The Role of Right and Left Parietal Lobes in the Conceptual Processing of Numbers

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Abstract

■ Neuropsychological and functional imaging studies have associated the conceptual processing of numbers with bilateral parietal regions (including intraparietal sulcus). However, the processes driving these effects remain unclear because both left and right posterior parietal regions are activated by many other conceptual, perceptual, attention, and response-selection processes. To dissociate parietal activation that is number-selective from parietal activation related to other stimulus or response-selection processes, we used fMRI to compare numbers and object names during exactly the same conceptual and perceptual tasks while factoring out activations correlating with response times. We found that right parietal activation was higher for conceptual decisions on numbers relative to the same tasks on object names, even when response time effects were fully factored out. In contrast, left parietal activation for numbers was equally involved in conceptual processing of object names. We suggest that left parietal activation for numbers reflects a range of processes, including the retrieval of learnt facts that are also involved in conceptual decisions on object names. In contrast, number selectivity in right parietal cortex reflects processes that are more involved in conceptual decisions on numbers than object names. Our results generate a new set of hypotheses that have implications for the design of future behavioral and functional imaging studies of patients with left and right parietal damage. ■

INTRODUCTION

The parietal regions, especially intraparietal sulcus (IPS), have been shown to be a major site of activation in neuroimaging studies of numerical processing (e.g., Nieder, 2005; Dehaene, Piazza, Pinel, & Cohen, 2003). For instance, comparing or estimating symbolic and nonsymbolic magnitudes, and performing arithmetical operations all activate parietal cortex (e.g., Dehaene et al., 2003). Whether left and right parietal lobes are similarly involved in number processing is currently a matter of debate. The essential involvement of left parietal areas for number processing comes from studies investigating how number tasks are affected by permanent neurological damage in patients or temporary disruption following transcranial magnetic stimulation (TMS). For instance, left parietal damage has been observed in patients who are impaired at processing numerical quantities (i.e., quantities expressed by numbers) but able to process continuous quantities, such as the physical size of objects (e.g., Lemer, Dehaene, Spelke, & Cohen, 2003; Polk, Reed, Keenan, Hogarth, & Anderson, 2001; Cipolotti, Butterworth, & Denes, 1991; Dehaene & Cohen, 1991). Moreover, TMS studies have reported impaired performance in terms of increased response times in number comparison when left IPS regions are stimulated (e.g., Cappelletti, Barth, Fregni, Pascual Leone, & Spelke, 2007; Andres, Seron, & Olivier, 2005).

On the other hand, right parietal lobe has been shown to be equally (e.g., Ansari, Dhital, & Siong, 2006; Castelli, Glaser, & Butterworth, 2006; Thioux, Pesenti, Costes, De Volder, & Seron, 2005) or even more strongly activated than the left in several imaging studies (e.g., Cohen Kadosh, Cohen Kadosh, & Henik, 2008; Naccache & Dehaene, 2001; Le Clec'H et al., 2000). Further evidence of the involvement of the right parietal areas comes from TMS studies (e.g., Cappelletti, Muggleton, & Walsh, 2009; Cappelletti et al., 2007) and from investigations on developmental dyscalculia showing that this is associated with right parietal dysfunctions (Price, Holloway, Räsänen, Vesterinen, & Ansari, 2008; Rotzer et al., 2008; Molko et al., 2003).

Numerical and Nonnumerical Processing in Left and Right Parietal Lobes

There are several reasons for the inconsistencies of previous results in terms of the involvement of the left and right parietal areas. In the case of neuroimaging studies, one reason may be that stimuli or tasks with different cognitive demands were used, for instance, comparing numbers or physical sizes relative to reading numbers or letters, therefore leading to different patterns of activation (e.g., Simon, Mangin, Cohen, LeBihan, & Dehaene, 2002; Chochon, Cohen, van de Moortele, & Dehaene, 1999; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). A second reason may be that the left and right parietal areas play different

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roles in numerical processing, with left parietal cortex more engaged in exact, language-dependent number processing, and right parietal cortex more involved in approximate number processing (e.g., Dehaene et al., 1999). Although this distinction explains the performance of some neuropsychological patients (e.g., Lemer et al., 2003; Polk et al., 2001; Dehaene & Cohen, 1991), some cases of developmental dyscalculia (e.g., Kucian, Loenneker, Dietrich, Martin, & von Aster, 2006), and some TMS results (Cappelletti et al., 2007), it still does not account for discrepant results in imaging studies that were not based on the exact versus approximate dichotomy.

A third reason why the involvement of left and right parietal lobes in numerical processing has been inconsistently reported, at least in neuroimaging studies, may be because other conceptual, perceptual, and response-selection processes have been shown to recruit parietal regions similar to those involved in number processing (e.g., Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Corbetta & Shulman, 2002; Culham & Kanwisher, 2001; Richter et al., 2000; Wojciulik & Kanwisher, 1999). That is, extracting and comparing learnt information from stimuli or selecting a response such as a left or right keypress might engage the same parietal areas irrespective of the cognitive task performed. It is therefore unclear to what extent parietal activations during numerical tasks are specific to numerical processing or merely a reflection of other nonnumerical processes including response selection.

Three approaches have recently been used to dissociate number processing from other processes that correlated with reaction times (RTs). The optimum approach is to equate RTs across different tasks, that is, equate task difficulty across tasks in order to achieve similar RTs (e.g., Pinel, Dehaene, Riviere, & LeBihan, 1999; Thioux et al., 2005). In this context, differences between stimuli cannot be attributed to differences in RTs. However, it is not always possible to satisfactorily equate response times and, in these circumstances, the second approach attempts to correct for response time differences by using regression analysis to factor out the effect of response times from number processing (Göbel, Johansen-Berg, Behrens, & Rushworth, 2004). Using this approach, Göbel et al. (2004) found that the main effect of response times over three different tasks (number comparison, vertical line judgment on numbers, and vertical line judgment on nonnumbers) activated the same left IPS areas as the main effect of number comparison relative to either of the other two tasks. No number-selective activations in right parietal lobe were reported. On this basis, the authors argued that number selectivity was indistinguishable from processes associated with RT changes in IPS. We note, however, that the RT effects reported by Göbel et al. were in left IPS, therefore they do not explain the right IPS activation previously associated with number processing.

The third approach avoids confounds associated with these RT-correlated processes by using an fMRI adaptation (fMRIA) paradigm, which avoids participants having to make a response. This technique is based on the observation that the BOLD signal is reduced when the same stimulus is presented repeatedly in a passive viewing, suggesting that a neuronal population is sensitive to a particular feature of the stimuli (e.g., Grill-Spector, Henson, & Martin, 2006). This paradigm has recently become popular in numerical cognition research, although it has yielded inconsistent results. For instance, reports that quantity processing activate parietal lobe bilaterally (e.g., Ansari et al., 2006; Cantlon, Brannon, Carter, & Pelphrey, 2006; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004) contrast with those reporting left-lateralized parietal activations (e.g., Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007 for abstract quantity processing) or even no number-selective activations (e.g., Shuman & Kanwisher, 2004). However, number selectivity was beyond the scope of most of these studies as no comparison of numerical and nonnumerical quantity processing was carried out. Moreover, although these fMRIA paradigms are simple and elegant, they were designed to look at passive number processing rather than the cognitive processes involved in more complex numerical tasks. Therefore, they do not allow more specific hypotheses on the role of the parietal regions in number processing to be tested.

One of these hypotheses is whether parietal lobes are engaged in processing numerical meanings not requiring magnitude manipulation, for instance, hours (e.g., 7.15 a.m.), dates (e.g., 2006), and mathematical constants (e.g., 3.14). Evidence suggesting that quantity and nonquantity number meanings may be distinct comes from lesion studies (e.g., Cappelletti, Jansari, Kopelman, & Butterworth, 2008; Dehaene & Cohen, 1991), although no investigations have so far tested quantity and nonquantity number meanings with the same stimuli and task demands. Another hypothesis is that parietal lobes respond to numbers irrespective of the task performed on them, that is, irrespective of whether the task requires conceptual manipulation or not (e.g., Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003).

We therefore aimed to (1) test whether there is any parietal region whose activation is higher for numbers in one condition relative to another, namely, *number selectivity*; (2) dissociate numerical processes from processes associated with RTs in parietal lobe; (3) investigate whether the parietal regions involved in quantity processing with numbers are also engaged in other conceptual operations that do not involve quantity manipulation; and (4) contrast the involvement of parietal lobes in these conceptual operations with numbers (both quantity and nonquantity) with perceptual operations with the same numerical stimuli.

The Present Study

The present investigation of the conceptual processing of numbers included three novel experimental features. First, we tested numerical (e.g., "23.07") and nonnumerical stimuli (i.e., object names, e.g., "desk") on identical conceptual and perceptual tasks in order to compare both stimuli under the same task demands and to identify parietal activation that was number selective, that is, higher for numbers than object names. Second, to dissociate parietal activation that was number-selective from activation that might be driven by response time effects, our statistical analyses factored out response times within and across conditions and subjects. Third, our nonquantity conceptual tasks with numbers required the extraction of learnt information but could not be based on a quantity strategy. We reasoned that if any parietal activation is driven by quantity processing, then this should be higher for the quantity than for the nonquantity tasks with numbers, object names, or both. Moreover, if parietal activation is higher for numbers than object names, then it is number selective. In contrast, if any parietal activation is common to quantity and nonquantity conceptual tasks on both numbers and object names, then this could be related to other processes including the extraction and comparison of learnt information.

METHODS

Participants

Participants were 22 right-handed volunteers comprising 10 men and 12 women with a mean age of 54.6 years (range = 23–62). All participants were neurologically normal native English speakers who gave informed consent and were screened prior to testing to ensure they were scanner compatible with normal or corrected-to-normal vision. The study was approved by the National Hospital and Institute of Neurology's joint ethics committee.

Experimental Design

The experimental design independently manipulated stimulus type (numerals, e.g., "23.07" or object names, e.g., "desk") and task. In all conditions, participants were simultaneously presented with two stimuli (either numbers or written object names). One stimulus was presented above a central fixation point and the other stimulus was presented below fixation. Above both stimuli was a two-word question. One word referred to the type of information that needed to be attended to (see below) and the other word indicated the type of stimulus (number or object).

The tasks were categorized on two levels (see Figure 1A and B). The first level distinguished between (i) conceptual tasks that necessitate access to the abstract meaning associated with a number/object name, from (ii) a perceptual task that involved a decision on the color of the physical stimulus (rather than its meaning). The second level distinguished between conceptual tasks that involved the extraction of either (i) quantity or (ii) nonquantity information.

The quantity tasks required decisions about relative size or numerosity (i.e., how many items?). The nonquantity tasks also required the extraction of learnt information but could not be based on a quantity strategy. This was possible by using nonquantity questions that focused on times and dates, both of which are on a circular rather than linear dimension. Thus, to identify a sleeping time, a simple quantity strategy (i.e., bigger number = later time = sleeping time) may not work as the target number could be either smaller (e.g., "2.40" vs. "11.05") or bigger in magnitude (e.g., "9.22" vs. "23.29") than the other number in the pair. Likewise, in the case of dates, the 1st month (January) is closer in time to the 12th (December) than the 3rd (March). Times were represented as two numbers referring to the hour followed by two numbers referring to the minute (e.g., 13.07 = 7 min past one). Likewise, dates were represented as two numbers referring to the day followed by two numbers referring to the month (e.g., 13.07 = 13th July). For objects, we distinguished between items that were used at night for sleeping (e.g., "bed") versus items that were used during office hours for working (e.g., "desk"). With respect to seasons, we distinguished between summer objects (e.g., "sunglasses") versus winter objects (e.g., "gloves"). We then selected questions that could be used for both the number stimuli and object name stimuli (see Figure 1A and B for examples). Specifically, there were a total of four different quantity questions for numbers: (i) larger number? (ii) smaller number? (iii) more numbers? (iv) less numbers?; with the same four questions for object names: (i) larger object? (ii) smaller object? (iii) more objects? (iv) less objects? Likewise, we also included four different nonquantity questions for numbers: (i) summer month? (ii) winter month? (iii) working time? (iv) sleeping time? The same four nonquantity questions were also used for object names, namely, (i) summer object? (ii) winter object? (iii) working object? (iv) sleeping object?

Our range of tasks/questions allowed us to minimize differences in the type of information that was extracted from numbers and object names but there were also some subtle differences. For example, for numbers, the questions "more versus less?" and "larger versus smaller?" are equivalent, but for object names, "more?" questions referred to the number of items (i.e., a numerosity judgment), whereas "larger?" questions referred to the size of the object. We therefore investigated whether the type of question (e.g., numerosity vs. size) influenced our effects of interest, that is, the effects of [conceptual vs. perceptual] and [quantity vs. nonquantity]. As our behavioral and imaging results did not reveal any significant effects of question type on our effects of interest, our final analyses (see below) summed over question type within the quantity and nonquantity conditions.

Stimuli

A total of 144 Arabic numbers and 144 object names were generated (see Appendix 1). Arabic numbers were presented as pairs of one or two digits, each separated by a dot, for example, 23.07. They referred to a linear dimension of quantity, to dates (e.g., 23rd July) or to

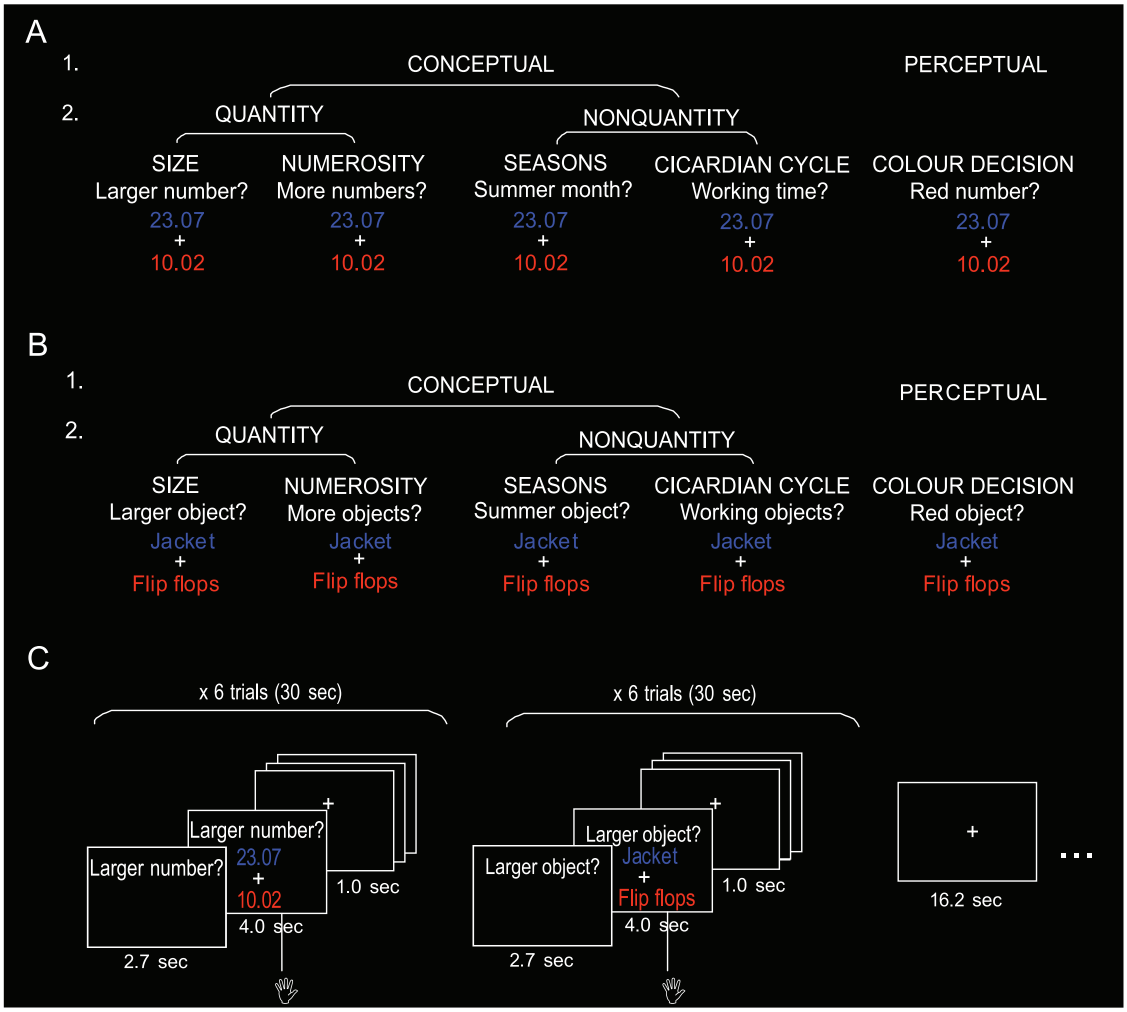

Figure 1. Experimental design. The same experimental tasks were used with pairs of (A) Arabic numbers and (B) object names, and can be distinguished at two levels: (1) conceptual versus perceptual tasks; (2) within conceptual tasks, quantity versus nonquantity tasks. For conceptual tasks, one of two possible questions was presented in different blocks in counterbalanced order (i.e., larger/smaller, more/less, summer/winter, working/sleeping). In each trial (C), participants viewed pairs of stimuli presented one above the other with a fixation cross in the middle of the computer screen. Both Arabic numbers and object names were each presented in one of four possible colors (red, yellow, blue, green). Subjects were instructed to indicate with a button press which of the two stimuli was the correct response to a question consisting of two keywords presented above the upper stimulus before and during the stimulus display. The six different conditions (3 tasks × 2 stimuli) were blocked (6 trials per block) and fully counterbalanced between and within subjects. In each task, the first block consisted of six trials with numerical stimuli (or object names), followed by another six-trial block of the same task with object names (or numerical stimuli) in a counterbalanced order. Presentation of blocks of the same task with both stimuli was followed by about 16-sec rest period where subjects were asked to maintain fixation on a cross in the middle of the computer screen. Trials, where the correct answer was the upper or the lower stimulus, were presented in equal proportion. Timing parameters refer to Paradigm 2.

times (e.g., 7 min past eleven at night). Numbers indicating quantities ranged from 1 to 31 for the first half of the numerical expression and from 01 to 59 for the second part (i.e., from 1.01 to 23.59). Numbers indicating dates were chosen to represent either summer or winter days in the Northern hemisphere; therefore, summer dates included the months of June, July, and August, winter dates included the months of December, January, and February. Dates were expressed in terms of day and month separated by a dot (e.g., 23.07). Numerals referring to a date ranged from 01 to 31 for the first half of each numerical expression and from 01 to 12 for the second part (i.e., from 01.01 to 31.12). Numbers indicating times were chosen to refer to either a sleeping or a working time approximately in terms of an 8 a.m. to 6 p.m. job. Therefore, working times were chosen between 8 a.m. and 6 p.m., and sleeping times between 10 p.m. and 7 a.m. Times were expressed in terms of 24-hr clock with the first pair of digits referring to the hour and the other two digits, separated by a dot, referring to the minutes past the hour (e.g., 16.30 is half past four in the afternoon). Numbers referring to a time ranged from 00 to 23 for the first half of each numerical expression and from 01 to 59 for the second part (i.e., from 00.01 to 23.59). Our numerical stimuli differed from those used in previous studies as we employed noninteger numbers. This decision was motivated by the nature of our nonquantity categorical tasks where noninteger numbers allow us to represent dates and times. To keep the stimuli constant across task, we also used the same noninteger numbers in the quantity task. Therefore, we were not able to compare integer and noninteger numbers but this was not the aim of the current experiment.

Object name stimuli referred to concrete, countable objects whose size could be unambiguously identified and that could be used in both the quantity (e.g., larger object: "sailing boat" or "desk"?) and nonquantity tasks (e.g., working object: "sailing boat" or "desk"?).

Irrespective of stimulus (numbers vs. words) or task (quantity, nonquantity, or perceptual), the two stimuli were presented in two different colors. Possible colors were red, yellow, blue, and green. Subjects needed to attend to the color in the perceptual task to make the color decision response but they were instructed to ignore the color in the quantity and nonquantity conceptual tasks.

Task Instructions

Participants were told that they would see pairs of numbers or object names and that above the stimuli, a two-word question would be presented before and during a block of six trials (see Figure 1C). On every trial, participants were instructed to make a keypress response to indicate which stimulus was the answer to the question. They were asked to press the upper key of a two-button keypad to select the upper stimulus and the lower key to select the lower stimulus. Trials where the correct answer was the upper or the lower stimulus were presented in equal proportion.

Participants were also told that the number stimuli could indicate either: (i) quantities, (ii) dates, or (iii) times. The instructions for the number stimuli were as follows: For the larger/smaller and more/less questions, participants were told that numbers referred to an amount and that they should choose the larger (or smaller) number in each pair irrespective of the wording of the question (i.e., "larger" or "more"). In this context, they were encouraged not to process the numbers according to any specific contextual meaning, for instance, "money." In contrast, for summer/winter questions, participants were told that each number indicated either a summer or a winter month in the Northern hemisphere (all participants were British and raised in the UK). They were told that summer months were "June," "July," and "August" and winter months were "December," "January," and "February" and that these months followed a day (1–31) separated with a dot (13.07) rather than the more familiar slash (13/07). They were instructed to select either the summer or the winter month in each pair of stimuli depending on the question. For the working/sleeping questions, participants were told that working or sleeping times were in terms of a 24-hr clock; and that working times were between 8 a.m. and 6 p.m., and sleeping times were between 10 p.m. and 7 a.m. Participants were discouraged from considering jobs that include night shifts. Finally, in the perceptual (color-decision) task, participants were asked to choose the stimulus whose color corresponded to the color indicated by the question above the stimuli. Subjects were instructed to select the stimulus according to the color of the ink and not according to the color of the object (e.g., they should not select red just because the object name was strawberries or cherries).

For object names, the instructions were the same as those for the numbers except that the processing required for "more/less" questions was not the same as that required for "larger/smaller" questions. Instead, during the more/less questions, participants were instructed to select the stimulus that was more (or less) numerous than the other, for example, "socks versus thermos," "stars versus moon," "bed versus blanket," "deck chair versus swimming pool," "snowflakes versus snowman," or "cherries versus melon." Prior to the fMRI experiment, participants underwent a practice session in order to familiarize themselves with the task procedure.

Presentation Parameters

The six different conditions (quantity, nonquantity, and perceptual-decision tasks × 2 stimuli) were blocked (6 stimuli per block) and fully counterbalanced between and within subjects. We used a blocked rather than an event-related design to minimize the cognitive cost of switching from one task to another and to maximize efficiency (Friston, Zarahn, Henson, & Dale, 1999). Although it may be possible that blocking stimuli introduces strategic differences in the way the stimuli are processed, these strategic effects can be dissociated from stimulus effects because the same stimuli were used in all three tasks, thus allowing us to distinguish between task-dependent effects and task-independent stimulus effects.

Six pairs of stimuli with a fixation between them were presented in each block. Each block began with a question that appeared before the first trial and remained on the screen for the duration of the block. A fixation was then presented between blocks (see Figure 1C). We used two versions of the same experiments [Paradigm 1 (P1) and Paradigm 2 [P2]). These paradigms differed in terms of number of subjects studied, the hand they used to respond, and timing parameters (see Table 1). The advantage of including two different sets of parameters is that we can conclude that any effects that are consistent for both paradigms cannot be attributed to hand of response, stimulus duration, or participants' age.

Data Acquisition

MR images were acquired using a 1.5-T Siemens Sonata MRI scanner (Siemens Medical, Erlangen, Germany). All three tasks (quantity, nonquantity, perceptual-decision) for each stimulus (numbers and object names) were presented within a run of 216 (P1) or 260 scans (P2) with each subject participating in three (P1) or four (P2) runs.

Table 1. Details of Paradigm 1 (P1) and Paradigm 2 (P2) in Terms of Participants and Timing Parameters

	Paradigm 1	*Paradigm 2*
Participants		
Number	14	8
Age (years)	average = 58.7; range = 22–74	average = 50.4; range = 22–69
Sex (*n*)	males = 7, females = 7	males = 3, females = 5
Handedness	Right	Right
Hand of response	Right	Left
Timing Parameters		
Duration of each stimulus pair (sec)	2.65	4
Fixation between stimulus pairs (sec)	0.5	1
Total time to respond (sec)	3.15	5
Total time for each block (sec)	18.9 (6 pairs × 3.15 sec)	30 (6 pairs × 5 sec)
Question before beginning of each block (sec)	3.78	2.7
Fixation between blocks (sec)	11.34	16.2
Number of scans per run	216	260
Number of runs	3	4
Total scanning time (min)	40.8	46.8

Participants' eyes were monitored using a compatible eye-tracker device to ensure that they kept awake during the scanning sessions. A gradient echo-planar image sequence was used to acquire functional images (repetition time [TR] = 3780 msec [P1], 2700 msec [P2]; echo time [TE] = 50 msec; field of view 192 × 192 mm; 64 × 64 matrix). Forty-two (P1) and 30 (P2) oblique axial slices of 2 mm thick (1 mm gap), tilted approximately 20° were acquired. Our final resolution was therefore 3 × 3 × 3 mm voxels. High-resolution anatomical reference image was acquired using a T1-weighted 3-D Modified Driven Equilibrium Fourier Transform (MDEFT) sequence (TR = 12.24 msec; TE = 3.56 msec; field of view = 256 × 256 mm; voxel size = 1 × 1 × 1 mm).

Data Analysis

For both P1 and P2, functional image analysis was performed using Statistical Parametric Mapping software (SPM5 software, Wellcome Trust Centre for Neuroimaging, London; www.fil.ion.ucl.ac.uk/spm).

The first four (P1) and six (P2) volumes of each fMRI session were discarded and the remaining 212 (P1) and 254 (P2) volumes were used for the analysis. Scans were realigned, unwarped, and spatially normalized (Friston, 1995) to the MNI standard space. Functional images were then smoothed in the spatial domain with a Gaussian kernel of 6 mm FWHM to improve the signal-to-noise ratio. A high-pass filter was used with a cutoff period of 128 sec.

The aim of our analysis was to examine whether (1) there were number-selective activations, that is, activations specific for [numbers > object names] for conceptual and/or perceptual decision tasks; (2) these activations were distinct from effects driven by RT-correlated processes. As we established that there was no difference between the subtasks used (see Methods section), we conducted two first-level analyses. In one analysis, response times were modeled as a covariate for each condition. In the other analysis, response times were modeled over numbers and object names for (a) the conceptual tasks and (b) the perceptual task separately. In each first-level analysis, each event-related stick function was convolved with a canonical hemodynamic response function and activation for each condition was compared to fixation according to the general linear model (Friston, 1995). For each of the two first-level analyses, we conducted two second-level ANOVAs to identify effects at the group level. To control for any correlation between conditions, a correction was made for nonsphericity using standard SPM5 procedures. Moreover, in each ANOVA, contrasts from P1 were modeled separately from P2 so that we could test for any interaction with the paradigm.

Analysis Set 1: RTs Modeled Separately for Each Condition

At the first level, the functional data were modeled in an event-related fashion with 12 regressors corresponding to the correct responses to each of the 12 condition types (3 tasks: 2 conceptual and 1 perceptual × 2 stimuli × P1 and P2) and a 13th regressor modeling all incorrect responses. In addition, for each subject, response times for each trial were entered as a covariate (parametric modulation) that interacted with condition. This allows us to compare the effect of RTs in different conditions. First-level contrasts were then entered into two second-level ANOVAs to identify four different effects at the group level.

ANOVA 1 modeled the main effects of conditions and interactions with 12 different conditions (6 per experimental paradigm). In addition, age and mean response times per subject for each condition were entered as two continuous covariates (i.e., across conditions). From this analysis, we identified effects that were:

(A) Common to numbers and object names by identifying the main effect of conceptual tasks (over quantity and nonquantity numbers and object names) relative to fixation. To ensure that these effects were not driven by one condition only, we used the inclusive masking option in SPM to identify the main effect of conceptual tasks relative to fixation in areas that were activated by both (i) conceptual tasks on numbers and (ii) conceptual tasks on object names at $p < .01$.
(B) Number selective (i.e., more activated by numbers than object names) over task and for each task separately (i.e., conceptual and perceptual).

ANOVA 2 modeled the effect of RT-correlated processes. The design matrix was almost identical to ANOVA 1, except that (i) the contrast images corresponded to the effect of RTs for each condition, rather than the effect of condition relative to fixation, and (ii) we did not include the covariate that modeled the mean RT-correlated processes for each subject. From this analysis, we identified effects of RTs that were:

(C) Common to all conceptual tasks.
(D) Number selective (i.e., more activated by numbers than object names) over task and for each task separately.

Analysis Set 2: RTs Modeled over Conditions

Analysis Set 1 (described above) allowed us to look at how the effect of RT-correlated processes differed for different conditions. However, if these effects varied across condition (task or stimulus), then differences between conditions are confounded by RT differences. For example, if conceptual decisions on numbers take longer than conceptual decisions on object names, then increased activation for numbers might be a consequence of more difficult response selection or other RT-related processes. Although our behavioral data did not indicate longer RTs for numbers than object names, we further ensured that our number-selective areas were not confounded with RT-related effects by conducting a second set of analyses that modeled these effects across numbers and object names. In this context, number-selective areas were identified after the main effect of RTs has been factored out.

In order to do this, we used a different design matrix at the first level. This modeled the functional data in an event-related fashion with five regressors corresponding to (1) the correct responses to the conceptual and (2) perceptual conditions across stimulus type, (3) numbers versus object names, (4) quantity versus nonquantity tasks, and (5) all incorrect responses. Response times were entered as covariates on the first and second regressors, thereby modeling RT-related effects over numbers and object names but separately for conceptual and perceptual trials.

These first-level contrasts were then entered into two second-level ANOVAs to identify effects at the group level.

ANOVA 3: Number selectivity when the main effect of RT-related processes was removed. This involved a t test on the contrast images for [numbers > object names on the conceptual tasks], that is, one contrast for each participant. From this analysis, we extracted the effect sizes for number > object names for each subject in the left and right parietal regions (sphere 8 mm radius) centered on the peak coordinates for number selectivity. A t test comparing the left- versus right-hemisphere effects allowed us to report the interaction of number selectivity with hemisphere.

ANOVA 4: RT-related effects over conditions. We examined the effect of RT-related processes for each task (i.e., conceptual and perceptual) over numbers and object names.

Statistical Threshold

For the main effect of task and number selectivity, regions were identified using a statistical threshold of $p < .05$, corrected for multiple comparisons across the entire brain using family-wise error correction. We also lowered the threshold to $p < .001$, uncorrected, in parietal lobes to fully characterize our effects. However, we only draw conclusions from effects that survived a corrected level of significance.

RESULTS

Behavioral Data

An ANOVA on the mean accuracy, with stimulus type and task type as within-subject variables and experimental paradigm as the between-subject variable, revealed a main effect of task [$F(2, 40) = 41.54$, $p < .001$], no effect of stimulus type ($p > .1$), but a significant interaction between task and stimuli [$F(2, 20) = 33.26$, $p < .05$]. Pairwise comparisons demonstrated a significantly higher accuracy for the perceptual decision relative to conceptual task for both numbers [$t(21) = 9.17$, $p < .001$] and object names [$t(21) = 8.25$, $p < .001$], for quantity relative to nonquantity for numbers [$t(21) = 2.07$, $p < .05$], and for nonquantity relative to quantity for object names [$t(21) = 2.00$, $p < .05$]. P1 and P2 did not differ [$F(1, 20) = 0.98$, $p = .98$].

The identical analysis on mean response latencies identified significant main effects of task [$F(2, 40) = 467.19$, $p < .001$], stimulus type [$F(1, 20) = 10.64$, $p < .005$], and a Task × Stimulus interaction [$F(2, 40) = 160.38$, $p < .001$]. P1 and P2 did not differ [$F(1, 20) = 3.45$, $p = .08$]. Pairwise comparisons of RTs demonstrated significantly faster RTs for perceptual decision relative to both conceptual tasks on numbers [$t(21) = 15.82$, $p < .001$] and object names [$t(21) = 12.15$, $p < .001$], for quantity relative to nonquantity conceptual tasks for numbers [$t(21) = 6.26$, $p < .001$], and for nonquantity relative to quantity for object names [$t(21) = 13.04$, $p < .001$]. Slower RTs for numbers than object names were therefore only observed on the nonquantity conceptual task. On the quantity task, RTs were longer for object names than for numbers. Therefore, any effect of number selectivity that is task independent cannot be explained by RTs.

In sum, perceptual judgments with numbers and object names resulted in the fastest and most accurate performance. More errors and slower RTs emerged when participants performed nonquantity judgments with numbers (e.g., summer month: "23.07" or "10.02"?) and quantity judgments with object names (e.g., larger object: "sailing boat" or "desk"?).

Functional Imaging Results

Analysis Set 1: When RTs Were Modeled for Each Condition Separately

(A) Main effect of conceptual task. Both conceptual tasks (quantity and nonquantity) on both types of stimuli (numbers and object names) increased activation in bilateral posterior IPS. In addition, these tasks activated bilateral occipital, right frontal, and cerebellar regions (Table 2; Figure 2, yellow areas).

(B) Number selectivity. There was no main effect of numbers more than object names across conceptual and perceptual tasks but there was an interaction between stimulus (numbers > object names) and task (conceptual > perceptual). This is because number selectivity was significant for conceptual decision (but not for perceptual decisions) in right posterior IPS extending into right angular gyrus, right superior parietal and right supramarginal gyri. There was also a significant number-selective activation in left supramarginal gyrus and right inferior frontal cortex (Table 3, Analysis 1). These effects were observed for both quantity and nonquantity number processing consistent

Table 2. Main Effect of Task on Brain Activation

		Coordinates			*Common Conceptual*	*Quantity Only*	*Nonquantity Only*	*Numbers Only*	*Object Names Only*
Area	*H*	*x*	*y*	*z*	*Z Scores*				
Occipital	R	24	−104	2	**6.5**	**5.7**	**6.2**	**5.7**	**6.2**
	R	28	−92	−4	**5.7**	**4.8**	**5.6**	**5.5**	**5.0**
	R	14	−106	6	**5.7**	**5.4**	**5.3**	**5.0**	**5.5**
		14	−106	16	**5.5**	**5.7**	4.5	4.0	6.0
	L	−18	−102	0	**7.5**	**6.8**	**7.0**	**5.6**	**6.8**
	L	−32	−96	−2	**5.7**	**5.1**	**5.4**	**4.8**	**5.7**
	L	−24	−88	−10	**5.8**	**5.0**	**5.8**	4.7	**5.9**
Posterior IPS	R	30	−58	56	**6.6**	**5.0**	**4.9**	3.8	3.5
	L	−26	−64	54	**5.3**	**5.1**	**4.9**	**5.3**	4.1
Inferior frontal	R	46	26	22	**5.0**	3.7	**5.4**	**5.4**	3.7
Cerebellum	R	38	−76	−20	**5.3**	**5.0**	**4.9**	4.7	**5.0**
		22	−78	−20	**4.8**	4.1	4.7	3.5	**5.2**

Activations common to all conceptual tasks relative to fixation, specific for quantity and nonquantity judgments, and for numbers and object names.

Values in **bold** indicate significance at $p < .05$, corrected for multiple comparisons.

H = hemisphere; L = left; r = right.

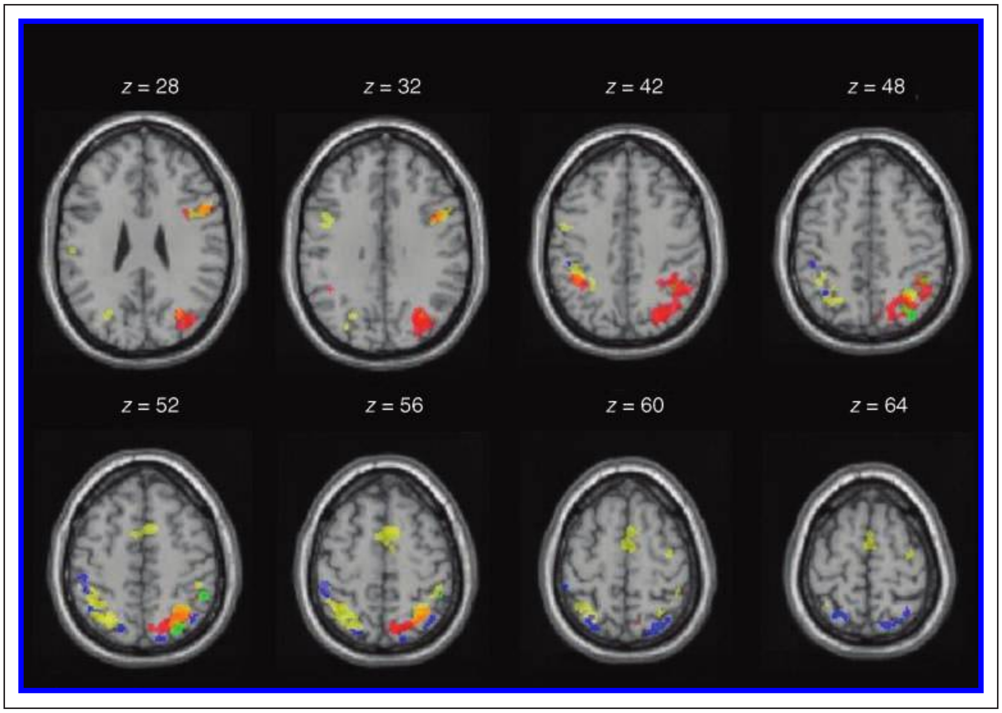

Figure 2. Main effect of conceptual task, number selectivity, and RT effects (Analysis 1). Activations rendered onto a template of axial sections (from $z = 28$ to $z = 64$) showing activations for conceptual decisions common to numbers and object names (yellow), numbers > object names (i.e., number selectivity, red), RT effects for all conceptual decisions for numbers and object names (blue), and RT effects for numbers > object names (green) averaged for Paradigms 1 and 2 ($p < .001$). Left is left.

with the absence of an interaction between [number > object names] and [quantity > nonquantity tasks].

The anatomical location of the number-selective effects is illustrated in red in Figure 2. Relative to the main effect of conceptual decisions for both numbers and object names, number selectivity was right lateralized and extended more inferiorly in parietal lobes.

(C) The main effect of RT-related processes (over numbers and object names). Nothing reached significance at $p < .05$, corrected for multiple comparisons across the whole brain. At a more lenient statistical threshold in parietal lobes ($p < .001$), a main effect of RTs (over numbers and object names) was observed in bilateral superior parietal cortex and very dorsal parts of angular and supramarginal gyri. The more dorsal locations of RT effects relative to number selective effects (reported in B above) are illustrated in blue in Figure 2.

(D) Number-selective RT effects. At an uncorrected threshold only ($p < .001$), there were only two areas in right dorsal angular gyrus and right dorsal supramarginal gyrus where activation correlated with number RTs more than object name RTs (Table 4, Analysis 1, and green areas in Figure 2).

Critically, the effects of condition (Analyses A and B) and RTs (Analyses C and D) never overlap, even when the threshold is lowered to $p < .05$, uncorrected. This is because the first-level analyses modeled the effect of RTs as covariates on the main effect of conditions, therefore condition effects are those after RTs are factored out. Conversely, RT-related effects are those after condition effects are modeled out.

Analysis Set 2: When RTs Were Modeled over Numbers and Object Names

Number selectivity. After the main effect of RT-related processes (over numbers and object names) was factored out, right parietal activation for numbers relative to object names remained significant after correction for multiple comparisons across the whole brain in extent (Table 3, Analysis 2; and red areas in Figure 3). However, consistent with the findings of Göbel et al. (2004), number selectivity was no longer significant in left parietal cortex, the highest peak being at −30, −76, 28 (Z-score = 2.8; 7 voxels on the left at $p < .01$ vs. 2988 voxels on the right at $p < .01$). The greater effect of number selectivity in the right compared to the left hemisphere was shown in a significant Hemisphere × Number interaction [$t(20) = -2.592$, $p < .02$; see Methods for details].

Response time related effects (over numbers and object names). Longer RTs increased activation in bilateral frontal and dorsal parietal areas (Table 3, Analysis 2; and blue areas in Figure 3). These effects were significant after correction for multiple comparisons in either height or extent.

In sum, our results have dissociated number-selective right parietal activation from other stimulus-independent task effects and RT-related effects. These effects were consistent across Paradigms 1 and 2. In other words, we can also exclude explanations in terms of hand of response, stimulus duration, and participants' age.

DISCUSSION

In this study, we aimed to dissociate parietal activation that was number selective from parietal activation driven by

Table 3. Number Selectivity

					Analysis 1				Analysis 2	
		Coordinates			Conceptual Only	Conceptual > Perceptual	Quantity Only	Nonquantity Only	Conceptual Only	No. of Voxels*
Area	H	x	y	z	Z Scores					
Posterior IPS	R	28	−70	32	**6.0**	4.9	**6.1**	4.8	4.7	340
		32	−66	32	4.2	3.8	4.0	3.2	4.3	
		32	−80	34	4.6	4.4	3.4	3.2	4.4	
Angular gyrus	R	42	−78	34	3.4[a]	*ns*	3.8[a]	3.1[a]	3.7	
		38	−78	30	4.6	4.0	**4.5**	3.5	3.9	
		32	−76	42	**5.2**	4.4	4.0	4.6	*ns*	433
		30	−62	46	3.9	3.0	2.8	3.2	4.2	
		32	−56	42	*ns*	*ns*	*ns*	*ns*	4.5	
Superior parietal	R	22	−68	56	**5.5**	4.9	**4.9**	4.1	4.3	
		18	−70	56	**5.4**	4.7	4.2	3.3	3.4	
		32	−64	54	**5.1**	4.1	**5.1**	**5.0**	3.2	
Supramarginal gyrus	R	48	−48	40	3.8	3.4	3.7	2.1	3.4	
		44	−44	48	4.0	2.8	2.6	2.8	3.3	
	L	−40	−44	40	**5.4**	4.8	4.5	4.8	*ns*	
		−52	−44	46	3.2	1.7	1.8	1.7	*ns*	

Activations for numbers > object names (number selectivity) for conceptual tasks only, conceptual > perceptual judgments, quantity and nonquantity judgments only in Analysis 1 (RTs modeled separately for numbers and object names) and for conceptual tasks only in Analysis 2 (RTs modeled over number and object names).

Values in **bold** indicate significance at $p < .05$, corrected for multiple comparisons.

H = hemisphere; L = left; R = right.

[a]Within 4 mm.

*$p < .001$.

other conceptual and response-related processes and to compare these results in the left and right hemispheres. Number-selective activation was identified by comparing numbers to object names during the same conceptual and perceptual tasks. Activation related to increasing RTs was identified by correlating RTs over numbers and object names separately (stimulus-independent effects) or for each stimulus separately (stimulus-dependent effects). Below, we discuss three novel findings from this study which can be summarized as follows.

First, in several right parietal regions, activation was selective for conceptual decisions on numbers even when RT-related processes were fully factored out. Second, the right parietal number-selective effects were task-dependent because they were observed during quantity and nonquantity conceptual tasks but not during a low-level color decision task. Third, we demonstrate a different pattern of effects in left and right parietal cortex, which has implications for the functional role of the left and right hemispheres and for the design of future patient and functional neuroimaging studies.

Throughout the discussion, we describe the anatomical locations of the different effects in terms of their relative position to one another. This is because the functional dissociation that we have observed does not fit neatly with anatomical labels or boundaries. For example, different regions of angular gyri expressed either number selectivity, response time related effects, or stimulus-independent task effects. Likewise, different parts of IPS and supramarginal gyri showed either number-selective or stimulus-independent effects.

Number Selectivity in Parietal Lobes

Number-selective effects were observed during conceptual tasks in right posterior IPS extending into right angular and supramarginal gyri. These effects dissociated from other activations in more dorsal right parietal regions and throughout left IPS.

Our finding of number-selective activations was in the context of several novel features of our experimental design and analysis. The experimental design carefully matched the numerical and nonnumerical conditions by using identical tasks with numbers and object names (with the exception of "more/larger number" vs. "more/larger object"). These tasks included quantity judgments, perceptual judgments, and a novel nonquantity conceptual task that required the extraction of learnt information (e.g., Does "10.07" indicate a summer month? Does "10.07" indicate a working time?) but was unlikely to be based on a quantity strategy. Our rationale for including this nonquantity task was as follows: If parietal activation was driven by quantity processing, then it should be higher for the quantity than nonquantity tasks for numbers, object names, or both. Our results did not identify any areas that met these criteria. In contrast, our results showed that in many left parietal and dorsal right parietal regions, activations were common to quantity and nonquantity conceptual tasks on both numbers and object names, suggesting that this could be related to other processes including the extraction of learnt information.

Another novel aspect of our approach is that our statistical analysis factored out any activation that correlated with response times within and across conditions and subjects, even though the overall mean response times for numbers and object names were not significantly different. The only other study that used a similar approach (Göbel et al., 2004) claimed that number selectivity in left parietal lobe could not be distinguished from response time effects. We replicate the pattern of effects observed by Göbel et al. (2004) in the left hemisphere, that is, left parietal activation is not number selective when response times are factored out. However, our final conclusion contrasts with that of Göbel et al. because we observed number selectivity in right parietal lobe that was not reported by Göbel et al. This key difference in our results is likely to be due to differences between our tasks and theirs. Specifically, we used the same conceptual tasks on both numbers and object names, whereas Göbel et al. contrasted number comparison with two low-level perceptual

Table 4. Reaction Time Effects on Brain Activation

Area	H	x	y	z	BA	*Analysis 1* Numbers & Object Names (Z Scores)	*Analysis 1* Numbers > Words (Z Scores)	*Analysis 1* No. of Voxels*	*Analysis 2* Numbers & Object Names (Z Scores)	*Analysis 2* No. of Voxels*
Superior parietal	R	26	−70	60	7	3.9	*ns*	65	3.4	494
		28	−72	50		2.8	*ns*		4.0	
		34	−62	60		3.7	*ns*		4.0	
		16	−80	54		4.1	*ns*	16	2.6	
Dorsal angular gyrus		34	−70	50		*ns*	3.9	43	4.5	
		40	−64	52		3.4	*ns*		4.5	
		36	−62	52		3.2	3.1		4.5	
		40	−56	54		3.1	*ns*		4.5	
Dorsal supramarginal		50	−44	54	40	*ns*	3.7	22	3.9	
Posterior IPS	R	30	−70	32		ns	ns		3.9	
Superior parietal	L	−24	−60	64	7	4.1	*ns*	41	2.5	71
Dorsal angular gyrus		−34	−56	50		4.3	*ns*	30	3.5	
		−30	−52	46		2.8	*ns*		4.0	
		−40	−52	56		3.5	*ns*		3.8	
		−34	−60	46		3.0	*ns*		3.5	
Dorsal supramarginal		−48	−36	56	40	3.8	*ns*	56	3.3	
Frontal	R	44	8	28		2.5	*ns*		5.7	137
	L	−48	28	20		2.5	*ns*		4.0	60

Activations for response time related effects for conceptual judgments for number and object names together and numbers > object names in Analysis 1 (RTs modeled separately for numbers and object names) and for conceptual judgments for number and object names together in Analysis 2 (RTs modeled over number and object names).

H = hemisphere; L = left; R = right.

*$p < .001$.

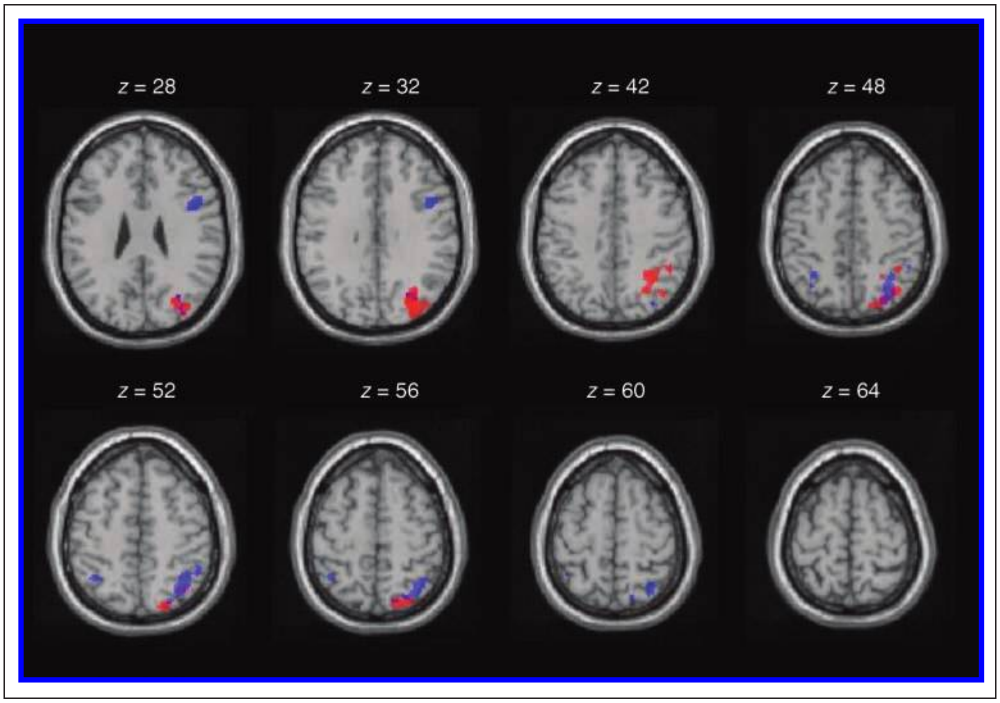

Figure 3. Number selectivity and RT effects (Analysis 2). Activations rendered onto a template of axial sections (from $z = 28$ to $z = 64$) showing number selectivity (red) once RT-related effects have been factored out, and RT effects summed over numbers and object names (blue) averaged for Paradigms 1 and 2 ($p < .001$). Left is left.

tasks, namely, vertical orientation judgment on numbers and nonnumbers.

Task-dependent Number Selectivity in Right Parietal Lobe

Our observation that number selectivity in right parietal lobe emerged only during the conceptual but not the perceptual tasks is consistent with the theoretical proposals that the parietal areas are engaged in the conceptual representation of numbers (Dehaene, 1998; Dehaene & Cohen, 1995). However, it differs from studies that observed similar parietal activations for numbers during conceptual and perceptual tasks (e.g., Tang, Critchley, Glaser, Dolan, & Butterworth, 2006; Thioux et al., 2005; Göbel et al., 2004; Shuman & Kanwisher, 2004; Eger et al., 2003). One possible explanation for this discrepancy is that previous tasks considered to be nonconceptual (such as "stimulus detection," i.e., distinguishing number stimuli from another types of stimuli; Eger et al., 2003) activated parietal lobes because they actually required conceptual processing in the form of identity recognition. Moreover, other nonconceptual tasks involved visual search processes (e.g., Tang et al., 2006; Thioux et al., 2005; Göbel et al., 2004) that previous studies have shown to activate the superior parietal lobes (e.g., Coull, Walsh, Frith, & Nobre, 2003; Pollmann et al., 2003).

Our key result was that number-selective right parietal activation was still observed during both the quantity and nonquantity conceptual tasks involving numbers, after controlling for task and response time effects. This suggests that right parietal activation might reflect conceptual processing that is involved in numbers more than object names. Recently, Ischebeck et al. (2007) provided evidence for the role of intraparietal areas in processing the ordinal aspect of numbers by demonstrating greater intraparietal activation during the generation of the names of the months, which requires an ordered sequence, compared to the generation of nonordered names of animals. Critically, they found no significant difference between ordered generation of months and numbers. Likewise, Gevers, Reynvoet, and Fias (2003) provided similar evidence based on chronometric techniques. Our study involved processing of ordered sequences, although not in terms of generating ordered information, and this processing may occur automatically in the presence of numbers but not in the presence of object names. In addition, our study suggests that number-selective conceptual processing is more related to right than left parietal lobes.

Number Processing in Left Parietal Lobe

Conceptual decisions on numbers and object names resulted in equal activation of left angular and supramarginal gyri as well as bilateral dorsal areas in IPS, where activation correlated with response times irrespective of the stimulus. Therefore, this suggests that left parietal lobe is involved in numerical processing, although not exclusively. By showing left and right parietal activations, our results draw together previous observations of number selectivity in right parietal lobe (e.g., Thioux et al., 2005; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Naccache & Dehaene, 2001; Pinel, Dehaene, Riviere, & LeBihan, 2001; Chochon et al., 1999; Dehaene et al., 1996) with other types of processing in left parietal lobe (Göbel et al., 2004). However, our results may appear to conflict with functional imaging studies that have reported left parietal number-selective effects (e.g., Cohen Kadosh et al., 2007; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Ansari et al., 2006; Cantlon et al., 2006; Piazza et al., 2004) and neuropsychological studies suggesting numerical impairments following left but not right parietal lesions (e.g., Lemer et al., 2003; Polk et al., 2001; Cipolotti et al., 1991; Dehaene & Cohen, 1991).

There are many possible reasons for the inconsistencies between studies. Number-selective effects can be driven by many different processes and they therefore depend on the nature of both the task and the stimuli. For example, in some of the studies reporting number activations in left parietal lobe, the direct comparison between numerical and nonnumerical stimuli was beyond the scope of the study, therefore it was unclear to what extent the effects were selective for numbers (Cohen Kadosh et al., 2007; Piazza et al., 2004, 2007; Ansari et al., 2006; Simon et al., 2002; Chochon et al., 1999). In other studies, numerical and nonnumerical stimuli have been directly compared but in conditions differing in task demands (e.g., Thioux et al., 2005; Le Clec'H et al., 2000; Pesenti, Thioux, Seron, & De Volder, 2000; Chochon et al., 1999). For instance, number quantity processing (e.g., which is larger: 3 or 4?) was compared to nonquantity tasks such as number reading or addition (e.g., Simon et al., 2002; Chochon et al., 1999; Dehaene et al., 1999), or to decisions on continuous, noncountable features (e.g., luminance or physical size; Cohen Kadosh, Cohen Kadosh, et al., 2008; Pinel, Piazza, Le Bihan, & Dehaene, 2004; Fias et al., 2003). The increased left parietal activation for number comparison reported by these studies might have reflected a more general process of the extraction and comparison of learnt information (consistent with the present findings for left parietal). Such general processes may have been more involved in number comparisons in these past studies because reading and addition can be based on rote verbal memory, whereas luminance and physical size judgments can be based on comparison of analogue magnitudes that do not need to be extracted from symbolic stimuli. Our suggestion, therefore, is that left parietal activation during conceptual tasks reflects the extraction and comparison of learnt information irrespective of stimulus type. As demonstrated by our results, left parietal activation does not depend on whether information is extracted and compared from numbers or object names, when response times are controlled. We also note that our left parietal activations are very similar to the brain networks previously described for either number comparison or distance effects (e.g., Pesenti et al., 2000; Pinel et al., 1999), consistent with the idea that these left-lateralized activations reflect the extraction and the comparison of numerical information.

Our results have provided new evidence that these processes are not specific for numerical stimuli, but they occur irrespectively of the stimulus used. Moreover, our results are in keeping with the proposal that the left parietal lobe is more engaged in exact processing of symbolic, language-based numerical information, as opposed to right parietal lobe being more involved in approximate, preverbal numerical representations (Izard, Dehaene-Lambertz, & Dehaene, 2008; Cohen Kadosh et al., 2007; Stanescu et al., 2000; Chochon et al., 1999). Exact representation of symbolic numbers requires extraction of information from the numerical symbols before processing, and we suggest that the left parietal regions may be the locus where this occurs, although not just for numerical stimuli (see also Cohen Kadosh, Lammertyn, & Izard, 2008 for a similar proposal).

How do these conclusions fit with the neuropsychological literature that has reported number-selective deficits following left parietal damage? Is it the case that left parietal damage impairs the extraction and comparison of learnt information, whereas right parietal damage impairs the processing of number semantics? At present, the answer is unclear because patients with difficulties processing numbers have not been tested on conceptual tasks such as those used in our fMRI experiment. It is therefore possible that left parietal lesions impair performance on such conceptual tasks involving object names (as well as numbers). However, it is also possible that left parietal lesions could impair performance on numbers more than object names even when the same tasks are used. This could arise if, after brain damage, a novel strategy was learnt that was more effective when the task was performed on object names than on numbers. Along the same lines, left and right parietal lobes may recover in different ways after brain damage such that, for instance, following right parietal lesions, the undamaged left parietal areas may still be able to extract and compare symbolic numbers, thereby masking the loss of number processing in the right hemisphere. Likewise, left parietal regions may not be able to fully compensate the role of the right parietal regions as shown by cases of developmental dyscalculia, which present with right parietal dysfunction (e.g., Price et al., 2008; Rotzer et al., 2008; Molko et al., 2003).

Another reason why numerical impairments are more often associated with left rather than right parietal lesions may be due to the fact that left-lesioned patients are routinely tested with symbolic number tasks rather than approximate nonsymbolic number tasks (e.g., Delazer & Benke, 1997; Cipolotti et al., 1991). Nevertheless, when the latter tasks have been used, selectively spared ability to approximate nonsymbolic numbers has been reported in patients with left parietal lesions (e.g., Lemer et al., 2003; Polk et al., 2001; Dehaene & Cohen, 1991). Similarly, the scarcity of neuropsychological patients with right parietal lesions and numerical impairments may be partly due to the fact that these patients are routinely tested with exact, symbolic number tasks, such as number comparison and arithmetical operations, which are usually preserved as they may be performed by intact left parietal regions (e.g., Priftis, Zorzi, Meneghello, Marenzi, & Umiltà, 2006; Zorzi, Priftis, Meneghello, Marenzi, & Umiltà, 2006;

Vuilleumier, Ortigue, & Brugger, 2004; Zorzi, Priftis, & Umiltà, 2002). The results of our study have therefore generated a new set of hypotheses that needs to be investigated with future behavioral and functional imaging studies with patients.

Summary and Conclusions

In summary, both left and right parietal regions are activated during conceptual decisions on numbers. On the basis of our own analyses and previous functional imaging data, we propose that the left parietal number activation reflects a range of processes correlating with RTs, including the extraction and comparison of learnt information. On the other hand, the right parietal number activation is more involved in conceptual processing of numbers than object names. These findings motivate the investigation of new hypotheses to be tested in patients with left and right parietal damage. They also highlight the importance of controlling for task and response time effects when searching for number-selective effects.

APPENDIX 1. Experimental Stimuli Used

Ant	Flies	Radiator
Armchair	Folder	Reindeer
Barbeque	Fork	Sailing boat
Bath	Gloves	Scarf
Bed	Hammer	Screwdriver
Bedroom	Heater	Seal
Bed-sit	Holly berries	Shawl
Bedspread	Hostel	Sheets
Bee	Hotel	Shelter
Bikini	Husky	Shelves
Bird nest	Ice lolly	Shoes
Biscuits	Ice skates	Shorts
Blanket	Igloo	Skipole
Blinds	Jacket	Sledge
Boots	Jumper	Slippers
Briefcase	Ladybird	Snowboard
Bunk bed	Lampshade	Snowflake
Butterfly	Lawn-mower	Snowman
Cactus	Lizard	Socks
Calculator	Mango	Sofa
Candle	Mattress	Spade
Car	Melon	Spoon
Chalet	Mince pies	Stamps

APPENDIX 1. (*continued*)

Cheque	Mittens	Stapler
Cherries	Moon	Stars
Chestnuts	Mouse pad	Stool
Clogs	Mug	Strawberry
Coat	Newspaper	Suit
Coconut	Nightdress	Sunflowers
Coffee maker	Notepad	Sunglasses
Computer	Office	Sweater
Cot	Paint-brush	Swim cap
Couch	Papaya	Swimming pool
Cricket bat	Paperclips	Swimsuit
Cricketball	Parasol	Teabags
Curtains	Peach	Teddy
Cushion	Pen	Telephone
Deck chair	Penguin	Tent
Desk	Picnic basket	Thermos
Diary	Pillow	Tinsel
Dormitory	Pine tree	Toothbrush
Drill	Pineapple	Toothpaste
Duvet	Pliers	Towels
Earplugs	Printer	Umbrella
Envelope	Pumpkin	Uniform
Fax	Purse	Wallet
Fireplace	Pyjamas	Watermelon
Flip-flops	Quilt	Woolly hat
00.01	2.11	30.11
00.16	2.12	31.01
00.25	2.40	31.07
01.01	2.47	31.08
1.03	2.49	31.10
1.06	21.01	4.08
1.07	21.05	4.25
1.09	21.06	4.52
1.11	21.58	5.02
1.32	22.02	5.06
1.36	22.10	5.08
10.01	22.30	5.09
10.15	23.11	5.10
10.41	23.29	5.30
11.05	23.30	5.55

APPENDIX 1. (*continued*)

11.07	23.45	6.03
11.08	23.48	6.04
11.45	24.01	6.50
12.02	24.03	6.54
12.07	25.02	6.56
12.11	25.03	7.00
12.51	26.01	7.05
13.02	26.06	7.08
13.07	26.07	7.10
13.12	27.01	7.12
13.24	27.06	7.28
13.51	27.08	7.38
14.07	28.02	7.43
14.10	28.08	7.44
14.43	28.09	7.50
14.57	28.11	7.58
15.09	29.03	8.01
15.19	29.06	8.05
16.02	29.07	8.10
16.06	29.08	8.11
16.30	29.08	8.12
17.00	29.11	8.15
17.02	3.02	8.25
17.03	3.03	8.32
17.07	3.08	8.45
17.55	3.10	8.47
18.03	3.17	8.52
18.08	3.20	8.56
18.20	30.03	9.08
18.55	30.05	9.11
2.02	30.06	9.11
2.06	30.09	9.22
2.08	30.10	9.56

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