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***The quantifying brain: a functional imaging  
approach to subitizing, counting, and  
numerosity estimation***

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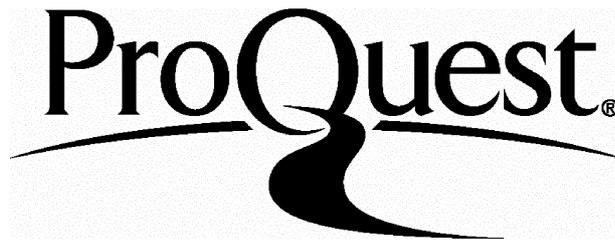
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## Summary

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The ability to estimate and count the number of objects in a collection is held to ground the development of symbolic numerical thinking. Nevertheless, we still lack understanding the neural code that supports the access to numerical quantity in these basic quantification tasks. In this thesis we present three experiments that, making use of functional imaging technique (functional Magnetic Resonance Imaging and Positron Emission Tomography) investigate the neural basis of estimation and counting in human adults. We first investigated the special status that small collections have in quantification. Small collections of up to 4 items are quantified fast and effortless, via a process called subitizing, in opposition to counting more than 3-4 items, where performance gets slow and error prone. It is held that this dichotomy reflects two *qualitatively different* processes. Using PET and fMRI, we showed that there is no brain circuit that is specialised for subitizing or counting: a bilateral occipito-fronto-parietal system is activated in both. However, the intensity of the activation in this circuit shows a sudden discontinuity between the two processes. We therefore demonstrated that subitizing and counting emerge from a qualitatively different recruitment of a set of brain regions, but that they are not anatomically segregated. In the third study we used fMRI to compare verbal counting to non-verbal numerosity estimation, using visual and auditory stimuli. Results showed that numerosity estimation emerges from the activity of a strongly right lateralised fronto-parietal circuit which is almost completely independent from the modality of stimuli presentation. This showed both the abstract and the non-linguistic nature of the numerosity-related computations. Counting also was independent of input modality, and recruited additional bilateral posterior parietal regions and linguistic regions of the left hemisphere. This showed that counting and estimation are hierarchically organised, and confirmed the linguistic and attentional nature of counting.

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# *Chapter I*

Anything we know has got a number: without numbers we could neither think nor understand things.

[Filolao, VI sec. BC, fragments]

## *Numerosity judgements*

### **1. Introduction**

Any set of individual elements has got a number, or numerosity, and can therefore be quantified on this continuum. Numerosity is a very abstract property of a set, because it does not depend on neither the modality (visual, auditory, somatosensory, motor), nor the mode (simultaneous or sequential) of stimuli presentation, nor on their physical characteristics (colour, pitch, and so one).

The numerosity ‘two’ can be attributed to two lions in the savanna, as well as to two melodies in a song, to two ideas in a speech, two movements in a ballet, and even to one set comprising of one sound and one colour. More formally, numerosity can be defined as the only property of sets that remains invariant under substitutions of any item in the set. How does the human brain grasp and access such an abstract property of the world? To what extent language and the counting procedures are necessary for making accurate numerosity judgements? How many ways there are to determine numerosity and which are the processes involved? Which is the functional neuroanatomy of such processes? This thesis attempts the investigations of some of these questions using behavioural and different functional imaging techniques in healthy human adults.

In this first chapter, we will introduce our studies in a larger framework where human numerical competence is seen in relation to its possible phylogenetic and ontogenetic ancestors, reviewing the most relevant data on numerosity judgements in animals and infants. Then we will focus on the human adults, reviewing the main behavioural, the neuropsychological, and brain imaging data on the different types of

numerosity judgements (counting, subitizing and estimation). We will structure this literature review around two main questions, that are also most relevant for the experimental work presented later. In the second, third, and fourth chapter, we will present 3 experiments that, using behavioural and functional imaging techniques, attempt to answer the previously proposed questions. Finally, in the fifth chapter, we will draw the main conclusions and indicate future development of this work.

## ***2. Numerosity judgements: a developmental overview***

Numbers could be thought to be a very recent cultural invention in the evolution of the human species. Indeed, the use of number words and digits are part of the human specific and evolutionary recent ability to create and mentally manipulate complex symbols. However, the concept of numerosity does not seem to be as recent, as traces of sensitivity to numerical properties of the world seem to be present also in numerous non-human species as well as in babies. In this first introductory part, we will review evidences for the presence of a numerosity sensitive behaviour in our phylogenetic and ontogenetic ancestors, structuring the discussion around two main points: 1) whether non human animals and human infants are genuinely sensitive to numerosity, and what is the nature of their representation of number, and 2) whether the ability to grasp numerosity is necessary for the development of symbolic numerical competence in humans.

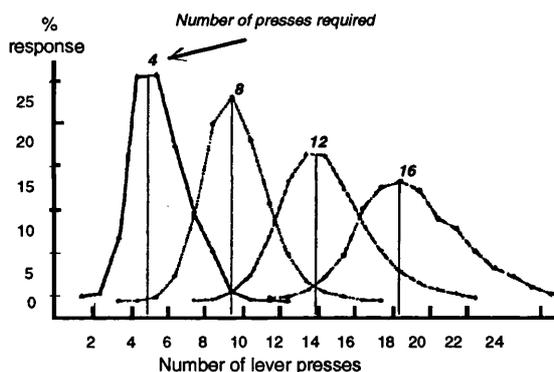
### **2.1- Numerosity estimation in the non-human animal**

Since the first experiment on birds by Koehler (Koehler, 1951), the idea that non-human animals can perceive numerosity as a feature of their environment started being investigated. Ever since, the ability to make numerosity judgements has been tested on many different species of animals (from pigeons to rats, racoons, dolphins and monkeys) both in the wild and in more controlled experimental settings in laboratory, with very different types of paradigms (Brannon & Terrace, 1998 ; Breukelaar & Dalrymple-Alford, 1998; Hauser, Carey, & Hauser, 2000; Meck & Church, 1983 ; Roberts & Mitchell, 1994; Washburn & Rumbaugh, 1991 ). Typically, animals are trained to respond differentially to a variety of numerically defined stimuli: the number of visual stimuli, the number of tones, as well as the number of responses to a manipulation and the number of reinforces (see (Davis & Pérusse, 1988) for a review). Initially, in those kinds of experiments, in order to exclude that animals respond on the

basis of physical parameters than co-vary with numerosity (like luminance, frequency, duration, hedonic value, etc.), stimuli were controlled for those non-numerical variables, by means of decorrelating numerosity with all those parameters. The rationale of using such decorrelation was that after this manipulation, a numerosity sensitive behaviour could only be explained by a genuine sensitivity to numerosity. However, the most sceptical have argued that even this control is not sufficient to conclude for a genuine abstraction of number in animals. In fact, there is still the possibility that animals indeed ground their judgements on those physical variables, varying from trial to trial their strategy, showing therefore a performance that could be interpreted as number-related. In our view, however, this possibility is rather implausible: for example, it would imply that animals required to respond to visual stimuli where numerosity de-correlated with luminance and density, would respond on the basis of luminance or density in a random fashion, and that this choice in some way correlates with numerosity. However, implausible as it is, this point has (as it should) been taken seriously. Two ways have been used in order to overcome this possible criticism: one is to look for the ability to *transfer* numerosity between *different modalities*, and the other is to look for the ability to *generalise* numerically relevant behaviour *to novel, non-differentially rewarded stimuli*. Quite a few experimental results using this logic indeed report convincing positive results (Brannon & Terrace, 2000; Church & Meck, 1984). For example, it was shown that rats initially trained on distinct auditory and visual numerosity discrimination tasks could later generalise to novel sequences in which auditory and visual sequences were mixed (Church & Meck, 1984). Thus, a rat trained to press a lever on the left in response to two flashes, and a lever on the right in response to four flashes or four sounds, spontaneously pressed the right lever when presented with a combination of two sounds and two lights. Given that no physical parameter could account for animal performance, these data strongly support the claim that animals do indeed have a genuine abstract representation of numerosity. In another study, two monkeys were trained to order sets of one to four items. After having learnt the task, they were presented with four totally different stimuli, which the monkey perfectly ordered on the basis of their number, irrespective of their physical characteristics (Brannon & Terrace, 2000). Moreover, and more crucially, monkeys were able to perform the same task on stimuli which numerosity varied from six to nine, showing the ability to discriminate numerosities and to generalise to numerically based behaviour to novel stimuli.

Once one has established that animals can represent numerosity, it is interesting to investigate the nature of such representation. In this respect, the most relevant and very well replicated behavioural finding is that, in numerosity judgements, the accuracy of the representation of a certain numerosity is proportional to its value: the higher the numerosity the larger the variability of the estimate across trials. For example, rats trained to make a certain number of lever pressing in order to get a reward always approximately produce the number of presses requested, and this approximation is such that the variability of the behaviour between trials is proportional to the mean of presses (see figure 1.1). This finding is held to reflect that representation of numerosity in animals is approximate, and not exact, and that its internal structure is organised according to the Weber's law<sup>1</sup>, like as many other physical continua (Weber, 1834).

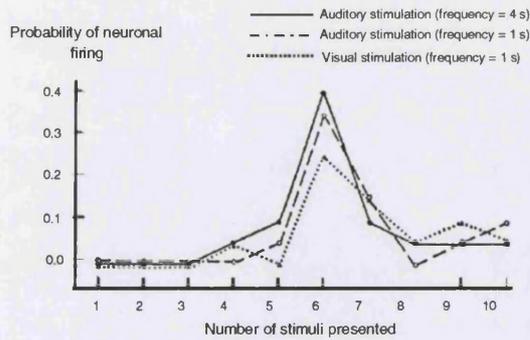
We will later discuss different theoretical accounts for this phenomenon.



*Figure 1.1 Distributions of rats lever presses (in %) as a function of number of presses fixed by the experimenter (modified from Mechner (1958)).*

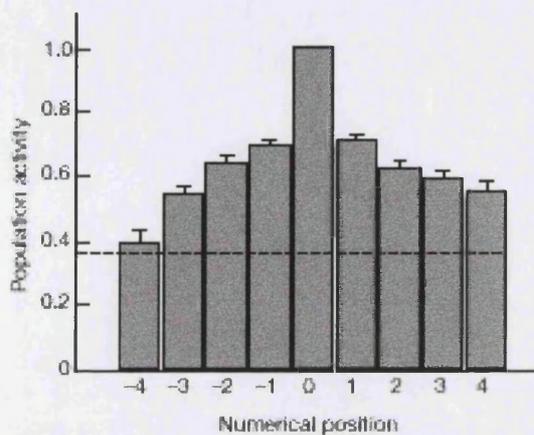
Which are the neural mechanisms that underlie animal ability to perform such complex abstract numerosity estimation tasks? The first, pioneer study that investigates elementary numerosity discrimination abilities in animals at a neuronal level dates back to the work of Thompson and colleagues (Thompson, Mayers, Robertson, & Patterson, 1970). They recorded from cells in the posterior association cortex of the anaesthetised cat (in an area that could be homologous to posterior parietal areas in monkeys and humans) and found preferential responses to a given numerosity, for instance, a sequence of three sounds or three light flashes (see figure 1.2).

<sup>1</sup> Strictly speaking, the Weber's law documents the relation between the size of a stimulus ( $I$ ) and the amount ( $\Delta I$ ) that needs to be added or subtracted for the observer to just notice the difference. It can be expressed as  $\Delta I = kI$  where  $k$  is constant. The proportion that the standard must be increased or reduced in order to produce a perceptive difference is then  $k = \Delta I/I$ . Generally, this law states that the magnitude of a perceived difference is proportional to the ratio of the absolute value of the stimuli.



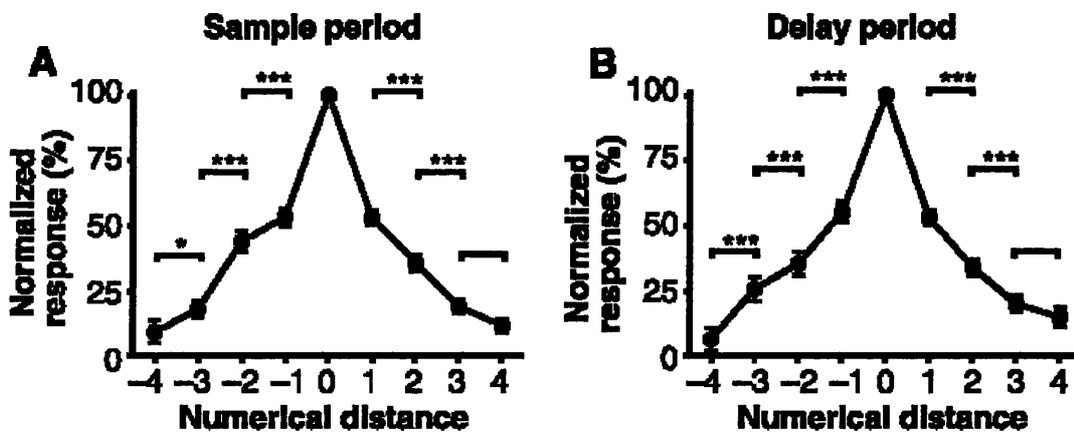
**Figure 1.2** Probability of discharge as a function of stimulus number in a series of stimuli for a particular neuron ('number 6 cell') from the posterior association cortex of an anesthetized cat. Redrawn from Thomson et al., 1970.

For many years this finding stood alone, while, very recently, two studies with macaque monkeys confirmed the existence of number coding cells located both in the intraparietal and in the frontal sulci. Tanji and colleagues trained a monkey to perform a push-movement with the hand 5 number of times in sequence, and then change to a turn-movement, perform it for 5 times, and so on. Total time being controlled by a careful experimental design, the very crucial variable that monkeys had to monitor was the exact number of movements performed. The experimenter, in the meantime, recorded many neurons in different regions of the monkeys' brain, and found that neurons located in the posterior intraparietal sulcus responded selectively to the numerical information (Sawamura, Shima, & Tanji, 2002). While some of these cells even specifically responded only for a single number (which varied from 1 to 5), the overall population response showed that its underlying metric is organized on a logarithmic continuum, according to the Weber's law, where the discriminability is proportional to the absolute value (see figure 1.3).



**Figure 1.3** Population responses of superior parietal neurons of primates in numerical position relative to a certain numerical peak response. From Sawamura et al., 2002

Unfortunately, however, it has to be noted that the numerical information relevant to perform the task in this study was more related to the numerical position in a sequence (*ordinal* number) than to the numerical quantity itself (*cardinal* number). Numerosity, by definition, refers to the cardinal value of a set, which is in principle different from its *ordinal* value (Giaquinto, 1995). Therefore, while this study represents a very elegant effort to “read” the neural code supporting the representation of number in the monkey brain, it doesn’t strictly tap on the concept of numerosity. However, an even more recent study indeed reported neurons tuned to cardinal number (Nieder, Freedman, & Miller, 2002). Macaque monkeys were trained to perform a match-to-sample task on successively presented visual displays containing between 1 and 5 randomly arranged items. During training, number was confounded with other visual parameters such as item size. However, after training, the monkeys spontaneously generalised to novel displays in which all of the relevant non-numerical variables were unconfounded, suggesting that they were attending to number. Each neuron was tuned to a specific numerosity between 1 and 5 (the maximal numerosity that was tested). A large proportion of such number-coding neurons was recorded in prefrontal cortex. The discrepancy between this localisation and the ones previously found will be briefly later discussed in chapter 4, §4.1.1. Overall, these data, confirming number-tuned neurons in the monkey brain, constitute a very strong support to the idea that animals are indeed sensitive to number.



**Figure 1.4** Normalised spike rate during sample (A) and delay (B) as a function of the numerical distance from the preferred number of items. Numbers closed to the preferred numerosity elicited higher spiking rates. Wilcoxon test (\*\*\*) =  $p < 0.001$ ; \* =  $p < 0.05$ . From Nieder, Freedman, & Miller, 2002.

## **2.2- Numerosity estimation in the pre-verbal human infant**

As in animals, abilities to discriminate sets on the basis of their numerosity seem to be present also in human pre-verbal infants. With the classic method of habituation-recovery of looking time, both new-borns and pre-verbal human infants have been shown to discriminate sets of visual object, as well as tones, or words that differed in the number of syllables, on the unique basis of their numerosity (Antell & Keating, 1983; Bijeljac-Babic, Bertoni, & Mehler, 1991; Starkey & Cooper, 1980; Strauss & Curtis, 1981; van Loosbroek & Smitsman, 1990; Wynn, 1996). Again, and crucially, there is also some evidence for cross-modal numerosity matching in preverbal infants. For example, it was shown that when 6-8-months-old infants hear either two or three drumbeats, and are given a choice between looking at a slide with two visual objects or another with three visual objects, they spend more time looking at the slide which numerosity matches the number of sounds they hear (Starkey, Spelke, & Gelman, 1983). This finding was not replicated in older infants of 3 years of age who were required to explicitly choose the set containing more objects between a visual and an auditory set (Mix, Huttenlocher, & Levine, 1996). However, the difference in task used in the two studies might account for the different findings. It is in fact possible that infants possess an implicit knowledge of number that is not accessible from conscious decision until later in development, and therefore could not perform such explicit task while showing an implicit sensitivity to numerosity. Supporting the idea of an abstract representation of numbers in the infant, recent experiments, using habituation techniques, have also showed that 5 months old can determine the number of collective entities (moving groups of items) when non-numerical perceptual factors are strictly controlled. This suggests that the number discrimination abilities in infants are not restricted to objects but can be applied to more abstract entities such as collections (Wynn, Bloom, & Chiang, 2002). What is the nature of the numerosity representations underlying infants' performance? Initially it was thought that the infants' ability to discriminate numerosity was limited to small number of objects, as they discriminate only between numerosity one versus two, two versus three, and sometimes between three versus four, while they fail to discriminate four versus five. This was suggested to reflect the operation of a mechanism within visual cognition dedicated to track multiple objects (object files) which has a limited capacity (Leslie, Xu, Tremoulet, & Scholl, 1998 ; Simon, 1997). More recent experiments, however, have shown that infants can discriminate also large numerosities, provided that their ratio is large (e.g., 8 versus 16)

(Xu & Spelke, 2000). This suggests that the mental representation of number in infants obeys to the same laws (Weber's) that govern numerosity representations in animals and in human adults. This representation is certainly non-verbal in nature, as neither animals nor the infants tested possess a symbolic language.

What are the neural mechanisms that underlie infants' ability to perform such complex abstract numerosity estimation tasks? Unfortunately, at present no studies investigating the neural correlates of numerosity perception in infants and/or babies has been published yet. The most probable reason for this lack of research in this field is that methodological and ethical problems make such kind of experiments particularly difficult to perform. Nevertheless, it is clear that it would be extremely important to understand the neural basis of such early and pre-verbal numerical abilities.

### **2.3- The development of verbal counting: a bridge from numerosity to numerical symbols?**

On the basis of the behavioural observation that preverbal infants and animals rely on internal representation of numbers that are governed by the same metrics (the Weber's law), different authors have proposed that infants and animals share a common, innate mechanisms to represent numerosity, emerging from cerebral circuits that are biologically determined (Dehaene, Dehaene-Lambertz, & Cohen, 1998). Along the same line, they also propose that this mechanism serves as a foundational core of numerical knowledge, providing humans with a start-up tool to the acquisition of numerical symbols. Some of those authors also propose that this initial pre-specialization will determine the brain circuits that will ultimately support high-level arithmetic in adults (Dehaene et al., 1998).

Others, on the contrary, refuse both this view of phylogenetic continuity between animal and human data, and stress the importance of verbal processing and of perceptual constraints in the emergence of the human understanding of number (Simon, 1999). According to this view, a special brain "module" for representing numerosity is *not* necessary for the development of numerical competence. The development of this ability is shaped only by the interplay of generic (not number specific) perceptual and linguistic functions. The two presented views differ as the first, or domain specific view, claims that counting and higher order numerical competence develop on the basis of a pre-existing ability to grasp and represent numerosity, while the second, or domain general, claims that counting and all the other numerical competences develop solely as

a co-ordination of domain general mechanisms for attention and language. At present, no data unambiguously refutes one or the other hypothesis. However, some straightforward contrasting predictions could be drawn from two such different views: 1) According to the first view, children who are particularly impaired in numerosity judgements should show impaired acquisition of counting and of numerical principles, while according to the second view, only children with impairment in language and/or perceptual processes should later show impaired acquisition of counting and of numerical principles. To our knowledge, these predictions have not been directly contrasted yet. 2) According to the first view, in healthy adults, brain regions that are necessary for performing numerosity tasks (representing a core numerical quantity system) should also be involved in symbolic numerical tasks, like counting, number comparison, and even arithmetic. According to the second view, this should not be the case. In chapter 5 we present a study that indirectly tests these predictions.

Despite the still open debate on the existence of an hypothesised numerosity specific module which would ground the ontogenesis of numerical knowledge, there is consensus on the fact that it is via learning how to count that the knowledge of numbers as abstract symbols for numerosity emerges. During the development, mastering the counting principles takes a relative long time (Wynn, 1992). During this process, children have first to learn a set of symbols (number words), and then understand that those symbols are to be used in a certain fixed order. Moreover, they need to understand (non necessarily in an explicit form) four basic principles: 1) the cardinal value principle: the last count word used represents the numerosity (cardinal value) of the set; 2) the order irrelevance principle: it does not matter the order one counts the objects in a collection; 3) the abstractness principle: it does not matter the nature of the objects to be counted; and 4) the one-to-one correspondence principle: each number word needs to be put to a one-to-one correspondence with each to-be-counted item (Gelman & Gallistel, 1978)(Gelman & Meck, 1983, 1986). Mastering the counting procedure, therefore, is essential to build a solid concept of numbers as symbols for numerical quantities and their governing principles.

#### **2.4- Numerosity judgements in adults**

In the last paragraphs we have reported evidence that language is not necessary to abstract the numerosity of a collection, as both non linguistic animals and pre-linguistic human infants are capable of making approximate numerosity judgements. In

the human adult, while this ability to make approximate, non-verbal estimations of numerosity is still present, the acquisition of a symbolic system – such as counting words – allows performing exact numerosity judgements, via counting. Overall, three main different types of numerosity judgements have been described in human adults: subitizing, counting, and estimation. We will briefly consider them in turn, and present those that, in our view, are the two main still open questions related to quantification processes in human adults.

*Subitizing* refers to the quantification of very small sets of elements. When subjects quantify small sets of visual stimuli, by responding to the question “how many are there?”, their performance is extremely accurate and fast, increasing very little as the number of object increases. While such extreme speed of identification of small numerosities has been observed since the end of the 19<sup>th</sup> century (Cattell, 1886; Jevons, 1871), the term “subitizing” (from the Latin adverb “subito” = suddenly) has been introduced by Kaufman and collaborators more than 50 years later (Kaufman, Lord, & Reese, 1949). Initially, this term referred to the rapid and accurate report of up to 6 or 7 items. With the advent of more accurate chronometric techniques, however, it was recognised that performance in the 4-7 range was linearly decreasing, and was therefore attributable to a serial counting process. However, in the 1-3 or 4 range, data seemed to suggest that quantification is indeed carried out by a special procedure which differ from serial counting, as reaction times increase very little (from 5 to 20ms, depending from different experimental conditions) and performance is at ceiling. Thus, the word subitizing is now used to define quantification in such 1-3 or 4 range, in opposition to counting.

*Counting* is the operation used in quantifying large sets of more than 3-4 items. It involves language and the application of a serial one-to-one operation between each individuated item and a particular sequence of number words. The time taken to count sharply increases up to 200 ms per items, and performance becomes error prone. The apparent discontinuity in performance around 3-4 items suggested that counting is a qualitatively different process from subitizing. However, this is still a matter of debate, as will be discussed in session 3.

*Numerosity estimation* is the ability to compare and match sets on the basis of an estimated numerosity, accessed without the use of verbal counting. Some refer to this ability as to non-verbal counting (Gallistel & Gelman, 2000). There is some evidence that the ability to perform numerosity estimation in human adults is not a function of the

linguistic system. However, questions remain on whether numerosity estimation abilities emerge from an abstract system specific for numerosity or it is based on different modality specific systems that only rely on perceptual information. This will be discussed in session 4.

Studies on quantification processes in adults have mainly focused, in our view, around two main questions: 1) Are subitizing and counting two qualitatively different and separate processes? 2) Does numerosity estimation rely on an abstract “number sense”? Therefore, in this section, the review of the literature on numerosity judgements is subdivided according to these questions.

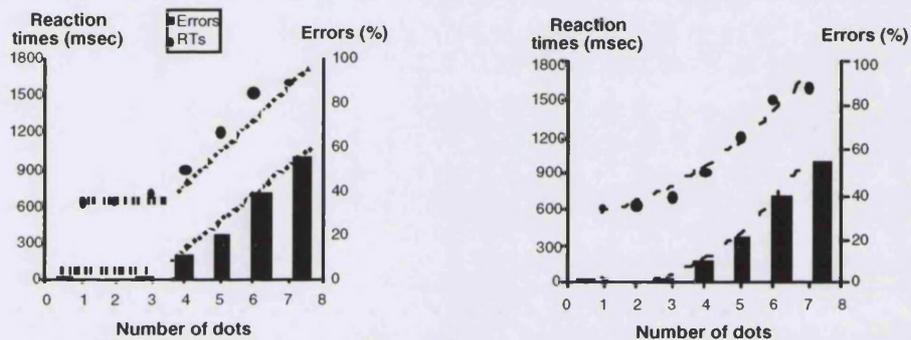
### ***3. Exact numerosity judgements in human adults: subitizing and counting***

In this session we review the relevant literature in the attempt to investigate cognitive and neural correlates of subitizing and counting.

#### **3.1- Counting and subitizing: two different processes?**

Whether subitizing and counting are two processes of a completely different nature is a question that has been intriguing cognitive psychologists since the last century (Cattell, 1886; Jevons, 1871; Kaufman et al., 1949). Since then, quite a large amount of experimental data has been collected. Still, the debate between those who hold that the two processes are radically different and those who claim that they simply reflect two different levels along a continuum of difficulty is still open. First, the putative subitizing range seems to vary from 2 to 5 between subjects and experimental conditions (as the exposition time, for example). Moreover, the methods for the individuation of this subitizing range have been in themselves a controversial issue. Sometimes the discontinuity in both mean response/error rate is individuated by simple visual inspection (Atkinson, Campbell, & Francis, 1976a; Atkinson, Francis, & Campbell, 1976b; Mandler & Shebo, 1982). More often it is individuated using simple statistical tests that look for deviations from linearity by detecting a presence of a quadratic trend in the data (Akin & Chase, 1978; Chi & Klahr, 1975; Trick & Pylyshyn, 1993). The first point at which a quadratic trend is individuated is the subitizing range. More recently, it has been proposed that the use of response time distributions (for which very large sets of data are necessary) could also be an appropriate tool for looking for discontinuities and therefore to individuate the subitizing range.

Interestingly, two articles, using such techniques, questioned the existence of any discontinuity in the quantification response times (Balakrishnan & Ashby, 1992; Balakrishnan & Ashby, 1991). Their analysis suggested that quantification response times can be interpolated with one single continuous function, and that two linear functions for subitizing and counting do not account for more variance in the data (see figure 1.5 for a schematic representation of such idea).



**Figure 1.5** Reaction times (RTs) and accuracy for quantification of random dot sets presented for 200 ms (redrawn from(Mandler & Shebo, 1982). On the left, RTs and accuracy data interpolated with two linear components, reflecting two processes: subitizing (1-3) and counting (4-8). On the right, same data interpolated with a single, non-linearly increasing function.

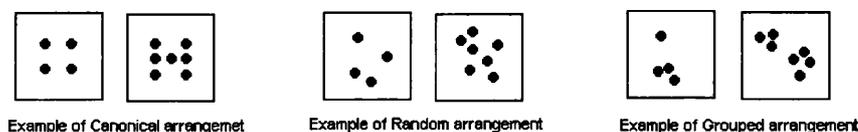
The issue of whether subitizing and counting are two separate processes has been approached with three different methodologies: behavioural, neuropsychological, and functional imaging. Behavioural studies look for experimental manipulations that influence selectively one but not the other process, and vice-versa, for demonstrating their cognitive nature, and therefore their dissociability. Neuropsychological studies could go one step further and limit the cognitive space giving neural constraints to the process. Imaging studies should refine the understanding of their neural implementation, and therefore the nature of the processes should be better revealed. Here we will first review the studies that made use of these three methodologies to investigate subitizing and counting and their dissociability. Secondly, we will review how the results from these studies have helped the development and evaluation of a number of models attempting to depict the functional architecture of the operations of subitizing and counting.

### 3.2- Behavioural studies

The main experimental manipulations that affect counting but not subitizing relate to: 1) ocular movements; 2) spatial arrangement of the items; 3) homogeneity of the array, 4) attentional focus in space, and 5) verbal short-term memory load.

*Ocular Movement.* The control of ocular movement is typically used to show the influence of attentional shift in space over the process of interest. In enumeration experiments, eye movement suppression (by shortening exposure times under 150 ms, the time for a saccade, or by presenting the stimuli in the form of afterimages) results in reduced reaction times in both subitizing and counting, and decreased accuracy in counting only, leaving subitizing flawless (Atkinson, Campbell, & Francis, 1976; Atkinson, Francis et al., 1976; Simon & Vaishnavi, 1996). This result suggests that eye movements are needed to obtain accurate performance in counting more than 4 items, while they are not needed in subitizing, for which covert attention is sufficient.

*Spatial arrangement of the items.* When the elements in the visual array are arranged so that they form symmetric geometrical shapes (like, for example, in dice layout, which is normally defined as “canonical” layout), or when group of chunks of 2-3-4 items are close together in space, counting is facilitated compared to condition in which the elements are all equi-spaced or randomly arranged (Atkinson, Campbell, & Francis, 1976; Mandler & Shebo, 1982). Subitizing, on the contrary, is not facilitated by either of these manipulations. See figure 1.6 for examples of different spatial arrangements.



**Figure 1.6** Example of different spatial arrangements of the dots used in different studies. Manipulating the spatial arrangement has an effect on counting but not on subitizing.

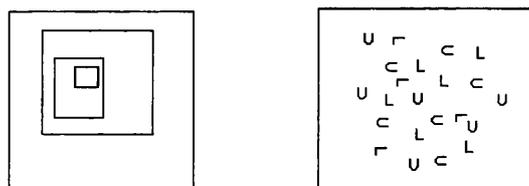
*Homogeneity of the array.* When there is no hint of spatial groupability (e.g., when items are all equi-spaced) the nature of the elements in the display is relevant:

arrays of different items (heterogeneous) are counted much faster and accurately than arrays of identical items (homogeneous) (Frick, 1987). Subitizing, on the contrary, is not affected by this manipulation. Heterogeneity helps in both individuating items to be counted, and in assigning spatial tags to keep track of already counted ones, and this manipulation shows that that these operations are crucial in counting, but not as much in subitizing.

*Attentional focus.* When the locations at which the dots will be presented are pre-cued (say, by the appearance of a coloured rectangles in the appropriate locations), counting is facilitated, while subitizing is not (Trick & Pylyshyn, 1993). Moreover, when the location cues are invalid (i.e., they do not predict the location of the dots), counting is impaired while subitizing is not. This shows that the attentional focus is needed in counting but not in subitizing.

*Verbal short term memory.* Counting has also shown to be influenced by a concurrent articulatory task. Subjects repeating an irrelevant speech sound as "...the the the.." showed substantial disruption in counting accuracy (Logie & Baddeley, 1987). Unfortunately, the authors did not discuss the impact of articulatory suppression on subitizing. Visual inspection of their graph, though, seems to show that the RTs started increasing for the suppression condition at around numerosity 6. This suggests that verbal working memory plays a fundamental role in counting but a less relevant one in subitizing.

The only experimental manipulation that has been shown to affect subitizing but not counting is one that prevents perceptual "pop-out" of the targets to be enumerated. The visual displays in these experiments are quite different from the classical ones used in enumeration studies (typically, dots or bars scattered in space on a homogeneous background). They either consists of objects embedded one into the other, or in displays containing both targets (the elements to be counted) and distractors (elements to be ignored), where targets differing from distractors by a combination of two features, like, for example, colour and orientation of bars (as used in displays for conjunction search) (see figure 1.7). In both cases enumeration RTs increase linearly from one element on, with no apparent discontinuity, suggesting that in those cases, one single serial counting mechanism is deployed (Trick & Pylyshyn, 1993).



A. Embedded figures display      B. Conjunction search display

**Figure 1.7** Example of two cases in which there is no evidence of dichotomy in performance between subitizing and counting. **A.** When the objects are embedded one in the other, and **B.** In conjunctive search displays, where the task is to quantify, for example, the number of “tilted L” among “L”, “U” and “tilted U”.

In summary, behavioural studies show evidence that counting is a complex operation that requires making ocular movements and the attentional focus to locate and mark single objects, or groups of objects, in space. Moreover, a sub-vocalisation process that continually registers the running total in the phonological store is involved. Subitizing, on the contrary, seems to be an operation that has minimum requirements to both the attentive visuo-spatial and the linguistic systems: it is not disrupted by the control of ocular movements, nor by manipulating the attentional focus, or by concurrent sub-vocalisation tasks, and it is not influenced by the nature of the objects in the display or by their spatial arrangement. The only experimental manipulation that disrupts subitizing is the lowering of the salience of the stimuli over the background (preventing their perceptual pop out). This suggests the possibility that subitizing is the result of a floor effect of a very fast but serial in nature operation of counting. Therefore, there is still the possibility that the two operations simply reflect two different levels along a continuum of difficulty. This point has been made by Balakrishnan & Ashby (Balakrishnan & Ashby, 1991, 1992) who analysed a large set of behavioural enumeration data with refined statistical tests, and showed no statistical evidence of discontinuity in the reaction times between subitizing and counting. However, it is well known that chronometric data are often ambiguous in separating parallel and serial models, given that this dichotomy is really relevant in the present debate. Neuropsychological studies, on the contrary, could be of great help in isolating the two processes, if a double dissociation can be found.

### **3.3- Neuropsychological studies**

The presence of a double dissociation between counting and subitizing in brain damaged patients would be strong evidence for the existence of two distinct processes. However, the evidence for a double dissociation is unconvincing in the literature.

#### ***3.3.1- Impaired counting and intact subitizing***

This dissociation is revealed in a study of a group of patients with simultanagnosia. Simultanagnosia is a deficit of the visual perception of complex scenes, with preserved recognition of individual objects, usually following bilateral parietal lesions (Balint, 1909; Coslett & Saffran, 1991; Hécaen & Ajuriaguerra, 1954). These patients usually fail to perceive a scene as a whole and report only one item at a time. Dehaene and Cohen ran a systematic computer-based testing of these patients showing that, while extremely impaired in counting, they could still subitize up to 2 or 3 objects (Dehaene & Cohen, 1994). Interestingly, those patients showed a good performance in a classic visual conjunction search task, (Treisman & Gelade, 1980) in that they explored all the visual display without missing any item. This suggests that the deficit in counting was not due to an impaired visual exploration of the set, but to the inability to keep track of the previously explored spatial location. The operation of spatial tagging, which is supported by parietal circuits, is more essential in counting than in subitizing.

#### ***3.3.2- Impaired subitizing and intact counting***

In the opposite direction, two cases have been reported, but they do not present compelling evidence for the impaired subitizing vs. intact counting dissociation. One patient, a developmental dyscalculic, Charles, when presented with sets of dots for unlimited time, was able to count to arbitrary limits, but showed an increasing monotonic function of 200ms per dot from a single dot, suggesting that he was counting even in the normal subitizing range (Butterworth, 1999b). Nevertheless, recent investigations that we carried out on this patient showed that, when dots were presented very briefly (100 ms.), his reaction time slope showed the typical discontinuous pattern around 4 (while he remained overall slower than normal controls). This result suggests that this patient had a problem of lack of self-confidence in such enumeration task that led him to adopt a slow counting strategy even in the subitizing range. The other case was a patient with severe acquired acalculia who could not, on command, say how many dots were in an array unless she was permitted to count them aloud and use finger

pointing (Cipolotti, Butterworth, & Denes, 1991). However, in this study, the investigators were not able to use computer-controlled presentation of dots, and the patient's counting limit was 4, since she could not recall numbers above 4. These data are not conclusive with respect to the neural dissociability of subitizing and counting processes.

### *3.3.3- Subitizing and awareness of spatial location: patients showing extinction*

Some neuropsychological data suggest that subitizing does not depend on awareness of objects' location in egocentric space. For instance, three patients showing extinction were tested by Vuilleumier and Rafal (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000). Extinction is a deficit (following right parietal lesions) for which a stimulus presented in the contra-lesional hemifield is not spontaneously attended when it is associated with another contemporary stimulus in the ipsi-lesional hemifield. With the same set of stimuli and exposure times, such patients were asked to perform two different tasks: an enumeration task and a spatial location task. Stimuli were visual objects briefly presented in the left, right, or both hemifields, and varied in term of numerosity: a single object or two objects, in either one or both the hemifields, resulting in a total of 1, 2, or 4 objects in the visual field. Patients were able report the number of items, but unable to consciously report the localization of the objects in the contra-lesional space when the ipsi-lesional space was concurrently stimulated. This result confirms previously discussed chronometric data that the ability to explicitly localise object in space is dissociable from the ability to subitize. It is worth noticing, however, that that particular spatial arrangement of objects –symmetric and with familiar shapes, such as horizontal line or square- could have transformed the counting task in an object recognition task (Mandler & Shebo, 1982). The way to control for this possibility should be to present the items in a more random arrangement, or all in a line.

In summary, neuropsychological data show that the ability to use spatial tags to keep track of object location is necessary for counting but not, or less, for subitizing, and that the neural circuits subtending the tracking are implemented in the parietal lobes. Moreover, it suggests that subitizing is dissociable from object localization in space, and that the operations involved in subitizing unlikely rely on those specific circuits of the parietal lobes that are important for the awareness of the spatial location.

Still, as for the behavioural case, neuropsychological literature failed to give evidence for the separability of the two processes: no specific neuropsychological deficit is found to affect subitizing selectively, leaving counting spared. One way to further investigate the neural circuits involved in the two processes and therefore clarify their nature, is the use of functional imaging techniques.

### **3.4- Functional imaging studies**

Results from functional imaging studies suggest that subitizing and counting are not dissociable at the neuroanatomical level, but do not unambiguously solve the problem of the nature of the two processes. One PET (Positron Emission Tomography) study made use of a visual search-type of display, consisting of 16 bars, containing 1 to 9 vertical bars in a variable number of horizontal bars (Sathian et al., 1999). The task consisted of reporting the number of vertical bars. Similar types of visual search display had previously been used to investigate subitizing, and they seemed to elicit the typical RTs slope of subitizing (Trick & Pylyshyn, 1993)<sup>2</sup>. The results showed that counting, relative to subitizing, activated a widespread network of brain regions comprising bilateral middle occipital and superior parietal, and right frontal regions. On the other hand subitizing, relative to single target detection, activated foci solely in the middle occipital extrastriate cortex. This was interpreted as supporting the idea that subitizing is a preattentive process, while counting is a qualitatively different serial process that involves shifting visual attention. However, interpretation of the results is not straightforward, since counting and visual search operations were confounded; moreover, the total number of elements in the display was held constant, and therefore the ratio between targets and distractors increased with the number of targets to be counted. This means that the perceptual salience of the targets was not matched in the subitizing (1-4) and counting (6-9) conditions, and so the attentive effort to isolate targets from the background may have led to brain activation that could not be strictly related to enumeration processes.

Another PET neuroimaging study made use of numerosity matching task, where subjects had to compare the numerosity of a visual array to 4 (Fink et al., 2001). Results show that numerosity matching was associated with striate, extrastriate, and inferior

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<sup>2</sup> A caveat in the use of those kinds of stimuli is necessary: a recent study (Watson & Humphreys, 1999) failed to replicate the typical deviation from linearity of the enumeration RTs using single feature enumeration (color, exp. 3b, and shape, exp. 3c). This shows that enumeration in searching arrays could involve operations that are different with respect to "classical" enumeration arrays.

frontal activation. This result was interpreted as evidence for subitizing as a preattentive visual parallel process. However, the matching task used could in principle be performed on the basis of information that is perceptual rather than numerical. Subjects could have deployed strategies such as matching the sets in terms of brightness, density and occupancy, which were not controlled in the display. This could explain the involvement of visual areas for numerosity matching.

In summary, functional imaging data on the dissociability between subitizing and counting are very sparse. Subitizing seems to be characterised at the neural level by activity restricted to the extrastriate occipital cortex, while counting seems to recruit a much larger network of regions. This might reflect a pre-attentive/attentive dichotomy of the two processes. Nevertheless, due to the nature of the task and stimuli used, results from previous studies can not be considered conclusive with respect to the question of the neural dissociability of the two processes of subitizing and counting.

### **3.5- Models**

Many models have been suggested to account for the apparent dichotomy subitizing/counting. These models can be classified into two groups: “domain general” and “domain specific”. Domain general models held that subitizing reflects some general properties of visual perception that are not specific to the number domain, and they are “the pattern recognition” and “FINST” models. Domain specific models held that subitizing reflects mental processes and representations that are *specific to numerosity* and consist in numerosity estimation. Those are the “accumulator”, and the “numerosity detector” model.

#### ***3.5.1- Pattern Recognition***

The core idea of these models is that subitizing consists in a recognition of pattern (Mandler & Shebo, 1982; Peterson & Simon, 2000). Based on the observation that the number of possible spatial configurations that few objects can take is very small, and resulting in either a linear, a triangular, and a quadrangular shape, the authors claim that adults have developed canonical perception for arrays of 2, 3, and maybe 4 items. In this perspective, the process of enumeration consists in matching the perceived pattern with an internal memorized “template”. These models account for the absence of errors in subitizing and also for the absence of facilitation in subitizing “canonical” patterns (as in figure 1.2.). However, there is a flagrant case in which these models appear to be inadequate, which is when items are arranged in linear arrays, where

performance mirrors the cases of randomly arranged displays. Still, there remains an open possibility that subitizing is performed by a recognition of a “canonical” array only in the cases where items are NOT arranged in a row, but are randomly spread. However, this account would need to be integrated in a broader theory in order to account for the entire set of data.

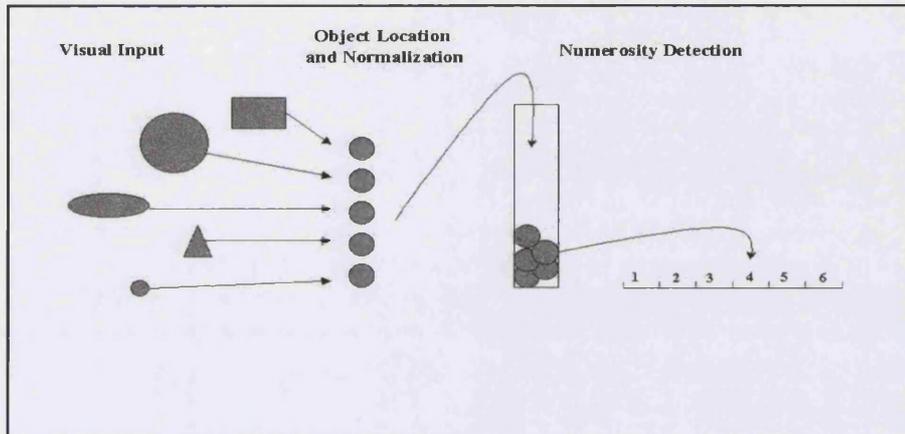
### *3.5.2- FINST*

This model has primarily been proposed as a general theory of visual attention. In particular, it relates to the problem of the limits in attentional resources. The core idea is that subitizing reflects a particular feature of the visual system: the possibility to assign the attentional focus to multiple but limited (to 3 or 4) objects in parallel, at a preattentive level (Pylyshyn, 1989). According to this model, at a primary stage of visual analysis, features and discontinuities are registered and grouped together to form “perceptive units”. After this stage, a limited (3-4) number of FINST (as Fingers of INSTantiation), or “reference tokens”, is assigned to qualify the items on which attentive visual routines can be subsequently performed. Subitizing is therefore a side effect of the way this system works, and consists of two operations: assignment of FINST, and choice of the numerical answer. The second operation consists in a fast but serial search through the sequence of number names, and the choice of the correct one. When, on the contrary, the number of items to be enumerated exceeds the number of FINSTs, a serial procedure of counting that involves shift of attention in space, starts. This model correctly predicts both the absence of errors in subitizing even at a very short exposure time (attributing this to the parallel assignment of FINST) and the small increasing RTs in subitizing (attributing it to the serial response choice stage). It correctly predicts also that when preattentive parsing of the scene is made impossible (such as by conjunction search displays or embedded figures, as shown in figure 1.7), then subitizing is impaired, and subjects use a serial exploration of the display. As for counting processes, the FINST theory predicts that after the first attempt at subitizing has failed, the attentional focus is serially moved from one object to another by means of reassigning the FINST. Each reassignment of FINST requires a certain amount of time, with the result that RTs increase linearly with each item to be counted in the counting range. Moreover, this model seems consistent with the finding that manipulation of attentional focus (for example with eye movements) affects counting and not subitizing, and with findings that cerebral lesion in loci that play crucial roles in

shift of spatial attention (i.e., parietal regions) result in impairment in counting but not (or less) in subitizing.

### 3.5.3- Numerosity detector

This model has initially been proposed to account for infants' and animals' abilities to discriminate and compare numerosities in the visual domain, even if, in principle, it could be extended to the other domains as well. The core idea is that subitizing is a form of very efficient numerosity estimation (Dehaene & Changeux, 1993). According to this position, humans are equipped with a preverbal mechanism specific for detecting numerosity, implemented in numerosity detector cells, that are located at the end of a chain of visual information elaboration stages that goes from the early visual system to the abstraction of a numerosity. In an initial stage, the retina registers visual stimulation and generate a *quantity code*. Then, "location cells" transform quantity codes into *location codes*, by means of which objects, regardless of their size, are represented as activation in space. This information is then transferred to "numerosity detectors cells" that sum up the activation of the previous ones and generate a *numerosity code*, which represent the numerosity of the array. The crucial point of this model is that, due to a non precise one-to-one correspondence between quantity code and location code, the variance of the generated output increases with numerosity of visual objects, according to the Weber's law. Therefore, there is a limit above which two consecutive numerosities cannot be reliably discriminated, and this limit is around four items: it is the subitizing range. As for numerosity over 4, the model predicts that, if requested to produce an exact answer, human adults change strategy and use verbal counting, which is a serial procedure of scanning space and is also a function of the general spoken language system. According to this model, numerosity sensitive cells should be located somewhere within the parietal cortex, in specific sub-regions that do not coincide with regions coding for visuo-spatial properties of the stimuli. Indeed, as previously discussed, the presence of numerosity sensitive cells in the posterior parietal cortex of the cat and of the monkey have been observed (Thompson, Mayers, Robertson, & Patterson, 1970; Sawamura, Shima, & Tanji, 2002). However, in humans, this seems unlikely to be the case, as simultanagnosic patients with lesions in parietal lobes (Dehaene & Cohen, 1994) show intact ability to subitize. However, there is still the open possibility that those numerosity sensitive cells are localized in regions that were not affected by the lesion. This possibility remains to be investigated.



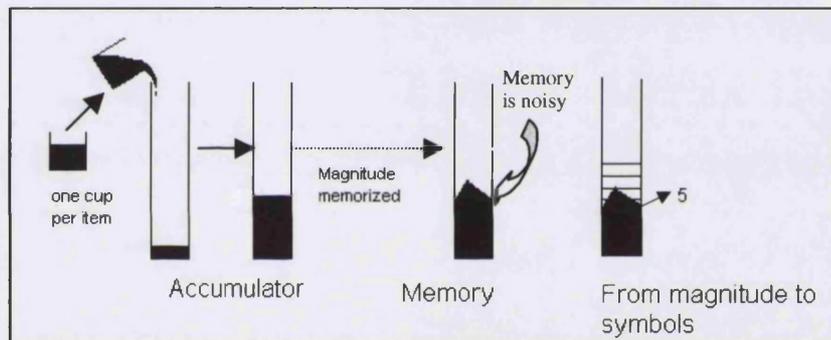
**Figure 1.8** Cartoon for the numerosity detector model in the visual system. The retina receives the visual input and generates a quantity code. Then, location cells perform objects normalization operations so that each object, regardless of its size, shape, and position in space, is represented as “one” unit of activation. This information is then transferred to “numerosity detectors cells” that represent the numerosity of the array. Since the normalization process is noisy, the variance of the output of this process increases with the numerosity of the visual objects, according to the Fechner’s law. Therefore, there is a limit above which two consecutive numerosities cannot be reliably discriminated, and this limit is around four items: it is the subitizing range.

#### 3.5.4- Pre-verbal Counting

This model has been proposed as a general account for perception of numerosity, and it is very similar to the previously presented one. Like the previous model, this model is also based on the idea that subitizing is a special case of numerosity estimation (also called “pre-verbal counting”) (Gallistel & Gelman, 1992, 2000). It is based on the Accumulator, a model first proposed to account for time estimation (Meck & Church, 1983). This is a mechanism that maps each member of a set onto the mental magnitude that represents it. It comprises of a pacemaker that gives a stream of impulse to an accumulator that sums the impulses. Then, a readout mechanism dumps the magnitude in the accumulator to memory (See figure 1.8). The accuracy with which the information is represented in memory obeys the Weber’s law: the standard deviation of the distribution of magnitudes increases in proportion to the mean magnitude. Therefore, as the numerosity increases, the accumulator becomes less and less precise,

and for sets of more than 3 or 4 items, the accumulator becomes unreliable. This is the point at which human adults, when they can, rely on verbal counting.

The main difference between this model and the numerosity detector model is that here the accumulator mechanism proceeds serially (it works with one item at a time), while for the numerosity detector model the estimation mechanism proceeds in parallel. Being serial, this model accurately predicts the small increase in RTs observable in subitizing, which is the main problematic aspect for parallel models. Unfortunately, however, this pre-verbal counting model does not give any specification as for its neural implementation.



**Figure 1.9** *Cartoon of the preverbal counting model. The non-verbal counting mechanism generates magnitudes that become the representation of numerosity into memory. The noise distribution in memory is scalar (i.e. standard deviation increases with the absolute value), therefore at numerosity larger than three or four, the system generates magnitudes that are too noisy to be mapped on the numerical symbols with high accuracy. This is the subitizing range. Adapted from Whalen et al., 1999.*

In summary, it seems that both the FINST model of Pylyshyn (Pylyshyn, 1989) and the two accumulator models (Dehaene & Changeux, 1993; Gallistel & Gelman, 1992, 2000), account for a large part of the behavioural data of subitizing. All claim in favour of the existence of two qualitatively different mechanisms for counting and subitizing. In light of the review of the available data, however, it is clear that that still needs to be proven true.

### **3.6- Subitizing and counting -Summary**

Behavioural, neuropsychological, and imaging data show evidence that counting is a complex operation that requires the co-ordination of the attentional focus to locate and mark objects in space and a sub-vocalisation process to update the running total in the phonological store. Subitizing, on the contrary, seems to be an operation that has minimum requirements to both the attentive visuo-spatial and the linguistic systems. One of the proposed models that accounts for the majority of such data suggests that subitizing is based on a pre-attentive ability of the visual system to keep track of multiple objects in parallel, while counting necessitates spatial attention. However, it is still not clear whether the engagement of spatial attention is a continuous function of the number of items to be enumerated even in the subitizing range, or it represents a real qualitative difference between subitizing and counting. A double dissociation in neuropsychological studies between subitizing and counting has not been described yet, and this would be the strongest proof of a qualitative distinction between the two processes. In chapter 2 and 3 we present two studies that use brain activation techniques in the attempt to solve this question.

## **4. Approximate numerosity judgements in human adults: estimation**

When humans are unable to use language and therefore counting, they still show some ability to perform judgements of numerosity, by estimation. The most striking feature of numerosity estimation judgements in humans is that it is almost identical to performance of other animals in similar tasks (see figure 1.10). Such performance is characterised by the fact that both the mean estimate and its variability are proportional to target value, suggesting that the internal representation of numerical magnitudes is organised on a logarithmic continuum. This similarity has led many authors to hold the idea that humans share with non verbal animals a system for representing numerosity.

### **4.1- Does numerosity estimation rely on an abstract “number sense”?**

As previously reviewed, many hold that human adults (as well as animals and infants) possess an abstract representation of number that is mainly used to perform numerosity estimation. Models of the cognitive processes involved in numerosity estimation are inspired by the scalar timing theory first proposed to account for time

estimation (Church & Meck, 1984; Gibbon, 1977). These models (see the numerosity detector and the accumulator models, in §3.5.3 and §3.5.4., respectively) hypothesise the existence of an internal numerosity-*accumulator* system (Dehaene & Changeux, 1993; Meck & Church, 1983) which is thought to transform objects and/or events into “abstract” items to be accumulated, irrespective of stimulus modality (visual, auditory, motor), mode (simultaneous or sequential), and physical characteristics (shape, position in space, duration, etc). The outputs of the accumulator are abstract magnitudes that are transferred into working memory, where they represent numerosity. In the final comparative decision stage, the actual magnitudes in the accumulator are compared with the stored magnitude in working memory, and a response is generated.

Many questions remain, however, regarding the nature of this representation and the processes that are used to construct it. In fact, a truly abstract representation of numerosity would apply to any set of discrete elements, whether events or objects, homogeneous or heterogeneous, simultaneous or sequential. Yet numerosity estimation is consistently found to be influenced by sensory properties of the stimulus, such as, for example, visual regularity. In both visual and auditory arrays, the presence of certain regularities influence the perception of numerosity. For example, the density and the grouping patterns of large visual arrays affect the numerosity judgements. Because of these perceptual influences, some explain numerosity estimation in terms of modality-specific perceptual process (e.g. texture perception for visual arrays), or in terms of processes specific to stimuli in certain formats (e.g. timing mechanisms for temporally distributed elements). For example, some computational models of human visual numerosity estimation predict human performance quite accurately, though they perform the numerosity judgement based on the detection of some physical stimulus properties such as area and density, which can be correlated with, but are *not* equivalent to numerosity (Allik & Tuulmets, 1991; Vos, van, Tibosch, & Allik, 1988). However, there is some evidence that seems to support the existence of an abstract non verbal representation of numerosity, even if the number of studies conducted in this domain are, unfortunately, still very few. Again, we group them according to the methodology used: behavioural, neuropsychological, and neuroimaging.

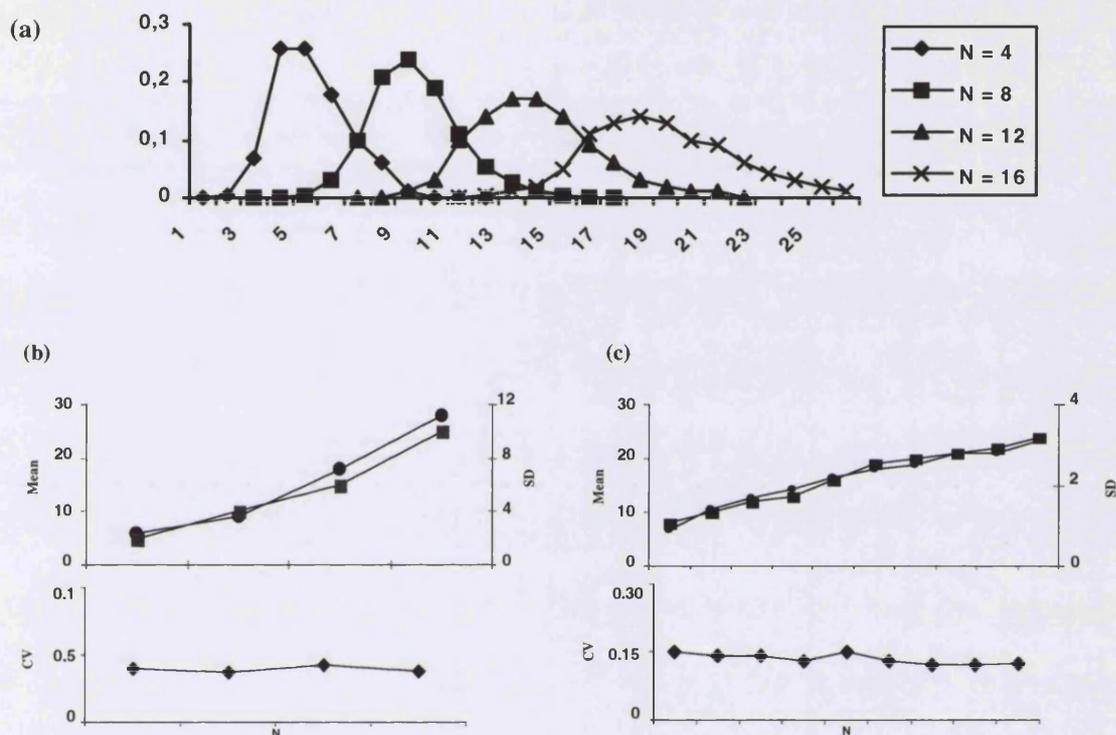
#### **4.2- Behavioural studies**

Behavioural studies that attempt to determine the existence of a truly abstract non verbal representation of numerosity on humans, are mainly inspired by the animal

literature, and follow two lines of research: (1) disentangling numerosity judgements from other judgements on possible co-varying factors, and (2) investigating the judgement of numerosity between different modality (e.g. visual and auditory) and mode (e.g., simultaneous vs. sequential) of stimulus presentation. (1) On one side, some studies systematically compare estimation of numerosity with estimation of other physical variables of the same set (e.g. time, for sequentially presented stimuli) that co-vary with numerosity. If numerosity estimation is performed on the basis of the estimation of the physical variable considered, performance in the estimation of the physical variable should account for performance on numerosity. In this logic, Whalen et al. (Whalen et al., 1999) presented numbers between 7 and 25 on a computer screen, and asked subjects to press a button as fast as they could until they had felt they had made approximately the indicated number of button presses. Results showed that both the mean estimate and its variability were proportional to target value, and the coefficient of variation (the ratio of the standard deviation and the mean) was constant across target size. These data perfectly mirror animal data (see figure 1.10). Then, in order to control if subjects relied on time estimation, they asked them to reproduce a time interval that was of the same order of the total key-presses. The coefficient of variation was then calculated and used to measure the precision of the judgement of time. Its value was much greater than the one found for the variation of the numerosity judgement, showing that subjects did not rely on estimated duration rather than on estimation of numerosity. Very similar results were found when subjects were presented with sequences of tones at a very fast rate, and had to estimate their number. Time estimation over the same stimuli did not account for numerosity estimation performance. In order to confirm the generality of such results, these manipulations should be systematically done also using simultaneously presented items.

(2) As a second line of research, some studies have investigated the cross-modal and cross-mode transfer of numerosity, using comparative judgements in order to exclude the possibility that subjects make use of verbal counting strategies (Bart, Kanwisher, and Spelke, personal communication). The logic of these studies is to look for computational costs in making numerosity judgements on stimuli presented in one only modality (e.g., two arrays of dots or two sequences of sounds) with respect to cross-modal (e.g., sequences of flashes vs. sequences of sounds), and cross-mode (e.g., arrays of dots vs. sequential) stimuli. Results show no evidence for computational costs for comparing numerosities across stimulus modality or mode, relative to accuracy on

intra-modal and intra-mode comparisons, which strongly suggests that adults' numerosity estimation is based on abstract representation of number. Nevertheless, this line of research is just at its beginning, and we will be able to conclude in favour of this hypothesis only after having collected a larger amount of evidence.



**Figure 1.10** Numerosity estimations in animals (panel a and b) and in humans (panel c). (a) The probability of breaking off a sequence of lever presses as a function of the number of presses in the sequence and the number required to get the reward. (b) The mean (circles) and standard deviation (squares) of the distribution in a, and the coefficient of variation (CV), which is the ratio between the mean and the standard deviation. Note that the CV is constant. (c) data from humans producing the sequences of lever pressing. The mean deviation (circles), standard deviation (squares), and the CV (coefficient of variation). Note the striking similarity between b and c. Adapted from Gallistel & Gelman, 2000.

### 4.3- Neuropsychological studies

Unfortunately, in the neuropsychological domain, investigations of numerosity estimation are very sparse. The first reported neuropsychological studies found that impairments in numerosity estimation are more likely to occur after right than left

hemisphere damage (McFie, Piercy, & Zangwill, 1950). Later it was shown that the right parietal lobe was the only locus relevant for estimation performance (Warrington & James, 1967), since, out of a pool of subjects with lesions in the three lobes of the two hemispheres, only the group with lesions in the right *parietal* were impaired at numerosity estimation. Indeed, a right hemisphere superiority in numerosity estimation was replicated using unilateral tachistoscopic presentation of stimuli to normal subjects (Kimura, 1966 ; Kosslyn et al., 1989; McGlone & Davidson, 1973; Young & Bion, 1979), but the specificity of parietal structures has never been further investigated. Moreover, it is worth noticing that the procedures used in all the aforementioned neuropsychological experiments show some problematic aspects:

1) stimuli always consisted of simultaneous, very brief, visually presented items; no other modality (auditory, or motor) or mode (sequential) of presentation was tested. This prevents any conclusions on the issue of whether numerosity estimation is an a-modal process, and whether the individuated neural substrate reflects this a-modal nature.

2) tasks involved the production of a number word. This could be problematic for investigations of non-verbal estimation because it is possible that subjects, having to generate a numerical result, may have used arithmetical strategies that depended on number symbols (such as counting by groups). In this sense, this procedure is not comparable with other studies in animals and infants in which no symbolic output is required, and where estimation is tested by means of comparison between numerosities. Clearly, a more systematic exploration of number estimation abilities in brain lesioned patients should be pursued, using different modality and mode of stimulus presentation.

#### **4.4- Functional Imaging Studies**

To date, no functional imaging study of numerosity estimation has been published yet.

#### **4.5- Numerosity estimation -Summary**

The very few existing behavioural studies of numerosity estimation in the human adults seem to suggest that indeed we can perform those kinds of tasks on the basis of a mechanism that treats entities as abstract entries into some kind of accumulator system specific for numerosity. Neuropsychological studies seem to point to cortical structure of the right parietal lobe as essential for performing such numerosity judgements. In the experiment described in chapter 4, we aimed at exploring the functional neuroanatomy

of such numerosity estimation in healthy human subjects using fMRI, in order to localise this process and to compare the brain regions involved in estimation with the ones involved in exact counting.

## ***5. Objectives of the present thesis***

As seen in the previous literature review, although much work has been done to understand the mechanisms involved in numerosity judgements in the human adults, still some unanswered questions remain.

With respect to counting and subitizing, data reviewed are still not able to determine whether the two processes are indeed qualitatively different, or whether they simply lie on a continuum of difficulty. We approached this problem in two steps: first, we investigated whether the two processes are implemented in separable regions in the brain using PET; then, using event related fMRI, we investigated whether they emerge from a qualitatively different recruitment of a set of relevant brain regions.

With respect to numerosity estimation, our knowledge on the critical regions involved, and of the nature of the representation in these regions (i.e., if it is a-modal, or dependent on the modality of stimuli) is still very poor. We approached this problem performing an fMRI study making use of stimuli from different modalities, which subjects have to quantify by either estimation or verbal counting. This allowed us to isolate regions involved in estimation and to explore whether they are dependent by stimulus modality or not.

## ***Chapter II***

### ***Experiment 1. Are subitizing and counting implemented as separate or functionally overlapping processes? A PET study***

#### ***1. Introduction***

In light of the previous review of the existing literature on subitizing and counting, we concluded that whether the two processes are indeed qualitatively different, or whether they simply lie on a continuum of difficulty is still an open question. Our reasoning was very simple: if, using functional imaging we are able to show that they rely on two distinct neural systems, then it would be quite a strong proof that they are also different in nature. Moreover, as a secondary research question, we wanted to investigate the validity of the pattern recognition models of subitizing (stating that subitizing simply consists in a pattern recognition, see chapter 1, §3.5.1). Given that the brain regions involved in recognition of visual patterns are fairly well known (i.e. occipito-temporal and fusiform areas) (Moore and Price 1999; Malack et al., 1997; 1998), our reasoning was very simple: if subitizing is a pattern recognition, it should activate brain areas typically found in object recognition, whilst counting should involve a wider network that may not involve strong activation of the areas related to subitizing. Therefore, we performed an experiment that made use of PET to investigate the following hypothesis: 1) That counting and subitizing are dissociable at the neural level; and 2) That quantifying familiar patterns of dots (canonically arranged arrays) relies on neural circuits linked to pattern recognition, and that this pattern recognition strategy could generally characterise subitizing (Mandler and Shebo 1982).

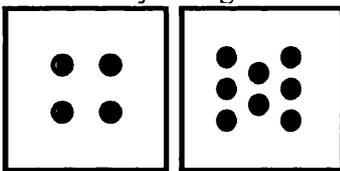
To ensure that the outcomes could be interpreted straightforwardly in terms of the normal behavioural results (unlike the previous imaging studies on subitizing processes, see chapter 1, §3.4), we used stimuli that are standardly used in enumeration tasks - black dots on a white background, that subjects had to quantify by saying aloud their answer.

## 2. Methods and materials

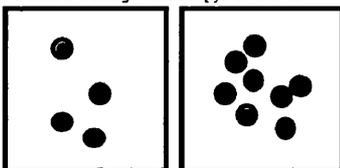
### 2.1- Subjects

Nine right-handed English speaking male volunteers (mean age 29, age range 22-45) with no history of neurological disorders gave informed consent to participate in 12 consecutive measurements of rCBF using PET. One subject suffered cramps during the acquisition of the 7<sup>th</sup> scan, and only 6 scans (out of 12) were included in the analysis. The study was approved by the local hospital ethics committee and the Administration of Radioactive Substances Advisory Committee (UK) (ARSAC).

Canonically arranged dots



Randomly arranged dots



*Figure 2.1 Examples of canonical and random arrangements of dots presented for quantification, for numerosity 4 and 8.*

### 2.2- Design and task

The experiment comprised a 2x2 factorial design with two baseline conditions. The variables manipulated were: (i) **numerosity of dots**, that had two levels: subitizing range (1-4 dots), and counting range (6-9 dots), and (ii) **spatial arrangement of dots**, that had two levels: canonical and random. For canonical arrangements, an easily recognisable and geometrical arrangement of dots was assigned to each numerosity, while for random arrangement, a disorganised distribution of dots was assigned to each numerosity (see figure 2.1). The task was to say aloud, as quickly and accurately as

possible, the number of dots presented. Responses were recorded using a microphone and used to measure RTs and accuracy.

The baseline conditions comprised of one baseline for the subitizing range, and one for the counting range. The former consisted of the presentation of one single dot, to which subjects were asked to respond with the word "one". The latter consisted of a combination of two different scans: in the first the stimulus always consisted of the same display of six dots, and the subjects were asked to simply respond with the word "six" without performing any counting; in the second baseline scan the stimulus was always a display of nine dots, and subjects were instructed to respond with the word "nine" without counting. These baseline conditions were included in order to control for the visual stimulation on the two numerosity ranges (1-4 and 6-9), and for verbal production, and auditory processing, even though the visual stimulation was not completely controlled in the case of the 1-4 range. Instructions were given prior to each scan.

### **2.3- Stimuli and procedure**

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

During each scan, 32 different stimuli were presented for 2500 ms each, at a rate of one every four seconds, preceded by a fixation point that lasted for 500ms, and followed by 1000ms of blank screen. Within each experimental scan, the same stimulus was presented 4 times. Therefore, within the experiment, random and canonical conditions were controlled within subjects so that any repetition priming effects would be equivalent in each condition. In order to facilitate a pattern recognition strategy for the canonical arrangement of dots, the subjects were familiarised with the canonical patterns being presented with each numerosity four times prior to the scanning session. In order not to trivialise the task, but also to maximise occurrence of crucial trials for each scan (Corbetta, Miezin, Shulman, & Petersen, 1993), we manipulated the probability of occurrence of each stimulus within each experimental scan. During the 45 sec. of data acquisition period, the probability of appearance of the crucial stimuli (e.g. 1-4 dots for the subitizing range condition) was 100%, but decreased to 30% in the

period preceding and following it. Non-crucial stimuli (e.g. 6-9 dots for the subitizing range condition) were randomly chosen from the other non-crucial conditions. For the baseline conditions, no non-crucial trial was presented, and therefore the probability of occurrence of the crucial stimuli was 100% through the whole scan.

#### **2.4- Imaging parameters**

The 12 PET scans were obtained using a SIEMENS/CPS ECAT EXACT HR+ (model 962) PET scanner (Siemens/CTI, Knoxville, TN, USA). Participants received a 20s intravenous bolus of H<sub>2</sub><sup>15</sup>O at a concentration of 55 Mbq ml<sup>-1</sup> and at a flow rate of 10 ml min<sup>-1</sup> through a forearm cannula. Images were reconstructed by filtered back projection into a 128 x 128 x 63 image matrix (voxel size 2.1 x 2.1 x 2.4 mm) using measured attenuation correction. For each subject, a T1-weighted structural magnetic resonance (MR) image was obtained with a 2 Tesla Magnetom VISION scanner (Siemens, Erlangen, Germany).

#### **2.5- Image processing and statistical analysis**

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

## *2.5.1- Main Effects*

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

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

### **2. Effects of Numerosity on Quantification**

#### **a) Activation for enumerating 6-9 dots versus 1-4 dots, irrespective of arrangement**

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

#### **b) Activation for enumerating 1-4 dots versus 6-9 dots, irrespective of arrangement**

The same procedure was used to identify areas more activate in enumerating 1-4 dots than 6-9 dots, irrespective of arrangement. Contrasts 1-4 random > 6-9 random, and 1-4 canonical > 6-9 canonical were combined using conjunction analysis masking with contrasts (1-4 random > 1-4 baseline) and (1-4 canonical > 1-4 baseline).

### **3. Effects of Spatial Arrangement on Quantification**

#### **a) Activation for canonical versus random arrangement, irrespective to numerosity**

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

**b) Activation for random versus canonical arrangement, irrespective to numerosity**

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

**2.5.2- Specific Effects**

**1. Effects specific for 6-9 dots randomly arranged (counting)**

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

**2. Effects specific for 6-9 dots canonically arranged**

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

**3. Effects specific for 1-4 dots randomly arranged**

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

**4. Effects specific for 1-4 dots canonically arranged**

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

For each of the above effects we discuss activation that reached significance at  $p. < 0.05$  corrected for multiple comparisons. A level of significance of  $p. < .001$  uncorrected for multiple comparisons will be accepted for the discussion only for specific regions of interest defined by previous neuroimaging and neuropsychological data. The *a priori* areas of interest were parietal regions that have previously been

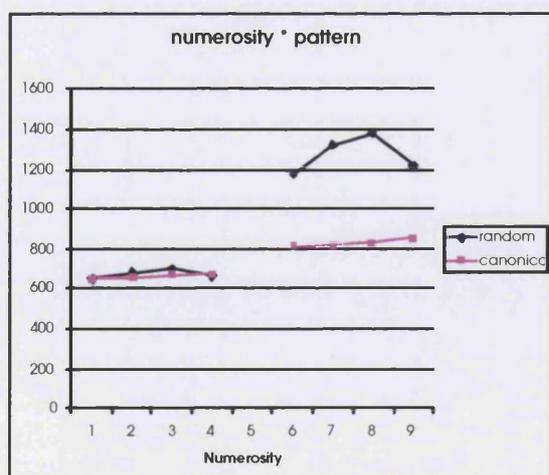
activated in neuroimaging studies of shifts of attention in space, and of attentional modulation of visual inputs. Interestingly, the same regions have been shown to play a crucial role in the manipulation of numbers (typically in number comparison and calculation) both in imaging and in neuropsychological studies (Cipolotti et al., 1991; Dehaene & Cohen, 1995; Dehaene et al., 1999; Pinel, Dehaene, Riviere, & LeBihan, 2001; Thioux et al., 1998; Pesenti, Thioux, Seron, & De Volder, 2000; Rickard et al., 2000)) A second region of interest is extrastriate occipito-temporal cortex, that has previously been activated in studies of pattern recognition and naming (Kanwisher, Chun, McDermott, & Ledden, 1996; Moore & Price, 1999a; Murtha, Chertkow, Beauregard, & Evans, 1999; Rolls, 1998) and may be one of the areas in which activity is strongly influenced by top-down attentional modulatory input from parietal cortex (Friston & Büchel, 2000).

### **3. Results**

#### **3.1- Behavioural results**

Overall, accuracy of performance was close to 100% for all 4 conditions, and therefore no further analysis of errors was performed. Figure 2.2 shows RTs as a function of number of dots and of arrangement. Subjects showed the expected subitizing-counting performance with the random arrangement, resulting in the discontinuity of the slopes in the subitizing range and in the counting range. The drop in RTs for nine dots was interpreted as due to a "guessing end effect" (Sathian et al., 1999; Simon, Peterson, Patel, & Sathian, 1998), and therefore was excluded from further behavioural analysis. Slopes for the canonical arrangement were approximately 8 ms for the subitizing range, and 13 ms for the counting range. For the random arrangement, they were 20 ms per item for the subitizing range, and 105 ms per item for the counting range. This last value was lower than usually found in counting experiments (see (Trick & Pylyshyn, 1993), for a review), probably because each random pattern was repeated throughout the experiment, leading subjects to "within experiment learning". Nevertheless, the RT data indicate the effect of subitizing and counting range for the random arrangement. The behavioural data also show that subjects were better at quantifying the sets with a canonical spatial arrangement in the counting range. This facilitation of the canonical arrangement over the random arrangement did not appear in the subitizing range. This is in agreement with what has previously been observed

(Dehaene & Cohen, 1994; Mandler & Shebo, 1982). These effects were tested entering reaction times on correct trials only into a 2x2 repeated measure analysis of variance, with number of dots (subitizing range [1-4 dots]; and counting range [6-9 dots]); and spatial arrangement of dots (canonical and random) as between subject factors. The analysis showed a significant main effect of number of dots ( $F[1,8] = 46.3, p < .0001$ ), with counting being much slower than subitizing (670 and 1112 ms.); a significant main effect of spatial arrangement ( $F[1,8] = 21.39, p < .005$ ), with random arrangements enumerated much slower than canonical arrangements; and finally, a significant number of dots x arrangement interaction ( $F[1,8] = 16.07, p < .005$ ). Planned comparison showed that the effect of number of dots was modulated by their spatial arrangement: for the random arrangement, counting was significantly slower than subitizing ( $F[1,8] = 61.327, p < .001$ ) while for the canonical arrangement the difference between subitizing and counting didn't quite reach significance ( $F[1,8] = 4.672, p = .062$ ). Moreover, planned comparisons also showed that in the counting range, the dots arranged in a random display were enumerated slower than when arranged in a canonical way ( $F[1,8] = 35.057, p < .0005$ ), while in the subitizing range there was no difference between the two arrangements.



**Figure 2.2** Mean of median reaction times averaged across subjects, in the quantification task, as a function of the number of dots and their spatial arrangements

## 3.2- Neuroimaging Results

### 3.2.1- Main Effects

#### 1. Effect of Task: The Quantification System (see table 1)

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

Areas	Talairach Coordinates			Cluster size	All > bsl	6-9 R > bsl	6-9 C > bsl	1-4 R > bsl	1-4 C > bsl	OTHER EFFECTS	
	x	Y	z								Number of voxels
Middle Occipital	R	36	-76	-12	} 4713	<b>5.8</b>	<b>5.1</b>	3.6	4.4	2.9	N
		36	-60	-14		<b>4.7</b>	<b>4.9</b>	3.4	4.4	n.s.	
	L	-32	-90	0	} 2523	<b>5.2</b>	<b>4.7</b>	3.5	3.2	3.0	N, C
		-48	-78	-14		<b>4.9</b>	<b>4.9</b>	3.4	2.9	n.s.	
Intra Parietal	R	-10	-92	-8		<b>4.5</b>	<b>4.6</b>	3.5	3.3	n.s.	
	L	30	-70	44		<b>5.2</b>	<b>5.9</b>	3.9	2.7	2.9	C
Midbrain		-28	-70	38	83	3.4	3.7	2.5	n.s.	n.s.	N
Middle Frontal	R	-2	-34	-10	449	<b>4.5</b>	3.9	<b>4.8</b>	n.s.	n.s.	n.s.
Middle Frontal	R	54	32	36	37	3.6	4.2	n.s.	n.s.	n.s.	n.s.
Cerebellum	L	-36	-40	-32	236	3.8	3.7	3.4	2.6	2.9	n.s.

**Table 1.**

*The quantification system. Regions that show increased activation during quantification tasks for all numerosities and arrangements relative to the baseline tasks, and relative z-scores. C = canonical arrangement; R = random arrangement; bsl = baseline. In Bold-type, Z-scores corrected for multiple comparisons, at  $p < 0.05$ , and related regions. In the column "other effects" regions that show increased activation as the Number of dots increases, irrespective of arrangement (N), and regions that showed*

\* This cluster is included in the right middle occipital one.

increased activation specifically in Counting 6-9 randomly arranged dots (C), are indicated.

## 2. Effects of Numerosity on Quantification

### a) Activation for enumerating 6-9 dots versus 1-4 dots, irrespective of arrangement (see table 2)

At a corrected level of significance, activation in the middle/inferior occipital extrastriate cortex bilaterally was enhanced for enumerating 6-9 dots compared with 1-4 dots, irrespective of spatial arrangement.

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

### b) Activation for enumerating 1-4 dots versus 6-9 dots, irrespective of arrangement

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

Area	Talairach coordinates	Cluster Size	All 6-9	6-9 R	6-9 C	
			> all 1-4	> 1-4 R	> 1-4 C	
	x y Z	Number of voxels	Z-scores			
Inf./Mid. Occipital	R	30 -92 -4	<b>5.1</b>	4.5	3.6	
		44 -88 -4	4.0	3.4	4.0	
	40 -88 10	3.9	3.4	4.0		
	62 -56 -26	54	3.9	n.s.	n.s.	
L	-36 -86 -2	} 291	<b>4.9</b>	<b>6.1</b>	3.4	
	-8 -100 -10		4.4	3.4	3.4	
Intra parietal	L	-28 -66 40	18	4.1	4.2	n.s.
Cerebellum	R	10 -72 -30	201	3.7	n.s.	n.s.

**Table 2.**

**Effects of Numerosity on Quantification.** Regions that show increased activation as the number of dots increases during quantification, irrespective of spatial arrangement scores (All 6-9 >all 1-4 ). For those regions all Z-scores for the random (R) and canonical (C) contrasts are reported separately. In Bold-type, z-scores corrected for multiple comparisons, at  $p < 0.05$ , and related regions.

## 3. Effects of Spatial Arrangement on Quantification

**a) Activation for canonical versus random arrangement, irrespective to numerosity**

Irrespective of numerosity, there were no areas that were more active for either random or canonical arrangements.

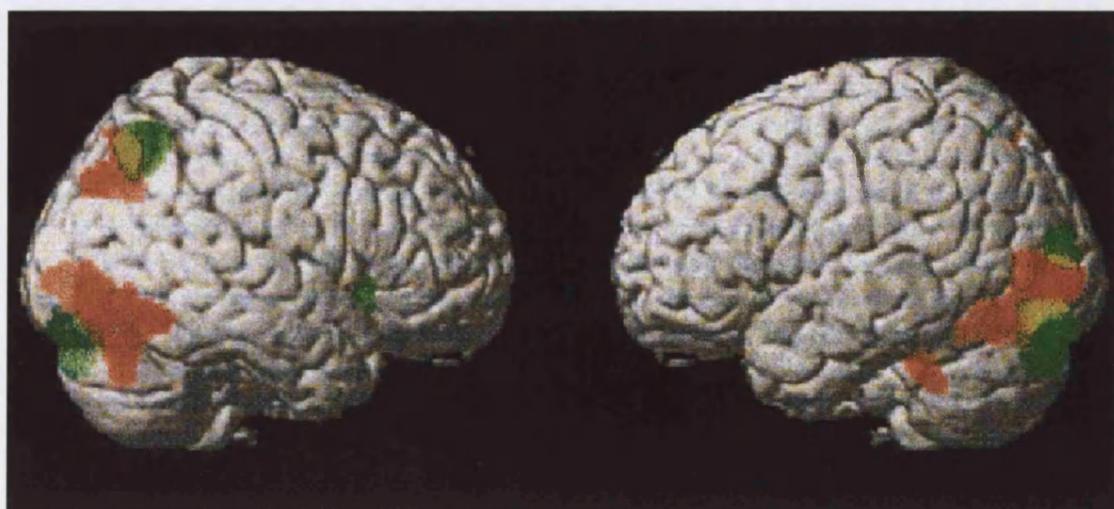
**3.2.2- Specific Effects**

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

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

Area	Talairach coordinates			Cluster Size Number of voxels	6-9 R	Interacti	6-9 R	6-9 R		
	x	y	z		> 6-9 C	on <sup>2</sup>	> 6-9 bsl	> 1-4 R		
Z-scores										
Superior Parietal	R	28	-68	50	462	<b>5.0</b>	3.6	<b>5.9</b>	<b>4.9</b>	
Inf./Mid. Occipital	L	-22	-86	-14	} 648	<b>4.8</b>	4.3	<b>4.6</b>	<b>6.1</b>	
		-16	-88	-26		4.3	3.7	4.6	n.s	
		-42	-86	-14		22	3.4	n.s	4.4	4.5
		-40	-92	12		100	4.4	3.6	4.5	4.0
Anterior Insula	R	38	18	-4	60	3.5	3.4	4.0	<b>4.8</b>	

**Table 3.** *Effects Specific to Counting. Regions that show increased activation that is characteristic for quantification of 6-9 randomly arranged dots (counting), with respect to 6-9 canonically arranged dots, and to all other conditions. In Bold-type, z-scores corrected for multiple comparisons, at  $p < 0.05$ , and related regions.*



*Figure 2.3 Counting and the Quantification system. In red, the occipito-parietal circuit activated during quantification tasks for all numerosities relative to baseline. In green, areas of increased activation specific for counting (6-9 randomly arranged dots). In yellow, the overlap.*

## 4. Discussion

This study tested two main hypotheses:

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

1) In relation to the dissociability of brain areas underlying counting and subitizing we found little evidence for subitizing or counting specific regions despite 18 scans per condition (9 subjects X 2). Subitizing does not seem to rely on a separate dedicated neural mechanism that is not also involved in counting. To the contrary, the results reveal a pattern of activation in bilateral middle occipital and parietal areas (see table 2), where intensity and spatial extent is modulated by the number of dots and their spatial arrangement. Activation increases as the number of items on the visual array increases, reaching a maximum peak and extent when counting 6-9 randomly arranged items is required. This modulation mirrors behavioural data, in that RTs are higher for quantifying arrays of 6-9 than for 1-4 dots, and within the 6-9 range, they are higher for counting randomly arranged than canonically arranged dots.

2) In relation to pattern recognition strategy in the quantification tasks, we found that areas linked with object recognition in the bilateral occipito-temporal cortex were activated for quantification irrespective of arrangement, and we did not find any effect specific to canonical spatial arrangement. It therefore appears likely that pattern recognition was evoked by all conditions, but when the configuration was not canonical (i.e. for random 6-9), there was additional contribution from the right superior parietal lobe.

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

*The middle occipital areas* are extrastriate visual areas that have been linked to object recognition even when visual input is controlled (Grill-Spector et al., 1998;

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<sup>2</sup> Numerosity x Arrangement Interaction

Moore & Price, 1999b). Activation in the middle occipital regions during quantification, even when no recognisable shape was present (in the counting random configuration condition) suggests that subjects may have tried in all conditions to deconstruct the array into patterns in order to count by groups. Previous studies have shown that subjects deploy this grouping strategy for counting, when they can (Atkinson, Francis, & Campbell, 1976; Mandler & Shebo, 1982; van Oeffelen & Vos, 1983). Our dots were not controlled for spatial proximity, in that some were closer than others (see one example in figure 2.1), and proximity is a very well known grouping principle. In fact it has been shown that subjects, when facilitated by grouping cues like spatial proximity, always adopt the strategy of counting by adding sub-clusters of dots (Atkinson, Francis et al., 1976; van Oeffelen & Vos, 1983). Therefore subjects are very likely to have applied this strategy in our study. In other words, when quantification was required, there was a top-down attentional effect on the visual input in order to perform sequential grouping. Other studies have also associated activation in middle occipital gyri with top-down attentional modulation of visual processing (Mangun, Buonocore, Girelli, & Jha, 1998). For example, these areas are active in tasks that required covert and overt shifts of visual attention in response to a cue, as compared with detecting the cue (LaBar, Gitelman, Parrish, & Mesulam, 1999; Luck, Girelli, McDermott, & Ford, 1997), quantifying sets of five or more targets among distractors, compared with sets with four or fewer targets, and quantifying sets of four or fewer targets among distractors compared with simply detecting a target (Sathian et al., 1999). In the two latter cases, from the paper by Sathian et al. discussed earlier, the activation in middle occipital areas was tentatively attributed to a form-discrimination process, and linked to the fact that subjects had to select and count vertical among horizontal bars. However, this interpretation does not hold for our study, because no particular form discrimination was necessary in order to isolate the objects to be counted.

*The intraparietal areas* have previously been associated with number processing, and their role in the circuit controlling finger movements has suggested an intimate involvement with counting (Butterworth, 1999a, 1999b). Supported by experimental and clinical evidence, Dehaene and his colleagues have proposed a neuroanatomical model of number representation: this model implies that areas within the intraparietal sulci bilaterally are the "cerebral localisation of a category-specific internal representation of numbers" ((Chochon, Cohen, van de Moortele, & Dehaene, 1999), page 625), that is involved in calculation, as well as in *quantification* operations,

and in comparison of numerical magnitudes (Dehaene & Cohen, 1995). Furthermore, the model proposed that right and left inferior parietal areas give differential contributions to number processing: the right hemisphere supports the *analogue* representation of numerical quantities (as, for example, in estimation processes), while the *left* parietal region connects the quantity representation with the linguistic code. Our study is consistent with this hypothesis because we show that left lateralised parietal activation is modulated by numerosity, and is *not* involved in subitizing 1-4 dots (see table 1). In other words, the left parietal area may relate to the internal subvocalization of the verbal number sequence, or some other kind of linguistic sequences, such as sequential additions of small numbers, as would occur when counting by groups (Logie & Baddeley, 1987; van Oeffelen & Vos, 1983). In contrast, the right lateralised parietal activation, which is present for subitizing but most extensive for counting randomly arranged dots, could reflect the access to domain specific representation of quantities and numbers (Chochon et al., 1999). Nevertheless, even if this account of parietal activation in our quantification task is interesting, it is not the only possible, and not even the most plausible explanation of our data. In fact, parietal cortices play a well-known role in visuo-spatial operations such as shifting attention in space and visuo-spatial working memory, and this account would very well fit with behavioural data that show that counting, more than subitizing, requires ocular movements to locate and mark objects (or groups of objects) in space (Atkinson, Campbell, & Francis, 1976; Atkinson, Francis et al., 1976). Data from lesion studies (see (De Renzi, 1982), for a review), and from functional imaging studies, indicate that the superior parietal cortex, especially in the right hemisphere, is often engaged in tasks that require shifts of spatial attention, with and without eye movement. (Anderson et al., 1994; Ashbridge, Walsh, & Cowey, 1997; Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta & Shulman, 1998; Nobre, Gitelman, Dias, & Mesulam, 2000 ), and visuo-spatial WM (Diwadkar, Carpenter, & Just, 2000; LaBar et al., 1999 ). These data support the involvement of shifts of attention among objects to locate them in space, and visuo-spatial WM to keep track of already counted objects during counting, but to a lesser extent subitizing and pattern recognition for 6-9 canonically arranged dots, as implied by behavioural studies of enumeration (Simon & Vaishnavi, 1996; Trick & Pylyshyn, 1993; Trick & Pylyshyn, 1994). The neuroimaging study of counting and subitizing processes by Sathian, Simon et al. (1999), also found activation in this same right parietal region for counting with respect to subitizing, but not for subitizing with respect to single target detection. This

pattern of data was interpreted as supporting the idea that subitizing is based on a preattentive process that does not involve attentional shifts, while counting is a serial process that does involve attentional shifts. On the contrary, in the present study, activation could be detected in parietal areas even for subitizing relative to the baseline condition. There are two possible explanations for this incongruity between the two studies: the first one is the threshold applied to the statistics: the threshold we applied was lower, and this might have allowed us to detect smaller activations. The second one is the nature of the baselines: in our study subjects did not have to deploy any spatial attention during the baseline task, since they only had to look at a single dot, while in the Sathian's experiment, subjects had to search for a single target in an array of distractors, and therefore the attentional requirement was much higher than in our case. This might have cancelled out the small supplementary activation in parietal areas for the subitizing range in their study. Moreover, neither our study nor that of Sathian et al. measured ocular movements. It is highly possible that in unlimited (as in Sathian et al.) or limited but long (as in the present study) stimulus presentation, the amount of eye movement differed between the subitizing and the counting condition, and this could well account for the higher parietal activation in counting than in subitizing.

What seems quite clear from our data is that subitizing does not rely on a dedicated circuit that is *not* involved in counting. On the contrary, both extrastriate and parietal areas get recruited along a continuum in relation to the numerosity and the spatial arrangement of the array. These data (i) suggest that subitizing and counting are not dissociable at the neural level, being implemented in a network where recruitment is modulated by the number of objects, and (ii) present complementary evidence to behavioural and neuropsychological evidence on the subitizing-counting issue. Interpreting subitizing and counting as lying on a continuum may appear to conflict with the behavioural data that show a dramatic increase in RTs between subitizing (1-4 dots) and counting (6-9 randomly arranged dots). However, we believe that our behavioural result is exaggerated (especially for the very small slope in the subitizing range) due to the block presentation that we were forced to use by the PET design. In fact, when numerosity 1-4 and 6-9 are presented as mixed trials, RTs are not always so dramatically dichotomically distributed, even if the difference in slopes for subitizing and counting seems to be present (Oyama, Kikuchi, & Ichiara, 1981; Simon & Vaishnavi, 1996; Trick & Pylyshyn, 1993). However, there is still no definitive account

of behavioural data from enumeration experiments, and the debate on how to interpret the apparent dichotomy in RT distribution remains open.

#### **4.1- Conclusion**

The aim of this study was to characterise subitizing and counting at a neural level in order to investigate whether they are implemented as separate or functionally overlapping processes. Our data suggest that no brain area is specific for subitizing or counting. On the contrary, results reveal a pattern of activation in bilateral middle occipital and parietal areas for both quantification tasks (subitizing and counting), and that this activation increases as the number of items in the visual array increases, reaching maximum peak and extent when counting 6-9 randomly arranged items (i.e. not facilitated by canonical configuration) is required. In relation to pattern recognition, we found that areas linked with object recognition in the bilateral occipito-temporal cortex were activated for quantification irrespective of arrangement, and we didn't find any effect specific to canonical spatial arrangement. It therefore appears likely that some form of pattern recognition was evoked by all conditions. Overall, these results do not confirm the existence of a dedicated neural system for subitizing that is not involved in counting. The previous hypothesis that subitizing and counting are two qualitatively different mechanisms based on two separate networks does not receive confirmation from the present study.

It is possible that operations like attentional shifts, eye movements, and on-line maintenance of visuo-spatial information, that are supported by the same occipito-parietal networks (or by separate sub-regions that are not dissociable with the present imaging techniques) are all engaged, in different proportions and intensities, in subitizing, counting, and pattern recognition. Clearly more work is needed to investigate the precise relation between activation and each numerosity at the single trial level. This will be addressed in the next study, with an event related design in fMRI.

## *Chapter III*

# *Experiment 2. Are subitizing and counting implemented as qualitatively different processes? An event-related fMRI study*

### **1. Introduction**

#### **1.1- Limitations of the previous PET study**

The previous study indicated that subitizing and counting are implemented in overlapping, not dissociable sites in the human brain. As it stands, this result represents a negative result, i.e., a failure to measure an anatomical segregation between subitizing and counting. It is clear that there is need for more evidence of such absence of a structural dissociation between regions supporting subitizing and counting. Moreover, the fact that these two processes recruit the same set of regions does not necessarily imply that they are not qualitatively different. In fact, there is still the possibility that the two processes result from a qualitative different involvement of the same set of regions. In that study, due to the constraints of the techniques used (PET), the activity evoked by different numerosities could only be measured in two distinct blocks (numbers 1-4, and numbers above 4). This did not allow us to investigate whether 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, with such block design, it was not possible to obtain a trial-by-trial measure of the brain activity. Such a measure might be crucial if subjects' reliance on subitizing versus counting is a probabilistic rather than deterministic process and shows a high degree of variability between subjects and trials, even for a fixed numerosity. Again, the

two main views of subitizing and counting being two different or a single process remained open.

### **1.2- The present study**

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 an MR-compatible microphone, we measured vocal responses in the magnet and correlated them with brain activation patterns. Our goals were to investigate whether activity in attention-related regions of the posterior parietal cortex shows a linear smooth increase with numerosity or a sudden discontinuity in the activity beyond the subitizing range. Moreover, we wanted to investigate the hypothesis of being able to detect whether, on any given trial, subjects deployed a serial exploration of the display (counting) or a parallel apprehension of numerosity (subitizing) on the basis of the activity in such regions.

## ***2. Methods and materials***

### **2.1- Subjects**

Ten, right handed, healthy volunteers (5 males and 5 females; age range 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.

### **2.2- Design, Task, Stimuli and 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 overall 4 sessions in which one quantification block of 28 trials (4 times the numerosity 1-7) was preceded and followed by a colour naming block of 4 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 1 and 7 white squares presented visually on the black background of a computer screen. The squares randomly varied in dimension between 3 and 6 mm radius (subtending 0.12 and 0.24 degrees of visual angle). They were presented at random locations within a 100 \* 125 mm rectangular area, centred on the screen, the contour of which was visible, and varied, from trial to trial, between 7 different colours

(see figure 3.1 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. In order 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 in order to measure accuracy.

For the colour naming task, stimuli consisted in 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 far from the subject, subtending a visual angle of 5 degrees. The experiment was programmed using Expe6 software (<http://www.ehess.fr/centres/lscp/expe/>). Trials were presented at a slow rate of one every 12 seconds (corresponding to 5 fMRI volumes acquisition period). Stimuli and responses occurred during the first fMRI acquisition, where the read-out gradient were 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.

### **2.3- 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 X 256 mm, matrix = 64 X 64]. The whole brain was acquired in 26 slices with a slice thickness of 4,5 mm. Synchronised with the beginning of each trial, the read out gradients were disabled for a period of 2.4 seconds (1 TR), followed by 4 whole brain scans. High-resolution images (3D gradient echo inversion-recovery sequence, TI(inversion time) = 700 mm, TR = 2400 ms, FOV = 192 X 256 X 256 mm, matrix = 256 X 128 X 256, slice thickness = 1 mm) were also acquired.

### **2.4- Image processing and statistical analysis**

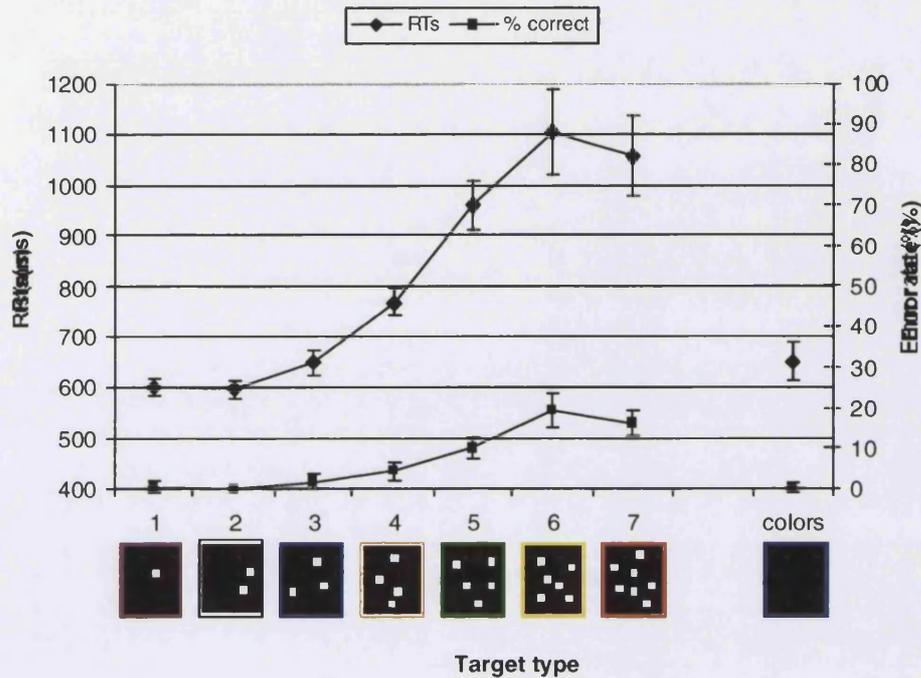
Data were analysed with SPM99 (<http://www.fil.ion.ucl.ac.uk/spm>). The first 4 volumes were discarded. All other volumes from each subject were realigned using the

first volume as reference then they were normalised to the standard T2\* template of the IMNI 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 hemodynamic response function (HRF). The data were high-pass filtered using a set of discrete cosine basis functions with a cut-off period of 120 seconds. 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  $p < 0.05$  corrected for multiple comparisons at the cluster level,  $p < 0.001$  at the voxel level. For the contrast showing non-linear 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**

#### **3.1- Behavioural results**

Correct response times measures were submitted to a one-way analysis of variance (ANOVA) with target type as the independent factor at 8 levels (quantification of 1 to 7 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 3.1). Crucially, the slope of response time showed the expected increase between the numbers from 1 to 3 (subitizing range) and in the numbers from 4 to 7 (counting range). This was tested by the presence of a quadratic trend in the 1 to 4 range [ $F[1,63] = 29.00$ ,  $p < 0.001$ ]. The drop in RTs for 7 is probably due to a "guessing end effect" (Sathian et al., 1999; Simon et al., 1998). This point was not included in the calculation of the slopes in the subitizing (1-3) and counting (4-6) range, which were of 24 ms for 1 to 3 items and of 168ms for 4 to 6 items, a significant difference ( $F[1,9] = 18.93$ ;  $p < 0.005$ ).



**Figure 3.1** Behavioural results and examples of stimuli. Mean reaction times and error rates for quantifying sets of 1 to 7 dots and naming the colour of a rectangular shape.

Responses for colour naming were overall very fast but slower than subitizing (597.92 and 651.76 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 4. 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, enumeration performance suggested the presence of a break between numerosities 3 and 4 in reaction time, and a similar trend is found in accuracy. Imaging data allowed us to assess whether behavioural discontinuity corresponded to the sudden engagement of attention-related cortical circuits.

### 3.2- Functional imaging results

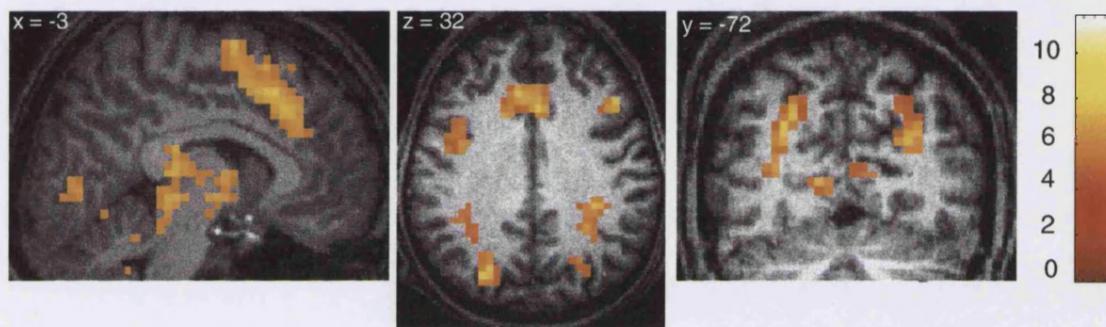
#### 3.2.1- Subitizing range

Even at the very low threshold of  $p = 0.05$  at the voxel level, no region showed greater activation in the subitizing range (1-3) than in the counting range (4-7) or than colour naming task. Moreover, and crucially, within the subitizing range, no region showed increasing activation from 1 to 3, even at very low thresholds ( $p = 0.05$  at the voxel level). This suggests that the processes that support subitizing are also active

during counting and the colour control, and that within the subitizing range those regions are not modulated by the number of items.

### 3.2.2- Counting range

Quantifying 4-7 elements, with respect to quantifying 1-3, activated a large network of areas (See table 4 and figure 3.2). This large network of regions probably subtends many different processes underlying the complex activity of counting, including visuo-spatial attention, word processing and their coordination.



**Figure 3.2** Regions showing greater activation when quantifying 4-7 elements (counting) than when quantifying 1-3 elements (subitizing). Group results are superimposed on capital, axial, and coronal slices of an individual normalized anatomical image.

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 4).

More interesting for understanding the neural processes supporting counting is to individuate the set of regions whose activity increases with the number of items to be counted. A linear contrast for numbers between 4 and 6 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 5). The activation in these regions increases linearly as the number of items increases from 4 to 6, 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, Frith, & Frackowiak, 1993; Fiebach, Friederici, Muller, & von Cramon, 2002). Thus, counting may involve coordinated spatial shifts and verbal working memory updates to keep the running total of the count (Logie & Baddeley, 1987).

Area	Hemisphere	Talairach coordinates			Counting > Subitizing	Counting > Colour naming	Non linear 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	-	-
<b>Intraparietal sulcus</b> (posterior)	R	32	-76	24	4.2	2.8	2.8
	L	20	-76	40	3.2	3.5	3.5 *
(anterior)	L	-28	-72	40	4.4	2.6	-
	R	36	-36	32	4.2	3.2	-
	L	-44	-44	36	3.9	3.3	-
<b>Precentral cortex</b> (lateral-FEF)	R	28	-4	56	3.8	3.0	3.3
	L	-40	0	32	3.8	2.5	-
(medial-SEF)		-24	-12	52	3.6	2.9	3.3
		8	8	60	4.8	-	2.3
<b>Cingulate cortex</b>		4	20	32	4.5	2.9	2.4
<b>DLPFC</b>	R	44	24	28	4.4	-	-
	L	-40	44	16	3.7	-	-
<b>Anterior insula</b>	R	32	24	0	4.8	2.4	4.3 *
	L	-36	20	-4	4.0	2.9	2.8
<b>Frontal operculum</b>	L	-44	16	4	4.0	2.6	2.8
<b>Orbito-frontal gyrus</b> (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	-
<b>Putamen/caudatus</b>	R	12	20	-4	3.7	3.1	2.7
	L	-16	16	-4	4.1	3.5	2.7
<b>Thalamus</b> (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	-
<b>Superior collicoli</b>	L	-20	-36	4	4.0	2.9	-
	R	12	-36	-16	4.3	3.1	-
	L	-4	-28	-8	4.0	4.0 *	-

**Table 4.** Coordinates of activation peaks for counting>subitizing, counting>colour naming, and non linear increasing with number. Stars (\*) indicate regions that were significant even in the whole brain search analysis. FEF= frontal eye fields ; SEF= supplementary eye fields ; DLPFC= dorsolateral pre-frontal cortex. In bold, regions that showed a non linear increase with number.

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 non-linear 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 4). Activation of these regions tightly mirrors the subitizing/counting behavioural dichotomy in that it shows a minimal or no increase from numerosity 1 to 3, a sudden discontinuous increase between numerosity 3 and 4, and a linear increase from 4 on.

Area	Hemisphere	Talairach coordinates			Z-scores
		x	y	z	
Intraparietal sulcus	(posterior) R	32	-76	24	4.1
	L	-24	-80	44	4.5
	(anterior) R	-28	-72	28	4.0
	L	40	-36	32	4.0
Medial precentral cortex (SEF)		-32	-44	32	3.7
		8	8	60	3.9
Anterior Insula/ Inferior frontal gyrus		8	12	44	3.7
	R	24	24	-16	4.6
Superior collicoll	L	-32	20	-8	3.8
		-8	-16	-12	3.9

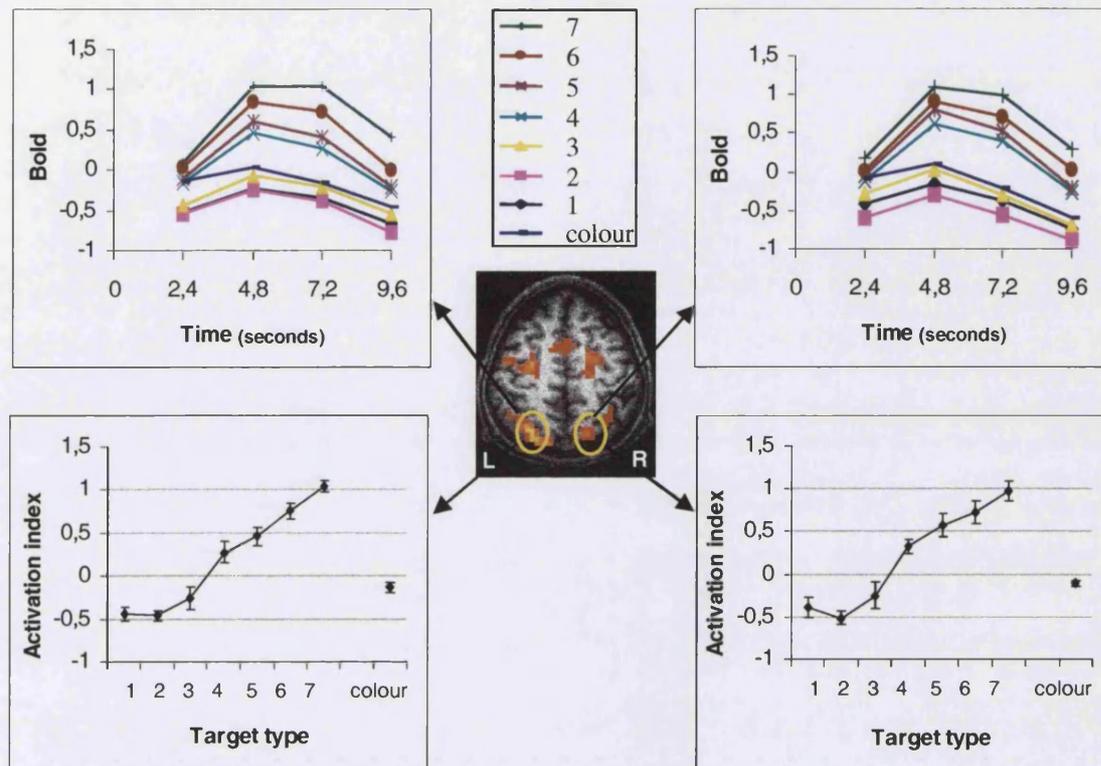
**Table 5.**  
*Coordinates of activation peaks for regions that show a linear increase with numerosity in the counting range. SEF= supplementary eye fields.*

### 3.2.3- A single-trial measure of posterior parietal activation

Posterior parietal regions, which have been associated with a variety of attention-related tasks (Corbetta & Shulman, 1998) (Culham & Kanwisher, 2001; Wojciulik & Kanwisher, 1999) 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 non linear increase with number (see, in figure 3.3, top, the time course of the activation as a function of the stimulus types). In order 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 normalised

BOLD signal at the four data points following each stimulus, and the standard SPM hemodynamic 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 activation index provides a relative, not an absolute measure of single-trial activation. In particular, negative values need not indicate a deactivation relative to the intertrial 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 response times. This showed a significant effect of target type ( $F[7,63] = 22.85$ ;  $p < 0.001$  for the right parietal cluster, and  $F[7,63]=35.54$ ;  $p < 0.001$  for the left parietal cluster). Moreover, a quadratic trend test (from 1 to 4) showed a significant discontinuity between numbers 3 and 4 ( $F [1,63]=12.93$ ,  $p < 0.05$  and  $F[1,63]=6.78$ ,  $p < 0.05$  for the right and left parietal clusters respectively). The sudden onset of activity at number 4 can be clearly seen in figure 3.3, where the increase in activity between 3 and 4 was higher than both the increase between 2 and 3 and between 4 and 5. Planned comparisons also showed that the activation for colour naming was significantly higher than the activation for quantifying sets of 1-3 elements ( $F[1,63] = 4.30$ ;  $p < 0.05$  and  $F[1,63]=5.21$ ,  $p < 0.05$  for the right and left parietal clusters respectively), but lower than when quantifying 4-7 ( $F[1,63]=33.55$ ,  $p < 0.001$  and  $F=52.39$ ,  $p < 0.001$ ) (see figure 3.3).



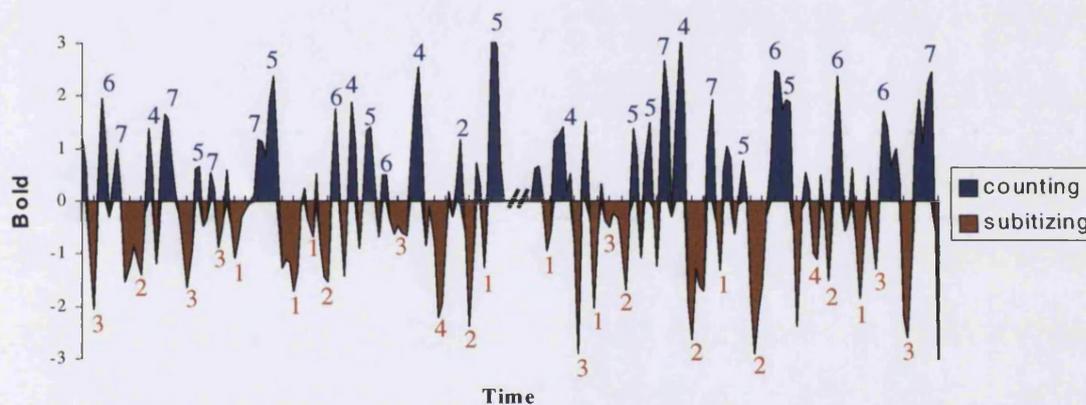
**Figure 3.3** Activation profile in regions showing a non-linear effect of number. Top: activation at posterior parietal peaks (averaged between all subjects). Centre: Axial view ( $z=50$ ) of the group results superimposed on an individual normalized anatomical image. Bottom: mean activation index for each target type (dots from 1 to 7 for quantification and an empty coloured rectangle for colour naming). Error bars indicate one inter-subjects standard error.

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 uses the linear combination of the right and left posterior parietal activation indexes and finds the best function to classify the trials in 2 classes: range 1-3 (subitizing), and range 4-7 (counting). We then applied this function to the new 3/4 of the data. This correctly predicted 76 % of the trials. All but one subject had high prediction scores (from 69% to 88%). By simply looking at the activity on those posterior parietal regions we were able to classify trials in trials where subjects were presented 1 to 3 objects and trials where they were presented with more than 4 objects. This means that the activation corresponding to quantifying 1 to 3 objects (subitizing) and the one corresponding to quantifying more than 4 objects

(counting) are very strongly clustered apart, thus confirming the different nature of the two processes.

### 3.2.4- Inferring subjects' strategies for quantifying 4 items

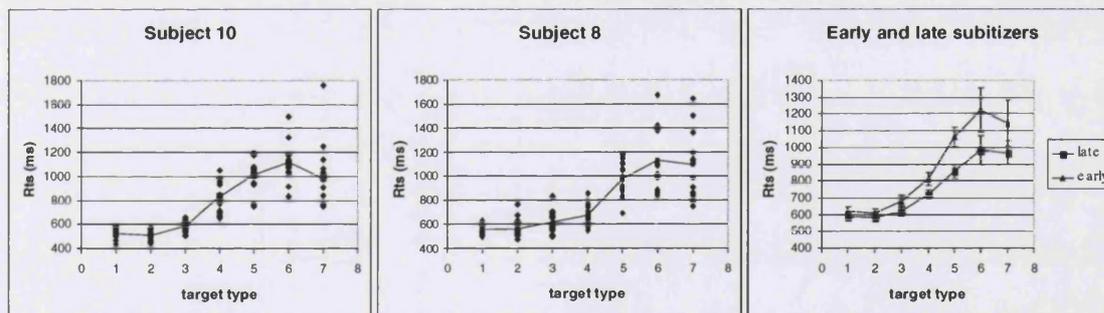
Over the 7 different numerosities, the worst predicted one was 4, with 60% trials classified as counting and 40% as subitizing. As shown in figure 3.4, among the trials at numerosity 4, there were some with a high activation and others with a low activation. This variability was confirmed by a close exploration of RTs. 4 was the first number at which the variance in RTs began to increase sharply, both across as well as within subjects (see figure 3.5).



**Figure 3.4** Time course of the non averaged 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 4 elements showed high activation, while trials with 1 to 3 elements showed low activation.

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 et al., 1978; Trick et al., 1993). For instance, Trick and Pylyshyn reported a series of experiments on visual object enumeration where the subitizing range varied from 2 to 6 between different subjects (Trick et al., 1993). In our data, examination of individual RTs suggested that different subjects subitized up to 3, 4 or even 5 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 (5 subjects per group). The “early activators” were those who showed high parietal activation (>70% of the trials classified as “active”) already at numerosity 3 or 4. The “late activators” were those who showed no strong parietal activation at numerosity 4 (<61 % of “active” trials), and whose activation started increasing later, at numerosity 5. We then went back to the response times of these two groups. As shown in figure 3.5, “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 1 and 6) showed a significant group x number interaction ( $F(5,40) = 2.42$ ;  $p = 0.05$ ). Planned comparisons showed that the two groups did not differ at numerosity 1 ( $p > 0.2$ ), 2 ( $p > 0.2$ ), or 3 ( $p > 0.1$ ), but started to differ at numerosities 4 ( $p < 0.05$ ), 5 ( $p < 0.01$ ) and nearly also at 6 ( $p = 0.08$ ). Thus, the activity in posterior parietal regions predicted for which numerosity subjects start to count.



**Figure 3.5** Variability of strategies from subject to subject and from trial to trial. Left and centre: behavioural results from two subjects showing a sudden increase in response time at 4 and at 5 respectively. Right: response times for early and late subitizers, as classified on the basis of their sudden onset of parietal activity.

For numerosity 4 there was also a large intra-individual variability in RTs, suggesting that the same subject might occasionally use subitizing or counting on different trials. Therefore, we also tested, within subjects, whether the trials with numerosity 4 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 vs. 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 predict whether, on any particular trial, subjects deployed a serial exploration of the display or a parallel apprehension.

## **4. Discussion**

The PET study of subitizing and counting presented in chapter 2, using a block design, showed that a set of parietal, occipital and frontal regions were more involved in counting than in subitizing. 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. Even stronger than behaviour, those regions showed essentially no increase in activation from numerosity 1 to 3, but a sudden increase between numerosity 3 and 4, and a linear increase from 4 on. Our results therefore support a two-process model with distinct operations underlying subitizing and counting.

A trial by trial analysis of the activity in bilateral posterior parietal regions allowed us to reverse the classical logic of functional imaging studies, and to go from brain activity to behaviour, capturing some of the inter-subjects and inter-trial variability in performance on the basis of activation in posterior parietal regions. This analysis suggests that, for a fixed numerosity of 4, subjects sometimes use a subitizing, and sometimes a counting strategy. Such a mixture of two processes may explain why purely behavioural measurement of quantifying time have not offered unambiguous evidence for dissociated processes of subitizing and counting. For instance, analyses of response time distributions do not reveal a sharp discontinuity in quantification performance around 3-4 items (Balakrishnan et al., 1991; Balakrishnan et al., 1992). 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 other domains, for instance to study the single-trial deployment of attention in feature and conjunction search tasks (Corbetta, Shulman, Miezin, & Petersen, 1995).

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 et al., 2001; Simon, Mangin, Cohen, Bihan, & Dehaene, 2002)). In particular, one study showed that the intensity of the activity in all these regions (as measured with the BOLD signal from fMRI) represents a direct measure of the number of saccades performed by subjects in a given interval (Kimmig et al., 2001). In our study, eye movements were prevented by flashing stimuli for 200 ms. Attentional movements, however, are consistent with the hypothesis that counting involves the serial attentional ‘tagging’ of each of the counted items (Trick et al., 1993). Indeed, posterior parietal regions were previously associated with marking of spatial locations (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Gottlieb, Kusunoki, & Goldberg, 1998) and shifting between features (Le, Pardo, & Hu, 1998) or between percepts in binocular rivalry (Lumer, Friston, & Rees, 1998), suggesting that those regions are generally involved in visual selection, possibly even beyond the selection of location (Wojciulik et al., 1999). Additional activation of the anterior insular/inferior prefrontal region in our study may reflect the coordination of this tagging process with the internal recitation of the series of words.

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 therefore their activity simply correlates with response time. This interpretation, however, was refuted by Wojciulik and Kanwisher (Wojciulik et al., 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 response time. Response times increased from 4 to 6, but were quicker with 7 than with 6 items (figure 3.1). Parietal activation, however, increased monotonically from 4 to 7 items (figure 3.3). One possible interpretation is that, on trials with 7 items, subjects often emitted their verbal response through a short-cut process of estimation, based on their knowledge that 7 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

(see chapter 1, §3.3). First, patients with ‘simultanagnosia’ arising from parietal damage, who experience severe difficulties in focusing their attention serially to multiple objects, fail in counting even 4 or 5 items. They frequently miss items or, conversely, may count the same items over and over again. Nevertheless, their ability to subitize 1, 2 or even 3 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 preattentive/attentive dichotomy of subitizing and counting (see chapter 1, §3.2). 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 (Trick & Pylyshyn, 1994; Atkinson et al., 1976b; Atkinson et al., 1976a; Simon, 1996; Oyama, Kikuchi, & Ichiara, 1981), and of perceptual grouping (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") (Trick et al., 1993; Trick et al., 1994). This double dissociation at the behavioural level fits with the hypothesis that subitizing relies on parallel preattentive mechanisms, whose disruption or unavailability beyond 3 or 4 items would force subjects to serially explore the visual array with attention or gaze shifts.

As reported in the first chapter, several models of subitizing have been proposed (see chapter 1, §3.5). The present observations do not allow us to select between those different models but it allows to exclude the validity of one between them, the preverbal counting model proposed by Gallistel and collaborators (Gallistel & Gelman, 1992, 2000). In fact this model defined subitizing as a fast but *serial* estimation process. On the contrary, the absence of increasing activity in attention-related region for quantifying 1-3 items suggests that this process is not carried out serially, but in a parallel fashion. This constitutes a negative, and therefore somewhat weak evidence against such model.

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, since the striate and

extrastriate activation expected given the presence of 1, 2 or 3 dots could not be detected. Further studies will be needed in order to elucidate the nature of subitizing, in order to explore whether it is based on a parallel detection of items, pattern recognition, or estimation of numerosity.

## *Chapter IV*

# *Experiment 3. Exploring the functional correlates of numerosity estimation processes*

### **1. Introduction**

As reviewed in chapter 1, quite a large amount of data has demonstrated that preverbal human infants and animals are capable of discriminating and comparing sets on the basis of their numerosity, suggesting that such ability is not parasitic of the linguistic system. The very few existing behavioural studies using comparable numerosity estimation tasks in the human adults also suggest that such numerosity estimation tasks are performed on the basis of abstract representations which are independent from language. Different behavioural studies using tachistoscopic presentation, and neuropsychological studies investigating brain lesioned patients, seem to point to cortical structure of the right hemisphere, particularly of the parietal lobe, as essential for performing numerosity estimation. The lateralization to the non linguistic hemisphere confirms the non linguistic nature of the numerosity estimation abilities, while the suggested specificity of the parietal lobe points to a possible link with symbolic number manipulation (e.g., exact/approximate calculation, and number comparison) that involve structure of the parietal lobe of the right as well as the left hemisphere. However, a critical review on the methodology used (see chapter 1, §4.3) evidenced the presence of several problems in all such studies, and therefore the need to further explore the neural basis of estimation abilities.

In the present study, we used fMRI to investigate brain responses to a non-symbolic numerosity estimation task, and to compare it to a symbolic exact counting task, using both visual and auditory stimuli. Specifically, the goals were:

- 1) To individuate the functional structures involved in numerosity estimation.

2) To investigate to what extent those structures are independent or specific to the visual or auditory modalities.

3) To compare the functional neuroanatomy of estimation and exact counting, in order to investigate whether brain structures involved in estimation were also always involved in counting, as suggested by some authors (see chapter 1, §2.3).

## 2. Methods and materials

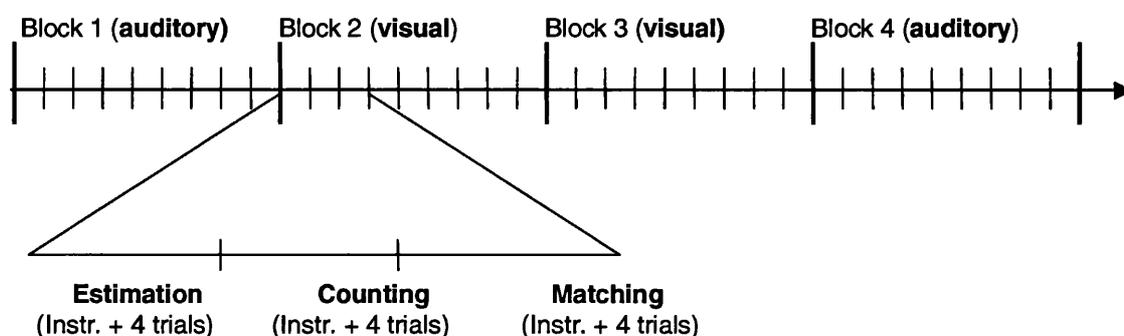
### 2.1- Subjects

Ten, healthy, right-handed volunteers (age 23 to 31, seven males, and three females) gave written consent. The subjects' right handedness was confirmed by means of the Edinburgh inventory. All had normal or corrected-to-normal sight and hear.

### 2.2- Procedure

#### 2.2.1- Design

We used a 2x3 factorial design, with two input modalities (auditory and visual), and three tasks (estimation, counting, and matching). The 25-minute single session experiment was organised into 4 modality specific blocks, presented in a counterbalanced order (Visual-Auditory-Auditory-Visual for 5 subjects and Auditory-Visual-Visual-Auditory for the other 5 subjects). Within each modality block, the three tasks were each repeated three times, and presented in alternating blocks of 4 trials each (see figure 4.1). Each task block was preceded by short instructions. Overall, subjects performed 24 trials for each of the 3 tasks in each input modality, making a total of 144 trials (24 X 2 X 3).



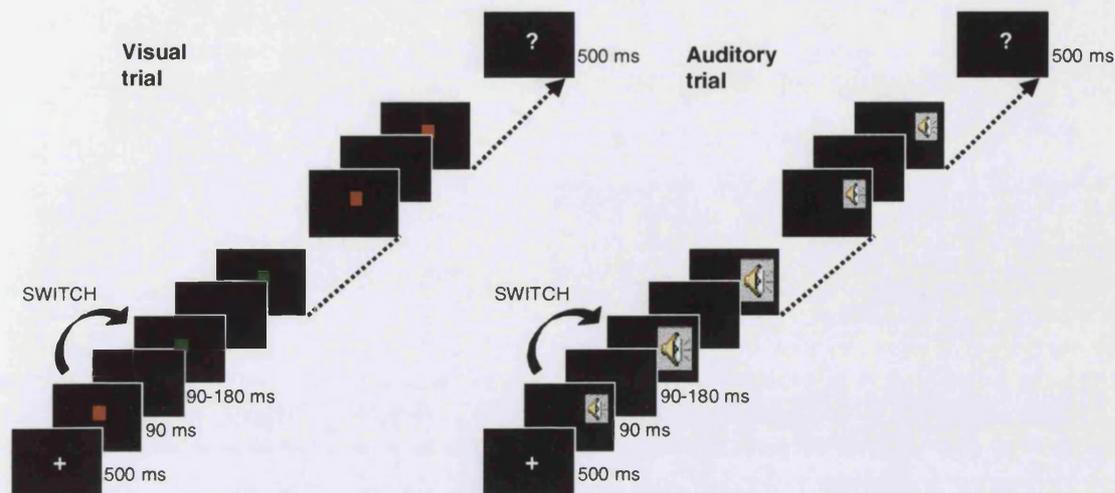
*Figure 4.1 Structure of experiment. The 25-minute single session experiment was organised into 4 modality specific blocks, presented in a counterbalanced order, where*

*stimuli were presented either visually or auditory. Within each modality block, there were three tasks (estimation, counting, matching), each repeated three times and presented in alternating blocks of 4 trials each.*

### **2.2.2- Stimuli**

Stimulation consisted of temporal sequences of two distinct categories of very rapidly presented visual and auditory stimuli. For the visual modality, the stimuli were green and red filled squares (subtending a visual angle of 1.5 deg.) presented one at a time on the centre of a black computer screen. The luminance of the two colours was assigned by averaging subjective equi-luminance values from five volunteers. For the auditory modality, the stimuli were high and low tones (1200 Hz and 400 Hz, respectively) presented binaurally through headphones. The intensity of the two tones was assigned by averaging subjective equi-loudness values (tested over the scanner noise) from five volunteers. The temporal structures of the visual and auditory stimulus sequences were identical. Each stimulus (coloured square or tone) lasted for 90 ms., and the interval between stimuli varied randomly between 90 and 180 ms., so that they were not presented at a constant rhythm. All sequences consisted of 30 stimuli overall, half from each category (i.e., 15 green and 15 red squares for the visual; 15 high and 15 low tones for the auditory). However, the relative clustering of events was manipulated so that 9 stimuli from one category (representing the 60%) appeared in a single "cluster" (i.e., a sequence of 9 identical stimuli), while the remaining 6 stimuli (representing the 40%) alternated with the 15 stimuli (100%) of the other category, grouped in smaller clusters of 2 to 6 items each. Overall, each sequence was made of either 7 or 8 alternated clusters of stimuli. The long cluster of 60% of the stimuli of one category could appear at random times along the sequence.

Figure 4.2 shows a schematic representation of trials in the auditory and in the visual modality. Each trial started with a fixation point that lasted for 500 ms, followed by the stimuli (a sequence of 30 events), that lasted for about 6.5 seconds, and ended with a question mark, after which subjects could give their answer, within 1.5 seconds, via key pressing. Overall, each trial lasted for about 9 seconds.



**Figure 4.2** Schematic representation of trials in the auditory and in the visual modality. Each trial started with a fixation point that lasted for 500 ms, followed by the stimuli (a sequence of 30 events), that lasted for about 6.5 seconds, and ended with a question mark, after which subjects could give their answer, within 1.5 seconds, via key pressing.

### 2.1.3- Tasks

For each of the two modalities there were three tasks, all requiring a two-choice button-press decision with the stimulus sequence held constant across tasks:

**Estimation:** subjects were asked to decide which of the two categories was the more numerous (the green or the red lights for the visual modality; the high or the low tone for the auditory modality). Since the number of stimuli from the two categories was always the same (15) in each sequence, subjects could not base their judgement on the total time taken by each stimulus type. However, as previous studies have shown, we expected the subjects' numerosity judgements to be biased towards the category that show the higher degree of clustering (Erlick, 1961, 1963). Behavioural measures allowed us to determine that subjects were actually paying attention to the numerosity, therefore carrying out the estimation task conscientiously if the pattern of judgements could be predicted by the degree of clustering.

**Counting:** subjects were asked to count (in their head) and decide if there were 6 or 7 switches between the clusters in the sequence (red to green, green to red in the visual sequences, high to low, low to high in the auditory sequence).

**Baseline:** subjects were asked to decide whether the last stimulus in the sequence was identical to the first one. This baseline task was designed to control for attending

the whole stimulus sequence, holding information in working memory for the whole stimulus period, and producing a two-choice button-press final response.

### **2.3- Imaging parameters**

A 2T Siemens VISION system (Siemens, Erlangen, Germany) was used to acquire both T1 anatomical volume images (1x1x1.5 mm voxels) and T2\*-weighted echoplanar images (64x64, 3x3 mm pixels, TE=40 ms) with BOLD contrast. Each echoplanar image comprised 32 axial slices (2.0 mm with a 0.5 mm slice interval, giving a resolution of 2.5 mm). A total of 518 volume images were taken continuously with a repetition time (TR) of 2.974 s/volume, the first six volumes in each session being discarded to allow for T1 equilibration effects.

### **2.4- Image processing and statistical analysis**

Data were analysed with statistical parametrical mapping (SPM99: Wellcome Department of Cognitive Neurology, London, 1999). All volumes from each subject were realigned using the first as reference and re-sliced using sinc. interpolation methods, adjusting for residual motion-related signal changes. A mean image was created using the realigned volumes and the anatomical MRI was co-registered to this mean image. This ensured that the structural and the functional images were spatially aligned. The functional images were spatially normalised to a standard T2\* template in the space of Talairach & Tournoux using non-linear-basis functions. This transformation was also applied to structural T1 volume. Data were then spatially smoothed with a 6 mm full width at half maximum isotropic Gaussian kernel, to compensate for residual variability after spatial normalisation and to permit application of Gaussian random field theory to provide for corrected statistical inference (Friston et al., 1995). A boxcar waveform convolved with a synthetic hemodynamic response function (HRF) was used as the reference waveform for each condition. Differences in global flow within subjects were removed using proportional scaling. The data were high-pass filtered using a set of discrete cosine basis functions with a cut-off period of 512 seconds. To condition temporal autocorrelation in the data, the time series were low-pass filtered using a symmetric HRF as the smoothing kernel.

Both individual and group analyses were performed. For the group analysis, data were analysed using a fixed effects model, in order to address:

#### ***2.4.1- Modality independent effects***

Areas that were more active for estimation than the baseline common for auditory and visual stimuli, were identified by the main effect of estimation > baseline. In addition, to ensure that the areas identified corresponded to increased activation *in each modality separately*, the main effect was inclusively masked with the estimation > baseline contrasts for each modality separately.

Areas that were more active for estimation than counting were identified by the main effect of estimation > counting masked with the simple main effects of (i) estimation > counting and (ii) estimation > baseline for each modality separately.

The same procedure was used to identify the areas involved in counting.

#### ***2.4.2- Modality specific effects: auditory > visual***

Areas that were more active for estimation than the baseline in the auditory modality only, were identified by masking the effect of estimation > baseline in the auditory modality with the modality (auditory > visual) by task (estimation > baseline) interaction. Areas that were more active for estimation than counting in the auditory modality only, were identified by masking the effect of estimation > counting in the auditory modality with (i) estimation > baseline in the auditory, and (ii) the modality (auditory > visual) by task (estimation > counting) interaction. The same procedure was applied to investigate modality specific effect in counting.

#### ***2.4.3- Modality specific effects: visual > auditory***

With the same procedures as in 2, we also identified effects for estimation and counting that were seen in the visual modality only.

For the group analysis, inferences were made at a voxelwise of  $p. < 0.05$ , corrected for multiple comparisons, and with a minimum cluster size threshold of 15 voxels. For each contrast, we also report the number of subjects showing a given effect with a voxelwise threshold at  $p. < 0.001$ , uncorrected for multiple comparisons. Masking was always performed at  $p.<0.001$ .

### **3. Results**

#### **3.1- Behavioural results**

Responses were analysed in terms of percentage correct. In the case of the estimation task, where there was no absolute correct answer (as the number of stimuli

was the same for the two categories of stimuli), correct responses were considered to be those predicted by the clustering manipulation (see Task session). Data confirmed that subjects were attending to numerosity in the estimation task, in that they were systematically influenced by this manipulation: all subjects performed above chance in the direction predicted by the clustering manipulation (ranging from 54% to 79% of “correct” answers). Overall, the answers were predictable by the clustering manipulation for an average of 62% of the trials in the auditory modality, and 65% in the visual modality, and significantly differed from chance ( $\chi^2$  (1d.f.) = 19.8,  $p < 0.001$ ). For the counting task, the percentage correct was 78% in the auditory and 79% in the visual modality. For the matching task, performance was 77% correct in the auditory modality and 80% in the visual modality. A 3x2 (Task x Modality) analysis of variance on error rate showed a main effect of Task ( $F[2,18] = 11.14$ ,  $p < 0.001$ ), indicating that the error rate was lower for the counting and matching tasks with respect to the estimation task. Critically, there was no effect of Modality, confirming that there was no difference between performance in the auditory and visual modality, and no interaction between Task and Modality.

### **3.2- Functional Imaging results**

#### *3.2.1- Modality independent effects*

##### *For Estimation*

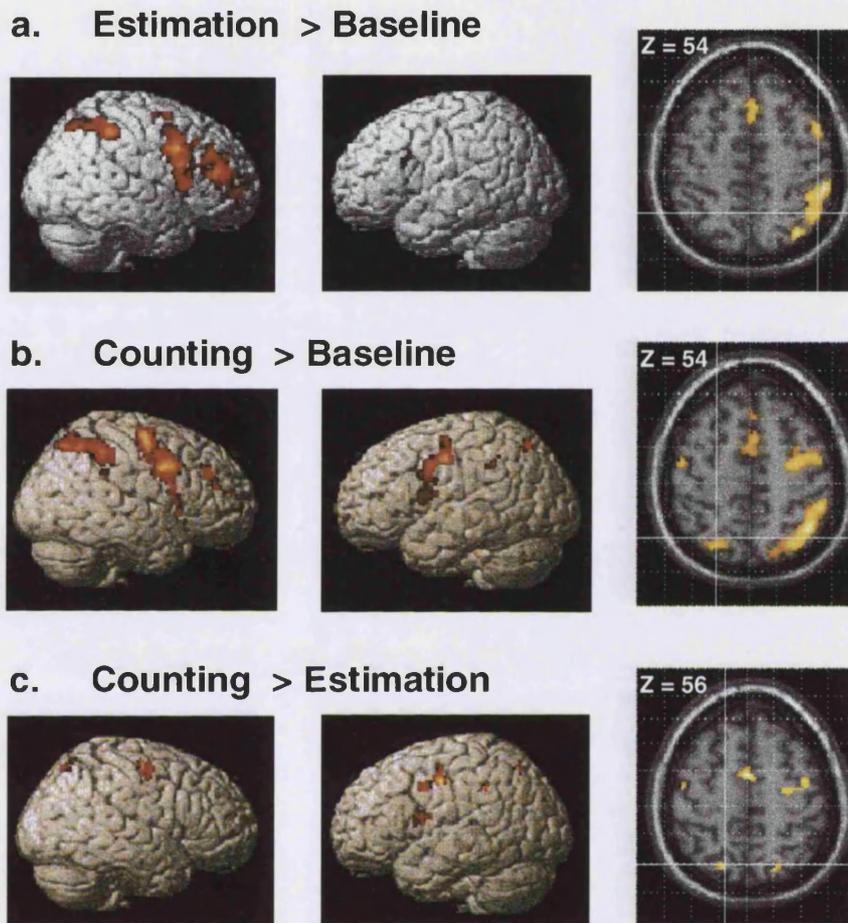
Activation for estimation relative to baseline, common for the two modalities, was almost completely right lateralised. It included a right fronto/parietal network comprising a large part of the intra-parietal sulcus, following all the horizontal segment, the inferior pre-motor cortex, dorsolateral prefrontal cortex extending rostrally to anterior inferior frontal gyrus, and a small area in the middle cingulate gyrus (see table 4, and figure 4.3). The only left hemisphere activation was a small cluster in the left premotor area. No other left hemisphere effects were seen even when the threshold was lowered to  $p < 0.001$  uncorrected.

There were no significant effects for estimation relative to counting.

##### *For Counting*

Activation for counting relative to baseline comprised all the regions involved in estimation. In addition, there was increased activation in (i) the posterior part of the intraparietal sulcus bilaterally; (ii) the left supramarginal gyrus; (iii) bilateral superior lateral and medial premotor cortex; and (iv) the left inferior prefrontal cortex (around

the classical language-related area). These additional effects were confirmed in the contrast of counting > estimation. (see table 6 and figure 4.3).



**Figure 4.3** Cortical regions of increased activation common to visual and auditory modality. Group results ( $n=10$ ,  $p < 0.05$  corrected for multiple comparisons) are visualised on a tree-dimensional rendering showing the left and the right hemisphere, and on a horizontal slice of an individual normalized anatomical image.

	Hemisphere	Estimation>baseline				Counting>baseline				Counting>Estimation									
		Z-scores	x	y	z	Cluster Size	N° subjects	Z-scores	x	y	z	Cluster Size	N° subjects	Z-scores	x	y	z	Cluster Size	N° subjects
<b>Intraparietal sulcus</b>	R																		
Ant. / lateral		>8	<b>56</b>	<b>-36</b>	<b>50</b>	<b>526</b>	<b>8</b>	>8	<b>42</b>	<b>-56</b>	<b>56</b>	<b>892</b>	<b>8</b>						
		>8	52	-42	54				50	-42	54								
Post. / lateral		7.6	44	-56	54			6.75	20	-74	56			7.6	20	-70	56	33	4
Post. / medial		>8	34	-70	54			7.29	28	-64	32				28	-64	32		
<b>Prefrontal Gyrus</b>	R																		
Lateral superior (FEF)		7.2	34	4	62	<b>58</b>	<b>10</b>	>8	28	-6	68								
		6.5	38	-8	64			>8	38	-8	62			7.6	30	-14	50	168	8
								>8	30	-12	58			7.6	42	-6	56		
Lateral middle/inferior		>8	50	10	44			>8	52	4	40	1410	9						
		>8	50	12	22			>8	48	12	20								
<b>Middle frontal gyrus</b>	R																		
Dorso-lateral		>8	50	40	14	1638	8	>8	42	36	32	154	6						
		>8	44	38	32			7.6	48	42	20								
Dorso-lateral Ant.		5.4	36	54	14			6.3	38	56	14								
<b>Cerebellum</b>	R																		
Ant. Cingulate Gyrus		7.2	4	12	56	125	8	6.0	2	14	50								
		6.7	4	22	52			6.5	4	24	52								
		6.0	4	30	40	15	5												
<b>Intraparietal sulcus</b>	L																		
Post. / medial								>8	-24	70	54	92	6	7.7	-16	-68	58	63	6
								7.6	-20	-68	56			7.7	-24	-70	52		
<b>Supramarginal gyrus</b>	L																		
Prefrontal Gyrus	L							7.4	-42	-42	38	63	6	7.2	-42	-40	36	16	6
Lateral middle/inferior		6.3	-56	16	28	23	5	>8	-54	2	40	451	7	>8	-50	-10	44	169	8
								>8	-50	-8	46			7.4	-52	4	40		
								>8	-48	-10	54			7.3	-46	-12	54		
Medial superior (SEF)								>8	-4	-6	64	435	9	>8	-2	-4	62	287	6
								>8	4	6	58			>8	6	-8	64		
<b>Inferior frontal Gyrus</b>	L							>8	-60	0	16	91	9	>8	-60	2	16	50	6
									-60	0	28								
<b>Cerebellum</b>	L							5.9	-32	-66	-34	16	8	6.9					

**Table 6**  
**Coordinates of activation peaks for estimation, counting, and counting> estimation, common to visual and auditory modality. In bold, the activation maxima and their anatomical localisation. FEF = frontal eye fields; SEF = supplementary eye fields.**

# These two are part of the cluster that peaks in the left SEF (comprising 435 voxels).

### *3.2.2- Modality specific effect: auditory > visual*

#### *For Estimation*

There were no significant effects for estimation > baseline or estimation > counting that were specific to the auditory modality.

#### *For Counting*

For counting > baseline two clusters were found in the right superior pre-motor cortex (cluster size=19; x=30, y=-4 z=64; Z=7.1) and left inferior premotor cortex (cluster size=27; x=-56 y=0 z=26; Z=6.6) .

For counting > estimation, small clusters were found in the middle cingulate gyrus (22 voxels at x=-14, y=-16, z=46, Z=6.9) and in the thalamus (16 voxels at x=-12, y=-8, z=-8, Z=5.6).

### *3.2.3- Modality specific effects: visual > auditory*

#### *For Estimation*

For estimation > baseline, activation was detected in the right cerebellar hemisphere (54 voxels at x=46, y=-54, z=-34; Z=7.3) but there were no significant effects specific to the visual modality for estimation > counting.

#### *For Counting*

For counting > baseline, two clusters were detected in the inferior occipito-temporal cortex bilaterally (21 voxels at x=-52, y=-64, x=-12; Z=7.5; and 41 voxels at x=50, y=-70, z=-10; Z=6.3) but there were no significant effects specific to the visual modality for counting > estimation .

## **4. Discussion**

We collected fMRI brain activations of 10 subjects performing a numerosity estimation and a verbal counting, and a perceptual matching tasks, over exactly the same temporal sequences of visual and auditory stimuli.

### **4.1- An amodal right hemisphere circuit for numerosity estimation**

One of the main results of the present study is the identification of a strongly right lateralised fronto-parietal circuit for numerosity estimation, comprising intraparietal, pre-motor and dorso-lateral prefrontal cortex, which is almost completely independent from the modality of presentation of the stimuli. This result confirms

previous studies which suggested a right hemisphere superiority for numerosity estimation (Kimura, 1966; Kosslyn et al., 1989 ; McFie et al., 1950; McGlone & Davidson, 1973; Warrington & James, 1967; Young & Bion, 1979). The absence of consistent activity specific to one or the other modality confirms that a unique system for numerosity estimation acts independently of the modality of stimulus presentation. This was also been indicated by previous behavioural studies that showed identical performance across modality of stimulus presentation and the transfer of numerosity across modality of stimulus presentation in animals and babies (Church & Meck, 1984; Starkey, Spelke, & Gelman, 1990) and more recently also in human adults (Bart, Kanwisher, and Spelke, personal communication). Moreover, the absence of activity in the left hemisphere linguistic areas confirms the non-linguistic nature of numerosity estimation, previously suggested by the fact that non-human animals as well as pre-verbal infants are able to perform similar tasks (Davis & Pérusse, 1988; Gallistel & Gelman, 1992; Starkey & Cooper, 1980).

#### *4.1.1- The functional implementation of the accumulator models for numerosity estimation: a proposal*

What is the nature of the computations performed by the frontal and parietal areas of the right hemisphere? One interpretation is that they reflect the functional implementation of the numerosity-accumulation mechanism previously sketched in the introduction (Dehaene & Changeux, 1993; Meck & Church, 1983). This mechanism can be decomposed into two stages:

- (i) transformation into abstract “oneness” (normalisation)
- (ii) maintenance/update in memory and comparison

During the normalisation stage, each stimulus is transformed into abstract “oneness” by discarding irrelevant physical information like shape, colour, intensity, position in space, duration in time, and so on. For example, in our experiment, information with respect to the shape and position in space of the visual stimuli were irrelevant, and so was information with respect to the duration or direction of the auditory stimuli. This kind of normalisation process is a typical computation that parietal regions perform. Parietal cortex is a high order cortex that receives direct and indirect projections from all sensory regions. It is involved in many tasks that involve attention and coordinates transformation in both spatial and temporal domains (Culham & Kanwisher, 2001; Duhamel, Colby, & Goldberg, 1992; Stricanne, Andersen, &

Mazzoni, 1996). Moreover, numerosity sensitive cell assemblies in animals have been found by electrophysiological recordings from areas that are homologous to parietal regions (Thompson et al., 1970; Sawamura, Shima, & Tanji, 2002). According to the present proposal, then, the process of abstraction of numerosity would primarily be a function of the parietal cortex. After the initial normalisation stage, the second stage consists of continuously accumulating the items in working memory and comparing them. These operations could be seen as emergent properties of the functional connections between parietal and frontal pre-motor and DLPF regions. Fronto-parietal functional loops are not specific for numerosity estimation, but common to a wide range of cognitive operations where the active maintenance of information on line is necessary (Friedman & Goldman-Rakic, 1994; Smith & Jonides, 1999). For example, they are involved in both time and frequency estimation where similar mnemonic and comparative processes are involved (Harrington, Haaland, & Knight, 1998; Roland, Skinhoj, & Lassen, 1981), and generally observed in different types of working memory tasks (Cohen et al., 1997; Jonides et al., 1993 ). Note that this model could also account the recent finding of numerosity tuned cells in the prefrontal cortex of the awake monkey performing a numerosity delayed match-to-sample task (Nieder, Freedman, & Miller, 2002). In fact, it is possible that such activity reflects the maintenance of the numerical information on-line in order to perform the task. This model predicts that number related activity should be first generated in parietal regions, and then be transmitted back and forth between parietal and pre-frontal cortex until the final decision stage is produced. However, the temporal dynamic of such flow of information is probably too fast to be investigated with the time resolution of fMRI. Cooling experiments with monkeys or human EEG/ERPs could be used in order to test such hypothesis.

#### *4.1.2- Numerosity estimation and time estimation*

Influential models of timekeeping and numerosity keeping are very similar, and this is because the psychophysics of numerosity and duration discrimination are themselves very similar (Gallistel & Gelman, 1992; Meck & Church, 1983 ). Indeed, models of numerosity estimation and their version in the timing domain differs only in that the variable to be represented is numerosity in one case, and time in the other. Contrary to the domain of number, many experiments have previously been performed on time estimation: typically, they require subjects to compare and match time intervals.

These experiments converge in highlighting the crucial role of subcortical structures like the basal ganglia and the cerebellum in the representation of time, together with a right lateralised fronto-parietal system attributed to subsidiary functions of the process of accumulation and comparison (Harrington et al., 1998; Macar, Vidal, & Casini, 1999; Malapani, Dubois, Rancurel, & Gibbon, 1998; Rao, Mayer, & Harrington, 2001; Tracy, Faro, Mohamed, Pinsk, & Pinus, 2000). In the present experiment neither basal ganglia nor the cerebellum showed increased activation for numerosity estimation. Does this result imply that representation of time and representation of numerosity rely on different brain systems? This is a plausible possibility that will require further investigation. For example, it would predict that patients with lesions in the cerebellum and/or basal ganglia that show impaired performance in time estimation should be perfectly normal in numerosity estimation tasks. To our knowledge, such comparison has not been performed yet. As proposed earlier, it is possible that the abstraction of numerosity would be a function implemented in intraparietal regions of the right hemisphere. Whether there are specific sub-sets of neurons that are involved in sensitive to numerosity but not to time has not been demonstrated yet. This was not tested in the present experiment, but could be easily testable, for example by directly comparing brain activity during time and numerosity estimation.

#### **4.2- Counting: an attentional and linguistic process**

The brain regions that showed increased activation in counting with respect to the baseline comprised the right fronto-parietal network that was also involved in estimation, with additional activation in posterior intraparietal and superior premotor regions bilaterally, the left supramarginal gyrus, and the left inferior precentral cortex.

Increased *posterior parietal* activation for counting is consistent with previously reported studies where this region is involved in shifting attention (in both space and time) and other visuo-motor tasks like pointing and grasping (Corbetta, 1998 ; Coull & Nobre, 1998 ; Simon, Cohen, Mangin, Bihan, & Dehaene, 2002). In fact, both the process of individuation<sup>3</sup> of each item and the tagging of already counted items, which are necessary for counting, require selective attention, and these processes are impaired after lesions to the posterior parietal areas (Dehaene & Cohen, 1994; Laeng, Kosslyn, Caviness, & Bates, 1999). In the experiment reported in chapter 3 on visual objects

counting, we find peaks of activity in regions that are very close to the one we observe in the present study. Also another previous PET study of counting had reported increased activation in those posterior parietal regions in closely matching voxels (Sathian et al., 1999). Interestingly, stimuli in those two studies consisted in simultaneous visually presented items, and therefore attentional shifts were deployed in space, while in the present experiment stimuli consisted in temporal sequences of both visual and auditory items, requiring therefore attentional shifts in time. This confirms the idea of an attentional system which is deployed in both space and time and localised in posterior parietal regions.

The *left inferior frontal cortex* and the *left supramarginal gyrus* were also more active for counting than for estimation. The inferior frontal gyrus of the left hemisphere is often associated with articulatory processes, and it has been proposed that, together with the left supramarginal gyrus, they constitute a functional network for verbal working memory (Hickok et al., 2000; Paulesu, Frith, & Frackowiak, 1993; Zatorre, Meyer, Gjedde, & Evans, 1996). Specifically, Hickok and Poeppel have proposed that the left supramarginal gyrus acts as an auditory-motor interface in language processing, connecting the left temporal auditory areas to frontal areas for articulatory speech production. The increase in activity of these regions in counting therefore confirms the crucial role of language and in particular of the phonological and articulatory loop in counting that was previously suggested by behavioural studies (Logie & Baddeley, 1987). Interpretation of activation in superior *pre-motor* cortex, *supplementary motor* areas and *cerebellar* hemispheres is not very clear. This motor related system may reflect subvocal articulation during counting or it may reflect finger movement during counting which occurs as a vestige of the learning process, even when no real movement is actually performed, or explicitly imaged. The historical basis of number words in many languages, including English, lies in body-part names, in particular in the names for finger and hand (Menninger, 1969), and it is also a near universal feature of learning both counting and simple arithmetic to use one's fingers (Butterworth, 1999a, 1999b; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). This hypothesis would also be supported by the existence of a neuropsychological syndrome that Gerstmann first described at the beginning of the century (Gerstmann, 1940) in which trouble with

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<sup>3</sup> Individuation is defined as an operation of selective attention that isolates items by "gluing" their features to particular points in space and/or time. When the items are less than four, in the putative "subitizing range", individuation doesn't seem to be necessary.

numbers co-occur with trouble in representing fingers (finger agnosia). An alternative very plausible possibility is that such network, in parallel/synergy with the posterior parietal regions, reflects the deployment of focal attention needed to individuate the items to be counted. Such lateral and medial premotor loci have been also called frontal and supplementary eye fields in light of their role in eye movements and in attentional movements together with posterior parietal regions (Corbetta et al., 1998; Everling & Munoz, 2000; Nobre, 2001).

Note that all these activation loci, including the prefrontal, the inferior frontal, and the posterior parietal, overlap very closely with the loci which activation was modulated by the number of items in our previous fMRI study on counting dots patterns (chapter 2). The fact that the same regions showed increasing activity for the same task (counting) under such completely different experimental conditions (simultaneous vs. sequential, and visual vs. auditory presented objects) constitutes quite a strong proof that we succeeded in individuating the neural correlate of such task.

#### *4.2.1- Always estimate when counting?*

Another finding of the present study is a complete inclusion of the brain regions underlying numerosity estimation in the brain regions underlying counting: the right fronto-parietal cortical circuits for estimation were also recruited for verbal counting, irrespective of modality of stimuli presentation, while estimation does not show regions of increased activation with respect to counting. This result could be interpreted as evidence at the neural level of what was predicted from developmental behavioural studies: counting is simply a more complex version of the pre-verbal quantification system, and recruits additional operations of (i) the attentional system, to locate events in exact spatio-temporal co-ordinates, and (ii) the linguistic system, to attribute number words, in a fixed sequence, to each items of the set. In this view, estimation should always be involved in counting.

In conclusion, in this study we used fMRI to isolate a strongly right lateralised fronto-parietal network of increased activation for numerosity estimation which is independent from the modality (visual or auditory) of stimuli presentation. This result is in agreement with previous neuropsychological results suggesting a right hemisphere superiority for numerosity estimation and reinforces the assumption of an a-modal and non-verbal system for numerosity detection and representation. Results also revealed

that counting recruited additional activity in the left hemisphere (in inferior frontal and supramarginal regions) in posterior parietal and inferior frontal regions bilaterally, thus confirming both its linguistic and attentional nature.

# *Chapter V*

## *General summary and Discussion*

We started this thesis with a review of the literature on quantification processes, and organised it around two still unanswered questions that we tried to later approach:

The first question related to subitizing and counting: the behavioural, neuropsychological, and neuroimaging data available did not allow to disambiguate whether the two processes are qualitatively different, or whether they simply lie on a continuum of difficulty.

The second one related to numerosity estimation. Again, the cognitive and neuropsychological data did not fully reveal the nature of the processes involved, neither their cerebral substrates.

### ***1. On subitizing and counting***

We approached the first question using functional imaging techniques in two steps: first, we investigated whether the two processes of subitizing and counting are implemented in separable regions in the brain using PET. The simple logic behind that study was that a different localisation would be quite a strong support for their dichotomy. Results from this first study indicated that no brain area is specific for subitizing or counting. On the contrary, we found activation in bilateral middle occipital and parietal areas for both subitizing and counting. This activation increases as the number of items in the visual array increases, reaching maximum peak and extent when counting 6-9 arranged items. This failure to measure an anatomical segregation between subitizing and counting, however, does not completely rule out the hypothesis of a different nature of the two processes. In fact, there was still the possibility that the two processes result from a qualitative different involvement of a common set of regions. In that study, due to the constraints of the techniques used (PET), the activity evoked by different numerosities could only be measured in two distinct blocks (numbers 1-4, and numbers above 4). This did not allow investigating whether the regions more active in counting showed a sudden, discontinuous engagement at a specific numerosity or

whether their activity increased linearly with each added item, even within the subitizing range. Moreover, with such block designs, it was not possible to obtain a trial-by-trial measure of the brain activity. Such a measure might be crucial if subjects' reliance on subitizing versus counting is a probabilistic rather than deterministic process and shows a high degree of variability between subjects and trials, even for a fixed numerosity.

Therefore, in a second step, using event related fMRI, we investigated whether the two processes emerge from a qualitatively different recruitment of a set of previously individuated common brain regions. Results revealed that activation in regions of the parietal and prefrontal cortex increase *non linearly* as the number of objects increases. In particular, concentrating on activity of the posterior parietal cortex, we showed that such increase shows a strong discontinuity around the numerosity 3, the putative subitizing range. Activity showed very little or no increase from one to 3 objects, a sudden increase at 4, and a linear constant increase with number beyond 4. These results are in strong support for a qualitative difference between subitizing and counting. We further demonstrated the robustness of such subitizing/counting discontinuity by predicting the numerosity range (subitizing or counting) of the stimuli that subjects were presented at any given trial, by simply looking at the level of activity in such parietal regions. This way of reasoning, reversing the arrow of causality classically oriented from behaviour to brain imaging, has been proven particularly useful in this study. We took this logic further, showing that even at the fixed intermediate numerosity of 4, where often a mixture of subitizing and counting strategies were deployed, we were able to predict the subject's strategy at the single trial level, therefore accounting for some of the otherwise unexplained inter-subject and inter-trial variability in performance.

In conclusion, with these studies on subitizing and counting we demonstrated that they emerge from a qualitatively different recruitment of a set of common brain regions related to both attention and language. While the activity of such cerebral network linearly increases with the number of objects in counting, there is no differential activation of such network with the number of objects in subitizing. Where, in the brain, the difference between a set containing one, two, three, or four items is coded, is still an open question, as we were not able to isolate a region responding differentially to different numerosity in subitizing. Moreover, as presented in the first

chapter, different models of subitizing have been proposed, some suggesting that it reflects a numerosity estimation process, other suggesting that it reflects a preattentive visual routine of grouping and/or pattern recognition. Our experiments do not allow us to select between those different models. More specific experiments should be envisaged in order to clarify the nature of subitizing.

### **1.2- Inferring cognitive processes from brain activation**

In passing, we would like to remark that in our second experiment we used brain activity to shed light on cognitive processes involved in our quantification task, in particular to separate trials where a subitizing-parallel or a counting-serial strategy was used. Such logic of going from brain activity to the cognitive processes, reversing the usual direction of functional imaging experiments, was only very seldom previously applied, for example to infer motor behaviour using fMRI signals from motor cortex (Dehaene et al., 1998) or to separate trials where subjects imagined a face or a house using fMRI signals from the fusiform face area (FFA) and the parahippocampal place area (PPA) (O'Craven & Kanwisher, 2000). Here, we 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-subjects and inter-trial variability in behaviour. In the present thesis such logic was functional to a specific question related to subitizing and counting, but we think that such an approach could (and should) have much broader applications, whenever behavioural data are not sufficient to shed light on the processes underlying a given overt behavioural and/or even covert mental event.

## ***2. On numerosity estimation***

The second question that we wanted to approach in this thesis relates to numerosity estimation. In particular, our knowledge of the critical cerebral regions involved in such processes, and of the nature of the numerosity representation in these regions (i.e., if it is a-modal, or dependent on the modality of stimuli) is still very poor. We approached these questions performing an fMRI study making use of stimuli from different modalities, which subjects had to quantify by either estimation or verbal counting. A perceptual baseline using exactly the same stimuli used in the quantification tasks allowed us to isolate regions involved in estimation, to explore whether they are

independent by stimulus modality or not, and to relate them with regions involved in counting.

Results showed that numerosity estimation relies on a strongly right lateralised fronto-parietal network, and that this activation (mirroring behaviour) is independent of the modality (visual or auditory) of stimuli presentation. This result is in agreement with previous neuropsychological results that had suggested a right hemisphere superiority for numerosity estimation and reinforces the assumption of an a-modal and non-verbal system for numerosity detection and representation. Results also revealed that counting recruited *additional* activity in the left hemisphere (in inferior frontal and supramarginal regions) and in posterior parietal regions bilaterally, thus suggesting a hierarchical relation with estimation and confirming both its linguistic and attentional nature.

## **2.1- Non symbolic numerosity manipulations and symbolic number processing**

If we think of the numerosity estimation system as representing approximate (analogical) numerosities, we can imagine it is also involved in symbolic number processing, especially in tasks that put great emphasis on numerical quantity, as numerals are symbols for numerosity. Indeed, a recent review on different neuroimaging studies of number processes evidenced that regions of the horizontal segment of the intraparietal sulcus, especially of the right hemisphere, are systematically activated whenever numbers are manipulated, independently of number notation, and with increasing activation as the task puts greater emphasis on quantity processing (Dehaene, Piazza, Pinel, and Cohen, 2002). Alone, at present, such results from functional imaging seem to be discrepant with lesion studies of symbolic number processing: in fact, acquired acalculias (resulting in different types of deficits of symbolic calculation) normally result from unilateral parietal lesions to the left hemisphere only (for a review, see van Harskamp & Cipolotti, 2001). However, our admittedly speculative hypothesis that the left lateralised symbolic number system, in normal subjects, works in complete synergy with a right lateralised non-symbolic numerosity system, would resolve such apparent discrepancy. Such hypothesis should be further tested, for example using within-subjects fMRI experiments with high spatial resolution, where each subject would perform both a non symbolic numerosity estimation task and a symbolic number manipulation task like number comparison or

calculation. This would allow us to directly compare regions of increased activation in both processes, and to confirm or disconfirm our hypothesised common, abstract, numerosity specific system.

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# *Annex 1. Scientific Publications*

- The essential of chapter 1 is contained in:

**Piazza, M.** (2002). “Les processus de quantification: subitizing, estimation et dénombrement”, chapter 5; In “*L’arithmétique cognitive*” Traités de Science Cognitive; Hermes, Bruxelles. In press

- The essential of chapter 2 is contained in:

**Piazza, M., Mechelli, A., Butterworth, B. and Price, C.** (2002). Are subitizing and counting implemented as separate or functionally overlapping processes? *NeuroImage*, 15:(2), 435-446.

- The essential of chapter 3 is contained in:

**Piazza, M., Giacomini, LeBihan, D., and Dehaene, S.** (2002). Single-trial classification of parallel pre-attentive and serial attentive processes using fMRI. *Proceedings of the Royal Society of London: Biological Sciences*. In press

- The essential of chapter 4 is contained in:

**Piazza, M., Mechelli, A., Price, C. and Butterworth, B.** (2002). The quantifying brain: functional neuroanatomy of numerosity estimation and counting. Paper under revision in *Journal of Cognitive Neuroscience*.

- The author has also participated in the following publications :

Dehaene, S., **Piazza, M.**, Pinel, P., and Cohen, L, (2002). Three parietal circuits for number processing. *Cognitive Neuropsychology*. In press

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