beginning of each trial, the read-out gradients were disabled for a period of 2.4 s (1 TR), followed by four whole-brain scans. High-resolution images (three-dimensional gradient echo inversion-recovery sequence, TI (inversion time), 700 mm;
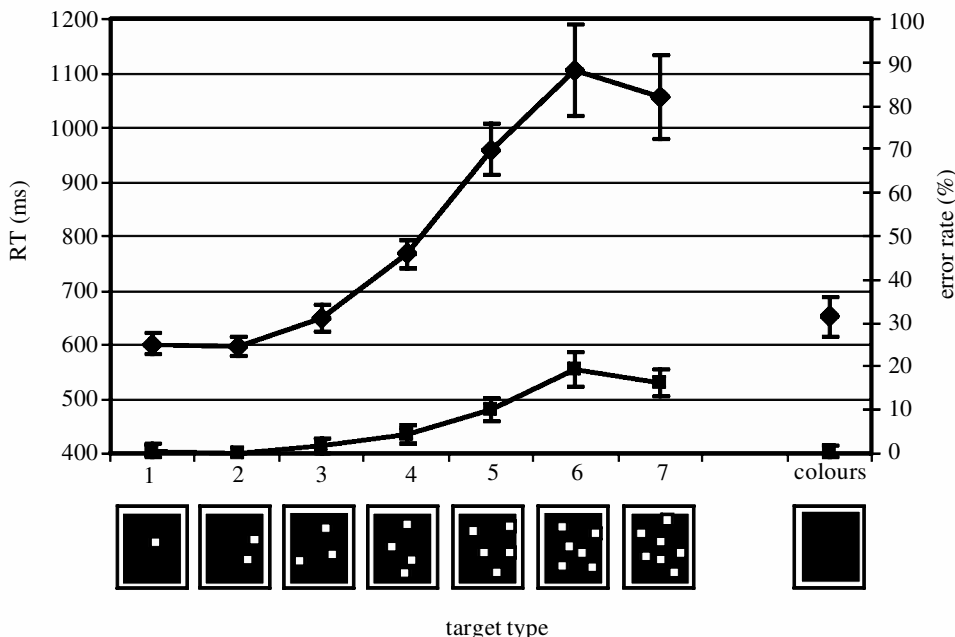
Figure 1. Behavioural results and example of stimuli. Mean RTs and error rates for quantifying sets of one to seven dots and naming the colour of a rectangular shape. Diamonds, RTs; squares, percentage incorrect.

TR, 2400 ms; FOV, 192 mm × 256 mm × 256 mm; matrix, 256 × 128 × 256; slice thickness, 1 mm) were also acquired.

(d) *Image processing and statistical analysis*

Data were analysed with SPM99 (http://www.fil.ion.ucl.ac.uk/spm). The first four volumes were discarded. All other volumes from each subject were realigned using the first volume as a reference, then they were normalized to the standard T2* template of the Montreal Neurological Institute using an affine transformation. Data were spatially smoothed with a 6 mm full width at half maximum isotropic Gaussian kernel, and convolved with a synthetic haemodynamic response function. The data were high-pass filtered using a set of discrete cosine basis functions with a cut-off period of 120 s. The contrasts of interest for each individual subject were then smoothed with a kernel of 5 mm, and a random-effect analysis was performed. To focus only on activation sites, all the contrasts were masked (at $p < 0.01$) with the regions that showed positive activation for that condition of interest. Unless otherwise stated, data are reported at $p < 0.05$ and corrected for multiple comparisons at the cluster level, $p < 0.001$ at the voxel level. For the contrast showing nonlinear increasing activation, and the contrast between counting and colour naming, the small-volume-correction option of Spm99 was used to search within a sphere of 6 mm radius placed around the maxima of the circuit activated more in counting than in subitizing. The voxelwise threshold was set to $p < 0.05$, and the clusters were reported if their extent was significant at $p < 0.05$, corrected for multiple comparisons across the small volume. The same effects were also explored with a classical whole-brain search (voxelwise, $p < 0.001$; cluster-level corrected, $p = 0.05$).

3. RESULTS

Cerebral activation was measured using fMRI while participants were briefly presented with arrays of one to seven small squares placed in a large rectangle in the centre of a screen. Their task consisted in quantifying the

array by saying the number aloud in a microphone that was placed in the coil. A control condition was also introduced, in which the large rectangle was empty, and the task consisted in naming its colour.

(a) *Behavioural data*

Correct RT measures were submitted to a one-way analysis of variance (ANOVA) with target type as the independent factor at eight levels (quantification of one to seven items, and colour naming). This analysis showed a significant effect of target type ($F_{7,63} = 31.10$; $p < 0.001$). Subjects were increasingly slower as the number of items increased (figure 1). Crucially, the slope of RT showed the expected increase between the numbers from one to three (subitizing range) and in the numbers from four to seven (counting range). This was tested by the presence of a quadratic trend in the one to four range ($F_{1,63} = 29.00$, $p < 0.001$). Such trend analysis looks for a deviance from linearity, testing for a presence of an increase from numerosity of three to four which is larger than the increase from one to three. The drop in RTs for seven is probably due to a 'guessing end effect' (Simon *et al.* 1998). This point was not included in the calculation of the slopes in the subitizing (one to three) and counting (four to six) range, which were of 24 ms for one to three items and of 168 ms for four to six items, a significant difference ($F_{1,9} = 18.93$; $p < 0.005$).

Responses for colour naming were overall very fast but slower than subitizing (651.76 and 597.92 ms, respectively) ($F_{1,63} = 10.19$; $p < 0.005$). Analyses on error rate showed a significant effect of target ($F_{7,63} = 12.00$; $p < 0.001$). Errors increased with the number of elements and started to be present at four. The error rates for colour naming and for subitizing did not differ (0.41% and 0.83%; $F_{1,63} = 0.02$; $p = 0.87$).

In summary, both enumeration speed and accuracy suggest a processing discontinuity between numerosities three and four, although they remained compatible with a con-

Table 1. Coordinates of activation peaks for counting > subitizing; counting > colour naming; more increasing in counting than in subitizing.
(Asterisks indicate regions that were significant at the cluster level in the whole-brain search analysis.)

area			Talairach coordinates			counting > subitizing	counting > colour naming	nonlinear increase with number
			x	y	z	z-scores	z-scores	z-scores
calcarine cortex			−12	−76	0	4.9	—	—
middle occipital cortex		L	−36	−80	8	4.0	—	—
intraparietal sulcus	(posterior)	R	32	−76	24	4.2	2.8	—
			20	−76	40	3.2	3.5	2.8
		L	−28	−72	40	4.4	2.6	3.5*
	(anterior)	R	36	−36	32	4.2	3.2	—
		L	−44	−44	36	3.9	3.3	—
precentral cortex	(lateral-frontal eye fields)	R	28	−4	56	3.8	3.0	3.3
		L	−40	0	32	3.8	2.5	—
			−24	−12	52	3.6	2.9	3.3
	(medial-supplementary eye fields)		8	8	60	4.8	—	2.3
cingulate cortex			4	20	32	4.5	2.9	2.4
dorsolateral prefrontal cortex		R	44	24	28	4.4	—	—
		L	−40	44	16	3.7	—	—
anterior insula		R	32	24	0	4.8	2.4	4.3*
		L	−36	20	−4	4.0	2.9	2.8
frontal operculum		L	−44	16	4	4.0	2.6	2.8
orbito-frontal gyrus	(lateral)	R	20	20	−20	4.2	3.0	3.1
		L	−32	16	−24	3.7	3.2	—
	(medial)	R	4	16	−20	3.5	2.7	—
putamen/caudatus		R	12	20	−4	3.7	3.1	2.7
		L	−16	16	−4	4.1	3.5	2.7
thalamus (anterior)		R	8	4	0	4.0	3.1	—
		L	−8	−4	−4	4.4	2.5	—
(posterior)		R	24	−36	0	3.9	3.1	—
		L	−20	−36	4	4.0	2.9	—
superior colliculi		R	12	−36	−16	4.3	3.1	—
		L	−4	−28	−8	4.0	4.0*	—

tinuous quadratic increase in difficulty (Balakrishnan & Ashby 1992). Imaging data allowed us to assess the presence of a sudden engagement of attention-related cortical circuits with four or more dots.

(b) fMRI data

(i) Subitizing range

Even at the very low threshold of $p = 0.05$ at the voxel level, no region showed greater activation in the subitizing range (one to three) than in the counting range (four to seven) or in the colour naming task. Moreover, within the subitizing range, no region showed increasing activation from one to three, even at the same low threshold.

(ii) Counting range

Quantifying four to seven elements, with respect to quantifying one to three, activated a large network of occipital, parietal, insular, prefrontal and subcortical areas (table 1; figure 2a). All regions within this network also showed increased activation when quantifying in the counting range was contrasted with colour naming (apart from two clusters in the occipital cortex) (see table 1). We then identified the regions whose activity increased with the number of items to be counted. A linear contrast for numbers between four and six identified a subgroup of regions of the previously individuated set, comprising the intraparietal sulci bilaterally, the medial precentral cortex (supplementary eye fields), the anterior insula/inferior frontal gyri bilaterally, and the superior colliculi (see table 2). The activation in these regions increases linearly as the number of items increases from four to six, tightly correlating with reaction times. The supplementary/frontal eye fields, superior colliculi and the posterior parietal cortex have been previously associated with serial shifts of attention and eye movements in space (Corbetta et al. 1998; Everling & Munoz 2000; Nobre 2001). The inferior regions of the frontal gyrus/insula are implicated in phonological and/or articulatory processing (Paulesu et al. 1993; Fiebach et al. 2002). Thus, counting may involve coordinated spatial shifts and verbal working memory updates to keep the running total of the count (Logie & Baddeley 1987).

Within the regions activated during counting more than during subitizing, we searched for regions with a significantly greater increase in activation with numerosity in the counting range than in the subitizing range. Such a nonlin-
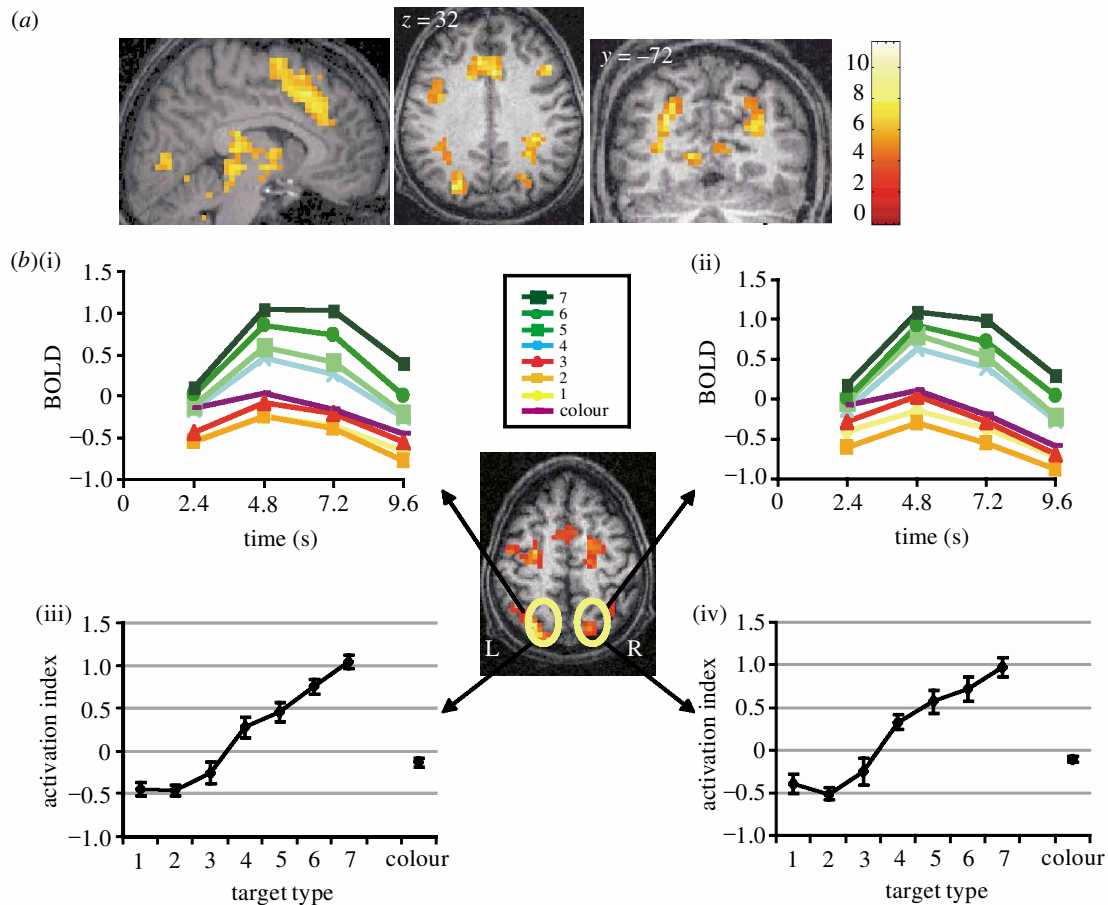
Figure 2. fMRI imaging of brain areas engaged in counting as opposed to subitizing. (*a*) Regions showing greater activation when quantifying four to seven elements (counting) than when quantifying one to three elements (subitizing). Group results are superimposed on sagittal, axial and coronal slices of an individual normalized anatomical image. (*b*) Left and right posterior parietal regions showing a nonlinear effect of number. Graphs (i) and (ii) show BOLD activation as a function of time, averaged across all subjects. The centre brain slice shows an axial view ($z = 50$) of the group results superimposed on an individual normalized anatomical image. Graphs (iii) and (iv) show the mean activation index for each stimulus type. Error bars indicate the inter-subjects standard error.

ear response, paralleling behavioural performance, was observed in the bilateral posterior intraparietal sulcus, the frontal and supplementary eye fields, the anterior cingulate cortex, the anterior insula, the orbitofrontal gyrus and basal ganglia (see table 1). Activation of these regions tightly mirrors the proposed subitizing/counting dichotomy in that it shows a minimal or no increase from numerosity one to three, a sudden discontinuous increase between numerosity three and four, and a linear increase from four onwards.

(iii) *A single-trial measure of posterior parietal activation*

Posterior parietal regions were the focus of further analyses. For each subject, we isolated the bilateral activation in the posterior parietal cortex with the contrast that showed a nonlinear increase with number. To compare brain activation with behavioural performance, we then calculated a single-trial index of the intensity of the activation. On each trial, a linear regression was calculated between the normalized blood oxygenation level dependent (BOLD) signal at the four data points following each stimulus, and the standard SPM haemodynamic function (without a constant term). Note that the BOLD signal is a relative measure where the reference point 0 is simply the mean activity of that region. Thus, the above acti-

vation index provides a relative, not an absolute, measure of single-trial activation. In particular, negative values need not indicate a deactivation relative to the inter-trial period, but merely indicate a low signal intensity with respect to the overall experiment.

We first submitted this activation index to a one-way ANOVA identical to the one applied to RTs. This showed a significant effect of target type ($F_{7,63} = 22.85$; $p < 0.001$ and $F_{7,63} = 35.54$; $p < 0.001$ for the right and left parietal clusters, respectively). Moreover, a quadratic trend test over progressively larger stimulus intervals showed that the first significant nonlinear increase was observed between numbers three and four ($F_{1,63} = 12.93$, $p < 0.05$ and $F_{1,63} = 6.78$, $p < 0.05$ for the right and left parietal clusters, respectively). The sudden increase in parietal activity at number four can be clearly seen in figure 2*b*, where the increase in activity between three and four is higher than either the increase between two and three, or between four and five.

We then used the activation index as a single-trial measure of the deployment of the parietal attention system, and attempted to use it to infer stimuli and subjects' strategy. On data from the first blocks of all subjects (1/4 of the total data), we performed a discriminant analysis, which finds the optimal linear combination of the right and left

Table 2. Coordinates of activation peaks for regions that show a linear increase with numerosity in the counting range.

area			Talairach coordinates			z-scores
			x	y	z	
intraparietal sulcus	(posterior)	R	32	−76	24	4.1
		L	−24	−80	44	4.5
			−28	−72	28	4.0
	(anterior)	R	40	−36	32	4.0
		L	−32	−44	32	3.7
medial precentral cortex (SEF)			8	8	60	3.9
			8	12	44	3.7
anterior insula/inferior frontal gyrus		R	24	24	−16	4.6
		L	−32	20	−8	3.8
superior colliculi			−8	−16	−12	3.9

activation indexes in order to classify the trials into two classes: range one to three (subitizing), and range four to seven (counting). We then applied this function to the remaining data. This correctly predicted 76% of the trials. All but one subject had high prediction scores (from 69% to 88%).

(iv) *Inferring subjects' strategies for quantifying four items*

Over the seven different numerosities, the worst predicted one was four, with 60% trials classified as counting and 40% as subitizing. As shown in figure 3, among the trials at numerosity four, there were some with a high activation and others with a low activation. This variability was confirmed by a close exploration of RTs. Four was the first number at which the variance in RTs began to increase sharply, both across as well as within subjects (see figure 4). Did this reflect measurement noise, or a genuine variability in the strategies used to quantify that numerosity? Inter-individual differences exist in how many items can be subitized (Akin & Chase 1978; Trick & Pylyshyn 1993). For instance, Trick and Pylyshyn reported a series of experiments on visual object enumeration where the subitizing range varied from two to six between different subjects (Trick & Pylyshyn 1993). In our data, examination of individual RTs suggested that different subjects subitized up to three, four or even five items. We therefore tested whether the sudden onset of activity of the posterior parietal region would allow us to predict the subitizing range of different subjects, as measured by their RTs. In order to do this, we classified subjects into 'early' and 'late' activators (five subjects per group). The 'early activators' were those who showed high parietal activation (more than 70% of the trials classified as 'active') already at numerosity three or four. The 'late activators' were those who showed no strong parietal activation at numerosity four (less than 61% of 'active' trials), and whose activation started to increase later, at numerosity five. We then went back to the RTs of these two groups. As shown in figure 4, 'early activators' showed a steeper counting curve, and an earlier onset of the linear part of the curve, than 'late activators'. An ANOVA with group as the between-subjects variable and number as a within-subjects variable (number between one and six) showed a significant group × number interaction ($F_{5,40} = 2.42$; $p = 0.05$). This indicated that the two groups did not differ at numerosity one, two or three ($p < 0.05$), but only in the coun-

ting range. Thus, the activity in posterior parietal regions partly accounted for inter-individual variability in counting performance.

For numerosity four there was also a large intra-individual variability in RTs, suggesting that the same subject might occasionally use subitizing or counting in different trials. Therefore, we also tested, within subjects, whether the trials with numerosity four that yielded high parietal activation corresponded to the use of a serial strategy, as measured by slower reaction times. We used a median split to separate, within each subject, the trials into two categories based on their level of parietal activation. Trials with high parietal activation were significantly slower than trials with low parietal activation (777 versus 737 ms, respectively; $F_{1,9} = 6.42$; $p < 0.05$). This result shows that, using the presence or absence of attentional shifts, as measured by activity in posterior parietal regions, we can partly account for some of the intertrial variability in performance, possibly associated with the deployment of serial versus parallel apprehension processes.

4. DISCUSSION

The objective of this study was to investigate whether we could separate parallel from serial attentive processes in a visual object quantification task. Previous imaging studies of visual object quantification using a block design showed that a set of parietal, occipital and frontal regions were more involved in counting than in subitizing (Sathian *et al.* 1999; Piazza *et al.* 2002). The present event-related design, while confirming this result, allowed us to measure the trial-by-trial engagement of different brain regions for each numerosity. The results revealed a set of bilateral fronto-parietal regions that were intensively active during counting, but to a much lesser extent during subitizing. Those regions showed essentially no increase in activation from numerosity one to three, but a sudden increase between numerosity three and four, and a linear increase from four onwards. Our results therefore support a two-process model with distinct operations underlying subitizing and counting.

The use of an automated algorithm to classify trials based on the level of posterior parietal activation suggests that, for a fixed intermediate numerosity of four, subjects sometimes use a parallel pre-attentive and sometimes a serial attentive strategy. Such a mixture of two processes
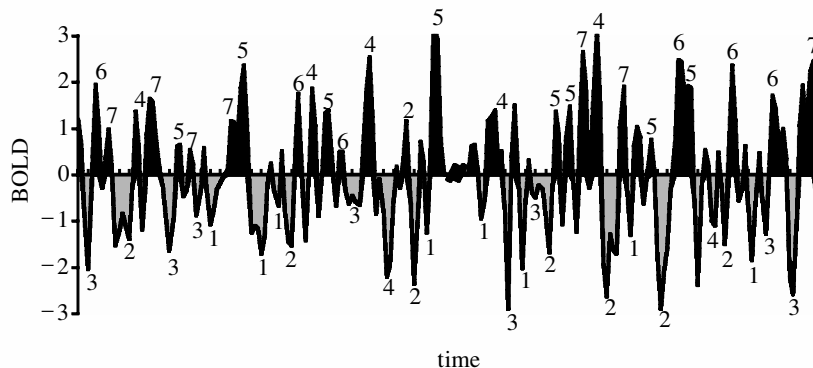
Figure 3. Time-course of the unaveraged activation profile of the right posterior parietal region for one subject. As shown here on a representative sample of two blocks (51 correct trials), almost all trials with more than four elements showed high activation, while trials with one to three elements showed lower activation. Black shading, counting range; grey shading, subitizing range.
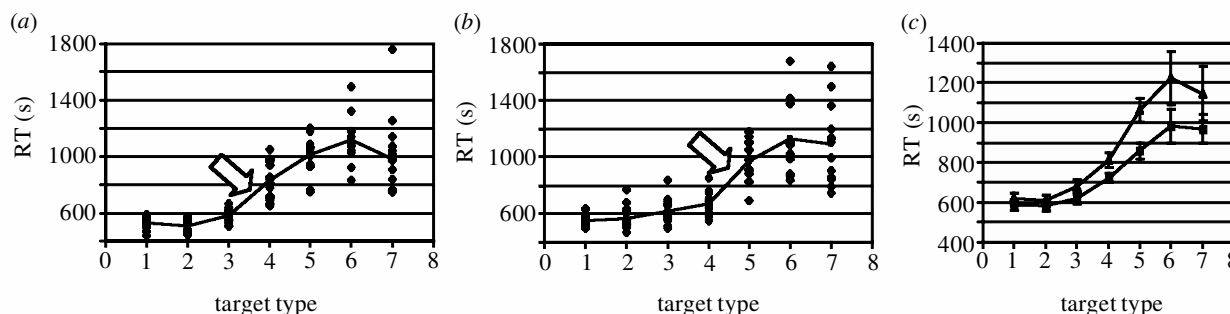

Figure 4. Variability of strategies from subject to subject and from trial to trial. (*a,b*) behavioural results from two subjects (10 and 8, respectively) showing a sudden increase in RT at four and at five, respectively. (*c*) RTs for early (triangles) and late (squares) subitizers, as classified on the basis of their sudden onset of parietal activity.

may explain why purely behavioural measurement of quantification time have not offered unambiguous evidence for dissociated processes of subitizing and counting. The present approach, relying on single-trial measurement and analysis of brain activation and its correlation with behaviour, provides a more powerful tool to evidence such a dissociation. Beyond the subitizing/counting debate, it may prove useful in order to separate pre-attentive from attentive processes in other domains, for instance, to study the single-trial deployment of attention in feature and conjunction search tasks.

The network of regions observed to underlie counting overlaps with the one classically associated with a variety of eye movement and attention-related tasks (for reviews see Corbetta 1998; Culham & Kanwisher 2001; Simon *et al.* 2002). In particular, one study showed that the intensity of the activity in the posterior parietal cortex and the frontal eye fields is proportional to the number of saccades performed by subjects in a given interval (Kimmig *et al.* 2001). In our study, eye movements were made ineffectual in performing the task by flashing the stimuli for 200 ms. Nevertheless, we also found a linear increase in activation of the same regions with the number of counted items, suggesting that this activation can be used to index the number of attention movements on a given trial. Attention movements are consistent with the hypothesis that counting involves the serial attentional 'tagging' of each of the counted items (Trick & Pylyshyn 1993). Nevertheless, we cannot exclude the remote possibility that eye movements, however ineffective for performing the task owing to very

brief stimulus presentation, were made more often with the higher numbers of items, perhaps in a reflex attempt to scan the display overtly.

Other elements of the active network may reflect the additional processes engaged in the complex coordinated activity of counting. In particular, the activation of the anterior insular/inferior prefrontal region may reflect the coordination of the spatial tagging process with the internal recitation of the series of number words. Also, the anterior (horizontal) segment of the intraparietal sulcus bilaterally was also strongly activated, with the same non-linear profile as the posterior parietal cortex. The present data add to a large set of experiments that have shown this region to be systematically activated whenever numbers are manipulated, independently of number notation, and with increasing activation as the task puts greater emphasis on quantity (Simon *et al.* (2002) and see Dehaene *et al.* (2002) for a review).

An alternative account of our results could be that the posterior parietal regions are generically related to the 'mental effort' required to perform the task, and that their activity simply correlates with RT. This interpretation, however, was refuted by Wojciulik & Kanwisher (1999), who showed that a difficult language task was not sufficient to activate posterior parietal cortices, and that an engagement of visual attention was required. Our results also show such a decorrelation of parietal activation and RT. RTs increased from four to six, but were shorter with seven than with six items (figure 1). Parietal activation, however, increased monotonically from four to seven

items (figure 2*b*). One possible interpretation is that, on trials with seven items, subjects often emitted their verbal response through a short-cut process of estimation, based on their knowledge that seven was the largest number presented. Subsequently, however, they probably verified their response by counting the whole set. This slightly later process of exhaustive counting was reflected in the fMRI activation curve, which sums activation over the entire trial, including processes occurring after the response is emitted.

The present observation of a strong contribution of the parietal attention system to counting, but not subitizing, is supported by two neuropsychological observations. First, patients with 'simultanagnosia' arising from parietal damage, who experience severe difficulties in focusing their attention serially to multiple objects, fail in counting even four or five items. Nevertheless, their ability to subitize one, two or even three items may be preserved (Dehaene & Cohen 1994). Likewise, patients with neglect and extinction, who fail to report visual items in their neglected field, can nevertheless accurately subitize them (Vuilleumier & Rafal 1999).

Behavioural manipulations also support the parallel/serial dichotomy of subitizing and counting. On the one hand, performance in the counting range, but not the subitizing range, is affected by manipulations that alter the orientation of gaze and/or attention (Atkinson *et al.* 1976*a*,*b*; Oyama *et al.* 1981; Trick & Pylyshyhn 1994; Simon & Vaishnavi 1996) and the perceptual groupability of the items (Mandler & Shebo 1982). On the other hand, subitizing, but not counting, is affected by manipulations that alter the parallel processing of items (perceptual 'pop-out'). When the parallel separation of targets from distractors is made impossible, for instance when quantifying Os among distracting Qs, subitizing disappears although counting can be largely unaffected (Trick & Pylyshyn 1993, 1994). This double dissociation at the behavioural level fits with the hypothesis that subitizing relies on parallel pre-attentive mechanisms, whose disruption or unavailability beyond three or four items would force subjects to serially explore the visual array with attention or gaze shifts.

We intended the colour naming task to serve as a control relative to which we could identify the neural systems implicated in subitizing. However, no area showed greater activation during subitizing than colour naming, even at a low threshold. This may imply that subitizing is an automatic process, which is deployed whenever one or more visual item is processed, and which was therefore activated even during the colour naming task. However, we cannot exclude a lack of power, because the striate and extrastriate activation expected given the additional presence of one, two or three dots could not be detected. While the speed and efficiency of subitizing hinder the elucidation of its neural bases, our work demonstrates that the slow serial process of attention orienting can easily be detected on single trials, thus supplementing the cognitive psychologist's toolbox of criteria for distinguish parallel pre-attentive from serial attentive processes.

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