THÈSE de DOCTORAT de l'UNIVERSITÉ PARIS 6

Spécialité : **Sciences Cognitives**

ÉCOLE DOCTORALE 158 CERVEAU-COGNITION-COMPORTEMENT (Paris)

UNITÉ INSERM-CEA de NEUROIMAGERIE COGNITIVE (Gif/Yvette)

Présentée par

Susannah Kyle REVKIN

Pour obtenir le grade de DOCTEUR de l'UNIVERSITÉ PARIS 6

Sujet de thèse:

INVESTIGATING THE PROCESSES INVOLVED IN SUBITIZING AND NUMERICAL ESTIMATION: A STUDY OF HEALTHY AND BRAIN-DAMAGED SUBJECTS

(Investigation des processus impliqués dans la subitisation et l'estimation numérique: Études de sujets sains et de sujets cérébro-lésés)

Soutenance effectuée le 25 octobre 2007 devant le jury :

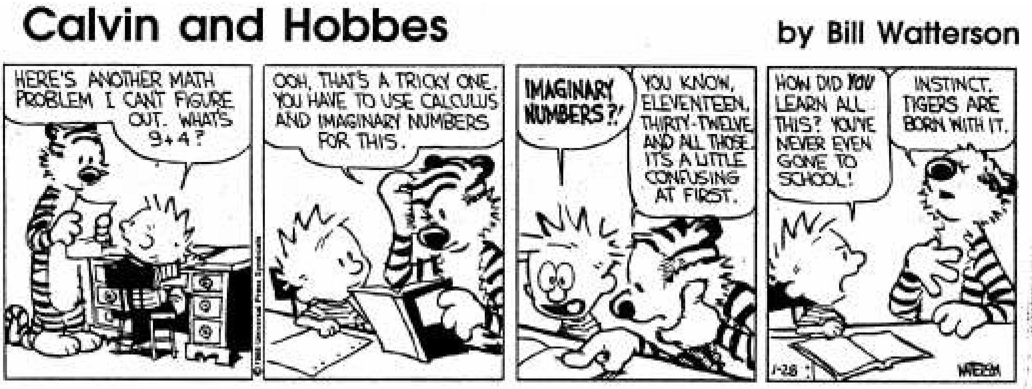
Stanislas DEHAENE Directeur de thèse

Laurent COHEN Codirecteur de thèse

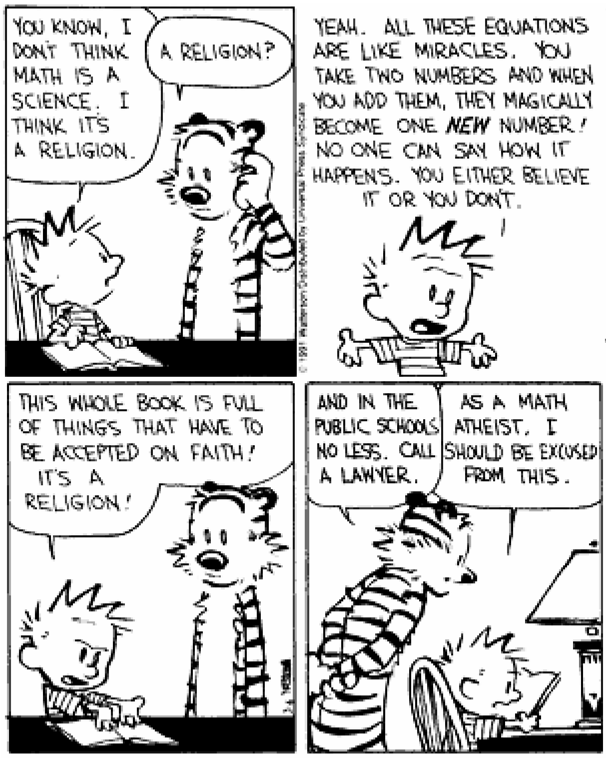
Paolo BARTOLOMEO Président du jury

Marie-Pascale NOËL Rapporteur

Marco ZORZI Rapporteur


Calvin and Hobbes
by Bill Watterson
HERE'S ANOTHER MATH PROBLEM I CAN'T FIGURE OUT. WHAT'S 9+4?
OOH, THAT'S A TRICKY ONE. YOU HAVE TO USE CALCULUS AND IMAGINARY NUMBERS FOR THIS.
IMAGINARY NUMBERS?!
YOU KNOW, ELEVENTEEN, THIRTY-TWELVE AND ALL THOSE. IT'S A LITTLE CONFUSING AT FIRST.
HOW DID YOU LEARN ALL THIS? YOU'VE NEVER EVEN GONE TO SCHOOL!
INSTINCT. TIGERS ARE BORN WITH IT.


TU M'AIDES AVEC MES DEVOIRS? ÇA FAIT QUOI 6+3?
6+3, HEIN? C'EST DIFFICILE.
BON, APPELONS "Y" LA SOLUTION, COMME DANS "Y A UNE SOLUTION?". "Y" DOIT ÊTRE UN NOMBRE CARRÉMENT ENTIER, ALORS DESSINONS UN CARRÉ AVEC 6 D'UN CÔTÉ ET 3 DE L'AUTRE PUIS ON MESURE LA DIAGONALE.
JE ME SOUVIENS PAS QUE LA MAÎTRESSE L'AIT EXPLIQUÉ COMME ÇA.
ELLE NE CONNAÎT PEUT-ÊTRE PAS LES MATHS MODERNES. QUAND TU JOUES AVEC DES CHIFFRES COMPLIQUÉS TU EN AS BESOIN!
MAIS CETTE DIAGONALE FAIT MOINS DE DEUX CENTIMÈTRES.
BON, D'ACCORD, JE DESSINE UN PLUS GRAND CARRÉ.


YOU KNOW, I DON'T THINK MATH IS A SCIENCE. I THINK IT'S A RELIGION.
A RELIGION?
YEAH. ALL THESE EQUATIONS ARE LIKE MIRACLES. YOU TAKE TWO NUMBERS AND WHEN YOU ADD THEM, THEY MAGICALLY BECOME ONE NEW NUMBER! NO ONE CAN SAY HOW IT HAPPENS. YOU EITHER BELIEVE IT OR YOU DON'T.
THIS WHOLE BOOK IS FULL OF THINGS THAT HAVE TO BE ACCEPTED ON FAITH! IT'S A RELIGION!
AND IN THE PUBLIC SCHOOLS NO LESS. CALL A LAWYER.
AS A MATH ATHEIST, I SHOULD BE EXCUSED FROM THIS.

ACKNOWLEDGMENTS

I would like to thank in particular...

Stanislas Dehaene and Laurent Cohen, for their enlightening supervision over these 3 years, for sparking and maintaining my interest for numerical cognition, for their scientific creativity and ingenuity which have been greatly inspiring;

Manuela Piazza, to whom I am extremely grateful for her generous constructive support, advice, encouragements, and supervision;

Patrik Vuilleumier, for welcoming me in the LABoratory of Neurology and Imaging of Cognition (LABNIC) in Geneva, for his enthusiasm, availability and greatly inspiring scientific supervision; the LABNIC team for their warm welcome, in particular, Nadia Lucas, Roland Vocat and Vincent Verdon for sharing office space with me in a friendly atmosphere; the Hôpitaux Universitaires de Genève, for providing me with access to patients;

Margarete Delazer, for welcoming me in the clinical department of neurology of the Innsbruck hospital, for her encouragements, support, positive contagious energy and valuable scientific supervision; the Innsbruck clinical department of neurology team for a welcoming atmosphere full of humour and generosity, in particular, Laura Zamarian and Anja Ischebeck for literally making office space for me and sharing their view on the beautiful Austrian mountains, as well as their scientific expertise and fuel (coffee and sweets); Thomas Benke, Thomas Bodner and Elfriede Karner for sharing their passion for and valuable clinical experience in neuropsychology;

Véronique Izard, whose collaboration was always carried out with great enthusiasm coupled to scientific rigor, and whose examples of ingenious Matlab programming have been of valuable use;

Marie-Pascale Noël and Paolo Bartolomeo, for accepting to be part of the jury and for their helpful scientific advice on on-going work delivered halfway through this PhD; Marco Zorzi for also accepting to be part of the jury;

The members of the U562 lab for their warm welcome, scientific professionalism, relaxed cheerfulness, generous help, advice or enlightening conversations, in particular: Emilie Qiao, for her efficient help in recruiting participants, Joachim Forget, Fabien Vinckier and Philippe Pinel for an introduction to and help with E-Prime; Lionel Naccache and Raphaël Gaillard for advice on masking and general helpful comments on on-going work; Ed Hubbard, for lengthy scientific discussions, advice and encouragements, shared over tasteless (Restau U) or great (Parisian restaurants) food; Anna Wilson for insights into organisational skills and statistical methods gained through my participation in a study on dyscalculia, as well as for her welcoming me when I first arrived in Paris; Marie-Hélène Baju and Laurence Labruna for their administrative help;

The institutional structures INSERM and Hôpital Pitié-Salpêtrière, in which I was able to carry out some of this work; the Pitié-Salpêtrière section of Psychiatrie de l'Enfant et de l'Adolescent, in which Pierre Mazet and David Cohen welcomed me; the Pitié-Salpêtrière Centre de Neuropsychologie et du Langage directed by Bruno Dubois, in which I was welcomed by Dalila Samri and Martine Galipaud who helped me with recruiting patients and organizing their testing; Marie-Thérèse Rigoard and Monique Plaza for warmly welcoming me as an office neighbour at the Psychiatrie de l'Enfant et de l'Adolescent;

The NUMBRA network for its financial and academic support, for the organisation of inspiring summer schools, for its atmosphere of a passionate, professional and welcoming scientific community, for an international experience rich in cultural, collaborative and scientific lessons;

Mark Wexler for his kind last-minute programming of a Python task;

Dominique Boulaine for her extreme kindness and efficiency in recruiting control participants in Paris;

All the patients and control subjects, from Paris, Geneva or Innsbruck, who accepted and took the time to participate in these studies, as well as colleagues and friends who participated as pilot subjects (in particular Lucian Hunziker for his faithful participation);

Last but not least, Christof, my family and my friends for their patience, encouragements, support and help.

OVERVIEW OF THE QUESTIONS ADDRESSED IN THIS WORK

Study of healthy subjects

Does subitizing, the fast and accurate apprehension of visually presented small quantities (1-3 or 4), represent estimation at a high level of precision, or does it reflect use of a separate system dedicated to small numerosities? (**CHAPTER 2**)

Three studies of neurological patients

How independent from visual spatial attention is numerical processing? Subitizing has been shown to be preserved in patients with neglect, a visual attention disorder in which patients do not attend to objects situated (usually) in left visual space, when a competing object is present in right space. Items situated in the neglected (left) field are taken into account when these patients are asked to enumerate up to 4 items, even though they cannot localise them. However, pattern recognition could have been used in this study to recognize the number of items, rather than subitizing. Is subitizing still preserved in neglect patients when items do not represent patterns? Is large numerosity quantification also spared in such patients? (**CHAPTER 3**)

How do we come to know *approximately* how many elements are present in a visual display? Do we go over each element of the visual set one after the other, in a counting-like fashion, or does the extraction of numerosity take all elements into account in parallel? Can it be spared in a patient who has visual attention difficulties that prevent her from counting (simultanagnosia)? (**CHAPTER 4**)

Does numerical estimation rely in part on executive functions, as it requires selecting plausible responses in a context of uncertainty? Does calibration, the adjustment of ones responses to external input (when given an example of the correct response), require executive functions, as one must keep the example in mind, and perhaps strategically compare each new item to the example to derive the approximately correct answer? (**CHAPTER 5**)

TABLE OF CONTENTS

1 CHAPTER 1: GENERAL INTRODUCTION

1.1 A DESCRIPTION OF SUBITIZING AND NUMERICAL ESTIMATION

As our experimental studies will mainly concern subitizing and estimation, we will focus on describing these processes before resituating them in the general context of numerical processing.

1.1.1 Subitizing

Subitizing, which has puzzled several researchers for many years, is the capacity to rapidly and accurately enumerate a small number of items (1-3 or 4). This capacity was documented as early as almost 100 years ago (Bourdon, 1908), and has since been thoroughly investigated, although its underlying processes still remain debated. Subitizing (from the latin “subito” which means suddenly, first coined by Kaufman, Lord, Reese, & Volkmann, 1949), is classically demonstrated when subjects are asked to enumerate visual sets of items, ranging for example from 1-7, as accurately and as fast as possible. In this case, responses times show a discontinuity between 3 and 4 (or 4 and 5), as there is very little increase in the 1-3 or 4 range (about 50ms/item) and much more for each additional item beyond this range (about 200-400ms/item) (e.g. Trick & Pylyshyn, 1994; Mandler & Shebo, 1982; Chi & Klahr, 1975).

Researchers have proposed that this reflects a distinction between two processes: the first, subitizing, would operate over the 1-3 or 4 range, whereas counting would be used for larger numerosities[1]. The dissociation between the subitizing and counting ranges has also been shown with paradigms where presentation is brief, and sometimes also masked, leading to a discontinuity also in response accuracy, as estimation or faulty counting takes over outside the subitizing range (e.g. Bourdon, 1908; Oyama, Kikuchi, & Ichihara, 1981; Mandler & Shebo, 1982; Green & Bavelier, 2003; Green & Bavelier, 2006) (see Figure 1-1).

[1] Subitizing, when it was first termed, was thought to extend to 6 items (Kaufman et al., 1949); however later studies showed that counting occurs already at 4 or 5 items.

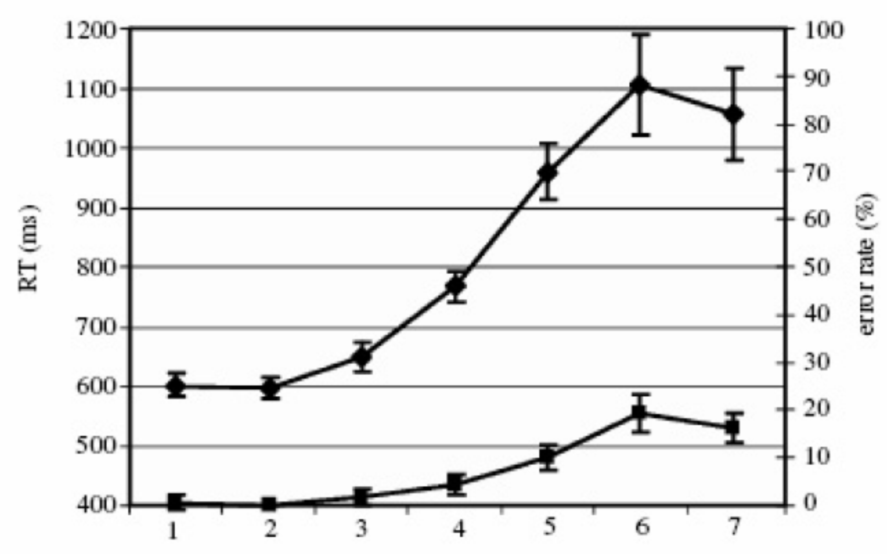


Figure 1-1 Mean reaction times and error rates in an enumeration task with brief stimuli presentation (diamonds: reaction times: squares: error rates). Both measures show an advantage for small numerosities (1-3) which is thought to reflect us of a separate process in this range, namely subitizing. Reproduced from Piazza, Giacomini, Le Bihan, & Dehaene, 2003.

Importantly, some studies have shown that subitizing occurs independently of ocular movements, as subjects are able to subitize even when presentation duration is too short to allow for saccades or when stimuli are presented as afterimages (Atkinson, Campbell, & Francis, 1976a; Atkinson, Francis, & Campbell, 1976b; Simon & Vaishnavi, 1996); in contrast, these modes of presentation affect performance in the counting range. Moreover, another manipulation of the stimuli presentation (cueing the area where items to be enumerated are going to appear) showed that subitizing did not require attentional focus, whereas counting does (Trick & Pylyshyn, 1993). These findings strengthen the idea that subitizing and counting are two dissociable processes (but, for studies suggesting a single enumeration process, see Balakrishnan & Ashby, 1991; Balakrishnan & Ashby, 1992).

1.1.2 Numerical estimation

When one is presented with a large number of items, two processes can be used to determine how many there are: counting or estimation. Although counting can be exact, it is slow and becomes error-prone when there are a lot of items to be counted, especially if they are arranged randomly, rather than in a line for example. In contrast, estimation is approximate, and can be used more quickly than counting with large numerosities. When estimating a set of numerosities presented each several times, performance follows a particular pattern. Indeed, mean response may be quite close to the correct answer, although there is variability in response. Numerical estimation judgments become less precise as numerosity increases: the variability in responses increases proportionally to the increase in mean response, a characteristic which is referred to as *scalar variability*, a signature of estimation processes, whether non-verbal (e.g. tapping on a lever a certain number of times; see Figure 1-2, top panel) or verbal (e.g. giving a verbal estimate of a set of dots) (Gallistel & Gelman, 1992; Whalen, Gallistel, & Gelman, 1999; Cordes, Gelman, Gallistel, & Whalen, 2001; Izard & Dehaene, in press).

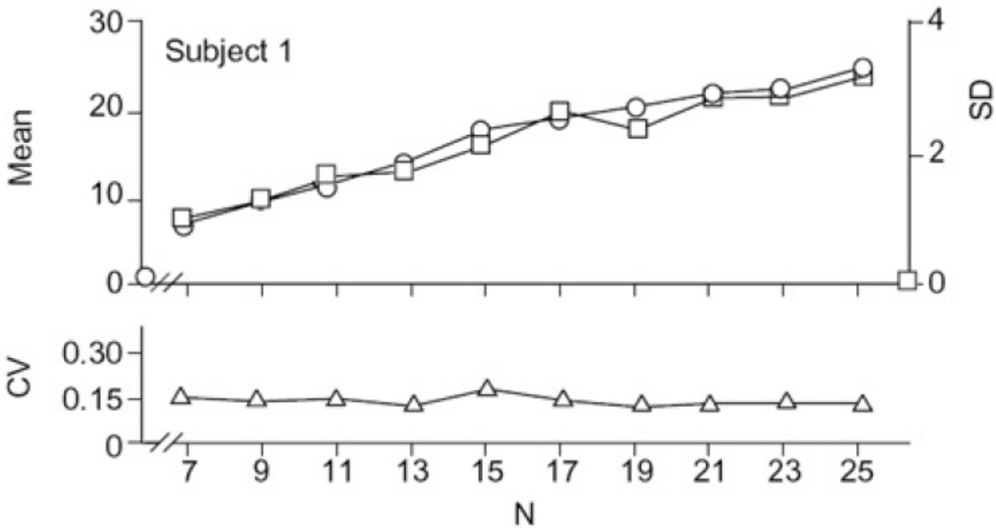


Figure 1-2 (**Top panel**) A subject's mean response (left axis) and variability in responses (standard deviation, SD, right axis) during a non-verbal estimation task. Adult subjects were instructed to press a button as many times as a given numerosity (N), without counting. Mean response increased as numerosity increased, and variability in responses (SD) increased proportionally. (**Bottom panel**) This resulted in a stable variation coefficient (CV) across presented numerosities. Data from Whalen et al., 1999, graph reproduced from Gallistel & Gelman, 2000.

This has been linked to Weber's law, which governs discrimination of numerosity, but also of other perceptual variables (weight, brightness, sound, etc.). Weber's law accounts for the fact that discrimination of two sets of numerosities becomes harder as the numerical distance between the sets decreases (*distance effect*). Also, at an equivalent numerical distance between the sets, increasing the numerosity of the sets also makes it more difficult (*size effect*). Discrimination of two quantities is thus proportional to their ratio. This is thought to reflect characteristics of the underlying representation of numerosity: representation of small numerosities would be more precise than larger ones: there would be an increase in overlap of numerosity representation as numerosity increases (e.g. Dehaene, 2007). This accounts for the distance and size effects: the larger the distance between the sets of numerosities to be compared, the less overlap, and the smaller the sets are, the less overlap. It also explains scalar variability: responses would become less precise as numerosity increases because there would be an increase in overlap of underlying representations. As mentioned before, scalar variability is reflected by a *proportional* increase in response variability, as presented numerosity (and mean response) increases: this yield a stable *variation coefficient* (standard deviation of mean response/mean response) across numerosities (see Figure 1-2, bottom panel; Whalen et al., 1999; Izard & Dehaene, in press). Mean variation coefficient across numerosities is thought to give an indication of the overall precision of the underlying representation (Dehaene, 2007).

Although subjects' estimation is coherent, there can be tendencies, as numerosities get larger, either to underestimate or overestimate (both tendencies: Minturn & Reese, 1951; underestimation: Izard & Dehaene, in press). This can however be countered by external calibration, that is, by giving the correct answer after subjects' responses or by showing an example of a correct estimate, bringing mean responses much closer to the correct response (Minturn & Reese, 1951; Izard & Dehaene, in press). External calibration using just one example has been shown to affect the whole range of numerosities in estimation of visually presented numerosities (Izard & Dehaene, in press). Its effect has also been shown to last for at least 8 months (Minturn & Reese, 1951).

As mentioned above, other non-numerical perceptual variables also lead to performance which obeys Weber's law. In fact, some of these variables co-vary with numerosity in most cases. For example, the area occupied by a set of dots gets bigger as numerosity increases (and concurrently, if using white dots on a black background, luminosity also increases); in this case, the size of the occupied area (or luminosity) may be used, instead of numerosity per se, to estimate numerical quantity. Other variables, such as dot density or dot size may also be used (e.g. if area is held constant, density will increase concurrently with numerosity, or dot size will decrease concurrently). In contrast to earlier studies of numerosity, many studies now carefully control for these confounds, for example by intermixing sets where area is held constant and with sets where density is held constant, to force subjects to estimate numerosity and not these other variables, or at least to be able to tell if they are using them rather than numerosity. Finally, some studies have showed influence of some of these variables, or of presentation configuration on estimates of numerosity. For example, regular patterns of dots are judged more numerous than random patterns (Ginsburg, 1976; Ginsburg, 1978; Ginsburg, 1991), which are themselves judged more numerous than clusters of dots (Ginsburg, 1991); estimates increase with increases of stimulus duration (Krishna & Raghubir, 1997); dense arrays are judged less numerous (Hollingsworth, Simmons, Coates, & Cross, 1991).

1.2 NUMEROSITY PROCESSING IN HUMAN ADULTS

In addition to subitizing and estimation described above, human adults possess a wide range of numerical capacities. We will now present an overview of some of these, as well as different studies showing their disruption in brain-damaged patients, anatomical correlates as revealed by imaging studies, and an anatomical model of numerosity processing in the parietal lobe.

1.2.1 Processing involving non-symbolic stimuli

In addition to subitizing and estimation, other processes involving non-symbolic stimuli (sets of dots, sounds, etc., rather than Arabic digits or number words) have been studied in adults. For example, paradigms presenting three successive sets of fairly large quantities of dots have been used to test addition of non-symbolic stimuli (subjects had to compare the quantity of the two first sets, taken together, to the third set). In summary, it has been shown that adults are capable of comparing, adding, or subtracting large quantities of non-symbolic stimuli, both presented visually (Lemer, Dehaene, Spelke, & Cohen, 2003; Pica, Lemer, Izard, & Dehaene, 2004; Barth et al., 2006), or in a cross-modal design (visual and auditory) (comparison: Barth, Kanwisher, & Spelke, 2003; comparison and addition: Barth et al., 2006). Moreover, no difference was found between conditions where stimuli were presented simultaneously or sequentially (Barth et al., 2003). In all studies, results conformed to Weber’s law, showing a ratio effect on comparison performance, whether it involved an arithmetic operation or not.

1.2.2 Mapping from quantity to symbols and back

Numerical quantity is referred to by a variety of symbols, ranging from Arabic digits (e.g. “5”), Roman numbers (“V”), to number-words (“five”; spoken or written). As we will see below in the section devoted to numerosity processing in infants and children, mapping from a given quantity to the corresponding symbol is a process which children must learn through counting. As we saw above concerning estimation in adults, it is a process which is still not evident, as adults have difficulties calibrating their verbal estimates without external input (as they show over- or underestimation with larger numerosities prior to external calibration).

Different adult studies have helped characterize the mapping from symbols to the underlying quantity, suggesting the link in this direction is very strong. For example, when subjects are asked to compare two digits and indicate which one represents the larger quantity, their reaction times show distance and size effects, just as when they are asked to compared non-symbolic quantities (Moyer & Landauer, 1967). This effect is also present when 2-digit numbers are used (Dehaene, Dupoux, & Mehler, 1990). Also, when the task consists in comparing digits according to their physical size, and subjects have to ignore numerical values, these interfere with their judgments, as response times are slower when numerical value and physical size are incongruent (for example comparing a physically big “5” with a physically smaller “9”) (Henik & Tzelgov, 1982). These studies show that access to numerical quantity from symbols is automatic in adults.

One study involving Arabic digits brought more insight about the underlying representation of numerosity (Dehaene, Bossini, & Giraux, 1993): subjects were asked to judge the parity of a given Arabic digit by pressing a left button if the digit was odd, and a right button if it was even. For another group of subjects, instructions were reversed (press the left button if the digit is even, and the right button if it is odd). An unexpected finding was than smaller digits were responded to faster with the left button, and larger digits with the right button. The authors named this effect the SNARC effect (Spatial-Numerical Association of Response Codes), and proposed that numerical quantities were represented on a number line which was oriented from left to right. Small numbers would therefore be associated with left space, and larger ones with right space (for a recent review on the associations between numbers and space, see Hubbard, Piazza, Pinel, & Dehaene, 2005). Moreover, this spatial-numerical association was replicated with spoken words and written number words (Nuerk, Wood, & Willmes, 2005). These findings suggest an automatic access to an amodal underlying numerical representation.

But how do we know that the underlying numerical representation is not shaped from years of learning, applying and manipulating numerical symbols? For example, it was suggested that the left to right orientation of the number line was linked to cultural factors: indeed, in subjects from cultures where one reads from right to left, and who have not been exposed to occidental culture, or very little, the SNARC effect is reversed (Dehaene et al., 1993). Are other characteristics of the number line dependent on exposure to language and education? Are adults’ capacities to apprehend and manipulate non-symbolic stimuli a consequence of use and manipulation of number words and Arabic digits (enumeration, calculation, algebra)? In other words, do basic numerical skills emerge from language? We will see below that evidence from non-human animal studies, and pre-verbal infants suggest the opposite. Additional evidence concerning the importance of language comes from the study of populations who have a small number lexicon. For example, the Mundurukù only have number words 1 to 5. For larger quantities, quantifiers such as “some” or “really many” are used. Moreover, this population has not been exposed to mathematical education, and does not possess a robust counting routine. Yet, the Mundurukù are able to perform approximate numerical additions and subtractions on quantities exceeding their numerical lexicon, presented as sets of dots (Pica et al., 2004). However, they fail at exact computations, even when the result falls within the range of their lexicon, suggesting that language (and in particular a counting routine) is important for exact computations, but not for approximate manipulation of numerosity (Pica et al., 2004). Additional evidence for approximate apprehension of non-symbolic numerosity without the corresponding number lexicon was provided by the study of another population, the Pirahãs, who, in a numerosity reproduction task, presented responses of increasing variability as the given numerosity increased (Gordon, 2004). Recently, the Mundurukù have also been shown to present understanding of basic geometrical concepts which may constitute foundations to more complex geometrical capacities in educated adults (Dehaene, Izard, Pica, & Spelke, 2006).

1.2.3 Neuropsychological patients

Neuropsychological double-dissociations are usually considered as strong evidence that two processes are independent. As regards subitizing, one developmental dyscalculic patient (Charles) was initially reported as presenting a deficit in subitizing, as counting (which was intact) was used in the subitizing range and above (Butterworth, 1999). The opposite dissociation was found in a few patients presenting a deficit in serial visual attention (simultanagnosia) which affected counting but not so much subitizing (Dehaene & Cohen, 1994). These two dissociations (impaired subitizing and preserved counting; preserved subitizing and impaired counting) taken together constitute a double dissociation. However, it was later established that Charles was able to subitize, as he had initially been counting in the subitizing range because of a lack of confidence in his responses; when stimuli were flashed at 100ms, and counting was therefore discouraged, Charles’ performance showed a discontinuity between subitizing and counting ranges. Another patient, with severe acquired acalculia, was reported as counting in the subitizing range (Cipolotti, Butterworth, & Denes, 1991), but as she was not able to recall (and therefore count) numbers above 4, it is difficult to conclude in a subitizing/counting dissociation in this patient. Finally, another patient, LEC, presented cerebral sequelae of hemorrage in the left intraparietal cortex, and, on the behavioral level, a complete Gerstmann's syndrome (Lemer et al., 2003). This syndrome is characterized by the association of four disorders: acalculia, agraphia without alexia, finger agnosia, and left-right disorientation (Gerstmann, 1940), and is generally found following damage to the left inferior parietal lobule (Cohen, Wilson, Izard, & Dehaene, 2007). LEC presented a deficit in subitizing, but also a general slowing of counting (Lemer et al., 2003). Unlike Charles, the subitizing deficit was present in an unlimited enumeration task (increase of about 540 ms per item from 1 to 3 items) but also when the dots were flashed to prevent counting (errors even in the subitizing range). However, counting was not completely preserved in this patient, as she was much slower than controls. In sum, the neuropsychological data does not bring very solid evidence in support of the dissociation between subitizing and counting which is clearer in behavioral performance in healthy subjects.

Subitizing has been shown to be preserved in patients presenting visual extinction, who present difficulties in attending to items situated in the space contralateral to their cerebral lesion (usually left space following right parietal damage) while another competing stimulus is present in the ipsilateral space (Vuilleumier & Rafal, 1999, Vuilleumier & Rafal, 2000). Taken together with the finding that subitizing is preserved in patients with simultanagnosia (Dehaene & Cohen, 1994), both these findings suggest that subitizing does not require visual attention, and therefore argue in favor of a parallel view of subitizing.

Studies of numerical estimation (using a task in which subjects are to give a verbal estimate of the quantity of a set of items) in neuropsychology patients are sparse. A first group study reported estimation impairment in patients with right parietal damage as opposed to patients with temporal or left parietal damage (Warrington & James, 1967). A second study reported a deficit in one patient with posterior cortical atrophy (bilateral parietal atrophy), in the context of general deficits in numerical processing, reflecting a semantic impairment in the numerical domain (Delazer, Karner, Zamarian, Donnemiller, & Benke, 2006). Finally, a third study presented a patient with visual agnosia following large left parietal, temporal and occipital, right temporo-occipital, and frontal lesions; in this case, estimation and numerical processing in general was clearly spared (Pesenti, Thioux, Samson, Bruyer, & Seron, 2000). These three studies suggest a role of the parietal structures, in particular the right parietal lobe, in numerical estimation. However, it is important to note that none of these studies controlled for co-varying non-numerical parameters in the visual displays that were used, making it difficult to ensure that *numerical* estimation was really measured in these patients.

As concerns other numerical processes involving non-symbolic stimuli, such as comparison or addition of clouds of dots, a study with controls for co-varying non-numerical parameters has reported impairment of theses processes in one patient, LEC, described above (Lemer et al., 2003). In addition to a deficit in non-symbolic numerical processing, she was impaired in some tasks involving symbolic stimuli. She presented deficits in subtraction and division, while multiplication and addition were relatively spared. She was also impaired in approximate addition but not in exact addition (with single digits). In fact, she reported not being able to pick the most approximately correct answer from two false solutions to addition problems presented with Arabic digits: rather, she reported always having to calculate the correct answer and compare it to the two possible responses to accomplish the task. Finally, she was also impaired in approximate comparison and approximate addition of two-digit Arabic numerals (corresponding to the same quantities and problems tested in the non-symbolic tasks). It was concluded that LEC presented a core deficit in numerical quantity processing.

This pattern of performance contrasted greatly with that of another patient, BRI, who presented frontal and temporal atrophy predominating in the left hemisphere, in the context of semantic dementia (Lemer et al., 2003). BRI performed as well as controls in the non-symbolic tasks (except she was generally slower); she also presented the opposite dissociations as LEC in the tasks involving symbolic stimuli, as subtraction was overall intact whereas multiplication was severely impaired; single-digit exact addition was impaired but not approximate addition; finally, approximate comparison and addition of two-digit numerals was preserved (although generally slower). It was concluded that this patient presented general sparing of quantity-based numerical processing, and impairment in numerical processes involving a verbal component.

As regards the first level of the double dissociation that these two patients constitute (core quantity-based processing vs. semantic knowledge), the dissociation between an intact numerical quantity system (coupled to intact parietal regions) and degraded other semantic categories (usually linked to verbal processes and thought to be sub-served by fronto-temporal structures) has been reported in several other studies (Cappelletti, Butterworth, & Kopelman, 2001; Butterworth, Cappelletti, & Kopelman, 2001; Thioux *et al.*, 1998; Zamarian, Karner, Benke, Donnemiller, & Delazer, 2006). Conversely, other patients than LEC have been found to have quantity-based numerical deficits (although these studies mainly used symbolic stimuli) with sparing of general semantic abilities (Dehaene & Cohen, 1997; Delazer & Benke, 1997; Delazer et al., 2006). This double dissociation suggests that quantity-based numerical processing represents a separate semantic category which is sub-served by the parietal lobes.

The second level of this double-dissociation concerns a distinction between two numerical tasks, subtraction and multiplication (both solved by mental calculation, not written). Multiplication is thought to strongly engage verbal processes. For example, multiplication tables are usually leaned by rote, and are thought to be solved by retrieving facts from verbal memory (Ashcraft, 1992), with no reference to numerical quantity. In contrast, subtractions are not memorized as tables in school, and therefore must be reached through online computation, requiring quantity-based processing. Addition can be solved either by accessing memorized facts, or by computation, and therefore is less likely to lead to a clear dissociation. As for divisions, the picture is also less clear, as they can be solved by applying different strategies, such as searching for the corresponding multiplication problem. Similarly to patient LEC, other patients have shown poorer performance in subtraction than in multiplication, associated with impairment in core quantity-based processing (as mentioned above: Dehaene & Cohen, 1997; Delazer & Benke, 1997; Delazer et al., 2006). Patients such as BRI showing the other dissociation in arithmetic operations have also been reported, usually also in the context of verbal deficits (Dagenbach & McCloskey, 1992; Pesenti, Seron, & van der Linden, 1994; Cohen & Dehaene, 2000).

Other numerical processes can be disrupted following cerebral damage, but which would not be due to a core quantity-based deficit, or to verbal processes. For example, some patients presented an intriguing deficit in association with visual neglect (a deficit related to visual extinction, in which items in the neglected, usually left, space are not acknowledged, even without a competing right stimulus) (Zorzi, Priftis, & Umilta, 2002). These patients were asked to perform a number bisection task: when presented with two spoken numbers, they had to find the number which fell exactly in the middle, without calculating (e.g.: “eleven” and “nineteen”; correct answer: “fifteen”). Their answers showed a clear deviation from the correct answer (“seventeen”, for the example mentioned above). The deviation pattern was related to the size of the numerical interval: it was deviated towards numbers larger that the correct response, increasingly so as the interval size increased, and was reversed (toward numbers smaller than the correct response; cross-over effect) for smaller intervals. This mirrored the rightward deviation and cross-over effect that these patients typically show when asked to bisect physical lines of varying length. It was therefore suggested that their impairment in the number bisection task reflected a deficit in orienting on the number line.

Finally, other numerical abilities such as transcoding (reading or writing Arabic numerals or number words), written calculation or conceptual numerical knowledge can be impaired in brain-damaged patients. We will however not discuss these here (for a recent review of numerical impairments following brain damage, see Cohen et al., 2007).

1.2.4 Anatomical correlates

Two studies investigating the anatomical correlates of subitizing and counting found no evidence of a difference between the cerebral areas involved in these two processes, which constituted a bilateral occipito-fronto-parietal network (Piazza et al., 2003; Piazza, Mechelli, Butterworth, & Price, 2002). However, these studies provided evidence for a stronger recruitment of this network in counting, compared to subitizing, showing a strikingly abrupt increase in activation between the subitizing and counting ranges. Moreover, a trial-by-trial analysis of activation in the bilateral posterior parietal regions allowed to predict whether subjects had subitized or counted a fixed number of items at the limit of the subitizing range (4): when the network was less recruited, subjects' behavioral data showed subitizing, and when there was a larger recruitment, behavioral data indicated that the 4 items had been counted (Piazza et al., 2003).

Piazza and collaborators also investigated estimation of non-symbolic quantities, using a comparison task (therefore obtaining a non-verbal response), presenting stimuli sequentially, both in the visual and auditory modalities (Piazza, Mechelli, Price, & Butterworth, 2006). This study revealed a right-lateralized fronto-parietal network for estimation, suggesting independence from areas involved in language processing; moreover, activation of the network was similar across modalities, underlining the abstract property of the estimation process. Additionally, activation during estimation was contrasted to that occurring during verbal counting, which revealed that the later recruited additional bilateral posterior parietal regions, and left hemispheric regions involved in language processing, again independently of stimulus modality (Piazza et al., 2006).

Other processes involving non-symbolic stimuli have also been investigated in imaging studies. Even the simple viewing of non-symbolic stimuli (sets of dots) has been studied and has shown to activate parietal areas bilaterally (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Cantlon, Brannon, Carter, & Pelphrey, 2006; but see Shuman & Kanwisher, 2004). Importantly, this paradigm showed that activity in the intra-parietal sulcus (IPS) was modulated by numerical quantity, following Weber's law. Indeed, after presenting a sequence of arrays all containing the same numerosity (habituation), a numerosity was presented (deviant) which varied according to its numerical distance from the habituation numerosity. Activation in the IPS during deviant presentation differed according to the numerical distance between the habituation and the deviant numerosities, increasing as distance increased. This suggests that the IPS sub-serves representation of numerosity. Other studies have converged to show the importance of the IPS, in particular of its horizontal segement (hIPS), in representation of numerosity. Importantly, in keeping with the strong link described above from symbols to quantities, this region has (in fact, initially) been shown to be systematically recruited when numerical tasks involve symbols rather than non-symbolic stimuli. For example, it is activated during different tasks involving Arabic digits: comparison (Pinel, Dehaene, Riviere, & LeBihan, 2001), addition (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999), and subtraction (Chochon, Cohen, van de Moortele, & Dehaene, 1999). Activity of the hIPS is modulated by numerical distance, even as presented with Arabic digits (e.g. Pinel et al., 2001; Piazza, Pinel, Le Bihan, & Dehaene, 2007), or with cross-notation stimuli (dots as habituation stimuli and digit as deviant, and vice-versa: Piazza et al., 2007). Activity of this area has also been found to depend on other variables which are thought to reflect the intensity of the recruitment of basic numerical capacities, as opposed to language- or education dependent abilities. For example, it is more activated during subtraction as opposed to comparison of digits, therefore showing a higher activation as the task becomes more difficult and recruits more quantity-based processing (Chochon et al., 1999); it is more activated in approximate than exact addition (Dehaene et al., 1999; however, this was not replicated: Venkatraman, Ansari, & Chee, 2005 ; Molko *et al.*, 2003); it is activated in subtraction but not in multiplication (Lee, 2000). The dissociation of activation between arithmetic operations (subtraction and multiplication) converges with the patient data. Multiplication has been shown to activate the left angular gyrus, linking it to language processing which occurs in the left hemisphere (Chochon et al., 1999 ; Lee, 2000). Also, a study investigating areas involved in learning complex multiplication facts showed that activation shifted from the hIPS to the left angular gyrus when comparing untrained problems with trained problems (matched for difficulty), suggesting that the former required quantity-based processing but that the later were solved thought more automatic fact retrieval (Delazer *et al.*, 2003). Another study replicated this and additionally showed that this shift was not present when subtractions were learned, again underlining the difference between these two tasks (Ischebeck *et al.*, 2006).

Finally, as regards the fact that numerosity often co-varies with other non-numerical continuous parameters, a study comparing activations during numerical, physical size, and luminosity comparisons showed that there was overlap in activation during these three tasks in the bilateral anterior IPS and in bilateral occipito-temporal regions (Pinel, Piazza, Le Bihan, & Dehaene, 2004). Using a Stroop paradigm, it showed that both behavioral interference effects and corresponding activation patterns suggested overlapping representation of numerical and physical size (anterior hIPS), but not of numerosity and luminosity (however, see Cohen Kadosh, Kadosh, & Henik, 2007); and overlapping representation of size and luminosity (in bilateral occipito-temporal and posterior intraparietal regions). However, this does not necessarily mean that the same neurons code for both numerosity and physical size, as the spatial resolution of functional magnetic resonance imaging (fMRI) is not high enough to observe the single neuronal level. Rather, it could be that populations of neurons sensitive to numerosity are intermingled with other neurons tuned to physical size, within the same parietal region.

1.2.5 Three parietal circuits

The convergence of different studies in adults (including neuropsychology and imaging studies) has been synthesized by a review article, proposing three parietal circuits of numerosity processing (see Figure 1-3; Dehaene, Piazza, Pinel, & Cohen, 2003).

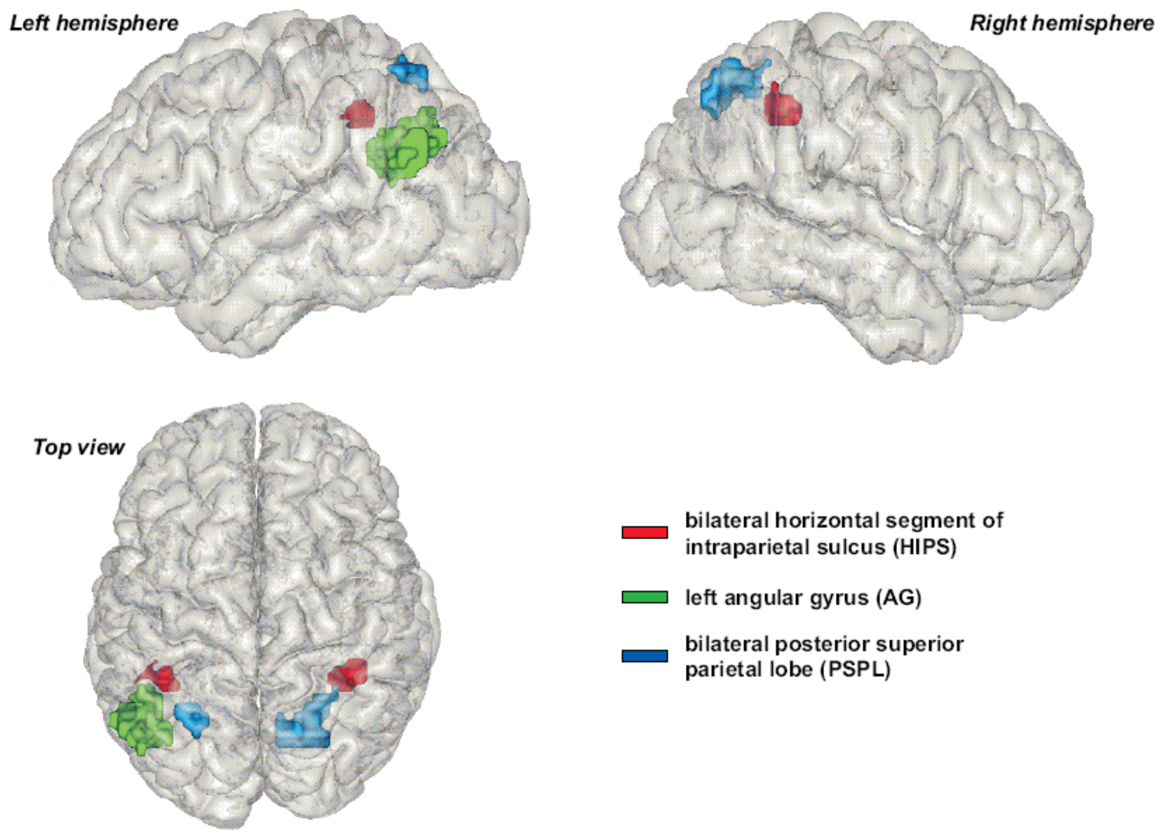


Figure 1-3 Three parietal circuits for number processing were determined by a meta-analysis of fMRI activation studies (intersection of activations clusters). Reproduced from Dehaene et al., 2003.

In sum, the hIPS has been shown to be involved in quantity-based processing, whether recruited by tasks presenting non-symbolic, symbolic, or both types of stimuli. This has been demonstrated by imaging studies, but also by neuropsychological cases of acalculia leading to a loss of basic numerical capacities. Evidence from different studies therefore suggests this circuit is involved in the semantic, abstract representation of numerosity. A second circuit involves the posterior superior parietal lobule, which contributes to counting, but also to other non-numerical abilities (spatial attention). Imaging studies have clearly shown its implication in counting, which requires attention shifting from item to item; additionally, patient studies have suggested it is involved in orienting attention on the number line. Finally, a third circuit concerns the left angular gyrus, which is thought to sub-serve numerical tasks that involve a strong verbal component, in particular the retrieval or storage of verbal arithmetic facts (typically multiplication facts which are learned by rote and memorised as verbal labels) as well as exact symbolic calculation. Imaging studies have demonstrated that this parietal area is activated during multiplication but not subtraction; patients with lesions to this area are no longer able to retrieve facts which they knew by heart, whereas they are still able to compute subtractions and accomplish basic numerical tasks such as non-symbolic comparison.

1.2.6 Conclusion

Human educated adults dispose of a large variety of numerical capacities. However, different studies have suggested that these rely on a more basic abstract numerical quantity processing ability, which is independent from language. This capacity to apprehend and manipulate quantities in an approximate fashion obeys Weber's law which also governs other perceptual judgements. This is particularly evident when non-symbolic stimuli are used.

Moreover, different studies have suggested that the basic representation of numerical quantities takes the shape of a number line, usually oriented from left to right. Repetitive use of symbols, such as Arabic digits, has lead to an automatic link to the underlying numerical representation. The strength of the link from numerical representation to symbols is subject to some variation. Adults are very accurate and fast at enumerating small quantities (1-3 or 4; subitizing), whereas exact verbal labelling of quantities becomes more error-prone and slower for larger quantities (counting). Adults may also use their basic approximate numerical quantification system to estimate larger quantities, which leads to patterns of verbal responses which obey Weber's law but also shows over- or under-estimation. This deviation during approximate mapping from quantity to verbal symbols can however be countered with external input (external calibration). Does taking into account this external output require executive functions? Could executive disorders disrupt the spontaneous mapping from quantity to verbal symbols without calibration? We will investigate these questions in our fourth study (chapter 5).

Studies of neuropsychological patients have suggested that subitizing is rarely disrupted following brain damage, and that it is independent of serial visual attention. On the other hand, counting deficits are found more frequently and often in association with serial visual attention deficits. Subitizing and counting have been shown to recruit the same areas, namely a bilateral occipito-parieto-frontal network, although activations are stronger for counting. Estimation has been linked, through patient studies, to the right parietal lobe, and through an imaging study, to a right fronto-parietal network.

Several numerical capacities have been shown to recruit the parietal lobes; an anatomical model was proposed to segregate the parietal regions into three areas which would show differential involvement in different numerical processes: the hIPS would be specifically recruited in quantity-related tasks (basic numerical quantity processing – number line); the bilateral posterior superior lobule would be used in numerical tasks with a strong spatial and attention component (counting, orienting on the number line); finally, the left angular gyrus would be recruited in numerical tasks which are strongly linked to verbal processes (multiplication facts, exact calculations).

1.3 NUMEROSITY PROCESSING IN NON-HUMAN ANIMALS

Humans are not the only specie endowed with numerical capacities. We will shortly present an overview of studies revealing the phylogenetic precursors of human numerical abilities, as well as their anatomical substrates.

1.3.1 Small numerosity processing

Monkeys have been shown to be able to discriminate 1 vs. 2, 2 vs. 3, and 3 vs. 4 sequentially hidden slices of apples, while failing with 3 vs. 8 and 4 vs. 8 slices (Hauser, Carey, & Hauser, 2000). These results are in violation with Weber's law, as the ratio differentiating 1 from 2 is the same as between 4 and 8, and suggest an object-tracking capacity limited to 4 objects. Cross-modal numerical discrimination of small numerosities is also possible in monkeys, who were able, in one study, without training, to correctly match the number of seen monkey faces to the number of heard monkey voices (2 or 3) (Jordan, Brannon, Logothetis, & Ghazanfar, 2005). Auditory discrimination between 2 and 3 sounds was found to be possible in untrained cotton-top tamarins, moreover over different formats and with controls for non-numerical parameters which usually co-vary with numerosity (tones and speech; Hauser, Dehaene, Dehaene-Lambertz, & Patalano, 2002). Moreover, monkeys are able to correctly anticipate the outcome of simple additions, if it does not exceed the upper limit of 4 (Hauser & Carey, 2003), and have also been shown to successfully predict subtraction outcomes with numerosities in the 1-3 range, without prior training (Sulkowski & Hauser, 2001).

1.3.2 Large numerosity processing

Non-human animals are capable of discriminating non-symbolic numerosities, and, importantly, show a pattern of performance that obeys Weber's law. For example, Meckner showed that rats could be trained to press a lever a certain number of times (4, 8, 16, or even 24 times) to obtain food, that responses were approximately correct but varied more as the demanded numerosity increased, a signature of Weber's law (Mechner, 1958, cited by Dehaene, 1997). Meck and Church successfully trained rats to activate one lever after hearing

2 occurrences of white sound, and another level after 8 sounds were heard (Meck & Church, 1983). This was also possible in response to flashes of light, and most importantly, to the combination of flashes and sounds, indicating that the rats were able to transfer numerical representations across modalities, moreover in conditions controlling for non-numerical parameters. Pigeons' performance also obeys Weber's law in discrimination of visual arrays controlled for non-numerical parameters (Emmerton & Renner, 2006). Finally, chimpanzees have been shown to be able to approximately add and compare sets of pieces of chocolates in order to successfully choose the more numerous collection (Rumbaugh, Savage-Rumbaugh, & Hegel, 1987).

1.3.3 Anatomical correlates

The first evidence suggestive of the existence of "number neurons" was discovered in 1970 (Thompson, Mayers, Robertson, & Patterson, 1970). In this study, cats were anesthetized and electrodes were introduced in their brains to record from singles neurons in the associative cortex, while they were presented with series of sounds, flashes, or single shock pulses. Some of these neurons responded preferentially to specific numerosities, in an approximate fashion, as they responded maximally to their preferred numerosity and less strongly to neighbor numerosities. Importantly, the same results were found when varying the intensity or rate of presentation of stimuli, showing that neurons were responding to numerosity and not these other variables. These results suggested the existence of number neurons coding numerosity in an amodal, approximate fashion.

Since then, other electrophysiological neuronal recordings have brought convincing and more detailed evidence for the existence of neurons tuned to numerosity (Nieder, Freedman, & Miller, 2002; Nieder & Miller, 2004). These were conducted in awake monkeys who were trained to respond in a numerosity-matching task (visual presentation), while cell recordings were taking place, originally in the frontal cortex (Nieder et al., 2002) and later also in the posterior parietal and anterior inferior temporal cortex (Nieder & Miller, 2004). Results showed that about 31% of tested neurons in the lateral prefrontal cortex and about 18% in the intra-parietal sulcus (IPS) responded to numerosity irrespective of co-varying non-numerical parameters (see Figure 1-4). Importantly, there were few numerosity-selective neurons in other parietal areas, or in the inferior temporal area investigated.

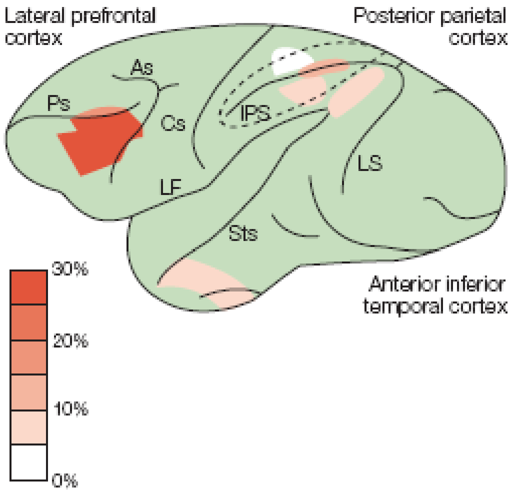


Figure 1-4 Lateral view of a monkey's brain. Proportions of neurons responding selectively to numerosity, color-coded according to the color-bar, are represented in the three areas in which recordings were conducted (lateral pre-frontal cortex, posterior parietal cortex, and anterior inferior temporal cortex). AS, arcuate sulcus; Cs, central sulcus; LF, lateral fissure; LS, lunate sulcus; Ps, principal sulcus; Sts, Superior temporal sulcus. Reproduced from Nieder (Nieder, 2005).

Interestingly, they responded in the same approximate fashion as the neurons recorded in the cats' associative cortex, responding maximally in response to a preferred numerosity, and less strongly to neighboring numerosities. In fact, response distribution was asymmetrical on a linear scale, as neurons tuned for 3 for example fired slightly for 2, maximally for 3, less strongly for 4 but also a little bit for 5 (see Figure 1-5).

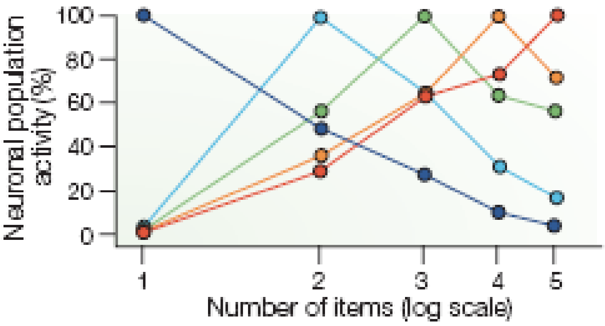


Figure 1-5 Distributions of activity of neurons tuned to numerosity are symmetrical when plotted against a logarithmic scale of number of presented items, showing that tuning is less precise as numerosity increases. Reproduced from Nieder (Nieder, 2005).

Also, distributions of responses were broader (covered a larger range of numerosities) as tested numerosity increased. These neurons' firing patterns therefore conformed to Weber's law, and suggest a compressed, logarithmic tuning to numerosity in these neurons (as shown by the fact that firing distributions represent Gaussian distributions of identical width on a logarithmic scale, with increasing overlap as number of items increases; see Figure 1-5). Similarly, the primates' behavioral responses during the task also obeyed Weber's law, showing the same progressive decrease in precision as numerosity increased. Importantly, analyses comparing activity in the pre-frontal cortex and in the IPS indicated that responses occurred first in the IPS and only later in the pre-frontal cortex, suggesting that numerosity was first extracted in the IPS and then transmitted and maintained online in the pre-frontal cortex (Nieder & Miller, 2004).

Finally, a recent study showed that numerosity-selective neurons situated in the IPS of primates could be sub-grouped into 3 populations (Nieder, Diester, & Tudusciuc, 2006): some neurons responded selectively to sequentially presented numerosities, whereas others to simultaneously presented numerosities, and finally, some neurons constituted the third group to which both other population signals converge to, and which codes abstract numerosity.

1.3.4 Conclusion

In conclusion, animal studies suggest the existence of two systems for the representation of numerosity. The first deals with small quantities (1-4) in an exact way, keeping track of each individual item, whereas the second apprehends larger numerosities in an approximate fashion, in conformity to Weber's law (Feigenson, Dehaene, & Spelke, 2004a). Furthermore, these systems can be used successfully to compute arithmetic operations such as additions. Also, apprehension of both small and large numerosities can be carried out in different modalities, or even across modalities, indicating abstract representation of numerosity. Finally, single-neuron recordings strongly point to a fronto-parietal network of numerosity processing, suggesting initial extraction of numerosity in the IPS and transfer to and online maintenance of numerical information in the pre-frontal cortex.

1.4 NUMEROSITY PROCESSING IN INFANTS AND CHILDREN

Next we will present the evidence for an ontogenetic precursor to human adults' processing of non-symbolic stimuli. We will also give an overview of the development of symbolic numerical processing in children, as well as briefly present dyscalculia (the developmental disruption of numerical capacities) and hypotheses as well as data concerning the processes involves. Before concluding, we will also summarize some of the literature on anatomical correlates of numerical processing in children.

1.4.1 Small numerosity processing

Several studies have investigated apprehension of small numerosities in infants and children. For example, a study of 10 and 12 month-old infants showed that, when confronted with choosing between hidden crackers of equal size, infants' discrimination had an upper limit of 3 items: indeed, discrimination of 1 vs. 2 cookies of equal size was successful, but not that of 2 vs. 4 or 3 vs. 6, although these quantities all differed by the same 1:2 ratio, therefore violating Weber's law (Feigenson, Carey, & Hauser, 2002). This suggests use of an object-tracking system for small numerosities. Additionally, this study demonstrated that when presented with one big cracker vs. two much smaller ones, infants chose the larger cracker (Feigenson et al., 2002). This finding suggests that in certain circumstances, the object-tracking system is influenced by non-numerical parameters such as total surface. Another study (Starkey & Cooper, 1980) reported discrimination of visual arrays (controlled for array density and length) in 22 week-old infants, as well as 2 year-old children. Results showed, for both ages, a limit of 3 items, as responses for trials involving more than 3 items did not differ from chance, and the authors suggested that this limited discrimination process reflected use of subitizing. In the same line, in 5 year-old children, a difference both in response times and error rate was found between the 1-3 range and above, again with visually presented stimuli (Chi & Klahr, 1975). Another study reported an evolution in subitizing range from 1-3 to 1-5 between the ages of 2 and 5 (Starkey & Cooper, 1995). In this study, the authors also tested the hypothesis that subitizing relies on recognition of canonical patterns (Mandler & Shebo, 1982): as aligned dots cannot form a triangle for numerosity 3 or a square for numerosity 4, subjects cannot rely on canonical pattern recognition to enumerate them. Their results did not support the canonical pattern recognition hypothesis, as subitizing limit and performance overall did not significantly differ between visual arrays of random or aligned dots. Furthermore, there is additional evidence that this system for small numerosities is not specific to a visual process, but rather that it supports abstract representations, as visual events and auditory sequences, such as puppet jumps or sounds (Wynn, 1996), or uttered syllables (Bijeljac-Babic, Bertoncini, & Mehler, 1991) are also discriminated by infants. Finally, this system is also able to carry out simple arithmetic operations on visual stimuli, as 4 month-old infants responses suggested they correctly anticipated the outcome of adding 1+1 or subtracting 1-1 dolls (Wynn, 1992).

1.4.2 Large numerosity processing

Infants as young as 6 months old have been shown to discriminate large numerosities presented visually (Xu & Spelke, 2000). Importantly, their performance showed a ratio effect, as discrimination was possible when numerosities differed by a ratio of 2, but not of 1.5. Another study (Lipton & Spelke, 2003) showed that infants' ability to discriminate large sets extended to auditory stimuli, again showing the same ratio effect (good discrimination with a ratio of 2, but not 1.5). Moreover, this study demonstrated that infant's discrimination becomes more precise with age (good discrimination with a ratio of 1.5 was achieved by 9 month-olds), however still independently from the acquisition of language and thus counting skills. Nine month old infants have even been shown to be able to add and subtract non-symbolic stimuli, controlled for non-numerical parameters, using numerosities well above the object-tracking (subitizing) range (McCrink & Wynn, 2004). Five year old children are also able to apply arithmetic operations to non-symbolic stimuli, successfully adding and comparing sets of stimuli (Barth, La Mont, Lipton, & Spelke, 2005; Barth *et al.*, 2006). Importantly, this was achieved not only in the visual modality (scrupulously controlling for non-numerical continuous parameters), but also across visual and auditory modalities (again controlling for non-numerical confounds), when two series of dots were to be added and then compared to a series of beeps, for example (Barth et al., 2005).

1.4.3 Mapping from quantity to symbols and back

As children get older, they are taught to count, which allows them to apprehend larger numerosities in an exact way. Children are thought to master counting at about 4 years of age, when all five counting principles, as defined by Gallistel and Gelman (Gelman & Gallistel, 1978) are acquired: *one-to-one correspondence* (only one number-word is attributed to each counted object), *stable-order* (the verbal sequence is always recited in the same order), *cardinality* (the last number-word of the verbal sequence represents the quantity of the set), *abstractness* (any set of objects can be counted, even sets of different objects), and *order irrelevance* (objects of the set can be counted in any order and still yield the same result, whether starting from the left or from the right, for example). Children also learn to map between non-symbolic quantity representation and numerals in an approximate fashion, and this estimation process undergoes modifications as children get older and learn more about numerosity. This was shown in a study of estimation in 8 to 12 year old children, using number line tasks (Siegler & Opfer, 2003). In these tasks, children were shown a vertical line labelled “0” on the bottom and “100” or “1000” on the top. In one task, they were shown a position on the line and asked to give a verbal estimate of the quantity represented at that position, and in another task, they were asked to indicate the position on the line corresponding to a verbal numeral. Results from both tasks using the 0-1000 number line suggested a compressive mapping in 8 year-old, as smaller numbers were represented as further apart from each other than larger ones. Results with the 0-1000 scale also showed that performance evolved with age to indicate use of a linear mapping, as 12 year old children's productions were linearly related to input. Moreover, a third finding was that children's performance with the 1-100 scale was more linear than compressive, even at 8 years old. This suggests that both compressed and linear mappings of numerosity can co-exist, but that children learn to apply the second mapping more often and to larger scales as they get older. Use of such a linear mapping in other estimation tasks, for example when asked to estimate a visually presented set of items, requires external calibration (which, in the number line task, is provided by the indication of the range of the scale). A study using this type of estimation task with 5 to 8 year-old children and numerosities in the 5-11 range suggested performance similar to adults and rats, as variability in responses increased concurrently to numerosity (scalar variability) (Huntley-Fenner, 2001); however, it also suggested a greater variability in responses in children compared to adults (larger variation coefficient), underlining, as in the previous study, the fact that mapping from non-symbolic representations to symbols is subject to some evolution before reaching the performance exhibited by adults.

1.4.4 Dyscalculia

Some children present specific difficulties in learning and mastering mathematics, although no general intellectual or neurological impairment is present (termed mathematical disabilities or dyscalculia). This disorder is thought to affect about 5% of the population (Gross-Tsur, Manor, & Shalev, 1996; Lewis, Hitch, & Walker, 1994; Shalev, Auerbach, Manor, & Gross-Tsur, 2000). Manifestations of dyscalculia are diverse, and different classifications have been proposed. For example, as dyscalculia is often associated to dyslexia (difficulties in learning to read), one classification has proposed that one type of dyscalculia (without dyslexia) stems from spatial impairments (due to right hemisphere dysfunction), whereas another type (dyscalculia with dyslexia) would be due to verbal deficits (left hemisphere dysfunction) (Rourke, 1993; Rourke & Conway, 1997). Another hypothesis proposes that dyscalculia is due to a core numerical deficit (Wilson & Dehaene, 2007), affecting numerical representations and/or access to them from symbolic input (this second impairment corresponds to the access deficit hypothesis, Rousselle & Noël, 2007). This implies that tasks that involve non-symbolic stimuli should be impaired, or that deficits should be manifest in symbolic tasks known to activate and rely on non-symbolic numerical representations, such as comparison of Arabic digits. There is some evidence in favor of this view as one study reported impaired processing of non-symbolic stimuli in dyscalculics (Landerl, Bevan, & Butterworth, 2004), and another in access to non-symbolic representations from symbols (Rousselle & Noël, 2007). The core numerical deficit hypothesis was tested by developing and administering a remediation software ("the Number Race") to 7-9 year old children with difficulties in mathematics (Wilson *et al.*, 2006a; Wilson, Revkin, Cohen, Cohen, & Dehaene, 2006b). This software was designed to train "number sense", the basic understanding of numerical quantity, as well as the link between numerical quantity representations and symbols (Wilson et al., 2006a). Preliminary results were promising, as performance in tasks tapping into numerical representation and their access from symbols (both symbolic and non-symbolic numerical comparison, subtraction, subitizing) was significantly improved after training with the software (Wilson et al., 2006b). Another recent study also used the "Number Race" remediation software but in a cross-over paradigm and using a control reading software in four to six year-old children with low socio-economic status, and found specific improvement in tasks tapping into access to numerical representation from symbols (digit and number word comparison tasks) after training with the numerical software (Wilson, Dehaene, Dubois, & Fayol, submitted). These children did not show improvement in the non-symbolic comparison task, therefore supporting the access deficit hypothesis (Rousselle & Noël, 2007). Concerning subitizing, a few studies have reported results suggesting a deficit of this process in dyscalculic children (Koontz & Berch, 1996, Landerl et al., 2004; in association to Turner syndrome: Bruandet, Molko, Cohen, & Dehaene, 2004).

1.4.5 Anatomical correlates

Few studies have investigated the neural correlates of numerosity processing in infants and young children compared to the adult population. However, there is a convergence from imaging studies and studies of special populations pointing to the implication of parietal structures. In particular, an imaging study involving non-symbolic stimuli has shown implication of the IPS in children as young as 4 years old (Cantlon et al., 2006). An ERP study in 3 month old infants suggested parietal activation in relation to discrimination of numerical quantity of non-symbolic stimuli (Izard, 2006). Other imaging studies of older children (within/over the range of 8-19 years old) suggest a progressive shift with age from predominant use of frontal to parietal areas in symbolic numerical processing, possibly reflecting a more automatic access to quantity representation from symbols (Rivera, Reiss, Eckert, & Menon, 2005; Ansari, Garcia, Lucas, Hamon, & Dhital, 2005). Studies of children presenting dyscalculia, often from special populations, have also brought evidence for involvement of parietal structures in numerical processing, through structural or functional parietal abnormalities (developmental dyscalculia: Soltész, Szucs, Dékany, Markus, & Csépe, 2007, Kucian *et al.*, 2006; Turner syndrome: Molko *et al.*, 2003; low birth weight: Isaacs, Edmonds, Lucas, & Gadian, 2001; fragile X syndrome: Rivera, Menon, White, Glaser, & Reiss, 2002; velocardiofacial syndrome: Barnea-Goraly, Eliez, Menon, Bammer, & Reiss, 2005, Eliez *et al.*, 2001).

1.4.6 Conclusion

These studies point to the existence of two numerosity systems in infants, one dedicated to small numerosities, and the other to large numerosities (Feigenson et al., 2004a). Small numerosities seem to activate an object tracking system, which is limited to 3 items, and which can easily be influenced by non-numerical continuous parameters. By contrast, larger numerosities are apprehended even when not co-varying with continuous parameters, and lead to a performance pattern which obeys Weber’s law (ratio effect). Some authors (Xu & Spelke, 2000) suggested that the object-tracking system would get overwhelmed when quantities are larger than its limit, but that numerosities well above the limit would not risk activating the object-tracking mechanism, and therefore infants would be able to use approximate numerical quantification in this case. Both small and large quantities seem to be represented in an abstract way, as these studies show “subitizing” and large numerosity discrimination within or across visual and auditory modalities. Additionally, theses studies show that both systems can be used not only to compare quantities, but also to perform arithmetic operations (addition and subtraction), either in an exact (small numerosities) or approximate way (large numerosities), well before children learn to count or to master symbolic arithmetic. Although infants and children’s performance show similarities to adults (“subitizing” of small quantities, ratio effect and scalar variability on performance with large quantities), their performance is less precise than adults’. These studies suggest not only an evolution at the non-symbolic level (greater precision with age in tasks involving only non-symbolic stimuli, and no verbal output), but also in the links from non-symbolic representation to symbols (enumeration and estimation tasks for example). In sum, these findings suggest that adults’ mathematical competencies rely on basic abstract numerical processing present at a very young age. Moreover, imaging studies and studies of children presenting mathematical difficulties (dyscalculia) suggest that this basic numerical capacity is sub-served by the parietal lobes.

1.5 SUBITIZING: WHAT PROCESS IS INVOLVED?

Although there is some evidence that subitizing is a distinct process from counting, there is still a debate as to which processe(s) it relies on. We will shortly summarize a selection of previous explanations and why they have been rejected, before presenting two prominent proposals for subitizing's underlying process.

1.5.1 Previous explanations

Different possible explanations of the underlying process of subitizing have been proposed. Some of these have been shown by experimental studies to be implausible.

For example, some authors suggested that subitizing relies on pattern recognition, as 2 dots form a line, and 3 most often form a triangle (Mandler & Shebo, 1982). For larger numerosities, too many different patterns would be associated with the same numerosity; pattern recognition would not be possible to immediately recognize larger numerosities, and counting would therefore be used for numerosity 4 and on. However, this theory has been rejected since it cannot account for the fact that subjects are able to subitize 3 items disposed in a line (Trick, 1987, cited by Trick & Pylyshyn, 1994; Atkinson et al., 1976a; Atkinson et al., 1976b; Starkey & Cooper, 1995). We will nonetheless be addressing this theory in one of our studies (chapter 3). Indeed, as mentioned above, results from one study suggested that patients with visual extinction present a preservation of subitizing (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000). One must point out that in this study, only numerosities 2 and 4 were tested; moreover, it has been suggested that pattern recognition could have been used, as numerosity 2 always forms a line, and as numerosity 4 was presented as a square pattern (Piazza, 2003). We will therefore test whether such patients are still able to subitize items displayed randomly or in lines.

Another theory was that the subitizing range represented the amount of items that one could hold in working memory at one point in time (Klahr, 1973, cited by Trick & Pylyshyn, 1994). However, experiments have shown that subitizing range or performance is not affected when distracter tasks or items constitute extra working memory load, whereas counting performance is disrupted (Logie & Baddeley, 1987; Trick & Pylyshyn, 1993), thus weakening the hypothesis that subitizing range represents a working memory storage limit. Now we will present two prominent accounts of subitizing: visual indexing and numerical estimation.

1.5.2 Visual indexing

We will first present the theory underlying the concept of visual indexing. Next we will describe a task which is thought to measure this capacity, and the different variations that this task may take on.

1.5.2.1 What is visual indexing?

Visual indexing, a process by which a limited number of items are individuated in parallel, is thought to be pre-attentive, occurring at an early stage of visual analysis during which objects are segregated and "pointed at" as individual entities (thus the initial term of "fingers of instantiation" to describe the pointers; Trick & Pylyshyn, 1994)[2]. This parallel tagging process would be limited to 3 or 4 items - serial attention being thus needed to take into account quantities larger than 3 or 4, which would be reflected by the onset of counting in an enumeration task (Trick & Pylyshyn, 1994). Up to 3 or 4 items, the system would only need to "read" how many pointers are activated to know immediately how many items there are (subitizing; Trick & Pylyshyn, 1994). The pre-attentive/parallel characteristic of visual indexing was demonstrated using feature and conjunction search tasks. The first type of task consists in detecting a target item among distracters which differ from them by one feature (for example, detecting the presence of a red bar among black bars). The second consists of detecting a target which differs by at least two features (for example, detecting a red vertical bar among red or black vertical or horizontal bars). Typically, detection in the feature task is easy, and targets "pop out"; reactions times are fast and do not get slower if more distracters are added to the display. In contrast, conjunction search is slower and reaction times increase as the number of distracters increases. Feature search is thought to engage a pre-attentive process, whereas conjunction search would require scanning from item to item, thus engaging serial attention (Treisman & Gelade, 1980). When one varies the number of *targets*, and asks subjects to enumerate rather that just detect them, subitizing occurs in the feature task but not in the conjunction task (Trick & Pylyshyn, 1993). Subitizing is also known to not occur in another situation: when stimuli are embedded objects (see Figure 1-6; Trick & Pylyshyn, 1993).

[2] A concept very similar to that of visual indexes is object-files (Kahneman, Treisman, & Gibbs, 1992), which we will not develop here for sake of conciseness.

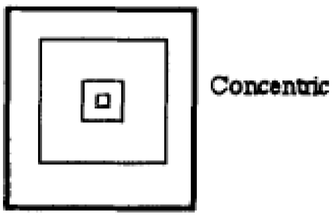


Figure 1-6 Example of embedded items (concentric rectangles) which cannot be subitized. Reproduced from Trick & Pylyshyn, 1993.

In both cases (conjunction enumeration and embedded objects enumeration), serial attention is required to clearly individuate distinct objects, and in both these cases, subitizing cannot operate and serial counting is used, as suggested by linearly increasing response times (Trick & Pylyshyn, 1993).

1.5.2.2 Multiple object tracking: a measure of visual indexing capacity?

Visual indexing presents itself as a good candidate for the underlying process of subitizing because of its limited capacity. Indeed, visual indexing was shown to have about the same limit as subitizing (4) by using multiple object tracking (MOT; Pylyshyn & Storm, 1988; Pylyshyn, 2000). In this task, subjects are presented with different items on a screen, some of which are cued as targets before all items start moving around. Subjects have to keep track of the targets during a few seconds, after which, all items stop moving and subjects have to indicate which items were targets (see Figure 1-7).

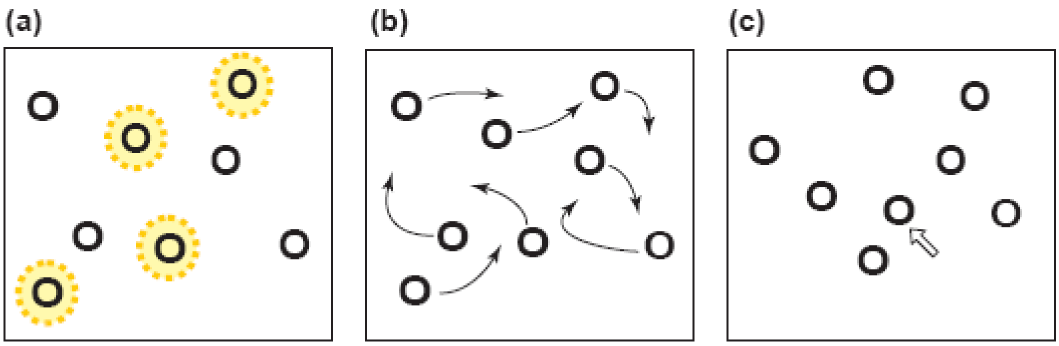


Figure 1-7 A version of the multiple object tracking task. The task starts when subjects are shown items on a screen, some of which are cued (flashing) as targets. (**a**) Shortly after, targets and distracters start moving randomly. (**b**) After a few seconds, items stop moving and subjects must indicate which items were targets by clicking on them with the mouse cursor. (**c**) Reproduced from Pylyshyn, 2000.

Typically, subjects can track a limited number of simultaneously moving objects, and multiple object tracking has thus been used as a measure of this limited visual indexing capacity (Pylyshyn, 2000). Individual differences have been shown to exist in multiple object tracking performance (Green & Bavelier, 2006), although the usual finding is that subjects can track 4 objects with more than 87% accuracy (Pylyshyn, 2000), which would explain why subitizing would occur up to 4 items.

1.5.2.3 Tracking under different conditions

Several studies have investigated subjects' performance on the MOT task using different paradigms, to establish the extent and limits of the tracking system, to infer the extent and limits of the visual indexing capacity. Among these studies, it has for example been shown that tracking takes place even without eye movements (Pylyshyn & Storm, 1988), or when moving targets are momentarily occluded (Scholl & Pylyshyn, 1999). Tracking also applies to stationary objects whose features change over time (tracking objects through feature modifications rather than spatial location changes: Blaser, Pylyshyn, & Holcombe, 2000). Tracking seems to apply to objects rather than features or "stuff", as it is difficult for example to track items whose movements resemble substances (e.g. pouring, VanMarle & Scholl, 2003). It also seems clear that objects are tracked rather than a region of space, as processing advantage for targets does not extend to distracters, even those situated very close to targets, thus suggesting that attention is divided between individual objects and weakening the possibility that attentional focus is simply broadened to encompass a larger area (Sears & Pylyshyn, 2000).

1.5.3 Numerical estimation

Theories of numerical processing have proposed an explanation to subitizing (Dehaene & Cohen, 1994; Dehaene & Changeux, 1993; van Oeffelen & Vos, 1982; Gallistel & Gelman, 1991), which we will resituate in two main numerical models later, and which has yet to be refuted. The gist of this proposal is that subitizing relies on numerical estimation (termed "non-verbal counting" by Gallistel & Gelman, 1991) which is characterized by the fact that it operates with high precision over small numerosities, and progressively decreasing precision as numerosity increases. Thus, subjects would be able to correctly and rapidly discriminate and name small numerosities (1-3 or 4), by relying on estimation, but then, following a speed-accuracy trade-off, have to switch to the slower process of counting for larger numerosities in order to give correct responses. In paradigms where stimulus presentation is short, subjects' accuracy scores would reflect the estimation process without switching to counting (exact for small numerosities, increasingly inaccurate for larger numerosities).

1.5.4 Conclusion

In sum, visual indexing represents a plausible underlying mechanism for subitizing. Like subitizing, it has been shown to operate independently from visual serial attention and to present a limitation in capacity similar to the subitizing range (4 items). On the other hand, the hypothesis that subitizing relies on numerical estimation seems equally plausible, proposing a theoretically grounded explanation for the limitation of subitizing to a small quantity of items. This second hypothesis has never, to our knowledge, been directly tested. This will be the aim of our first study (chapter 2).

1.6 MODELS OF NUMEROSITY EXTRACTION

We have seen that human adults, non-human animals, preverbal infants and children present evidence for a non-verbal approximate numerosity extraction process (usually applied to large numerosities). We will now present two main models that have characterized this process, and have also proposed a link between this process and subitizing.

1.6.1 The preverbal counting model

Gallistel & Gelman (Gallistel & Gelman, 1992) suggest that all numerical judgments rely on a serial counting-like process; they propose that approximate numerical information is extracted through use of the fast preverbal counting mechanism proposed by Meck & Church in their animal studies (Meck & Church, 1983), and that this mechanism can become verbal and exact in children and adults through mapping to the verbal and written number symbols (verbal counting).

Meck & Church's preverbal counting mechanism (Meck & Church, 1983) consists in the accumulation of a series of pulses which are "counted" as they pass through a gate: "the gate closes for a short fixed interval once for each stimulus in the sequence being counted, so that the magnitude in the accumulator at the end of the sequence is proportionate to the number of elements in the sequence" (Gallistel & Gelman, 1992, p. 52). Although this model has been derived from an experiment where the items to be enumerated consisted of a sequence of sounds, Gallistel & Gelman (Gallistel & Gelman, 1991, Gallistel & Gelman, 1992) have used it to explain enumeration of visual sets of items presented in parallel (e.g.

subitizing). They stress the parallel between this preverbal mechanism and the verbal counting mechanism, describing the incrementing of elements in the preverbal counting mechanism as serial: “The accumulation process passes through the intervening magnitudes en route to the cardinal magnitude just as the verbal counting process passes through the intermediate count words en route to the cardinal count word” (Gallistel & Gelman, 1992, p. 65). However, the preverbal counting mechanism would lead to increasingly imprecise estimates as numerosity increases, as noise in the memory of the accumulated counts would concurrently increase (see Figure 1-8).

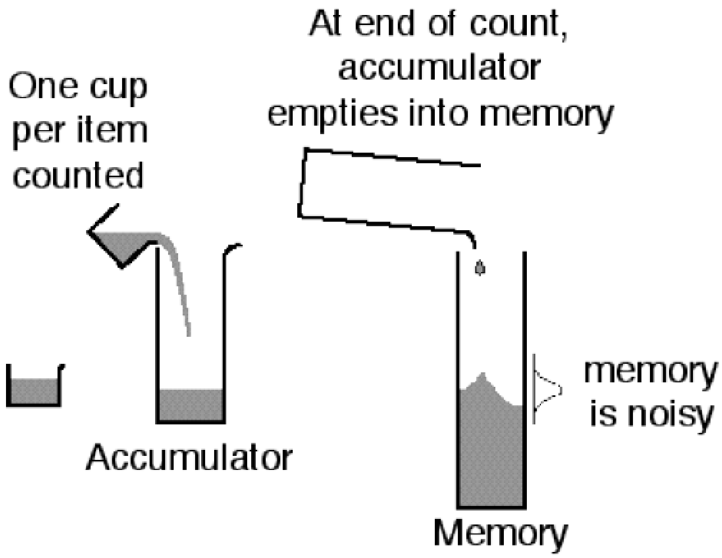


Figure 1-8 The pre-verbal counting model. Items are serially counted by the accumulator, that is, quantities are incremented one by one, as a cup would be poured into a graduated recipient; the result of the count is read out in memory where it has been stored, but memory is noisy and therefore leads to different estimates of the number of counts on different occasions. The amount of noise in memory increases concurrently to the numerical quantity that is being counted (scalar variability: the variability in the estimates is proportional to the mean of the distribution of estimates). Reproduced from Gallistel & Gelman, 2005.

As more and more counts are accumulated, there would be more and more chances of errors in keeping the exact count. Therefore, in this model, numerosities would be represented on a linear scale (same distance between two neighboring numerosities) but representations would get increasingly broader due to increase in noise in the preverbal counting process. Therefore, there would be a progressive increase in overlap of numerosity representation, as numerosities increase. The authors postulated that this could account for subitizing: the accumulation process would be sufficiently precise with smaller quantities to allow for their exact enumeration through estimation (preverbal counting), but thereafter, when representation overlap would get too large, verbal counting would be used to allow for a correct response.

1.6.2 The Log-Gaussian model

We will first present a computational model which has later been integrated in the larger scope of the Log-Gaussian model.

1.6.2.1 A parallel numerosity detector

Dehaene & Changeux (Dehaene & Changeux, 1993) have proposed a numerical model in which all approximate numerosity judgments (estimation, comparison, and so on) rely on a numerosity detector mechanism that is parallel in nature.

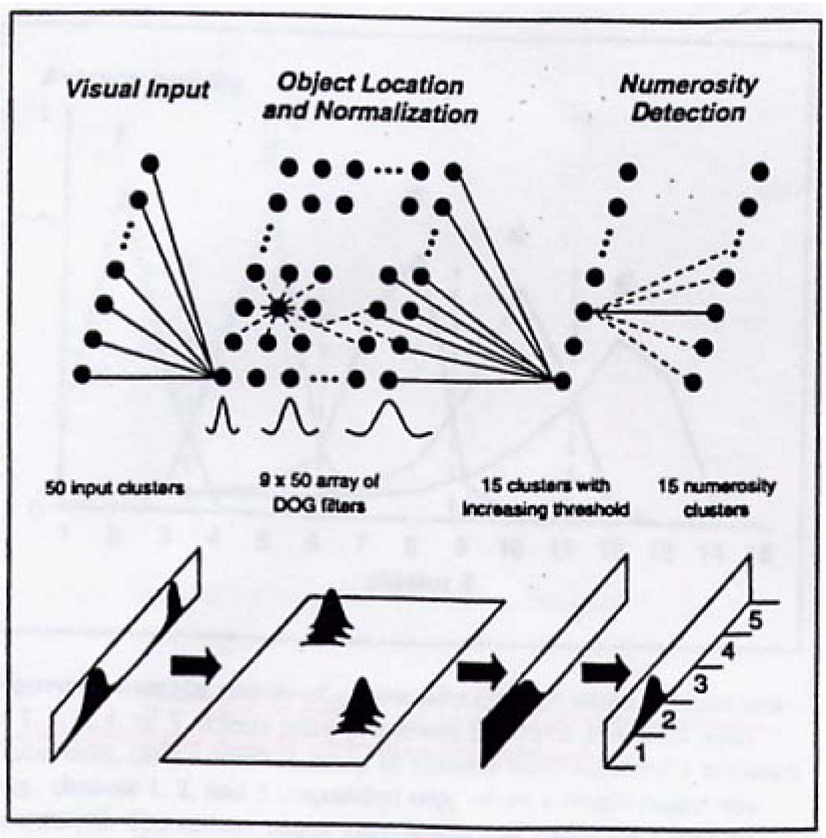


Figure 1-9 The parallel numerosity detection network of Dehaene & Changeux (1993; see text for a description). Reproduced from Dehaene & Changeux, 1993).

In this model (see Figure 1-9), after an initial stage where visual input objects are normalized onto a location map, they project to a set of 15 “summation clusters” which detect in parallel the total activity generated by the objects. Some of these summation clusters are activated and others not, depending on the number of presented objects (increasing threshold of activation). Finally, “numerosity clusters”, which each code for different numerosities, are activated in response to the activity at the summation clusters level. Computational simulations of the model (with visual, but also with auditory input) yielded results which can account for specific characteristics of approximate numerical judgments (e.g. the distance effect). The increasingly approximate coding is represented by two facts in this neuronal model: first, as numerosity increases, the number of neurons coding numerosities decreases, following a logarithmic scale; second, in the large numerosity range, each neuron codes for a broader range of numerosities. The compressive nature of underlying numerosity, as proposed by this model, has found a neural implementation by the “number neurons” recently discovered in monkeys (Nieder et al., 2002; Nieder & Miller, 2004), as they present asymmetries in the tuning curves compatible with a compressive scale (Dehaene, 2007).

Because parallel processing is modeled, the authors concluded that approximate numerical judgments could be explained by a mechanism different in nature from serial verbal counting which is used for exact numerosity quantifications. However, as the numerical detection follows Weber’s law and therefore becomes less precise as numerosity increases, they proposed that exact quantifications of *small* numerosities (subitizing) could reflect the higher precision end of the estimation process[3]. This model differs from the preverbal counting mechanism as it postulates that subitizing would rely on a parallel, and not a serial process.

1.6.2.2 The Log-Gaussian model

The parallel numerosity detection model can be integrated in a larger scale of work which has since been carried out by Dehaene and different collaborators over the years (Dehaene, 2007). This has lead to the proposal of a Log-Gaussian model of representation of numerosity, which postulates a compressive number line with fixed (Gaussian) noise. This constitutes another difference with the preverbal counting model (linear number scale). The Log-Gaussian model proposes that numerosity is represented on a log scale, explaining therefore that smaller numerosities may be represented in a more precise way, whereas larger

[3] However, it is worth noting that the simulation was conducted with numerosities one through five (that is, mainly in the subitizing range).

ones are more compressed and therefore overlap more. Each representation would have the same fixed Gaussian noise (the width of the Gaussian distribution), but the compression would account for the increase in overlap as numerosity increases (see Figure 1-10).

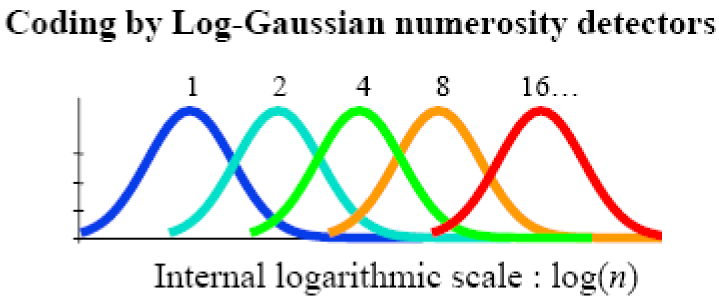


Figure 1-10 Numerosity (*n*) is represented on an internal logarithmic scale with fixed Gaussian noise (width of activation distributions), which accounts for an increase in overlap of representations as numerosity increases. Reproduced from Dehaene, 2007.

The width of the Gaussian distributions determines the precision of the underlying representation, and could therefore explain individual differences. The term *internal Weber Fraction* is used to refer to the Gaussian's width; this determines the precision in subjects' performance in numerosity discrimination for example. A smaller Gaussian width will mean less overlap in numerosity representation, and thus a more precise discrimination. The precision of the discrimination is measured directly during performance by the behavioral Weber Fraction: it refers to the difference in ratio necessary to discriminate two quantities (usually at 75% correct) (for a detailed description of different possible measures of the behavioral Weber Fraction, see Izard, 2006). However, it is mathematically possible to estimate the internal Weber Fraction using performance scores from a discrimination task (Izard, 2006; Dehaene, 2007). It is postulated that the internal Weber Fraction could also account for precision in numerical estimation, as measured by the variation coefficient (Izard, 2006; Dehaene, 2007). Indeed, the variation coefficient (standard deviation of responses/mean response) represents a measure of the width of response distributions which would be related to the width of internal numerosity representation distributions.

1.7 A PARALLEL OR SERIAL NUMERICAL EXTRACTION PROCESS?

Both the preverbal counting and the Log-Gaussian models can account for many effects found in different numerical tasks (distance and size effects, scalar variability in estimation processes...) due to the increasingly approximate characteristic of the number representation they describe. In the preverbal counting model (Gallistel & Gelman, 1992), the preverbal form of the counting mechanism leads to more approximate judgments as numerosity increases because noise in the serial process concurrently increases (linear representation of numerosities with increase in noise). The Log-Gaussian model (Dehaene, 2007) postulates that approximation becomes less precise as numerosity increases because the underlying numerosity representations overlap more in the range of the great numbers, as on a compressed scale (logarithmic representation of numerosities with fixed noise).

Both propose that subitizing is estimation at a high level of precision. However, they diverge as regards the serial/parallel characteristic of the numerosity extraction process. Although there is evidence suggesting that subitizing relies on a parallel process (Dehaene & Cohen, 1994; Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000), this is not conclusive as to whether the approximate numerosity extraction is also parallel. Indeed, as exposed above, it is not clear whether subitizing relies on numerical estimation or not. We will investigate the serial/parallel nature of approximate numerical processing of large quantity, and in particular estimation, in our second and third studies (chapters 3 and 4).

1.8 INSIGHT FROM COMPUTATIONAL MODELS OF NUMERICAL PROCESSING

Different computational models, like the parallel numerosity detector model, have tried to account for different effects reported in the numerical cognition literature at the behavioral or neural level. We will briefly summarize how some of these models relate to some of these effects, in particular the subitizing range in enumeration and/or the distance and size effects in numerical comparison.

1.8.1 Peterson and Simon's model

Peterson & Simon (Peterson & Simon, 2000) developed computational models that seemed to suggest a range of 3 or 4 in a quantifying process of sets of non-symbolic stimuli (presented in a hypothetical 4 x 4 grid of possible locations in which up to 6 objects could be presented, or in a 6 x 6 grid with up to 8 objects). This range emerged from a pattern matching model, suggesting that subitizing range is constrained by the number of possible configurations the network has to memorize to later match input to stored configurations, this number being much lower for up to 3 or 4 items, and becoming much larger as numerosity increases. Results obtained with their simulations further suggested that subitizing emerged after pattern-response associations were learned through initial counting procedure. However, as Zorzi and collaborators note (Zorzi, Stoianov, & Umiltà, 2005), this is difficult to reconcile with findings that small numerosities can be successfully discriminated by pre-verbal (and therefore pre-counting) young infants (Xu & Spelke, 2000; Lipton & Spelke, 2003).

1.8.2 Verguts and Fias' model

Verguts and Fias (Verguts & Fias, 2004; Verguts, Fias, & Stevens, 2005) elaborated on Dehaene and Changeux's neuronal model (Dehaene & Changeux, 1993) to develop a computational model of numerical processing of both non-symbolic and symbolic stimuli (Fias & Verguts, 2004). They found that processing of non-symbolic stimuli by their network (Verguts & Fias, 2004) showed strikingly similar characteristics to those exhibited by "number neurons" as reported by Nieder and collaborators (Nieder et al., 2002; Nieder & Miller, 2004). Indeed, the network showed filter property, as well as increasing bandwidth as numerosity increased, these two properties allowing to account for the distance and size effects respectively. These findings argue for a compressive logarithmic representation of numerosity. As regards the hypothesis that subitizing might rely on numerical estimation, tested numerosities of this computational model and of the single neuron recordings both ranged from 1 to 5, that is, mostly over the subitizing range. In both cases (computational model, and single neuron recordings), therefore, non-symbolic input lead to behavioral performance which obeyed Weber's law, but did not show a clear discontinuity in performance after 3 or 4 numerosities.

This study (Verguts & Fias, 2004) also showed that when symbolic input was fed into the network in conjunction with non-symbolic input, the network (same nodes) developed capacities to process this symbolic input as well. However, output differed somewhat when symbolic input was then used alone, being much more precise and showing linear characteristics (see Figure 1-11).

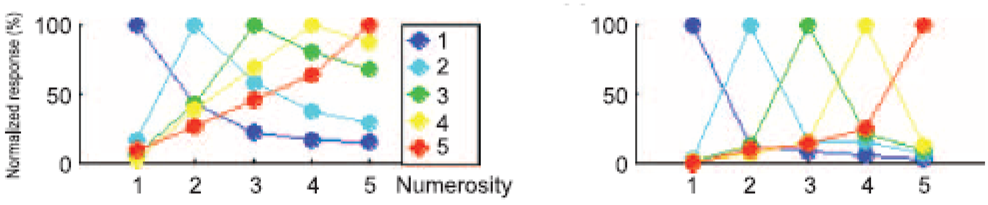


Figure 1-11 Responses distributions of Verguts & Fias's neural network. (**left graph**) after non-symbolic input, showing skewed response distributions which become increasingly less precise as input numerosity increases (suggesting logarithmic scaling); (**right graph**) after symbolic input, showing more precise response distributions of equal precision regardless of input numerosity (suggesting linear scaling). Reproduced from Verguts & Fias, 2004.

This brings evidence for the idea that a same brain area can deal with both non-symbolic and symbolic stimuli and sub-serve both approximate and exact numerical processing (Dehaene, 2007).

In this study, the authors (Verguts & Fias, 2004) also argued against the idea that numerosity extraction might be innate, using the argument that their network learned quite quickly how to discriminate numerosities, therefore proposing that sensitivity to numerosity in babies and animals reflects use of an ontogenetic rapidly learnable capacity. However, as pointed out by Feigenson and collaborators (Feigenson, Dehaene, & Spelke, 2004b), the initial structure of the network itself was designed in a way that it already possessed numerical properties.

In a follow-up study (Verguts et al., 2005), Verguts and collaborators showed, with symbolic input only, that learning was directly related to the frequency of exposure to the different symbolic input (as modeled by corresponding to the frequency of occurrence of numerals in every-day life, based on data from another study - Dehaene & Mehler, 1992). They therefore argued that some effects are due to matching from number representation to symbolic output, rather than to properties of the number representation, therefore accounting for effects reported in the literature but unexplained by previous numerical models (the absence of a size effect in naming and parity judgment, as well as symmetries in priming studies of number naming and parity judgment).

1.8.3 Zorzi and Butterworth's model

A recent review of computational models of numerical cognition (Zorzi et al., 2005) compared the different models of underlying numerical representation, and also presented evidence in favour of the numerical magnitude model (Zorzi & Butterworth, 1999). This model assumes a linear representation of numerosity, in which each numerosity set is represented by a corresponding number of nodes, in such a way that it contains the smaller sub-sets, such as a “thermometer” representation (see Figure 1-12.A.).

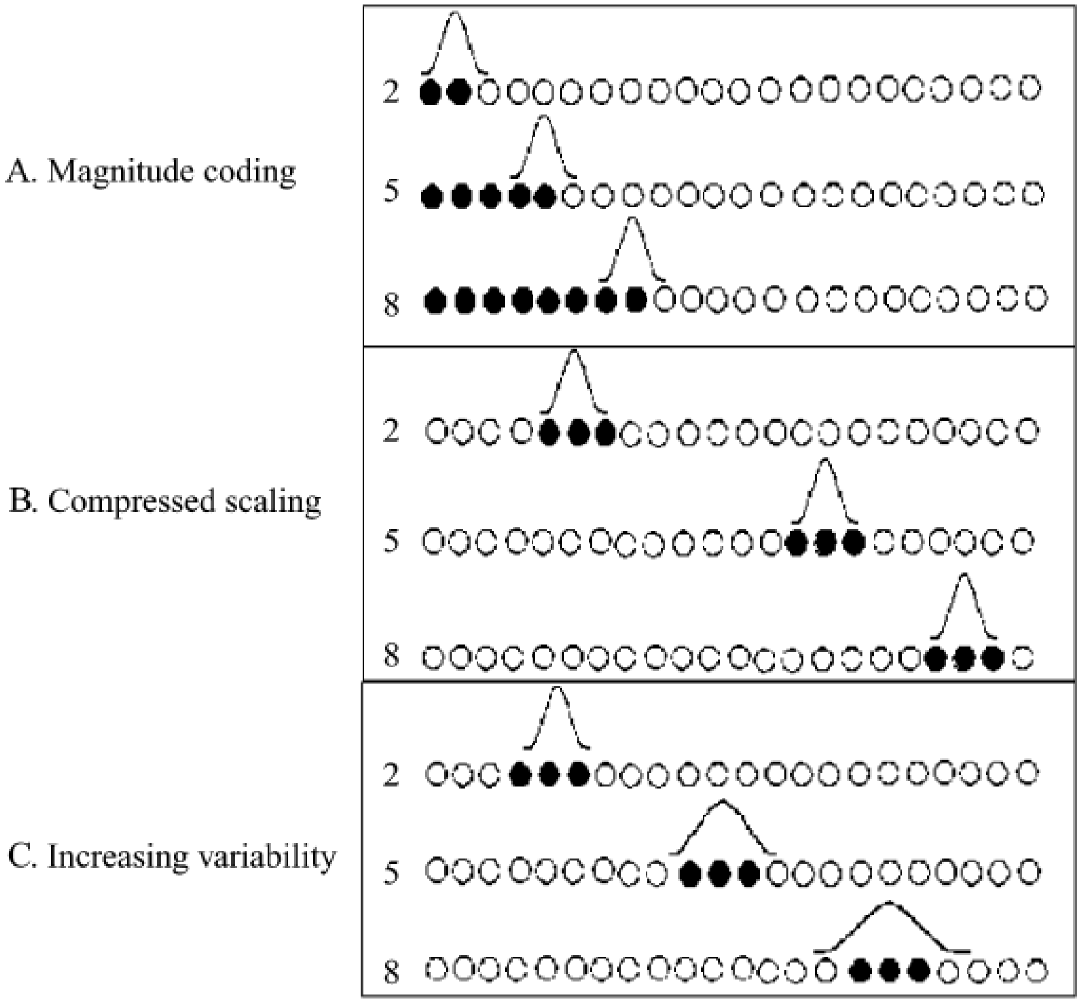


Figure 1-12 Graphical representation of (**A**) magnitude coding (numerical magnitude model of Zorzi & Butterworth, 1999, (**B**) compressed scaling (e.g. Log-Gaussian model of Dehaene, 2007), and (**C**) increasing variability (preverbal counting model of Gallistel & Gelman, 1992). Reproduced from Verguts et al., 2005.

In this way, larger numerosities are more similar, as they share more nodes that smaller numerosities. This model therefore represents numerosity in a non-compressive way, and does not assume scalar variability either, as the preverbal counting model does (Gallistel & Gelman, 1992). The distance and size effects, which represent asymmetric performance in the classical comparison task, and which have previously been explained by asymmetry at the representational level (compressive scale – Log-Gaussian model Dehaene, 2007; scalar variability – preverbal counting model Gallistel & Gelman, 1992), are explained in this model by the non-linearity of the response system, and not of the representation of numerosity itself (see Figure 1-12 for a comparison of underlying numerical representation as modelled by the magnitude model, the compressive scale model and the scalar variability model).

This model successfully simulates the distance and size effects in number comparison (Zorzi & Butterworth, 1999), while also correctly simulating the distance-priming effect (Zorzi, Stoianov, Priftis, & Umiltà, 2003, cited by Zorzi et al., 2005) which is symmetric and which the Log-Gaussian and scalar variability models cannot account for. However, the neural implementation of such a model seems costly, as it implies an equivalent number of neurons to each numerosity, contrary to the Log-Gaussian model, for which a decreasing number of neurons is needed as numerosity increases.

1.8.4 Conclusion

In sum, different computational models yield interesting results as concerns the simulation of behavioural and neuronal performance. Most of them simulate the approximate characteristic of numerical processing, therefore accounting for several effects reported in the literature (e.g. distance and size effects). However, their results do not allow disentangling of different claims about the nature of the scale of underlying representation of numerosity, that is, whether it is compressive (supported not only by Verguts & Fias' simulations as well as Dehaene & Changeux' simulations exposed in the previous section, but also by the single neuron recordings in monkeys previously described) or linear (supported by Zorzi & Butterworth's simulations). Moreover, and importantly for one of our studies, they do not provide a clear answer as to whether subitizing might rely on numerical estimation. Indeed, Peterson & Simon's model suggested a discontinuity in quantification between 3 or 4 items and above, whereas Dehaene & Changeux's simulations and Verguts & Fias' showed no clear discontinuity over the 1-5 range. Of course, these differences might have depended on the *a priori* set by the models, as Peterson & Simon were interested in simulating a discontinuity in enumeration between exact and approximate performance, whereas Dehaene & Changeux and Verguts & Fias were aiming to model only approximate processes.

1.9 CONCLUSION AND AIMS OF OUR DIFFERENT STUDIES

Different studies have shown that human adults possess a basic approximate numerical capacity which is relatively independent from language, as it is shared with babies, non-human animals, indigenous populations who do not have counting series for quantities larger than five, as well as brain-damaged patients with verbal deficits. Different imaging studies converge with neuropsychological reports to show the implication of the parietal lobe, more specifically the horizontal segment of the intra-parietal sulcus (hIPS), in the use of this "number sense". Importantly, it has been shown to be involved in numerical judgments even when stimuli are controlled for other possible parameters that usually co-vary with numerosity, such as the area occupied by the items or the density of the items, therefore reflecting a specifically numerical process. Although this process is independent from language, language (or symbols in general) is needed in certain numerical tasks to express the result of the quantification process. This is the case in enumeration and estimation of quantities. In these tasks, different processes are thought to be used: subitizing (exact quantification of small quantities 1-3 or 4), counting (exact quantification outside the subitizing range), and estimation (approximate quantification outside the subitizing range). However, it remains unclear whether subitizing and estimation truly represent two distinct processes. It has been proposed that subitizing represents estimation at a high level of precision. Alternatively, similarly to infants and non-human animals, human adults could dispose of two separate numerical systems, one dedicated to small numerosities, and the other to large numerosities. A third possibility is that exact quantification of small numerosities relies on a more general process, not specific to the numerical domain, but shared with general visual processes for example, such as visual indexing. With the aim of shedding some light on this issue, we will directly test the hypothesis that subitizing relies on numerical estimation in our 1st experimental study (chapter 2). We will also investigate processing of small and large numerosities (subitizing and estimation) in patients with visual extinction, to see if quantification can occur without spatial attention, as has been suggested for small numerosities by a previous study (chapters 3). Another question that arises in the literature on numerical cognition pertains to the nature of human adults' approximate numerical capacity. Does this process operate in a serial or parallel fashion? Do all elements of a visual set have to be extracted one by one, with a serial preverbal counting process, or in parallel, as suggested by the Log-Gaussian model? We will turn to a neuropsychological patient whose serial visual processing is disrupted to try to answer this question, focusing mainly on estimation, in our

3rd study (chapter 4). Finally, we will address a last question in our 4th study (chapter 5) which concerns the use of symbols to express the output of the basic approximate quantification process. Does this approximate mapping from quantity to symbols require executive functions, as it involves calibration which might call upon strategic processes? We will investigate this question in a case study of a patient presenting executive deficits.

2 CHAPTER 2: DOES SUBITIZING REFLECT NUMERICAL ESTIMATION?[4]

Susannah K. Revkin[1,2,3*], Manuela Piazza[4], Véronique Izard[5], Laurent Cohen[1,2,3,6,7], & Stanislas Dehaene[1,2,3,8]

[1] INSERM, U562, Cognitive Neuroimaging Unit, F-91191 Gif/Yvette, France

[2] CEA, DSV/I2BM, NeuroSpin Center, F-91191 Gif/Yvette, France

[3] Univ Paris-Sud, IFR49, F-91191 Gif/Yvette, France

[4] Functional NeuroImaging Laboratory, Center for Mind Brain Sciences, Trento, Italy

[5] Department of Psychology, Harvard University, Cambridge, U.S.A.

[6] AP-HP, Hôpital de la Salpêtrière, Department of Neurology, F-75013 Paris, France

[7] Univ Paris VI, IFR 70, Faculté de Médecine Pitié-Salpêtrière, F-75005 Paris, France

[8] Collège de France, Paris

* Corresponding author

[4] This chapter is an article which is in press in *Psychological Science*.

2.1 ABSTRACT

Subitizing is the rapid and accurate enumeration of small sets (up to 3-4 items). Although subitizing has been extensively studied since its first description nearly 100 years ago, its underlying mechanisms remain debated. One hypothesis proposes that subitizing results from numerical estimation mechanisms which, according to Weber's law, operate with high precision for small numbers. Alternatively, subitizing might rely on a distinct process dedicated to small numerosities. In this study we tested the hypothesis of a shared estimation system for small and large quantities in human adults using a masked forced-choice paradigm in which subjects named the numerosity of sets with either 1-8 or 10-80 items, matched for discrimination difficulty. Results showed a clear violation of Weber's law, with a much higher precision over numerosities 1-4 in comparison to 10-40, thus refuting the single estimation system hypothesis and supporting the notion of a dedicated mechanism for apprehending small numerosities.

2.2 INTRODUCTION

For nearly 100 years, the fast, accurate and seemingly effortless enumeration of 1 to 3-4 items has presented an enigma to psychologists (for a first account, see Bourdon, 1908). Indeed, adults' enumeration of a visual set of items shows a discontinuity between 3-4 items and above. Numerosity naming is fast and accurate for sets of 1 to 3-4 items, but suddenly becomes slow and error prone beyond this range, showing a linear increase of about 200-400ms/item (e.g. Bourdon, 1908; Oyama et al., 1981; Mandler & Shebo, 1982; Trick & Pylyshyn, 1994; Green & Bavelier, 2003; Green & Bavelier, 2006). This dissociation is held to reflect two separate processes in exact enumeration, "subitizing" for small numerosities and counting for larger ones.

How subitizing operates remains debated. One view proposes that subitizing reflects the use of a numerical estimation procedure shared for small and large numbers (van Oeffelen & Vos, 1982; Gallistel & Gelman, 1991; Dehaene & Changeux, 1993; Izard, 2006). It is now well demonstrated that subjects can quickly estimate the approximate quantity of a large array of dots, without counting. This estimation is subject to Weber's law: judgments become increasingly less precise as numerosity increases, and the variability increases proportionally to the mean response, such that numerosity discrimination is determined by the ratio between numbers (Gallistel & Gelman, 1992; Whalen et al., 1999; Cordes et al., 2001; Izard, 2006; Piazza et al., 2004). Weber's law can be accounted for by a logarithmic internal number line with fixed Gaussian noise (Dehaene, 2007) – a hypothesis that we adopt here for simplicity of exposition, although a similar account can be obtained with the "scalar variability" hypothesis (noise proportional to the mean on a linear scale; Gallistel & Gelman, 1992).

Because Weber's law implies that the variability in the representation of small numbers is low, it has been suggested that it may suffice to explain the subitizing/counting transition. In an unlimited exact enumeration task, the hypothesis is that subjects would first generate a quick estimation, which would suffice to discriminate a numerosity n from its neighbors $n+1$ and $n-1$ when n is small, but would then have to switch to exact counting when n is larger than 3 or 4 and the estimation process becomes too imprecise to generate a reliable answer (Dehaene & Cohen, 1994).

An alternative account postulates a cognitive mechanism dedicated to small sets of objects. Studies of numerosity discrimination in young infants and animals have suggested the existence of two different systems for small and large numerosities (for a review, see Feigenson et al., 2004a). Although babies and animals show a ratio effect for the discrimination of large numerosities, under some circumstances their performance with small numerosities (1-4) escapes Weber's law: they perform well when the quantities to be compared are smaller than 3 (or 4 for monkeys), but performance falls down to chance level when one of the numbers is larger than this limit, even if the ratio is one at which they succeed when both quantities are large.

These studies suggest a distinct system for small numerosities in infants, which is supplemented for larger numerosities by an estimation system similar to that found in adults. Trick and Pylyshyn (Trick & Pylyshyn, 1994) have proposed that a similar distinction exists in adults, in whom a dedicated mechanism of visual indexing would operate over small sets of 1 to 3-4 objects. This parallel tagging process would be pre-attentive, occurring at an early stage of visual analysis during which objects are segregated as individual entities. It would be limited to 3 or 4 items, thus requiring a serial deployment of attention to enumerate quantities larger than 3 or 4, as reflected by the onset of counting in an enumeration task.

In summary, two prominent accounts of subitizing have been proposed: the hypothesis of a single numerical estimation system common to small and large sets, and the hypothesis of a tracking system dedicated to small sets. The present experiment was designed to separate them. We reasoned that if subitizing relies on numerical estimation, performance should be similar in a naming task with numerosities 1-8 compared to the same task with quantities 10-80 (decades). If Weber's law is all that matters, these numerosities should be strictly matched for discrimination difficulty (same ratio between 1 and 2 versus 10 and 20, etc.; see Figure 2-1).

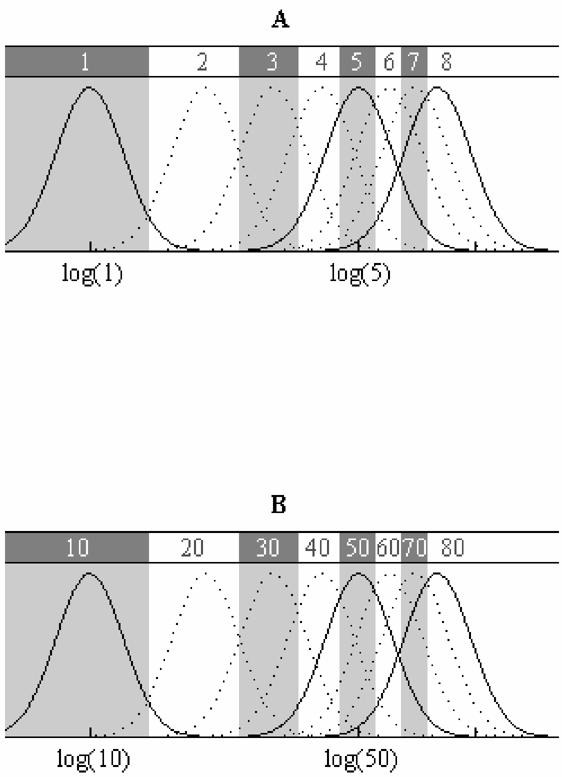


Figure 2-1 The naming tasks according to the log number line model: an optimal response grid for the logarithmic scale of underlying numerical representation is depicted, where response criterion used to distinguish between two adjacent response labels is optimally placed where the two underlying distribution curves meet. According to this model, numerosities from the 1-8 task (**A**) are of equivalent discrimination difficulty as those from the 10-80 task (decades) (**B**), and should thus lead to equivalent naming performance pattern, that is almost flawless naming over the first numerosities of each task (little underlying representation overlap), and progressively less precise naming as numerosity of each task increases (increase of overlap).

Therefore, once subjects are trained with using only decade numbers, the disproportionately higher precision expected over the 1-4 range should also be seen in the 10-40 range: we should see “subitizing” even for large numbers as long as they are sufficiently discriminable. If this were not the case, it would clearly indicate that Weber’s law does not suffice to account for subitizing, and that a distinct process must be at play with numerosities 1-4.

We further reasoned that if subitizing arises from approximate estimation, its range should be determined by subjects' numerosity discrimination capacities (as measured in a large-number comparison task). Specifically, subjects with better discrimination capacities should be more precise in both the 1-8 and 10-80 naming tasks, and in particular have a larger subitizing range.

Our paradigm was designed so that conditions were identical for the 1-8 and 10-80 naming tasks. To prevent counting, sub-grouping or arithmetic-based strategies, stimuli were masked and subjects responded within a short delay. Importantly, we calibrated subjects, as subjects spontaneously underestimate larger quantities, but can be trained to accurately label them (Izard, 2006). To reinforce this calibration process, we also gave feedback at the end of each trial. Finally, because naming small quantities is a much more familiar task than naming decades, subjects were intensively trained.

2.3 METHOD

2.3.1 Subjects

18 right-handed subjects (8 men; mean age = 24.9 years, range 18-38) with no history of neurological or psychiatric disease, and normal or corrected-to-normal vision, gave written informed consent.

2.3.2 Tasks and procedure

Tasks were programmed using e-prime software (Schneider, Eschman, & Zuccolotto, 2002) and administered on a portable computer at a viewing distance of 57 cm. Subjects performed a comparison task and two naming tasks.

2.3.2.1 Dots Comparison task

Subjects were presented with two dot arrays, and were to judge as accurately and as fast as possible which one contained the most dots. Comparison difficulty was manipulated by having a reference numerosity (16 for half the trials, 32 for the other half) from which the deviant could differ by one of 4 possible ratios: 1.06, 1.13, 1.24, 1.33. These variables were randomized across blocs. Subjects responded by pressing the mouse button on the same side as the larger array (using their left or right indexes). The dots, present on the screen until subjects responded, were black and appeared in two white discs on a black background on either side of a central white fixation spot (after a delay of 1400 ms). On half the trials, dot size of deviant clouds was held constant, and on the other half, the area of the envelope of the deviant clouds was held constant, whereas the reference stimuli varied on both parameters at once. This was designed to prevent subjects from basing their performance on these non-numerical parameters. Subjects first performed 16 training trials with accuracy feedback. They performed a total of 128 trials (32 trials per ratio category).

2.3.2.2 Naming tasks

Subjects performed two naming tasks, one with numerosities 1-8 and one with numerosities 10-80 (decades), in two sessions in which both tasks were administered. The tasks order was counterbalanced across session and subjects. Procedure was identical in both tasks. Subjects were explicitly informed which quantities were going to be presented and instructed to name the number of dots as accurately and fast as possible, within one second (otherwise trial would be discarded). They were first calibrated by being shown 16 examples of the stimuli which consisted of random patterns of dots. In order to make sure subjects' estimation was based on numerosity and not on other continuous parameters, for both the calibration and test trials stimuli were generated so that half were of constant dots density and the other half of constant dot size. During calibration, examples and the correct answer were presented for up to 10 seconds according to the subject's need. Test trials began with a central cross which flashed twice to announce the arrival of the dots, which was followed by a flicker mask and finally a black screen (see Figure 2-2).

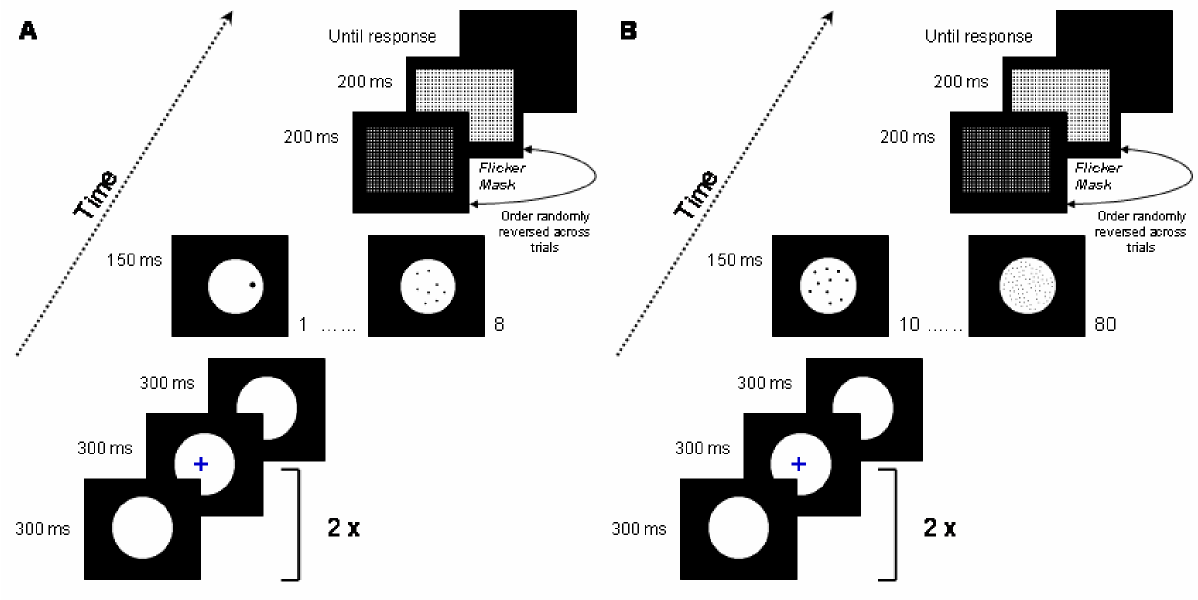


Figure 2-2 (**A**) 1-8 naming test trial: after seeing a flashing cross, subjects were shown groups of dots ranging from 1 to 8 followed by a mask and had to name the presented numerosity as fast as possible using labels 1 to 8. (**B**) 10-80 naming test trial: procedure was identical except that only numerosities 10-80 were presented and subjects used only decades names 10-80 as labels.

Subjects responded using a microphone. Responses given within one second were entered by the experimenter using the keyboard and subjects then received feedback (the correct response was displayed if the response had been incorrect). If responses exceeded one second, a slide was displayed encouraging faster responses. Each numerosity was presented 5 times in random order. This procedure (including calibration) constituted one bloc (40 trials), and subjects performed 4 blocs of each test in each session for a total of 8 blocs (320 trials, 40 presentations of each numerosity) over the two sessions. The first two blocs of each test were discarded as training, and analysis was therefore limited to a maximum of 160 trials per test (20 trials/numerosity/test or less if subjects responded too slowly on some trials).

For analysis, error rate, mean response time (RT), mean response, and variation coefficient (SD of response/mean response) were calculated for each numerosity and each subject. Scalar variability and Weber's law are reflected by a stable variation coefficient (VC) across numerosities (Whalen et al., 1999; Cordes et al., 2001; Izard, 2006), and the VC thus gives an indication of the overall precision of the underlying numerical representation (Izard, 2006).

2.4 RESULTS AND DISCUSSION

2.4.1 Dots Comparison Task

Accuracy was used to calculate the estimate of the internal Weber Fraction (w), a measure of the precision of underlying numerical representation, for each subject, using a method previously described (maximum likelihood decision model, Supplemental Data from Piazza et al., 2004). This basically estimates the SD of the theoretical Gaussian distribution of underlying numerosity on a log scale (see Figure 2-1). Mean w across subjects was 0.18 (SD = 0.06, median = 0.16). Subjects were divided by median split into two groups according to their discrimination precision: low ($w > 0.16$; 7 subjects) and high ($w <= 0.16$; 11 subjects). The two groups did not differ on overall RT ($t(16) = 1.50$, $p = .15$).

2.4.2 Numerosity Naming Tasks

Few trials were excluded because of excessive RT (1-8 task: mean (M) = 3.44, SD = 2.31; 10-80 task: M = 6.78, SD = 3.95). For each task, preliminary ANOVAs showed that the data was similar for error rate, RT and VC across order groups, session and type of control; data was therefore collapsed across these factors. The data was then analysed in a 2 x 2 x 8 ANOVA with factors of numerosity range (1-8 vs. 10-80), discrimination precision group (low vs. high) and rank-order numerosity (1 or 10, 2 or 20, etc, until 8 or 80).

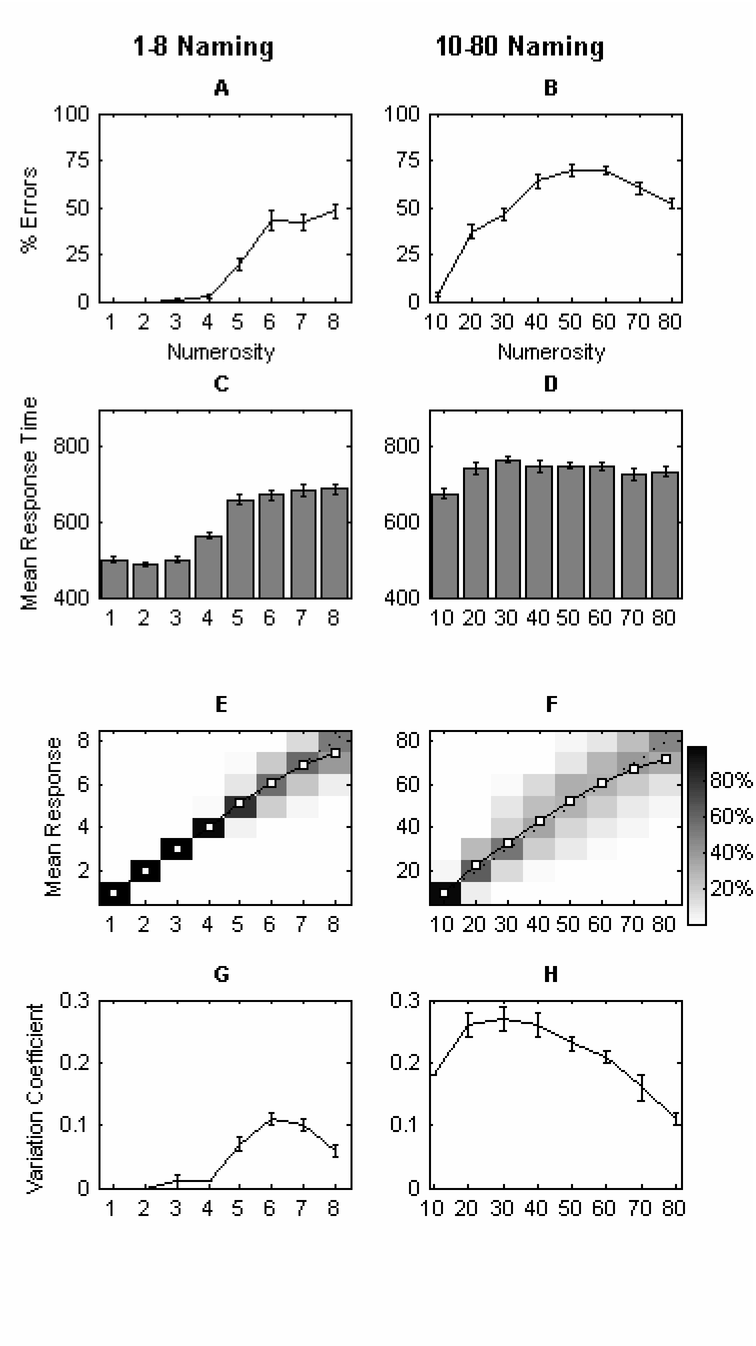


Figure 2-3 Results of the two tasks for which subjects named quantities of dots 1-8 or 10-80 (decades). Percentage of errors (**A**: 1-8; **B**: 10-80), response time (**C**: 1-8; **D**: 10-80), mean response (**E**: 1-8; **F**: 10-80) and variation coefficient (**G**: 1-8; **H**: 10-80) are plotted against presented numerosity and all show a clear advantage for the 1-4 range but not for the 10-40 range. Error bars represent ±1 standard error; in response graphs (**E**: 1-8; **F**: 10-80), dotted line indicates ideal performance and bar on right indicates response frequency in relation to total number of responses.

2.4.2.1 Error rate

Error rate was significantly lower in the 1-8 range (*M* = 21%, *SD* = 7%) compared to the 10-80 range (*M* = 51%, *SD* = 6%) ($F(1, 256) = 518.32$, $p < 0.0001$), and in subjects from the high precision group (*M* = 32%, *SD* = 4%) compared to the low group (*M* = 39%, *SD* = 2%) ($F(1, 256) = 30.06$, $p < 0.0001$); there was also a significant effect of rank-order ($F(7, 256) = 104.49$, $p < 0.0001$), error rate being lower for small numerosities within each range.

Crucially, the interaction between range and rank-order was highly significant ($F(7, 256) = 32.64$, $p < 0.0001$), thus violating the prediction of a constant performance in both ranges, as derived from Weber's law. In the 1-8 range errors were essentially absent for numerosities 1-4, and began to rise steeply from numerosity 5 (see Figure 2-3.A). By contrast, in the 10-80 range, errors were frequent even for numerosities 20 and 30 (see Figure 2-3.B).

The group factor interacted significantly with rank-order ($F(7, 256) = 3.65$, $p < .001$), as error rate was lower for subjects with high precision in numerical comparison particularly for ranks 6-8. The triple interaction was also significant ($F(7, 256) = 4.17$, $p < .0005$), subjects with high precision making less errors especially in the large task over most numerosities and in the small task over numerosities 5-7. Importantly, there was no difference between groups in the 1-4 range.

In sum, results showed a clear difference between the 1-8 and 10-80 tasks, error rate being much lower in the 1-8 task especially for numbers 1-4. Numerosities from the 10-40 range yielded many more errors than those from the 1-4 range, and did not show a clear discontinuity with the following numerosities, in contrast to the 1-8 task. Also, subjects with a higher discrimination precision made fewer errors, especially in the 10-80 task and only outside the subitizing range in the 1-8 task.

2.4.2.2 Response Times

Results revealed a main effect of range ($F(1, 256) = 517.40$, $p < 0.0001$), RTs being faster in the 1-8 range (*M* = 588 ms, *SD* = 32 ms) compared to the 10-80 range (*M* = 737 ms, *SD* = 44 ms). Subjects with a high discrimination precision were slightly slower (*M* = 672 ms, *SD* = 30 ms) than those with a low precision (*M* = 655 ms, *SD* = 41 ms) ($F(1, 256) = 8.09$, $p < .005$). There was also a main effect of rank-order ($F(7, 256) = 31.36$, $p < 0.0001$), RTs increasing from 1-5, then stabilizing. Crucially, a range by rank-order interaction ($F(7, 256) = 27.14$, $p < 0.0001$) again showed differential processing of the small numbers 1-4, with much faster RTs than either the numbers 5-8 or 10-80 (see Figure 2-3.C and 2-3.D). This result again shows a distinct processing within the subitizing range, contrary to predictions derived from Weber's law.

Finally, range also interacted with group ($F(1, 256) = 9.03$, $p < .005$) as subjects with high precision were slightly slower (M = 751 ms, SD = 36 ms) than those with a low precision (M = 715, SD = 48 ms) in the 10-80 task only. All other effects were non significant.

In sum, clear differences were again seen between the 1-8 and 10-80 ranges, subjects being much faster in the first than in the second and showing a "subitizing effect" only over the 1-4 range. Also, discrimination precision only influenced performance in the 10-80 task, suggesting that variability in the 1-8 range was governed by other principles than large-number estimation accuracy.

2.4.2.3 Mean response and variation coefficient (VC)

In both 1-8 and 10-80 ranges, mean response was quite close to the correct one, and variability in responses increased as numerosity increases, a signature of estimation processes (see Figure 2-3.E and 2-3.F). However, a clear broadening of the response range appeared already at numerosity 20 in the 10-80 range, whereas a comparable broadening did not appear until much later (from numerosity 5) in the 1-8 range.

To validate these observations statistically, we estimated mean response and SD of responses by fitting the cumulative response distribution for each numerosity and each subject with the cumulative of a Gaussian distribution function. Fitting was overall excellent for both the 1-8 range[5] (R2: M = 1.00, SD = 0.00) and the 10-80 range (R2: M = .99, SD = .006), except for extreme numerosities for which it was sometimes disrupted because of anchoring effects (very little response variability). Extreme numerosities were therefore excluded from the VC analyses for both ranges, and data were analysed in a 2 x 2 x 6 ANOVA with factors of range, group and rank-order numerosity.

There was a main effect of range ($F(1, 192) = 636.25$, $p < 0.0001$), VC being much lower in the 1-8 range (M = 0.05, SD = 0.02) compared to the 10-80 range (M = 0.23, SD = 0.04). There was a trend towards a main effect of rank-order ($F(5, 192) = 2.31$, $p = .05$), VC being lower for the extreme numerosities, presumably due to a remaining anchoring effect. Crucially, a range by rank-order interaction was again observed ($F(5, 192) = 26.52$, $p < 0.0001$), VC being drastically lower in the 1-4 range compared to the 5-8 range, while no such effect was seen for the 10-40 versus 50-80 (Figure 2-3.G and 2-3.H).

[5] Variability in response was null for most subjects for numerosities 1 to 4, resulting in a null variation coefficient without fitting response distributions in these cases.

A main effect of group ($F(1, 192) = 25.45$, $p < 0.0001$) indicated that subjects with a high precision had a lower VC ($M = 0.13$, $SD = 0.03$) than subjects with a low precision ($M = 0.16$, $SD = 0.02$). No group by range interaction or triple interaction was found; however, subjects with a higher precision had a lower VC over numerosities 20-70 ($t(16) = -2.27$, $p < 0.05$) and 5-7 ($t(16) = -4.62$, $p < 0.0001$), but not 2-4 ($t(16) = -0.74$, $p = 0.47$), (see Figure 2-4).

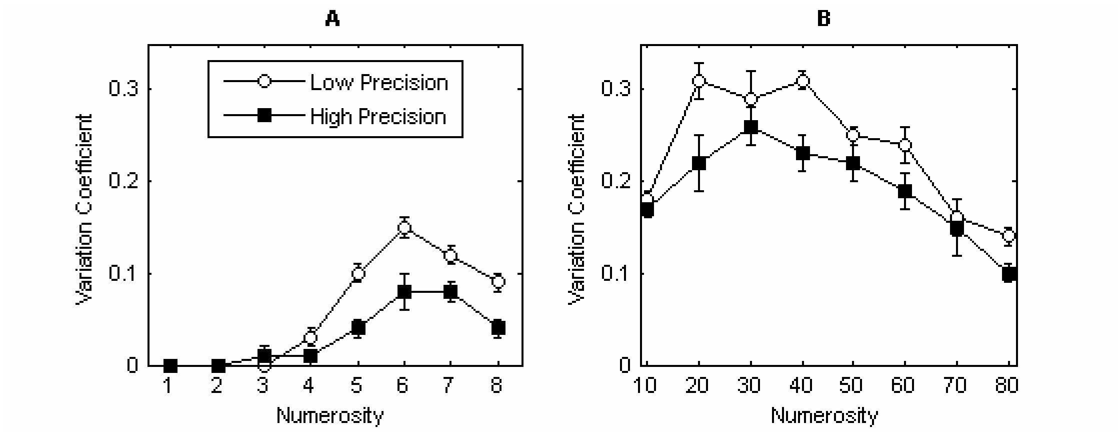


Figure 2-4 Variation coefficient according to discrimination precision group (Low Precision or High Precision), showing a higher naming precision (lower variation coefficient) for subjects from the High Precision group only for numerosities 5 and above in the 1-8 range (**A**) and over most numerosities in the 10-80 range (**B**). Error bars represent ±1 standard error.

In summary, responses showed an abrupt increase in variability between numerosities 4 and 5, not expected from a purely Weberian estimation process. No such discontinuity was found in the 10-80 range. Also, subjects with a higher discrimination precision had a lower VC, particularly in the 10-80 range and outside the subitizing range in the 1-8 range.

2.4.3 Predictors of subitizing range and response precision

Correlation analyses were conducted to further explore the links between different measures of response precision, and the results are presented in Table 2-1.

		Dots Comparison	1-8 Naming				10-80 Naming
		w	RT Range	VC 2-7	VC 2-4	VC 5-7	VC 20-70
Dots Comparison	*w*	1	-.03 (.92)	**.68 (<.01)**	.27 (.28)	**.76 (<.01)**	.42 (.08)
1-8 Naming	RT Range		1	-.08 (.76)	.36 (.16)	-.22 (.41)	-.31 (.22)
	VC 2-7			1	**.69 (p<.01)**	**.98 (p<.01)**	**.80 (p<.01)**
	VC 2-4				1	**.57 (<.05)**	**.52 (<.05)**
	VC 5-7					1	**.78 (p<.01)**
10-80 Naming	VC 20-70						1

Table 2-1 Correlations between measures from the different tasks. P-values are indicated in parentheses. Significant correlations ($p < .01$ or $p < .05$) are in bold. *w* = estimated internal Weber fraction, RT = Response Time, VC = Variation Coefficient.

First we determined a subitizing range for each subject using the data from the 1-8 naming task. The subitizing range was estimated by fitting the full RT curve (excluding numerosity 8) with a sigmoid function of numerosity, and taking the inflexion point of that curve (called “RT range” in Table 2-1; one outlier subject was excluded). Data fitting was excellent (mean $R^2 = .91$, $SD = .12$) and yielded a mean subitizing range of 4.38 ($SD = 0.25$)[6]. The validity of this measure was further demonstrated by its significant correlation across subjects with another classical measure of the subitizing range, the onset of the linear increase in RT in an unmasked timed numerosity naming task [7] ($r = .62$, $p < .01$). If subitizing is due to a single process of estimation for small and large numbers, subitizing range, Weber fraction in numerosity comparison, and precision of numerosity naming should be tightly correlated across subjects. Contrary to this prediction, subitizing range did not correlate with discrimination precision (*w*), nor with other naming precision measures (1-8 and 10-80 VC) (see Table 2-1).

[6] See graphs of the fit for each subject in Appendix 1.
[7] In another task, subjects enumerated 1-8 dots as accurately and as fast as possible. Stimuli resembled those of the 1-8 naming task, but weren’t masked and were presented for up to 10 seconds. Correct RTs were fitted with a four-parameter hyperbola, with a horizontal asymptote (corresponding to subitizing performance) and an oblique asymptote (counting performance); subitizing range was determined as the numerosity where the two asymptotic lines intersected.

Table 2-1 also shows the correlations between *w* and VC over the 1-8 and 10-80 ranges. Correlation between *w* and VC from the 1-8 task was significant, subjects with a higher discrimination precision also having a higher 1-8 naming precision. Given the big difference between VC in the 1-4 and 5-8 ranges (see main analysis), correlations were also calculated separately for these ranges and showed that estimation precision correlated significantly with discrimination precision only in the 5-7 range. Correlation between *w* and VC from the 10-80 task was also positive but non significant. As one would expect, VC measures correlated significantly with one another. Importantly, correlation of VC in the 10-80 task was higher with the 5-7 range VC than with the 2-4 range.

2.5 DISCUSSION AND CONCLUSIONS

Subjects performed a non-symbolic numerosity comparison task, allowing us to measure the precision of numerosity discrimination (internal Weber Fraction *w*), as well as two numerosity naming tasks, each covering a different range of numerosities matched for ratios (1-8 and 10-80). In conflict with Weber's law, but in agreement with the hypothesis of a dedicated process for small numbers, various measures revealed a disproportionate precision in the range of numerosities 1-4. Variation coefficient approached zero for these numerosities, indicating null or very little variability in response, errors being exceedingly rare. In contrast, there was no clear advantage over the 10-40 range in the 10-80 task. In particular, the variation coefficient was very high, reflecting errors and high response variability.

Analyses of inter-individual variability confirmed the special status of the subitizing range. Subjects with a high precision in discrimination of large numerosities made fewer errors (in the 10-80 task over most numerosities and in the 1-8 task outside the subitizing range) and were overall more precise than those with a low discrimination precision. However, the subitizing range did not correlate either with discrimination precision, or with naming precision.

In sum, the clear difference in performance pattern across the two naming ranges, with a unique advantage for numerosities in the subitizing range, and the absence of correlation between subitizing and large-number performance strongly suggest that there is a separate system dedicated to small numerosities (1-4), and go against the hypothesis that subitizing is estimation at a high level of precision (van Oeffelen & Vos, 1982; Gallistel & Gelman, 1991; Dehaene & Changeux, 1993). Our results are in line with young infant and animal studies, which provide evidence for a separate apprehension of small quantities in these populations (for a review, see Feigenson et al., 2004a).

Our study also allowed us to investigate the link between numerosity comparison and numerosity naming. According to the log number line model (Dehaene & Changeux, 1993; Izard, 2006; see Figure 2-1), a single parameter, the internal Weber fraction, should directly influence both tasks. Our data support this hypothesis, as subjects with a higher discrimination precision were also more precise in naming. Those results are in line with a recent mathematical theory that shows how performance and RT curves in those classical numerical tasks can be derived from first principles based on the log number line hypothesis (Dehaene, 2007).

Our data contrasts with those of Cordes et al. (Cordes et al., 2001), who found no difference in variation coefficient within and outside the subitizing range and therefore argued for a continuous representation of small and large numerosities. Although our data suggest a distinct exact system for small numerosities, it is possible both approximate and exact systems co-exist for small numerosities, but that their use depends on task conditions. In Cordes et al.'s study (Cordes et al., 2001) stimuli were Arabic numerals and responses were non-verbal fast tapping. Perhaps there is a separate system for the apprehension of small numerosities which predominates in situations of parallel visual perception.

Importantly, for both naming tasks, subjects had been intensively trained and received regular feedback to counter a possible effect of familiarity with naming smaller numerosities. Although one could object that this training was still insufficient, the clear discontinuity in the 1-8 task between numerosities 1-4 and 5-8 would still need to be explained. Such a discontinuity is perhaps not surprising in RTs in a classical subitizing task (unlimited presentation), because subjects are thought to switch strategies and start counting at about 4 or 5 items (Piazza et al., 2003). However, in our study, the masking and short response delay prevented subjects from counting, and indeed RTs showed no serial increase whether in the subitizing range (1-4) or in the counting range (5-8). Because counting was prevented, tenants of the subitizing-as-estimation hypothesis would have to argue that the entire curve over the 1-8 range was due to numerosity estimation – yet the results clearly indicate that estimation was drastically more precise over the range 1-4 than over the range 1-5, in disagreement with a system obeying Weber's law. Current models of numerosity estimation, such as Dehaene and Changeux's (Dehaene & Changeux, 1993) or Verguts and Fias' (Verguts & Fias, 2004) model, show Weber's law even in the small number range, and are thus unable to account for the present data with a single process.

Although our study argues against estimation as the underlying mechanism of subitizing, the question remains open as to whether subitizing relies on a domain-specific *numerical* process or on a domain-general cognitive process. 100 years after its discovery, the mechanisms of subitizing remain as mysterious as ever – but we now know that they are not based on a Weberian estimation process.

Acknowledgments: this study was supported by INSERM, CEA, two Marie Curie fellowship of the European Community (MRTN-CT-2003-504927; QLK6-CT-2002-51635), and a McDonnell Foundation centennial fellowship.

3 CHAPTER 3: DIFFERENTIAL PROCESSING OF SMALL AND LARGE QUANTITIES IN VISUAL EXTINCTION[8]

Susannah K. Revkin[1,2,3], Manuela Piazza[4], Stanislas Dehaene[1,2,3,5], Laurent Cohen[1,2,3,6,7], Nadia Lucas[8], & Patrik Vuilleumier[8,9]

[1] INSERM, U562, Cognitive Neuroimaging Unit, F-91191 Gif/Yvette, France

[2] CEA, DSV/I2BM, NeuroSpin Center, F-91191 Gif/Yvette, France

[3] Univ Paris-Sud, IFR49, F-91191 Gif/Yvette, France

[4] Functional NeuroImaging Laboratory, Center for Mind Brain Sciences, Trento, Italy

[5] Collège de France, Paris

[6] AP-HP, Hôpital de la Salpêtrière, Department of Neurology, F-75013 Paris, France

[7] Univ Paris VI, IFR 70, Faculté de Médecine Pitié-Salpêtrière, F-75005 Paris, France

[8] Laboratory for Behavioral Neurology & Imaging of Cognition, Department of Neuroscience & Clinic of Neurology, University of Geneva, Geneva, Switzerland

[9] Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland

[8] This chapter is an article in preparation.

3.1 ABSTRACT

Patients with visual extinction have been shown to process some characteristics of items that are extinguished in a localisation task. This particular deficit therefore proves to be a useful tool to determine what information may be extracted independently from spatial attention. Here, we apply this logic to investigate processes of numerosity extraction (subitizing and estimation). Subitizing (the fast and accurate enumeration of small quantities of items) has been reported to be globally spared in patients with visual extinction, arguing for a parallel mechanism which can operate without spatial attention. In the present study of two patients presenting visual extinction, we replicated this finding while ensuring that canonical pattern recognition was not used rather than subitizing *per se*. We also investigated numerical processing of large quantities in one of these patients. Results suggested that numerical estimation of large quantities cannot operate independently from spatial attention when stimuli form two separate objects which strongly compete for attention. We discuss these results in relation to models of numerical processing.

3.2 INTRODUCTION

Neglect patients sometimes present “extinction”, that is, they fail to attend to a stimulus presented in the hemifield contralateral to their lesion when a competing stimulus is simultaneously presented in the ispilateral field (e.g. Karnath, 1988). Some manipulations of stimuli have been shown to influence extinction, reducing or even eliminating it, when perceptual grouping occurs (for e.g. through collinearity, connectedness, or surroundedness; Humphreys, 1998).

In this line of research, one study revealed that patients presenting visual extinction were able to some extent to report the number of items presented over the whole visual field (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000). That is, left items were taken into account to determine how many items had been presented in both fields, although patients were rarely able to localise them (extinction). This means that a difference in task demands, as opposed to a difference in stimuli, can also influence extinction, through a similar process to perceptual grouping (Driver & Vuilleumier, 2001). This study used small quantities (2 and 4 items), and therefore suggests that enumeration of small quantities, *subitizing*, does not require spatial attention. Subitizing is the fast and accurate enumeration of 1-3 or 4 items, and is thought to rely on a parallel pre-attentive process, therefore differing from counting, which calls upon a serial displacement of visual attention from item to item (Trick & Pylyshyn, 1994; Piazza et al., 2003). Indeed, response times show a discontinuity between the subitizing range and above, with a much steeper and lineally increasing slope outside the subitizing range, reflecting use of serial counting (e.g. Trick & Pylyshyn, 1994; Mandler & Shebo, 1982; Chi & Klahr, 1975). Moreover, subitizing is disrupted in conditions which prevent parallel processing (Trick & Pylyshyn, 1993), indicating that it relies on such a pre-attentive process. Therefore, patients with visual extinction may perceive these small quantities as “a set of 2 (or 4)”, rather than 2 (or 4) individual items which compete for attention (Vuilleumier & Rafal, 1999), similarly to the effect of perceptual grouping.

Although subitizing is an enumeration process, it is unclear whether it results from a domain-specific numerical process (Dehaene & Cohen, 1994; Dehaene & Changeux, 1993; van Oeffelen & Vos, 1982; Gallistel & Gelman, 1991), or whether it relies on general properties of the visual system (Trick & Pylyshyn, 1994). Indeed, one model of subitizing (Trick & Pylyshyn, 1994) proposes that it relies on visual indexing, which is the process by which elements of a visual scene are “pointed at” at an early stage of visual analysis. Visual indexing would have a limited capacity (4; Pylyshyn & Storm, 1988; Pylyshyn, 2000) which coincides well with the subitizing range (3 or 4).

Another model proposed that subitizing relies on recognition of canonical patterns (Mandler & Shebo, 1982): 2 dots can be seen as representing a line, 3 dots most often form a triangle, and four dots, a square. From numerosity 5 and on, the correspondence between numerosity and a single canonical pattern is no longer possible. Therefore, subjects could use pattern recognition up to numerosity 4 to accurately and quickly enumerate items, and then switch to counting. This theory has however been rejected, as lines of 3 or 4 dots can be subitized (Atkinson et al., 1976a; Atkinson et al., 1976b; Starkey & Cooper, 1995).

However, of importance for our study, the investigation of subitizing in patients with visual extinction used only numerosity 2 (which forms a line) and numerosity 4 disposed as a symmetrical square pattern (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000). Therefore, canonical pattern recognition might have been used by these patients, rather than subitizing *per se* (Piazza, 2003). We address this issue in the first part of our study, by comparing enumeration in patients with visual extinction with line, random and canonical shape patterns of dots. Given the evidence that subitizing relies on a pre-attentive process (Trick & Pylyshyn, 1993), and the fact that symmetry does not improve enumeration time in the subitizing range (in contrast to the counting range: Howe & Jung, 1987), we hypothesized that patients with visual extinction would be able to subitize lines and random asymmetrical patterns.

Another question which arises, and which we address in the second part of our study, is whether extraction of large quantities (a domain-specific numerical process) might operate without spatial attention. Estimation is an approximate numerical process which is thought by some researchers to operate in parallel (Dehaene & Changeux, 1993), whereas others view it as a serial process (pre-verbal counting: Gallistel & Gelman, 1992). Estimation is thought to rely on a non-verbal amodal approximate quantity processing capacity, which adults share with non-human animals and pre-verbal infants (for a review, see Feigenson et al., 2004a). This core approximate quantity system is thought to be sub-served by the parietal lobes, more specifically the hIPS (horizontal segment of the Intra-Parietal Sulcus) bilaterally (Dehaene et al., 2003). This region could be spared in neglect patients, as this disorder occurs most often after right lateralized lesions which involve different parietal areas (such as the inferior parietal lobule or the temporoparietal junction: e.g. Mort *et al.*, 2003; Vallar & Perani, 1986; or, for recent strong evidence of the importance of fronto-parietal connexions in neglect, see Thiebaut de Schotten *et al.*, 2005).

We therefore tested numerical estimation of large quantities in one patient with visual extinction. First, we reasoned that estimation should be spared in the intact visual field, due to the difference in parietal regions involved in spatial attention and numerical processing. We further reasoned that if estimation does not require spatial attention, it should also be spared in the extinguished visual field. This finding would argue for a pre-attentive (parallel) process. Finally, as mentioned above, it is know that extinction can be reduced or even eliminated when perceptual grouping occurs (Humphreys, 1998). A central cloud of dots could perhaps be perceived as an object through perceptual grouping by proximity, as opposed to the condition where two separate clouds of dots are presented (one on the left, and the other on the right, but with a larger distance in between left- and right-sided dots than for the central cloud). We therefore used these two presentation modes to see if it would influence estimation performance.

3.3 EXPERIMENT 1: SMALL NUMEROSITY PROCESSING

For this experiment, we report data collected from two different patients, JM and FC.

3.3.1 Patient JM: methods and results

3.3.1.1 Case description

We examined a 79 year-old right-handed patient who had obtained a master in education, worked as a museum curator, and who was retired but working as a volunteer for an international organisation. About two weeks prior testing, she presented several episodes of confusion which led to her hospitalisation, during which she was found to present a left sensory-motor hemiparesis, a left inferior quadranopsia and a left neglect syndrome. Brain imaging (see Figure 3-1) revealed a cerebral right posterior temporo-parietal vascular infarction due to an embolism, as well as an ancient left cerebellar infarction.

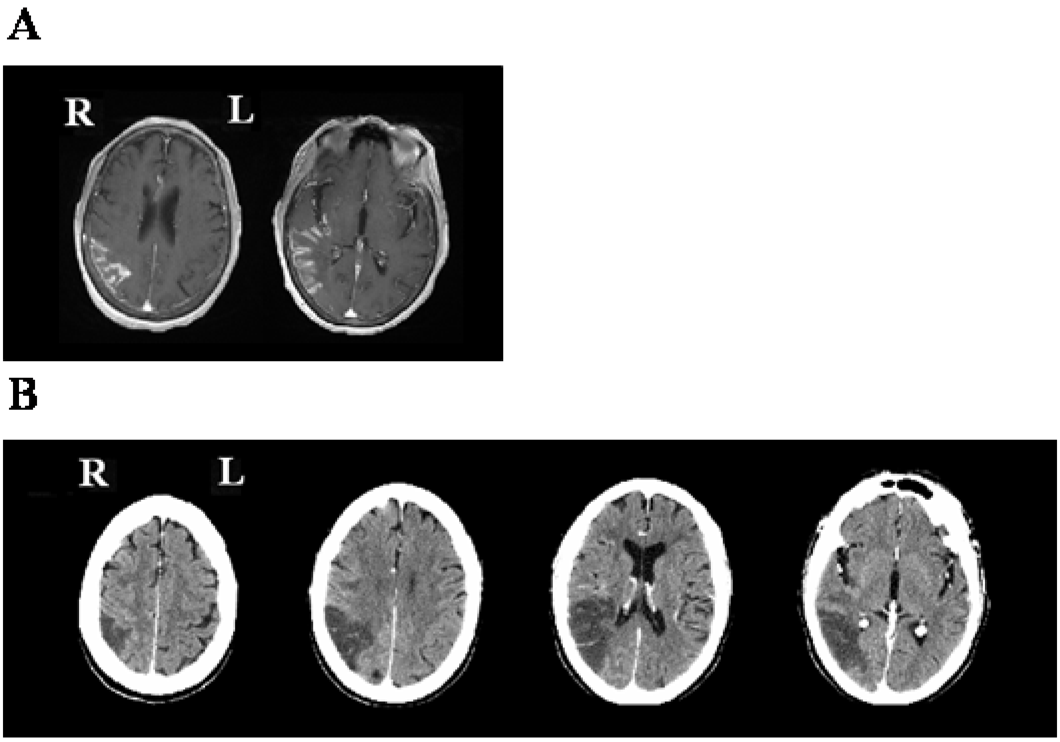


Figure 3-1 Structural imagery of patient JM's brain showing a parietal and temporal posterior right cerebral vascular infarction. (**A**) MRI. (**B**) CT-scan.

A neuropsychological examination carried out about one week before numerical tests were conducted revealed important signs of spatial (body-centred) neglect affecting performance in several tasks: in two cancellation tasks (Bells test, Gauthier, Dehaut, & Joanette, 1989; Ota test, Ota, Fujii, Suzuki, Fukatsu, & Yamadori, 2001) the patient started cancelling items on the right, and omitted many items in the left space; in bisecting lines, she placed the middle of the line further to the right than it should be; finally, she presented spatial dyslexia, omitting words on the left of the page, although this could be countered by strong verbal prompting. Multimodal extinction (visual, auditory and tactile) was also present. Additionally, the patient presented signs of constructive apraxia, psychomotor slowing, as well as discrete signs of executive dysfunction. In sum, results were compatible with a right fronto-parietal disturbance, disrupting the spatial attention network. The patient gave her informed oral consent prior to her inclusion in the study, and testing was conducted over 5 sessions spaced over a 2 week period.

3.3.1.2 Enumeration vs. localisation of small quantities of dots

3.3.1.2.1 METHOD

Both tasks were administered with exactly the same stimuli and in the same conditions. Only instructions varied. In the localisation task, the patient was instructed to localise the sets of dots as having appeared on both sides of a preceding central fixation cross, on its left side, or on its right side. In the enumeration task, she was asked to name the quantity of dots present in the set (2, 3 or 4). The enumeration task was administered first, to ensure that a better performance in this task (as hypothesized) could not result from familiarity with the stimuli or attention being brought to the left following instructions from the localisation task. Stimuli consisted of sets of black dots on a white background, and contained 2, 3 or 4 dots. Dots always appeared either in left space, right space, or bilaterally. They were arranged in different patterns according to 3 different conditions, in a virtual 3 (lines) by 8 (columns) grid. Half the columns were situated on the left part of the screen, and the other half on the right, leaving an empty middle column of a width of about 3°. In the first condition, dots formed *canonical shapes*, 2 dots forming a line, 3 dots a triangle, and 4 dots, a square. In the second condition, dots formed a horizontal *line*. In the last condition, dots formed pseudo-*random* patterns, using predetermined patterns controlled to never form a line or canonical shape. Given that numerosity 2 always forms a line, we used a greater distance between dots in the condition “random” to distinguish this condition from the two others, reasoning that canonical shape/line perception is less evident when distance between the two dots is larger (less perceptual grouping). Again concerning numerosity 2, we used horizontal lines in the “line” condition, and diagonals in the “canonical shape” condition, to distinguish them, reasoning that a horizontal line was more representative of a line that a diagonal (see Figure 3-2 for examples of the stimuli in the bilateral condition).

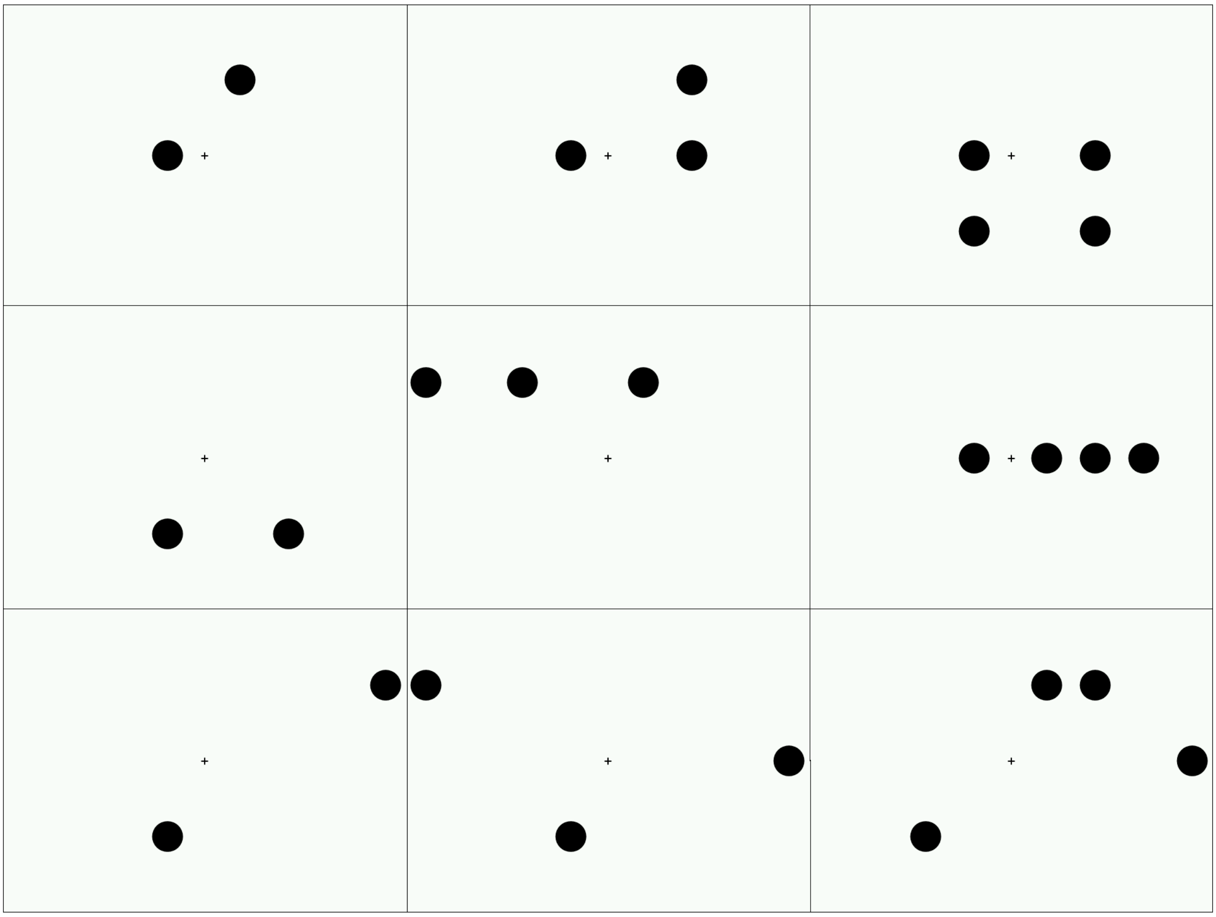


Figure 3-2 Example of stimuli from Experiment 1 (from the bilateral condition only). The first line depicts stimuli taken from the condition "canonical shape", the second shows examples taken from the condition "line", and the third represents examples from the condition "random". The first column shows examples for numerosity 2, the second for numerosity 3 and the third for numerosity 4. The fixation cross is depicted in the examples but only preceded stimuli presentation in the tests.

During each trial, a black fixation cross (of a width and height of 0.5° of visual angle) flashed twice on a white background (duration of the cross presentations and empty white backgrounds were each of 250 ms) and was followed by a set of black dots (presented for 400 ms; visual angle of dots was of 2.2° of width and height). Each half of the total grid (left or right space) subtended 12.4° of width and 13° of height, and distance between columns was of 1.2°, and distance between lines of 3.2°. After stimuli presentation, the screen remained white until the patient's response which was entered by the experimenter using the keyboard, before moving on to the next trial. Duration of the set of dots was determined before the tests were administered by presenting a small sample of the same stimuli bilaterally, in the left field, or in the right field, and asking the patient to localise the dots with regards to the preceding central fixation cross by responding "both sides", "left" or "right". This was repeated with different durations, in order to determine a duration for which extinction occurred. The patient performed the task at a distance of about 57 cm from the screen. For each task, there were 8 stimuli in each condition for each numerosity and each space, except for the conditions random and line for numerosity 4 presented bilaterally, in which there were 9 stimuli. For each task, there were 110 trials in the first bloc, and 108 in the second, amounting to a total of 218 trials. Variables were distributed randomly within each bloc.

3.3.1.2.2 ACCURACY RESULTS

Accuracy was analysed using χ^2 tests to compare results according to the task (localisation vs. enumeration), across the different conditions. First, accuracy was analysed for each space separately, across numerosities and types of patterns.

3.3.1.2.2.1 Effect of task in relation to space

Task had a significant effect only in bilateral space. In both left and right space, localisation (left: 56%; right: 89%) was therefore not significantly different from enumeration (left: 46%; right: 83%) (left: $\chi^2(1) = 1.12$, $p = .34$; right: $\chi^2(1) = 1$, $p = .35$). Importantly, in the bilateral condition, performance in localisation dropped to 0%[9], reflecting extinction, and in contrast, performance was much higher in enumeration (45%) ($\chi^2(1) = 42.80$, $p < .001$). Looking only at results from the bilateral condition, we further examined the effect of task according first to type of pattern, and then to numerosity, and finally to both.

3.3.1.2.2.2 Bilateral space: Effect of task in relation to type of pattern and numerosity

All results from the bilateral space are presented in Table 3-1.

[9] Responses showed a typical extinction pattern, as most errors (96%) consisted in “right” responses.

Accuracy (%)	**Task**		**χ^2 value**	**p-value**
	Localisation	Enumeration	(df = 1)	(bilateral)
Type of pattern				
Canonical shape **	0	50	16.00	< .001
Line **	0	54	16.55	< .001
Random **	0	39	10.44	< .005 §
Numerosity				
2 **	0	86	34.29	< .001
3 **	0	46	14.27	< .001
4	0	12	3.18	.24 §
Numerosity 2				
Canonical shape **	0	75	9.60	< .01 §
Line **	0	100	15.00	< .001 §
Random **	0	83	10.37	< .005 §
Numerosity 3				
Canonical shape *	0	63	7.27	< .05 §
Line *	0	63	7.27	< .05 §
Random	0	13	1.07	1 §
Numerosity 4				
Canonical shape	0	13	1.07	1 §
Line	0	0	-	-
Random	0	22	2.25	.47 §

Legend: (*) = patient significantly differs from controls' at $p < .05$; (**) at $p < .01$; (§) = Fisher's exact test

Table 3-1 Patient JM's performance in localisation and enumeration of small quantities presented bilaterally, according to type of pattern and numerosity.

The patient's accuracy in the localisation task was always lower than in the enumeration task, and this difference was significant for all three types of patterns. Looking at different numerosities, localisation always led to less accurate performance than enumeration, but this difference was significant only for numerosities 2 and 3. Accuracy scores showing influence of pattern type for each numerosity separately in the bilateral space are reported in Table 3-1 and Figure 3-3, contrasting performance in localisation and enumeration.

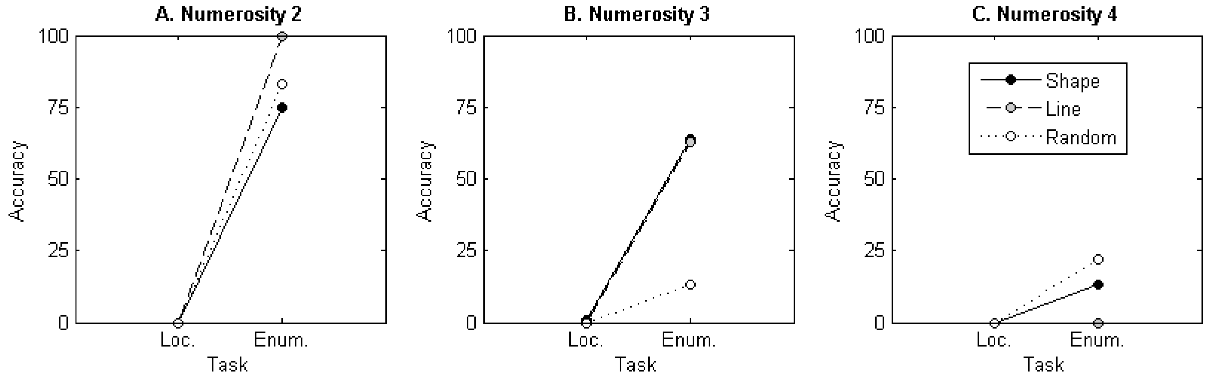


Figure 3-3 Patient JM's performance in localisation (Loc.) vs. enumeration (Enum.) of small sets of items presented bilaterally, as a function of numerosity (**A**. 2 items; **B**. 3 items; **C**. 4 items) and pattern type (canonical shape, line, or random)

Analyses revealed, for numerosity 2, that task had a significant effect for each type of pattern. For numerosity 3, task effect was significant only for canonical shape and line patterns, not for random pattern. Finally, for numerosity 4, task had no significant effect, independently from pattern type.

3.3.1.2.2.3 Left space: Effect of task in relation to type of pattern and numerosity

All results from the left space are presented in Table 3-2.

Accuracy (% correct)	**Task**		**χ^2 value**	**p-value**
	Localisation	Enumeration	(df = 1)	(bilateral)
Left Space				
Type of pattern				
Canonical shape	56	50	0.12	.73
Line	56	37	1.32	.25
Random	56	50	0.15	.70
Numerosity				
2	57	88	3.88	.10 §
3	60	59	0.01	.96
4 **	52	0	15.49	< .001
Numerosity 2				
Canonical shape	50	100	2.86	.20 §
Line	33	67	0.90	.52 §
Random	80	100	1.53	.42 §
Numerosity 3				
Canonical shape	80	75	0.04	1 §

(Table 3-2 continued)

Accuracy (% correct)	**Task**		**χ^2 value**	**p-value**
	Localisation	Enumeration	(df = 1)	(bilateral)
Left Space				
Numerosity 3				
Line	83	43	2.24	.27 §
Random	0	57	3.59	.19 §
Numerosity 4				
Canonical shape	43	0	4.29	.08
Line	43	0	3.34	.19 §
Random **	71	0	8.57	< .01 §
Right Space				
Type of pattern				
Canonical shape	92	92	0	1 §
Line **	100	74	7.18	< .001 §
Random	75	83	0.51	.48
Numerosity				
2	88	96	1	.61 §
3	96	92	0.36	1 §
4	83	63	2.64	.19
Numerosity 2				
Canonical shape	88	88	0	1 §
Line	100	100	-	-
Random	75	100	2.29	.47 §
Numerosity 3				
Canonical shape	88	100	1.07	1 §
Line	100	100	-	-
Random	100	75	2.29	.47 §
Numerosity 4				
Canonical shape	100	88	1.07	1 §
Line **	100	25	9.60	< .01 §
Random	50	75	1.07	.61 §

Legend: (*) = patient significantly differs from controls' at p < .05; (**) at p < .01; (§) = Fisher's exact test

Table 3-2 Patient JM's performance in localisation and enumeration of small quantities presented in left and right space, according to type of pattern and numerosity.

The patient's accuracy in the localisation task did not significantly differ from accuracy in the enumeration task for all three pattern types. Looking at different numerosities, there was again no significant effect of task, except for numerosity 4, for which localisation led to a significantly better performance than enumeration. Accuracy scores showing influence of pattern type for each numerosity separately in the left space are also reported in Table 3-2, contrasting performance in localisation and enumeration. There were no significant effects, except an effect of task for numerosity 4 with random patterns only, as enumeration was much lower than localisation in this condition.

3.3.1.2.2.4 Right space: Effect of task in relation to type of pattern and numerosity

All results from the right space are presented in Table 3-2. The patient's accuracy in the localisation task did not significantly differ from accuracy in the enumeration task for canonical shape and random patterns; however, with line patterns, localisation led to significantly better performance than enumeration. Looking at different numerosities, there was no significant effect of task. Accuracy scores showing influence of pattern type for each numerosity separately in the right space are also reported in Table 3-2, contrasting performance in localisation and enumeration. There were no significant effects, except an effect of task for numerosity 4 with line patterns only, as localisation accuracy was much higher than enumeration in this condition.

3.3.1.2.3 RESPONSE ANALYSIS

Responses from the enumeration task were analysed from the bilateral condition only (mean responses and results of these analyses are reported in Table 3-3).

Numerosity	Left quantity	Right quantity	Mean response	χ^2 value	df	p-value
2	1	1	2.08	-	-	-
3	2	1	2.13	-	-	-
3 *	1	2	2.63	7.27	1	< .05§
4	3	1	2.33	-	-	-
4	1	3	3.33	2.40	1	0.46§
4	2	2	2.33	2.40	1	0.46§

Legend: (*) = patient significantly differs from controls' at p < .05; (§) = Fisher's exact test; (-) not tested (see text for explanation)

Table 3-3 Patient JM's mean responses in enumeration of small quantities presented bilaterally (excluding data from type "canonical shape").

Responses were analysed excluding the type “canonical shape” to avoid confusion with canonical pattern recognition, but collapsing across types “line” and “random” (there was not enough data to analyse these separately). We used χ^2 tests to statistically compare the patient’s distribution of responses to theoretical distributions representing perception of right-sided dots only. We reasoned that a significant difference would indicate that the patient’s mean response was higher than expected if left dots had not been taken into account for enumeration. Some data was not analysed, as in some cases the theoretical distribution corresponded to “1” responses only, which the patient could not have given (this forced-choice paradigm proposed only responses 2, 3, and 4). Results showed that for numerosity 3, the patient’s response distribution significantly differed from the theoretical one, indicating a higher mean response than expected. For numerosity 4, results were non-significant, in line with the accuracy results which suggested that numerosity 4 did not lead to an advantage of enumeration over localisation.

3.3.1.2.4 DISCUSSION[10]

Localisation results showed a clear extinction pattern, as accuracy was worse in the bilateral condition than in left or right space. However, in the bilateral condition, enumeration lead to a significantly better performance in comparison to localisation. This effect was significant when dots were disposed to form a canonical shape, replicating a previous study (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000). Crucially, when they were presented as lines, enumeration performance was also significantly better than localisation. However, the enumeration advantage with both canonical shapes and lines was present only for numerosities 2 and 3, not for 4. A significant advantage was found for enumeration in contrast to localisation with random patterns but only for numerosity 2. The finding of better enumeration of 3 items disposed as a line (compared to their localisation) is a new finding, as the previous study of subitizing in visual extinction (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000) had not included numerosity 3. Also, it clearly argues against enumeration performance relying on canonical pattern recognition, as 3 dots forming a line cannot be interpreted as forming a triangle. Response analyses suggested, as the accuracy results did, that dots from the extinguished field had been taken into account in the enumeration task (at least for numerosity 3). Finally, the fact that there was no advantage of enumeration over

[10] We also had the subject perform an additional enumeration task to control for non-numerical parameters which usually co-vary with numerosity; these results suggest that enumeration of small quantities was based on numerosity of the set and not on other continuous parameters (see Appendix 2).

localisation for numerosity 4 might indicate that this patient has a subitizing range of 3, and that she must therefore rely on serial counting to enumerate 4 items.

3.3.2 Patient FC: methods and results

3.3.2.1 Case description

We examined a 73 year old right-handed retired patient who had worked as an electrician. Almost 3 years before testing, he suffered a right temporo-parietal stroke of probable cardio-embolic origin which resulted in left motor and spatial neglect, with spatial alexia and visual, auditory and tactile extinction, as well as signs of executive dysfunction. Additionally, he presented a left sensitivo-motor hemi syndrome and a left lateral homonymous hemianopsia. A CT-scan taken shortly after the stroke revealed softening of the right parieto-occipital junction territory.

A neuropsychological examination carried out about one month after the stroke revealed persistence of the neglect syndrome. Indeed, the patient failed to take into account elements in the left spatial field in several tasks: he failed to retrieve objects placed on the left side of a desk; when asked to draw or copy simple items, he left out elements from their left part (indicating object-centred neglect), or, in copying a figure with several objects, left out the objects on the left; in bisecting lines, he placed the middle of each line on the extreme right; in describing a complex figure (Goodglass cookie-theft picture), he left out items on the left[11]. Moreover, he presented spatial agraphia and alexia, writing on the right side of the piece of paper, and reading only the words on the extreme right of a text. In some cases, under strong verbal prompting, he could counter his neglect and take into account some items in his left space. The examination also showed that neglect extended to representational space (close and far). The patient also presented dysarthria and a slight hypophonia, a fluctuating temporal disorientation, constructive apraxia, a deficit in movement perception, executive deficits (perseverations, difficulties in following task instructions and intrusions in the memory tasks), and a verbal memory disorder which could be countered with categorical priming. Finally, there were no more signs of left lateral homonymus hemianopsia (however it was hard to definitely exclude because of the patient’s difficulties in following task instructions). Also, importantly for the present study, there were no signs of acalculia, as the patient’s performance in mental calculation (with simple and complex problems) was good, as was

[11] Visual extinction was also tested, but results were not interpretable as the patient presented important difficulties in following instructions in this task at this time.

written calculation, once spatial difficulties were countered. An MRI taken at the time of the second neuropsychological examination showed sequelae of an ancient looking ischemic stroke affecting the left thalamic and opercula area, a recent ischemic stroke in the right hemisphere in the border area between the anterior and middle cerebral arteries as well as cortical-sub-cortical atrophy (see Figure 3-4).

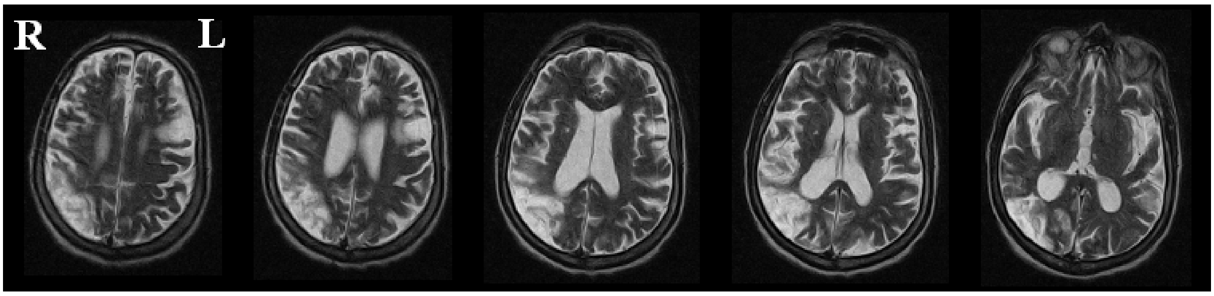


Figure 3-4 Patient FC's MRI showing a right ischemic stroke in the parieto-occipital junction area.

The patient gave his informed consent prior to his inclusion in the study. Before the patient was presented with the numerical tasks, we also tested him again on a neglect task to ascertain the persistence of his visual neglect syndrome. In this variation of the Bells Task (Bells task: Gauthier et al., 1989) he was to circle all the rabbits he could find on a sheet of paper, presented among distractors; his performance showed signs of neglect, as he started his search on the right side of the paper, and omitted 6 rabbits on the left side (in addition to 1 on the right side, and 1 in the centre).

3.3.2.2 Enumeration vs. localisation of small quantities of dots

3.3.2.2.1 METHOD

Method and procedure were identical to those described for patient JM, except stimulus duration which was of 100 ms. Also, sets with only 1 dot were added (catch-trials), to ensure that the patient did not systematically respond "two" when perceiving only one dot on the right and extinguishing the other left dot. In the first task, the patient was therefore instructed to name the quantity of dots present in the visually displayed set choosing response 1, 2, 3 or 4. For each test, the patient therefore performed 114 trials in the first bloc (4 additional trials with 1 dot), and 112 in the second (4 additional trials with 1 dot), amounting to a total of 226 trials.

3.3.2.2.2 ACCURACY RESULTS

Accuracy was analysed using χ^2 tests to compare results according to the task (localisation vs. enumeration), across the different conditions. First, accuracy was analysed for each space separately, across numerosities and types of patterns.

3.3.2.2.2.1 Effect of task in relation to space

Task had a significant effect in all three spaces, but direction of this effect differed. In both left and right space, localisation (left: 85%; right: 90%) led to a better performance than enumeration (left: 52%; right: 77%) (left: $\chi^2(1) = 17.45$, $p < .001$; right: $\chi^2(1) = 4.51$, $p < .05$). Importantly, in the bilateral condition, performance in localisation dropped (31%)[12], reflecting extinction, and in contrast, performance was much higher in enumeration (67%) ($\chi^2(1) = 17.63$, $p < .001$). Looking only at results from the bilateral condition, we further examined the effect of task according first to type of pattern, and then to numerosity, and finally to both.

3.3.2.2.2.2 Bilateral space: Effect of task in relation to type of pattern and numerosity

All results from the bilateral space are presented in Table 3-4.

[12] Responses were not as expected in extinction, as the patient's errors consisted in "right" (56%) but also in "left" responses (44%). It seems that the patient may have had some left-right naming difficulties, as he sometimes pointed left while responding "right" and vice-versa. However, as other tests clearly indicate signs of *left* neglect, we believe extinction of right dots is improbable.

Accuracy (%)	**Task**		**χ^2 value**	**p-value**
	Localisation	Enumeration	(df = 1)	(bilateral)
Type of pattern				
Canonical shape **	29	74	9.41	< .005
Line	27	46	1.70	.19
Random **	38	80	9.16	< .005
Numerosity				
2	42	55	0.76	.38
3 *	40	75	5.53	< .05
4 **	15	69	15.44	< .001
Numerosity 2				
Canonical shape	25	71	3.23	.13 §
Line	38	14	1.03	.57 §
Random	63	75	0.29	1 §
Numerosity 3				
Canonical shape	50	50	0.00	1 §
Line *	20	88	5.92	< .05 §
Random	43	88	3.35	.12 §
Numerosity 4				
Canonical shape **	13	100	7.33	< .001 §
Line	22	33	6.33	.66 §
Random **	11	78	4.45	.14 §

Legend: (*) = patient significantly differs from controls' at $p < .05$; (**) at $p < .01$; (§) = Fisher's exact test

Table 3-4 Patient FC's performance in localisation and enumeration of small quantities presented bilaterally, according to type of pattern and numerosity.

The patient's accuracy in the localisation task was always lower than in the enumeration task, although this difference was significant only for canonical shape and random patterns. Looking at different numerosities, localisation always led to less accurate performance than enumeration, although this was significant only for numerosities 3 and 4. Accuracy scores showing influence of pattern type for each numerosity separately in the bilateral space are reported in Table 3-4 and Figure 3-5, contrasting performance in localisation and enumeration.

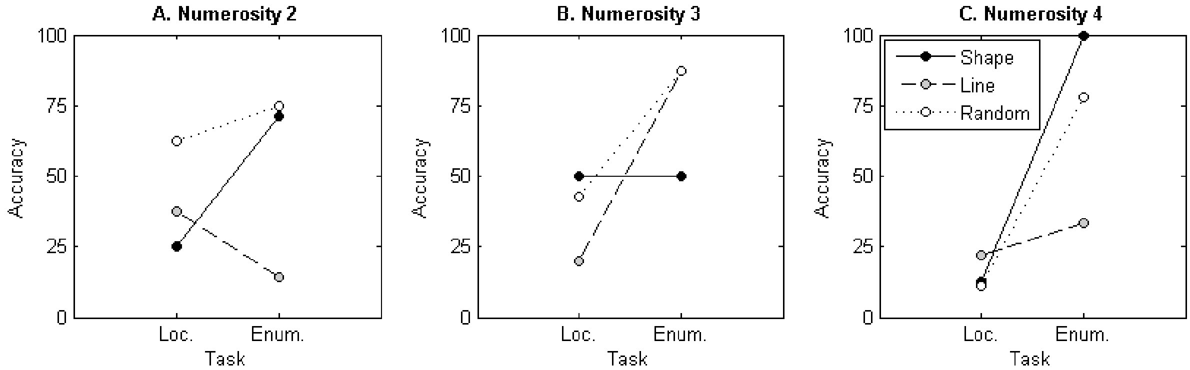


Figure 3-5 Patient FC's performance in localisation (Loc.) vs. enumeration (Enum.) of small sets of items presented bilaterally, as a function of numerosity (**A**. 2 items; **B**. 3 items; **C**. 4 items) and pattern type (canonical shape, line, or random).

Analyses revealed, for numerosity 2, that task had no significant effect, independently from type of pattern. For numerosity 3, only line had a significant effect, enumeration leading in this case to significantly better performance than localisation. For numerosity 4, both canonical shape and random pattern led to a significantly better performance in enumeration.

3.3.2.2.2.3 Left space: Effect of task in relation to type of pattern and numerosity

All results from the left space are presented in Table 3-5.

Accuracy (% correct)	**Task**		**χ^2 value**	**p-value**
	Localisation	Enumeration	(df = 1)	(bilateral)
Left Space				
Type of pattern				
Canonical shape **	91	55	7.33	< .01
Line *	79	44	6.33	< .05
Random *	86	58	4.45	< .05 §
Numerosity				
2 **	86	17	22.30	< .001
3	77	71	0.19	.66
4	92	71	3.42	.14
Numerosity 2				
Canonical shape **	100	13	11.48	< .005 §
Line	75	25	4.00	.13 §
Random **	86	13	8.04	< .05 §
Numerosity 3				
Canonical shape	71	50	0.63	.59 §

(Table 3-5 continued)

Accuracy (% correct)	**Task**		**χ^2 value**	**p-value**
	Localisation	Enumeration	(df = 1)	(bilateral)
Left Space				
Numerosity 3				
Line	75	100	2.02	.47 §
Random	86	63	1.03	.57 §
Numerosity 4				
Canonical shape	100	100	-	-
Line	88	13	9.00	< .05 §
Random	88	100	1.07	1 §
Right Space				
Type of pattern				
Canonical shape	96	83	2.16	.19 §
Line **	100	61	11.62	< .005 §
Random	75	88	1.23	.46 §
Numerosity				
2	96	71	5.40	.05 §
3	79	83	0.09	1 §
4	96	78	3.26	.10 §
Numerosity 2				
Canonical shape	100	75	2.29	.47 §
Line	100	50	5.33	.08 §
Random	88	88	0.00	1 §
Numerosity 3				
Canonical shape	100	71	2.64	.20 §
Line	100	100	-	-
Random	38	75	2.29	.32 §
Numerosity 4				
Canonical shape	88	100	1.07	1 §
Line **	100	29	8.57	< .01 §
Random	100	100	-	-

Legend: (*) = patient significantly differs from controls' at p < .05; (**) at p < .01; (§) = Fisher's exact test

Table 3-5 Patient FC's performance in localisation and enumeration of small quantities presented in left and right space, according to type of pattern and numerosity.

The patient's accuracy in the localisation task was significantly higher than in the enumeration task for all three pattern types. Looking at different numerosities, task effect was present only for numerosity 2, for which localisation led to a significantly better performance than enumeration. Accuracy scores showing influence of pattern type for each numerosity separately in the left space are also reported in Table 3-5, contrasting performance in localisation and enumeration. Theses analyses show that the task effect found with numerosity 2 was significant for both canonical shape and random patterns, for which localisation led to better performance than enumeration. There was no significant effect for numerosities 3 and 4.

3.3.2.2.2.4 Right space: Effect of task in relation to type of pattern and numerosity

All results from the right space are presented in Table 3-5. The patient's accuracy in the localisation task did not significantly differ from accuracy in the enumeration task for canonical shape and random patterns; however, with line patterns, localisation led to significantly better performance than enumeration. Looking at different numerosities, there was no significant effect of task. Accuracy scores showing influence of pattern type for each numerosity separately in the right space are also reported in Table 3-5, contrasting performance in localisation and enumeration. There were no significant effects, except an effect of task for numerosity 4 with line patterns only, as localisation accuracy was much higher than enumeration in this condition.

3.3.2.2.3 RESPONSE ANALYSIS

As for patient JM, responses from the enumeration task were analysed from the bilateral condition only (mean responses and results of these analyses are reported in Table 3-6).

Numerosity	Left quantity	Right quantity	Mean response	χ^2 value	df	p-value
2 **	1	1	2.45	44.00	2	< .001
3 **	2	1	3.00	24.00	1	< .001
3 **	1	2	3.17	17.14	2	< .001
4 *	3	1	3.00	8.57	2	< .05
4	1	3	3.67	6.00	1	.06§
4 **	2	2	3.86	28.00	2	< .001

Legend: (*) = patient significantly differs from controls' at p < .05; (**) at p < .01; (§) = Fisher's exact test

Table 3-6 Patient FC's mean responses in enumeration of small quantities presented bilaterally.

Responses were collapsed across types of pattern, as results excluding the type "canonical shape" essentially yielded the same results. Analysis procedure was the same as for JM, except that all the data was analysed from FC's responses, as catch-trials allowed him to use the response “1”. Results showed that for all numerosities, the patient’s response distribution significantly differed from the theoretical one (or approached significance in one case), indicating a higher mean response than expected. This confirms the accuracy analysis. However, it is important to not that in some cases, surprisingly, mean responses were higher than the correct response (for numerosities 2 and in one condition, for numerosity 3).

3.3.2.2.4 DISCUSSION[13]

In the localisation task, results showed a clear extinction pattern, as accuracy was worse in the bilateral condition than in left or right space. However, in the bilateral condition, enumeration lead to a significantly better performance in comparison to localisation. This effect was significant when dots were disposed to form a canonical shape, as was shown also for JM and again replicating a previous study (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000). Crucially, when they were presented randomly, enumeration performance was also significantly better than localisation. Although presentation of dots as a line did not yield a significant advantage for enumeration in comparison to localisation when collapsing across numerosities, it did when looking only at numerosity 3. This is a new finding, as previously stated for patient JM also. However, there was no accuracy advantage for enumeration over localisation for numerosity 2.

A slightly unexpected finding was that localisation was significantly better than enumeration in both left and right space, rather than equivalent. This could be due in part to the fact that in the localisation task, the patient had more chances of responding correctly if he was not sure, as there were 3 possible answers (left, bilateral, or right) compared to the enumeration task for which there were 4 possible answers (1, 2, 3 or 4). Also, localisation was administered after enumeration, so a higher familiarity with the stimuli might also have helped performance in localisation.

Response analyses suggested, as the accuracy results did, that dots from the extinguished field had been taken into account in the enumeration task, although in some cases they indicated over-estimation of quantity, which is difficult to explain, and might indicate some use of guessing.

[13] We also had the subject perform an additional enumeration task to control for non-numerical parameters which usually co-vary with numerosity; these results suggest that enumeration of small quantities was based on numerosity of the set and not on other continuous parameters (see Appendix 2).

3.4 EXPERIMENT 2: LARGE NUMEROSITY PROCESSING

For this task, we tested only the second patient, FC, in one session with rests, about a month and a half after testing had been conducted with small numerosities.

3.4.1 Estimation of large quantities of dots

3.4.1.1 Method

In this forced-choice estimation task, the patient was asked to estimate the total number of dots presented in different sets. The total quantity could vary between 40, 60 and 90 dots (variable “numerosity”), and the patient was explicitly informed that he should use these quantity labels to respond as accurately but also as fast as possible. To de-correlate quantities presented in the left and right visual fields, each set was composed of two sub-sets, each forming a half cloud. One sub-set was always of fixed quantity (20 dots), situated on half the trials in the left field, and the other of a varying quantity (20, 40 or 70 dots) in the other field (variable “varying sub-set”: either left or right). To investigate the importance of perceptual grouping, both sub-sets were either presented as one object (completely adjacent to one another, forming one central could) or two separate half-clouds (separated by a distance of 3° of visual angle) (variable “object”). To prevent the patient from using non-numerical continuous parameters that usually co-vary with numerosity (such as the size of the total area occupied by the set of dots, or the size of dots), half the sub-sets had a constant area, and the other half were of constant dot size. When one type of control was used for the left sub-set of dots, the other type was always used for the right sub-set (variable “type of control”, constant area in the left sub-set, or constant dot size in the left sub-set). The stimuli were constructed by first generating sets of dots of quantities 30, 60 and 105. Then, for each set, 33% of the dots (respectively 10, 20 and 35) were removed from the right part of the cloud, to obtain left sub-sets of 20, 40 and 70 dots. Removing the same percentage of dots from each set assured that the non-numerical parameter was still constant across numerosities. More sub-sets of 20 dots were generated than sub-sets of 40 or 70, as 20 constituted the fixed quantity but also a varying quantity. The right sub-sets were obtained by vertically mirroring left-subsets. A right sub-set was never matched with the left-subset that it mirrored, as left sub-sets of constant area were always matched with right sub-sets of constant dot size, and vice-versa (for a few examples of stimuli, see Figure 3-6).

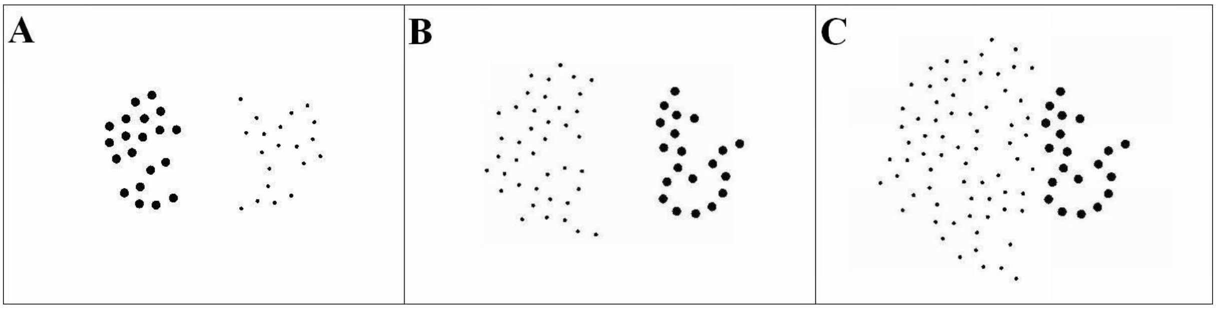


Figure 3-6 Example of stimuli from Experiment 2, in the condition of varying left hemi-cloud (right hemi-cloud always contains 20 dots). (**A**) Numerosity 40 in the “2 objects” condition with left hemi-cloud of constant area. (**B**) Numerosity 60 in the “2 objects” condition with left hemi-cloud of constant dot size. (**C**) Numerosity 90 in the “1 object” condition with left hemi-cloud of constant dot size.

The task was administered in two sessions of two blocs each, with a rest in between sessions (variable “session”). During each trial, a black fixation cross (of a width and height of 0.5° of visual angle) flashed twice on a white background (duration of the cross presentations and empty white backgrounds were each of 250 ms) and was followed by a set of black dots (presented for 100 ms[14]; visual angle of dots varied from 0.2° to 0.5°, and area occupied by each sub-set from 4° to 9° of width, and from 6.5° to 13° of height). The screen remained white until the patient responded. After each trial, the experimenter entered the patient’s response using the keyboard before moving on to the next trial. The patient performed the task at a distance of about 57 cm from the screen. There were 96 trials in each bloc, amounting, across blocs and sessions, to a total of 384 trials (16 stimuli from each condition). Variables were distributed randomly within each bloc. The first session was preceded by 24 training trials. The patient did not wear his corrective glasses during the first bloc of the first session. However, data was collapsed across blocs of the first session as preliminary analyses revealed no effect of this variable.

3.4.1.2 Results

Responses were analysed in a 3 x 2 x 2 x 2 x 2 ANOVA with, respectively, numerosity (40, 60 or 90), varying sub-set (left or right), object (one or two), type of control (constant area or dot size in left sub-set) and session (first or second) as variables. There was a main effect of numerosity, as responses increased as numerosity increased (F (2, 334) = 22.96, p < .0001). There was also a main effect of varying sub-set, as responses were higher when the

[14] Duration of the sets of dots was determined before the estimation test was administered, by using a short localisation task in order to determine a duration for which extinction occurred (see below).

varying sub-set was on the right (F (1, 334) = 31.58, p < .0001). Responses were also higher when sub-sets formed one object (F (1, 334) = 7.13, p < .01). Finally, responses were higher when area was held constant in the left sub-set (F (1, 334) = 23.91, p < .0001) and also overall in the second session (F (1, 334) = 11.97, p < .001). There were four significant double interaction effects. Firstly, the effect of numerosity was present only in trials where area was held constant in the left sub-set (F (2, 334) = 9.73, p < .0005). This suggests that area, which co-varies in the right (non-extinguished) sub-set on such trials, might have been used to estimate numerosity. Secondly, the effect of numerosity was present only in trials where the varying sub-set was on the right (F (2, 334) = 7.74, p < .001). This suggests that varying numerosity could not be extracted in the extinguished left field (but see below). Thirdly, when the varying sub-set was on the left, mean response was higher on trials where sub-sets formed one cloud (F (1, 334) = 5.24, p < .05). This suggests that perceptual grouping may have prevented extinction of the varying numerosity in the “one object” condition. Finally, mean response was higher when area was held constant in the left sub-set, only in trials where the varying sub-set was on the right (F (1, 334) = 7.66, p < .01). This suggests that area, which co-varies in the right (non-extinguished) sub-set on such trials, might have been used to estimate numerosity, which varied in the right sub-set on these trials. There were two significant triple interactions. Firstly, mean response was influenced by numerosity when the left sub-set varied only when it formed one object with the right sub-set (see Figure 3-7.A.); in contrast, when the right sub-set varied, response was influence by numerosity whether sub-sets formed one or two objects (see Figure 3-7.B.).

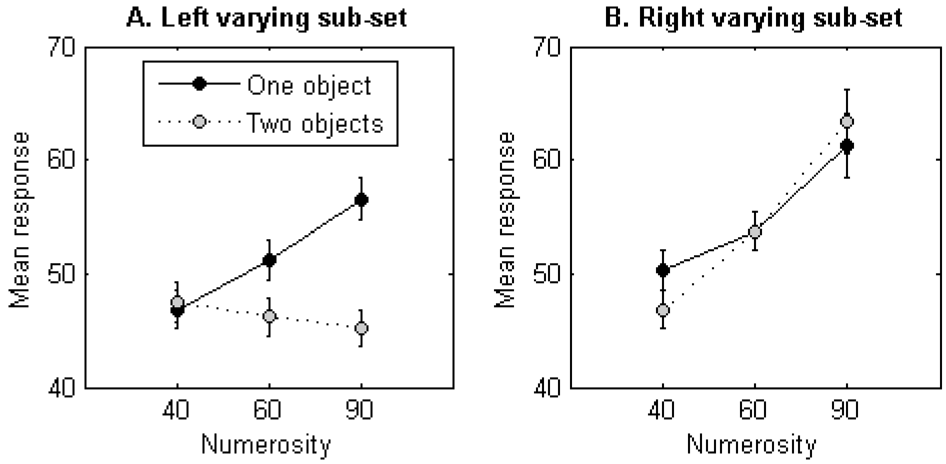


Figure 3-7 Patient FC's performance in estimation when the varying sub-set is on the left (**A**) or on the right (**B**). Results show that in the first condition (**A**), response increases with numerosity only when sub-sets form one object; in the second condition (**B**), response increases with numerosity whether sub-sets form one of two objects (Error bars represent ±1 standard error).

This suggests that a competing right object prevents numerosity extraction of a left object, but that the right part of an object does not prevent extraction of numerosity of its left side. The second triple interaction revealed that type of control had an effect only when the right sub-set varied and only for numerosity 90.

3.4.2 Localisation of large quantities of dots

Before the patient performed the estimation task, a localisation task was administered mainly to determine stimulus duration time. To this effect, the same stimuli were used (a subset of them) but were also presented sometimes completely on the left (left condition) or completely on the right (right condition) of the previous fixation cross, in addition to the condition where they were presented in both hemi fields simultaneously (bilateral condition). No much data was collected, so results must be considered with caution. However, these results showed that in the bilateral condition, extinction was greater when stimuli formed two objects (50% errors, that is, 6 responses "right" out of 12 trials) compared to when they formed one object (25% errors, that is, 3 responses "right" out of 12 trials). This is consistent with previous reports that manipulations of sets of 2 objects which induce perception of a single object reduce or eliminate visual extinction (Humphreys, 1998). This suggests that a central cloud of dots may be perceived as an object (even if its left side looks different from its right side), which could explain the better estimation performance in this condition. In contrast, two separate sets of dots seem to lead to clear extinction, preventing estimation processing of the left hemi-set. Performance in left and right conditions was not optimal, but errors consisted only in response “both”, perhaps because the two hemi sets of dots differed in appearance (because of the different controls for non-numerical parameters); the patient might have found it difficult not to respond “both” while perceiving what looked like two different objects.

3.4.3 Discussion

This data suggests that the patient was sensible to a varying left numerosity only when it was « connected » to the right half-cloud – when there were two distinct hemi-clouds, extinction of left numerosity occurred (first triple interaction effect). The object-individuation process (which leads to the extinction of a clearly distinct left object) therefore precedes and hinders the estimation process (for the left object). Moreover, this data suggests that the patient used area in the right field to estimate numerosity, but that type of control (non-numerical parameters) had no significant influence on his estimation in the left field (second triple interaction effect).

3.5 GENERAL DISCUSSION

We investigated numerical processing of small and large quantities in patients presenting visual extinction, to discover whether such processes can occur independently of spatial attention.

First, as concerns small numerosity processing, we report results of two patients which suggest sparing of subitizing even when items to be enumerated cannot be localised when competing items are present. We thus replicate previous studies which had also suggested sparing of enumeration of 2 or 4 items forming canonical patterns across visual fields (2 as a line, 4 as a square; Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000). We extend this previous finding to include sparing of subitizing of numerosity 3, as well as demonstrate that this occurs even when dots are arranged to form a line, ruling out the possibility that canonical pattern recognition is used in patients with visual extinction rather than subitizing *per se* (Piazza, 2003). This is also supported by the finding in one patient of intact processing of random patterns of 4 items, which clearly do not form a symmetrical canonical square. Our results also suggest that subitizing did not rely on non-numerical continuous parameters which usually co-vary with numerosity. In sum, these results support the original view that subitizing can occur without spatial attention (Vuilleumier & Rafal, 1999; Vuilleumier &

Rafal, 2000) and are in line with other studies which suggest that subitizing relies on a pre-attentive parallel process (healthy subjects: Trick & Pylyshyn, 1993; patients with a deficit in serial visual processing: Dehaene & Cohen, 1994), moreover which doesn't rely on symmetry (Howe & Jung, 1987). Our results are thus in line with the view that the preservation of subitizing in patients with visual extinction might be due to grouping of stimuli into specific, easily recognizable sets of quantities (Vuilleumier & Rafal, 1999), and further show that such grouping mechanism cannot be reduced to *classical* Gestalt ones (i.e., canonical shape perception).

Second, as concerns large quantity processing, we tested one of the patients with an estimation task involving quantities well above the subitizing range (40, 60 and 90). This allows to test numerical extraction processing, as subitizing might rely on domain-general processes such as visual indexing (Trick & Pylyshyn, 1994) rather than a process specific to the numerical domain, or represent a different core quantity system dedicated to small numerosities, as it has been shown for non-human animals and pre-verbal infants (Feigenson et al., 2004a; see also Revkin, Piazza, Izard, Cohen, & Dehaene, in press for similar evidence in human adults).

Results from this task suggest that estimation in the intact visual field may indeed be spared in a patient presenting visual extinction, suffering a right parietal cerebral lesion. Even though a recent study suggests that non-verbal estimation relies on a right-lateralised fronto-parietal network (Piazza et al., 2006), this network would not include the parietal regions usually affected in neglect (e.g. Mort *et al.*, 2003; Vallar & Perani, 1986). However, the patient's performance in the intact visual field was sometimes influenced by non-numerical continuous parameters, such as the area occupied by the set of dots, although this only happened for one of the three tested numerosities (90). As we tested only three numerosities, it would be useful in future studies to use a more extensive set of quantities to make sure that non-numerical parameters do not play a great role in the sparing of numerical judgments in the intact field of patients with visual extinction, and, generally, compare performance to control subjects to clearly state that estimation is preserved in the intact field of patients with visual extinction.

Results from this task further suggest that estimation cannot take place without spatial attention when items are disposed to form two separate objects: in this case, the left object is clearly extinguished and its numerical quantity is not processed. In the condition where items form a central object, results are more difficult to interpret. Localisation of the two halves of a central cloud seemed to suggest that the left half was less extinguished than when the two halves formed two clearly distinct objects. Estimation was improved in this central cloud condition, and it is more probable that this occurred because the left dots were perceived consciously often enough to allow intact estimation, rather than because estimation can operate implicitly over the left side of single objects. It is known that neglect can apply in the context of within-object processing or between-object processing, or both (Humphreys, 1998). Thus, it may be of interest in future studies to investigate estimation in patients with only within-object neglect (who neglect the left side of objects, wherever they may be situated), and compare their performance to patients with only between-object neglect (who neglect whole objects in left space) (e.g. Humphreys & Heinke, 1998). Patients with between-object neglect might be able to numerically process only a central cloud of dots. In contrast, patients with within-object neglect might present intact numerical processing of two separate clouds but not one central cloud. Patient FC had presented within-object neglect shortly after his stroke, however, we did not retest him for this type of neglect at the time of this study, at which time he presented clear between-object neglect.

Finally, as concerns the parallel (Dehaene & Changeux, 1993) or serial (Gallistel & Gelman, 1992) mechanism of numerical estimation, it is difficult to conclude from this study. When clouds of dots were separated to clearly form two competing objects, extinction occurred, and the patient’s estimation responses were not influenced by left numerosity, suggesting that estimation relies on spatial attention. However, it does not necessarily mean that it requires *serial* visual attention. If estimation had been preserved without spatial attention, it would have clearly supported the idea of a parallel underlying mechanism (Dehaene & Changeux, 1993). We believe that the absence of such a sparing does not lead to such a clear-cut conclusion. The fact that visual extinction reflects competition between stimuli might account for estimation processing being prevented in the extinguished field, even if this process might rely on a parallel mechanism.

An interesting finding which arises from this research is the fact that subitizing can occur independently from spatial attention, but not estimation of large quantities. This brings further evidence for separate systems for small and large quantities in human adults (Revkin et al., in press), as in non-human infants and pre-verbal infants (Feigenson et al., 2004a). Future investigations are needed to determine what allows subitizing to operate without spatial attention, and why this is not possible in the case of numerical estimation.

4 CHAPTER 4: NUMEROSITY PROCESSING IN SIMULTANAGNOSIA: WHEN ESTIMATING IS EASIER THAN COUNTING[15]

Susannah K. Revkin[1*], Manuela Piazza[2], Véronique Izard[3], Dalila Samri[4], Michel Kalafat[4], Stanislas Dehaene[1,5], & Laurent Cohen[1,4,6]

[1] Unité Inserm-CEA de NeuroImagerie Cognitive, CEA/SAC/DSV/DRM/NeuroSpin, F-91191 GIF/YVETTE, FRANCE

[2] Functional NeuroImaging Laboratory, Center for Mind Brain Sciences, University of Trento, 38068 Rovereto (TN) Italy

[3] Department of Psychology, Harvard University, Cambridge, MA, U.S.A.

[4] AP-HP, Hôpital de la Salpêtrière, Service de Neurologie, F-75013 Paris, France

[5] Collège de France, 75005 Paris, France

[6] Université Pierre et Marie Curie, Paris, France

* Corresponding author

[15] This chapter is an article which is currently in revision for *Neuropsychologia*.

4.1 ABSTRACT

Simultanagnosia, a disorder which usually affects patients with bilateral parietal damage, causes impairments in tasks requiring serial analysis of a visual scene, while perception of individual objects is spared, as well as performance in tasks where a parallel exploration of the visual scene is sufficient. In the numerical domain, it has previously been shown that, in accord with this serial/parallel dissociation, simultanagnosic patients present a severe deficit in counting visual sets of dots (which requires serial visual processing) while subiziting (the parallel enumeration of 1-3 items) can be preserved. However, there exists a debate as to whether *approximate* numerical judgments (estimation, comparison, addition, etc.) rely on a parallel or a serial process. We reasoned that if they rely on a parallel process, they should be preserved in simultanagnosic patients, in contrast to counting. We report results of a simultanagnosic patient which support this hypothesis, as she presented a severe impairment at counting sets of dots, which contrasted greatly not only with her performance at subitizing, but also with performance at estimation, comparison, and addition of large sets of dots, which were globally preserved.

4.2 INTRODUCTION

Simultanagnosia is a disorder which usually accompanies bilateral parietal damage and causes severe difficulties in perceiving complex visuals scenes (e.g. Balint, 1909, cited by Rizzo & Vecera, 2002). Typically, patients show intact perception of individual objects, but striking limits in reporting more than one object at a time, as well as severe difficulties in orienting in space when more than one object has to be tracked and searched for. These disorders can be very invalidating in everyday life, up to the point that these patients, for example, cannot find their way to the door when exiting the examination room, even after several visits, or cannot find the fork or knife on a table, even when the disposition of cutlery respects their usual table setting principles. In laboratory tests, these patients are impaired in tasks involving serial exploration of visuo-spatial displays (e.g. as required in feature conjunction search); however, in tasks where a parallel exploration is sufficient (e.g., feature – "popout" – search), they show intact performance (e.g. Coslett & Saffran, 1991).

Further evidence of impairments of serial explorations of visual displays in simultanagnosia comes from the disruption of patients' counting abilities. Dehaene and Cohen (Dehaene & Cohen, 1994) reported the case of a group of simultanagnosic patients who were unable to quantify sets when they comprised more than 2 to 3 objects. In fact, it is well established that the enumeration of sets of more then 3 or 4 items requires exploring all the items in sequence, by means of successive switches of attention (Trick & Pylyshyn, 1994; Piazza et al., 2003). On the contrary, quantification of small sets can occur "at a glance", with no cost for additional items up to 3 or 4 (errors are not modulated by the number in this small range, and reaction times show only a very slight increase) (Trick & Pylyshyn, 1994; Mandler & Shebo, 1982). For this reason, the quantification for one to three items, often referred to as "subitizing", is considered to rely on parallel processes.

For larger sets, when counting is not possible (for example when the items are presented for a very short time), the quantity of objects can only be apprehended approximately. In such estimation tasks, subject's responses are on average quite accurate. However, their variability across trials increases as the number increases. This pattern of response distribution, typical of estimation judgments also in perceptual domains (such as brightness or loudness estimation) is often referred to as scalar variability or Weber's law (Izard, 2006; Whalen et al., 1999). Interestingly, generally, reaction times in such estimation tasks are quite long (in the range of seconds) and not modulated by the number of items to be estimated. Does such a numerosity estimation process rely on a very fast exploration of the visual set by which each element is taken into account one after the other in a serial fashion (i.e., counting-like), or does the extraction of numerosity take all elements into account in parallel (subitizing-like)? Some have proposed that the estimation of numerosity relies on a pre-verbal counting-like process which is serial in nature (Gallistel & Gelman, 1992; Meck & Church, 1983). Others (Dehaene & Changeux, 1993) have proposed that the extraction of numerosity relies on a numerosity detector mechanism that is parallel in nature.

Here, we explore the mechanisms underlying estimation of large numerosities. In particular, capitalizing on the fact that serial exploration of space is impaired in simultanagnosia, we ask if and to what extent explicit and serial deployments of visual attention are necessary to apprehend and estimate the number of elements in a visual display.

Although simultanagnosia typically occurs after bilateral parietal lesions, often in relation to posterior cortical atrophy, the areas involved in spatial attention orienting are thought to be situated in the superior parietal lobule, and thus their lesion in simultanagnosia may spare the regions related to numerical judgments (anterior horizontal IntraParietal Sulcus segment, or hIPS) (Dehaene et al., 2003). Indeed, resting cerebral metabolism in posterior cortical atrophy patients presenting visuo-spatial deficits (such as the one presented in the present study) shows hypoactivation of the superior parietal lobule (Nestor, Caine, Fryer, Clarke, & Hodges, 2003). This area is strongly associated with both eye movements and movements of attention in space (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000) and can also be involved in numerical processing, in particular in serial counting (Piazza et al., 2003), but is clearly not specific to the number domain (Dehaene et al., 2003). With the idea that *number sense* itself, the core approximate numerical capacity (mediated by the hIPS) may be spared in simultanagnosic patients, we address the question whether use of number sense for approximate judgments of large quantities requires serial shifts of visual attention (mediated by the superior parietal lobule). According to Dehaene & Changeux's model (Dehaene & Changeux, 1993), it should not. This model therefore leads to the somewhat counter-intuitive prediction that a simultanagnosic patient who is unable to count should in contrast be able to subitize small quantities, but also estimate, compare, and manipulate large non-symbolic numerosities (granted the numerosity extraction process itself is intact). Alternatively, if large numerosities are extracted through a serial counting-like process, the patient should not be able to access numerosity for sets containing more than 3 objects.

Different accounts of the underlying deficits in simultanagnosia have been reported, sometimes related to different types of simultanagnosia: difficulties in linking spatial location of objects with their identity (Coslett & Saffran, 1991), a coarse coding of the spatial location of object features (McCrea, Buxbaum, & Coslett, 2006), impaired explicit access to spatial feature location or even spatial relationships which would nonetheless be correctly coded at a preattentive stage (Kim & Robertson, 2001), difficulties in disengaging attention from one of several stimuli (Pavese, Coslett, Saffran, & Buxbaum, 2002; Darlymple, Kingstone, & Barton, 2007). We will not examine which one of these accounts best explains the simultanagnosic profile of the patient we tested, but assume that our study should nonetheless inform us whether one or several of these different possible underlying processes are required for estimation of visually presented large quantities.

4.3 METHODS AND RESULTS

4.3.1 Case description

The patient we examined was a 60 year old right-handed native French speaking woman who had worked as an accountant and had no contributive medical history. She started presenting difficulties in writing and reading about five years prior to testing, and these difficulties were not accompanied by a reduction in visual acuity. The patient was later diagnosed with posterior cortical atrophy (Benson syndrome; Benson, Davis, & Snyder, 1988). MRI conducted during the testing period showed cerebral atrophy predominating in the parietal regions (see Figure 4-1).

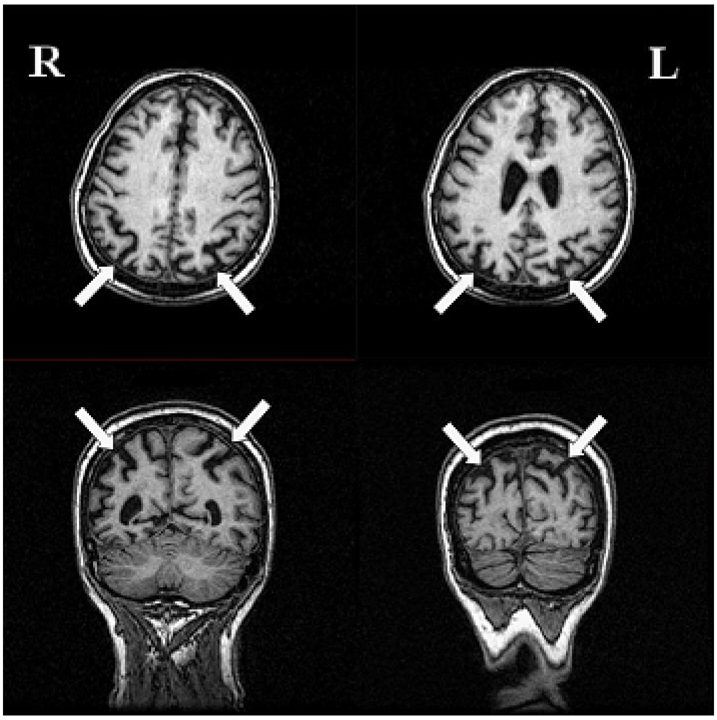


Figure 4-1 MRI - arrows indicate parietal damage, more pronounced in the left hemisphere.

Cerebral perfusion tomoscintigraphy showed severe hypoperfusion of bilateral posterior associative cortices; this hypoperfusion was more marked on the left side and in left peri-sylvian regions (see Figure 4-2).

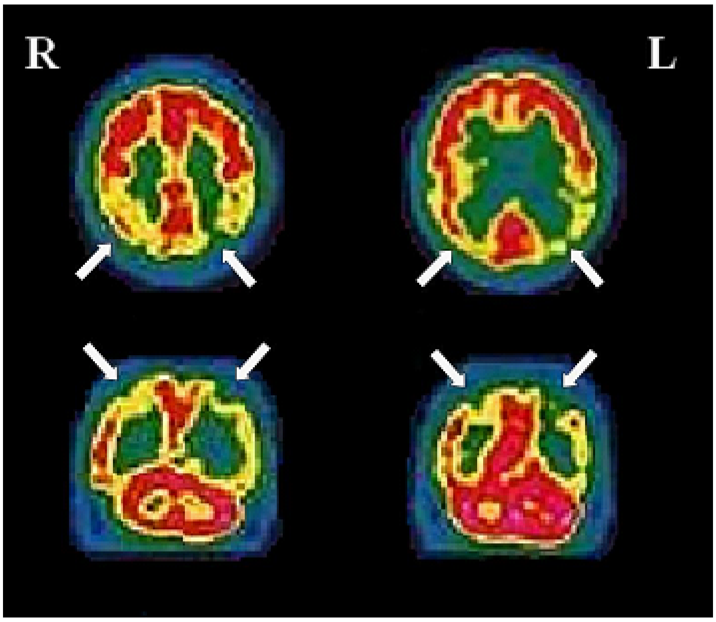


Figure 4-2 Cerebral perfusion tomoscintigraphy - arrows indicate parietal hypoperfusion, more pronounced in the left hemisphere.

She gave her informed written consent prior to her inclusion in the study, which was performed in accordance with the Declaration of Helsinki.

4.3.2 Control Subjects

For most tasks, we compared the patient's performance to that of five control subjects. These subjects were all right-handed native French speaking women, aged 61 to 65, and with a similar or slightly higher level of education than the patient. They all gave their informed written consent prior to their inclusion in the study, which was performed in accordance with the Declaration of Helsinki.

4.3.3 Neuropsychological examination

A neuropsychological evaluation was carried out one month before numerical testing began. It revealed a severe Balint syndrome (simultanagnosia, optic ataxia, discrete gaze apraxia) (De Renzi, 1996). In particular, her simultanagnosia was very severe, with disrupted performance in several tasks: piece-meal description of the Cookie Theft picture (see Appendix 3 for a transcription), severe deficits in the space perception subtests of the Visual Object and Space Perception Battery (VOSP, Warrington & James, 1991; Dot Counting: 1 correct out of 10; Position Discrimination: 10 correct out of 20; Number Location: 0 correct out of 10; Cube Analysis: 0 correct out of 10), difficulties in perceiving overlapping figures ("Overlapping Figures Task", Gainotti, D'Erme, & Bartolomeo, 1991). In contrast, single objects were correctly identified. The difficulties due to simultanagnosia were also present in everyday life. For example, the patient reported not being able to find different goods in the refrigerator, although her husband stated they were always kept in the same location; her husband reported that, while not being aware of quite obvious objects, her attention would however be drawn to a very small detail that he would not notice (spot of dust on his shirt); she could not find the door when leaving the testing room which she had been to many times. The patient also presented other visuo-spatial disorders (signs of right unilateral spatial neglect, visual and tactile extinction, important difficulties in planification and spatial organization during the copy of a complex figure). Moreover, the patient showed difficulties in working memory (in both verbal and visuo-spatial modalities) and in topographical orientation, alexia, agraphia due to both spatial and praxic difficulties, spatial acalculia, reflexive apraxia and difficulties in miming actions.

The experimental testing was carried out over 7 sessions which covered a period of 5 months. All computerized tasks were programmed and administered using e-prime software (Schneider et al., 2002).

4.3.4 Feature and conjunction search tasks

4.3.4.1 Method

The patient's goal in these tasks was to examine a set of bars and indicate whether it contained a red vertical bar (target) or not. In the *feature search task*, the target was presented among distractors that differed from it only by one feature, namely colour (distractors were white vertical bars). In the *conjunction search task*, distractors could differ from the target by one or two features, namely colour (white) and orientation (horizontal). In both tasks, the number of distractors was manipulated (3, 8, or 15). The bars (~0.1° thick and ~0.6° long) were arranged in an imaginary 2 by 2, 3 by 3 or 4 by 4 grid (respectively 3, 8 or 15 distractors; mean occupied area of ~6.5°). The set of bars was presented on a black background and remained present for 15 seconds or until the patient gave her response. Each trial was preceded by a small white fixation star presented centrally (1 second). The patient was asked to respond out loud as accurately as possible, but also as fast as possible[16]. Data was collected in one testing session and the experimenter controlled trial pace. The patient performed the feature search task first. For each task, the patient completed a total of 48 test trials which were presented in one bloc, and trials which differed according to number of distractors were randomized within each task. Target was present in about half the trials for each condition (number of distractors) and each task.

4.3.4.2 Results

Overall accuracy in the feature task (Figure 4-3.A) was optimal (100%), whereas the conjunction task yielded some errors (77% correct responses, see Figure 4-3.C).

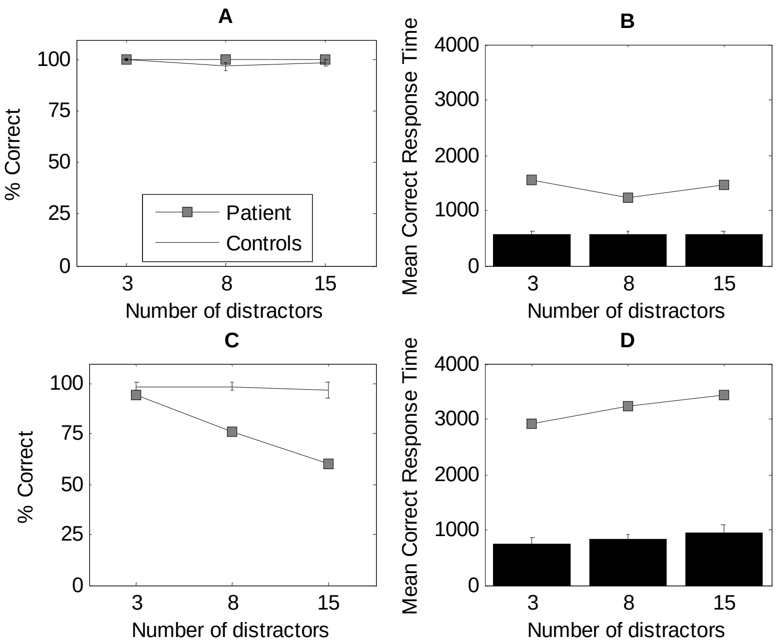


Figure 4-3 Patient's vs. controls' performance in the feature search task (**A**: accuracy; **B**: response times) and in the conjunction search task (**C**: accuracy; **D**: response times). (Error bars represent ±1 standard deviation).

A 2x3 Chi-squared analysis (task x number of distractors) revealed a significant effect of task ($\chi^2(1) = 11.2$, $p < .01$), whereas the effect of number of distractors was not significant. In the conjunction search task, accuracy (Figure 4-3.C) seemed to decrease linearly as the number of distractors became higher, although this effect did not reach statistical significance

[16] As the patient was unable to use the keyboard to respond herself, response times (RTs) were measured by experimenter keypress and must therefore be interpreted with caution.

in a χ^2 analysis. However, a direct comparison of conditions with 3 (94% correct) vs. 15 distractors (60% correct) yielded a significant effect ($\chi^2(1) = 4.9$, $p < .05$, difference in accuracy = 34%). Correct response times (RTs) were analysed in a 2x3 independent ANOVA (task x number of distractors). Overall correct RTs were twice as long in the conjunction task (3119 ms, see Figure 4-3.D) as in the feature task (1418 ms, Figure 4-3.B), a significant difference ($F(1, 77) = 85.11$, $p < .01$). There was no main effect of number of distractors nor interaction, although correct RTs in the conjunction task increased as the number of distractors became higher (difference of RTs in the conjunction task between the condition with 3 distractors vs. 15 = 534 ms ; much smaller and inversed difference in the feature task: -108 ms).

4.3.4.3 Comparison to controls[17]

For analysis of the patient’s performance in comparison to controls, we used a statistical program developed specifically for analysis of single case studies (for comparison on single measures, such as mean accuracy scores, mean RTs, difference in accuracy scores, intercept, etc.: Crawford & Garthwaite, 2002; Crawford & Howell, 1998; for slope comparison: Crawford & Garthwaite, 2004; for correlation comparison: Crawford, Garthwaite, Howell, & Venneri, 2003) for these tasks as well as most others (see below free estimation of large sets of dots, forced-choice estimation of large sets of dots, dots comparison of large sets of dots, and addition and comparison of large sets of dots).

In the feature task, the patient did not statistically differ from controls on any of the accuracy measures (see Table 4-1; see Figure 4-3 for graphs of all the data).

[17] Controls performed these search tasks in exactly the same conditions as the patient, except that they performed twice as many trials and answered themselves using the keyboard.

	Patient	Controls		t-value	p-value
		mean	SD	(df = 4)	(two-tailed)
Accuracy (%)					
Overall					
Feature Task	*100*	*99*	*1*	*0.91*	*0.41*
*Conjunction Task ** *	*77*	*98*	*2*	*-9.59*	*< 0.01*
*Difference Feature - Conjunction ** *	*23*	*0*	*2*	*-10.50*	*< 0.01*
With 3 distractors					
Feature Task	*100*	*100*	*0*	-	-
Conjunction Task	*94*	*99*	*2*	*-2.28*	*0.09*
With 8 distractors					
Feature Task	*100*	*97*	*2*	*1.37*	*0.24*
*Conjunction Task ** *	76	99	2	*-10.50*	*< 0.01*
With 15 distractors					
Feature Task	100	99	2	*0.46*	*0.67*
*Conjunction Task ** *	*60*	*97*	*4*	*-8.44*	*< 0.01*
Difference 15 - 3 distractors					
Feature Task	*0*	*-1*	*2*	*0.46*	*0.67*
*Conjunction Task ** *	*-34*	*-2*	*5*	*-5.84*	*< 0.01*
RTs (ms)					
Overall					
*Feature Task ** *	*1418*	*563*	*54*	*14.37*	*< 0.01*
*Conjunction Task ** *	3119	843	99	20.99	*< 0.01*
*Difference Feature - Conjunction ** *	*-1701*	*-204*	*59*	*23.16*	*< 0.01*
Difference 15 - 3 distractors					
*Feature Task * *	*-108*	*11*	*28*	*-3.88*	*< 0.05*
*Conjunction Task ** *	*534*	*215*	*55*	*5.30*	*< 0.01*

* Patient significantly differs from controls' at p < .05; ** at p < .01

Table 4-1 Comparison of patient's vs. controls' results in the feature and conjunction search tasks.

In contrast, in the conjunction task, she was significantly worse than controls on all these measures except accuracy with 3 distractors (Table 4-1). Moreover, compared to controls, the patient presented a significantly greater difference in overall accuracy between the two tasks (Table 4-1). Finally, compared to controls, the patient presented a significantly greater difference in RTs between the conditions with 15 vs. 3 distractors in both the feature and the conjunction tasks; however, this difference was much greater in the conjunction task and indicated a steeper increase in RTs compared to controls, whereas the difference in the feature task showed a slight decrease (whereas controls showed a very slight increase).

4.3.4.4 Comment

These results point to preservation of a fast parallel process of feature detection, and underline the difficulties that the patient presents in the use of a serial visual process.

4.3.5 Basic numerical examination[18]

The patient was able to count out loud from 1 to 20, and backward starting from 20 (although backward counting was quite slow). Her performance at reading one- and two-digit Arabic numerals was spared, although performance with three and more digits was perturbed. Writing Arabic numerals also proved difficult and yielded errors at both the lexical and syntactic levels, as well as distortions of individual digits and intrusions (which sometimes resembled letters from the alphabet). Performance on basic arithmetic tasks was generally spared: addition and subtraction trials (operands ranging from 0 to 9) presented visually and simultaneously read out to the patient yielded 80-100% correct responses depending on problem type, with RTs varying from 2 to 4 seconds, whereas performance at multiplication (operands ranging from 0 to 9) was slightly inferior (75% correct in 2-5 seconds). Results of a comparison task involving pairs of digits 1 through 9 presented one digit at a time were good (97% correct response out of 31 trials: 1 error). The patient also performed a cognitive estimation task, which consisted of 20 questions related to everyday life (e.g. "What is the mean length of a fork?") or about encyclopedic knowledge (e.g. "How high is the Eiffel tower?") and yielded only a few extreme answers (mostly overestimations, for e.g., when asked what the mean length of a bus was, she answered "300 meters" instead of something close to 12 meters).

4.3.6 Tasks involving non-symbolic stimuli

Here we describe and report results for the five main numerical tasks involving non-symbolic stimuli, namely enumeration of small sets of dots, free estimation of large sets of dots, forced-choice estimation of large sets of dots, comparison of pairs of large sets of dots, addition and comparison of large sets of dots. Each task allowed us to estimate whether the patient's responses varied qualitatively with numerosity in the same manner as in normal subjects. We also obtained quantitative estimates of the precision of numerical estimation. In the three first tasks, we measured the variation coefficient (standard deviation divided by mean response) and its relation to numerosity. Indeed, when a subject is asked to estimate the number of items in a set (either by producing a verbal response or by reproducing the numerosity in a non-verbal fashion, for example by means of finger tapping), judgments become less precise as numerosity increases in such a way that the variability in responses increases *proportionally* to the increase in mean response, thus yielding a constant variation

[18] Norms were not obtained for these tasks; an optimal performance is expected for most of them in healthy adults (except for the cognitive estimation task).

coefficient, a characteristic which is referred to as "scalar variability" (Gallistel & Gelman, 1992; Whalen et al., 1999; Izard, 2006). We examined if this relation still held in our patient. In the last two comparison tasks, another measure, the behavioral Weber Fraction, was used to apprehend the precision of the numerical comparison process. This measure is based on the fact that, in non-symbolic numerical comparison, performance typically improves with the ratio of the numbers to be compared. Although more complicated fits can be used (see Dehaene, 2007, in press), the Weber fraction can be approximated as w=r-1 where r is the ratio leading to 75% correct (as estimated by interpolating the accuracy curve with a sigmoid function of ratio). For both the coefficient of variation and the behavioral Weber fraction, we tested if the patient's values were higher than those of controls, which would indicate a reduced precision of numerical estimates.

4.3.6.1 Enumeration of small sets of dots (unlimited presentation)[19]

4.3.6.1.1 METHOD

In this task the patient was presented with one to eight dots and was instructed to enumerate them, by counting them if necessary. She was asked to respond as accurately as possible but also to minimise response time. The dots were black (mean visual angle of 0.9°) and appeared in a white central disk (mean visual angle of 8.4°), and were always preceded by a black screen for 1.5 seconds. The dots remained on the screen until the patient gave a response and in any case never more that 10 seconds. Distance to the screen was about 80 cm. RTs were measured using a vocal key, and the experimenter took note of the patient's responses. The patient completed a total of 128 test trials (4 blocs of 32 trials), enumerating each numerosity 16 times in random order.

[19] Norms were not obtained for this task; an optimal performance is expected in healthy adults.

4.3.6.1.2 RESULTS

The patient made as much as 55% errors (Figure 4-4.A.).

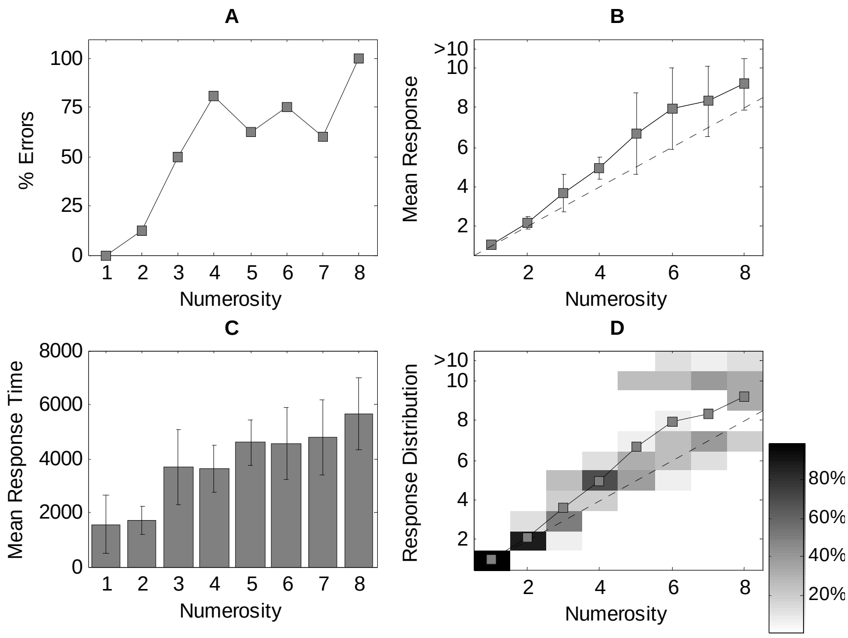


Figure 4-4 Patient's performance in enumeration of small sets of dots. (**A**) Percentage of errors. (**B**) Mean response. (**C**) Response times. (**D**) Response distribution. (Error bars represent ±1 standard deviation; note that 5 extreme answers (4x "20" and 1 x "50") have been recoded as >10 in graphs B and D; in graph D, the bar at right indicates response frequency in relation to total number of responses).

Interestingly, her errors were not distributed randomly across numerosities ($\chi^2(7) = 51.2$, $p < .01$). She made very few errors for numerosities 1 and 2 (respectively 0 and 13%, a non significant difference). However, there was a sudden significant increase between numerosities 2 and 3 ($\chi^2(1) = 5.2$, $p < .05$). The percentages of errors for 3 (50%) and above (mean (*M*) of 76%, ranging from 50 to 100) were much higher. This suggests that a parallel enumeration process for small numbers (subitizing) might be partially preserved and shows a range of 2 items. The pattern of RTs confirmed the error rate pattern: mean RTs for numerosities 1 (1562 ms; *SD* = 1098 ms) and 2 (1713 ms; *SD* = 531 ms) (a non significant difference) were much faster than for numerosities 3-8 (mean RT across these numerosities = 4472 ms, *SD* = 1198 ms). A linear regression indicated a general influence of numerosity on RTs ($R = 130.62$, p < .01, see Figure 4-4.C). A linear regression restricted to RTs in the 3-8 range still indicated an influence of numerosity ($R = 10.53$, $p < .01$). The first significant increase of RTs between consecutive numerosities was detected between numerosities 2 and 3

($t(28) = -5.0$, $p < .01$). A possible indication that the patient's RTs might not be related to counting, but perhaps to estimation, comes from the fact that the correlation between RTs and the presented numerosities ($r = .74$, $p < .01$) was significantly higher than the correlation between RTs and responses ($r = .51$, p < .01) ($t(125) = 4.31$, p (two-tailed) < .01; Williams' significance test for differences between non-independent correlations: 1959, cited by Crawford, Bryan, Luszcz, Obonsawin, & Stewart, 2000). Although our patient's error rate was very high, her response pattern did not reflect chance performance: her responses were positively correlated to the presented numerosities ($r = .63$, p < .01) and increased significantly with numerosity ($R = 80.24$, $p < .01$; slope = 1.52) (see Figure 4-4.B for mean response and Figure 4-4.D for response distribution). Variation coefficient ($M = .34$, $SD = .31$) increased with numerosity ($R = 7.33$, $p < .05$, slope = .09).

4.3.6.1.3 COMMENT

Results from this task show a severe impairment in counting visual sets of dots. However, the patient's correlation of responses with presented numerosities, associated with a preservation of subitizing, suggests that a parallel approximate process, such as numerical estimation, might have been used by the patient although she clearly cannot rely on exact serial counting anymore. This supposition also relies on the fact that the variability in the patient's responses to a given numerosity increased concurrently with the mean response, suggesting scalar variability. Yet another possibility is that the patient was simply still using a faulty counting process and that the variance in her responses reflects counting errors. We therefore used further tests to investigate whether numerosity estimation of briefly presented large sets of items was preserved.

4.3.6.2 Free estimation of large sets of dots (short presentation: 3 seconds)

4.3.6.2.1 METHOD

In this task the patient was presented with sets of dots which represented the following 11 numerosities: 10, 13, 17, 22, 29, 37, 48, 63, 82, 106, 138. The patient was instructed to estimate as accurately as possible the quantity of dots present in the display without counting. In order to prevent the patient from using non-numerical parameters that usually co-vary with numerosity (e.g. density or the area of the envelope of the clouds of dots), half the stimuli consisted of groups of constant density across numerosities, and for the other half, constant envelope of the clouds of dots (with randomization of this variable across trials). Data was collected over three testing sessions. In each session, the patient performed 3 blocs (each bloc containing calibration and 22 test trials). Calibration consisted of examples of stimuli other than those tested, but sampling the same range (numerosities 15, 60 and 140). Two examples of each calibration numerosity were presented, one from a set of constant density, and one from a set of constant total occupied area, while the patient was informed of the exact numerosity (e.g.: “Here are 15 dots”). Calibration dots remained on the screen for 10 seconds or until the patient was ready to see the next set. During the first session only, the patient was not explicitly informed of the range of test stimuli (10 to 140). Test numerosities were each presented 6 times in random order during each session. The patient completed a total of 198 test trials, enumerating each numerosity 18 times. During test trials, the dots remained on the screen for 3 seconds (1400 ms in the first session). The dots were black (mean visual angle of 0.2°) and appeared in a white disc (mean visual angle of 8.4°) which remained on the screen throughout the experiment. RTs correspond to experimenter key press, who entered the patient’s response directly on the computer keyboard. After each response was entered, the white disc remained empty for 700 ms before the next set of dots appeared.

4.3.6.2.2 RESULTS[20]

During the first session, in which the patient was not informed of the range of presented numerosities, she responded “1000” 8 times in association to numerosities ranging from 63 to 138. In the two other sessions, she was both calibrated and instructed of the approximate range, which led her to reduce but not totally eliminate her responses “1000”. All responses “1000” (11 in total) were removed from the data, as we considered that this particular response might reflect a purely categorical appreciation of numerosity (“a lot”) rather than continuous numerical evaluation.

[20]Unless specified otherwise, we report results and analyses excluding data from the extremes numerosities (10 and 138) to avoid noise from anchoring effects.

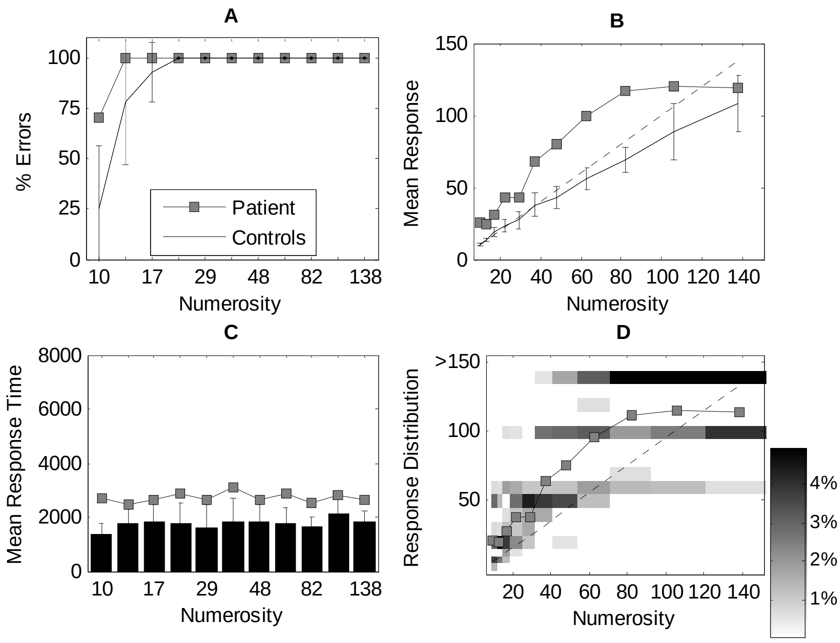


Figure 4-5 Patient's vs. controls' performance in free estimation of large sets of dots. (**A**) Percentage of errors. (**B**) Mean response. (**C**) Response times. (**D**) Response distribution. (Error bars represent ±1 standard deviation; note that responses "1000" have been removed; in graph D, only the patient data is depicted, and the bar at right indicates response frequency in relation to total number of responses).

The patient's error rate was very high (100% for all numerosities except for 10 for which she made 71% errors; see Figure 4-5.A). RTs (*M* = 2720 ms, *SD* = 779 ms; see Figure 4-5.C) were stable across numerosities (linear regression is non significant; intercept = 2675, slope = 1). However, one must interpret the RT results with caution as they correspond to experimenter key press. The high percentage of errors and relatively flat RT function are expected even in healthy subjects since the task conditions (limited stimuli duration) and instructions are meant to induce an approximate estimation process and do not allow for exact counting. The patient's responses increased with numerosity (*R* = 210.64, $p < .01$), and there was clearly a tendency to overestimate, as mean response was consistently superior to the correct response across numerosities (except for the largest extreme) (Figure 4-5.B). There was a high correlation between the presented numerosities and the patient's responses (*r* = .76, p < .01). The spread of the patient's responses (Figure 4-5.D) tended to increase as numerosity increased, suggesting scalar variability. Indeed, the patient's mean variation coefficient was .44 (*SD* = .17) and was essentially constant, decreasing only very slightly across numerosities (*R* = 9.66, $p < .05$; intercept = .63, slope = -.004). One can also observe from the response distribution (Figure 4-5.D) that some verbal responses, such as responses

60, 100 and 140, were used more often than others, covering large ranges of numerosities. Finally, additional analyses suggest that our patient's responses could have been influenced by non-numerical parameters. There was indeed a significantly greater correlation between numerosity and response in trials of constant density (r = .88, p < .01) compared to trials of constant total occupied area (r = .66, p < .01) (z = 3.55, p < .01). There were however no significant differences between these two types of trials as regards overall percentage of errors and mean variation coefficient.

4.3.6.2.3 COMPARISON TO CONTROLS[21,22]

The patient did not statistically differ from controls' regarding overall error rate, mean RT, regression of RTs or response against numerosity, or numerosity-response correlation (see Table 4-2; see also Figure 4-5 for graph of controls' data).

	Patient	**Controls**		**t-value**	**p-value**
		mean	SD	(df = 4)	(two-tailed)
Errors (%)					
Overall	100	97	5	0.55	0.61
Constant density	*100*	*98*	*4*	*0.46*	*0.67*
Constant area	*100*	*96*	*6*	*0.61*	*0.58*
RT (ms)					
Overall	2720	1790	561	1.51	0.21
Regression of RT against numerosity					
Intercept	*2675*	*1684*	*749*	*1.21*	*0.29*
Slope	*1*	*2*	*7*	*NA*	*within 2 SDs*
Response					
Regression of response against numerosity					
Intercept	*17.65*	*5.48*	*4.66*	*2.38*	*0.08*
Slope	*1.12*	*0.79*	*0.17*	*NA*	*within 2 SDs*
Numerosity-response correlation coefficient	0.76	0.82	0.05	-1.05	0.35
Constant density	*0.88*	*0.83*	*0.03*	*1.44*	*0.22*
Constant area	*0.66*	*0.83*	*0.06*	*-2.02*	*0.11*
Mean variation coefficient *	0.44	0.27	0.05	2.98	< 0.05
Constant density	*0.34*	*0.28*	*0.05*	*1.10*	*0.34*
Constant area	*0.42*	*0.24*	*0.06*	*2.74*	*0.05*
Regression of variation coefficient against numerosity					
Intercept *	*0.63*	*0.18*	*0.09*	*4.56*	*< 0.05*
Slope *	*-0.004*	*0.002*	*0.001*	*-4.47*	*< 0.05*

* Patient significantly differs from controls' at p < .05
NA: statistical analysis was not possible due to differences among the controls' error variances

Table 4-2 Comparison of patient's vs. controls' results in the free estimation task.

[21] Controls performed this task in exactly the same conditions as the patient, except that they performed a total of 132 trials and that, although calibrated, they were never explicitly informed of the stimuli range.
[22] Unless specified otherwise, we report results and analyses conducted after excluding data from the extremes numerosities (10 and 138) to avoid noise from anchoring effects.

However, the patient's mean variation coefficient across numerosities was statistically higher than controls', and the components of the linear regression of variation coefficient against numerosity were also significantly different (Table 4-2). Regarding effects of non-numerical parameters, the patient did not statistically differ from controls on error rate, numerosity-response correlation or mean variation coefficient when looking separately at trials controlled for density or for area (see Table 4-2); however, controls did not present a difference in numerosity-response correlation between the two types of trials (for both types, r = .83), in contrast to the patient. Similarly to the patient, controls' mean variation coefficient in trials of constant density was not significantly different in comparison to trials of constant area.

4.3.6.2.4 COMMENT

In sum, several measures of the estimation performance of the patient indicate partial preservation of estimation and no difference from controls. However, the patient's responses were overall less precise and more influenced by non-numerical parameters with respect to controls, indicating that the estimation system might not be completely intact. Could these differences and the repetitive use of some verbal labels (60, 100, 140, 1000) be reduced with the use of a forced-choice paradigm and calibration for all the presented numerosities? We used another estimation task in which our patient was instructed to select the appropriate answer among a specific and limited set of possibilities. Also, she was calibrated for all possible answers.

4.3.6.3 Forced-choice estimation of large sets of dots (decades)

4.3.6.3.1 METHOD

In this task the following numerosities were presented: 10, 20, 30, 40, 50, 60, 70, 80. The patient was instructed to estimate as accurately and as fast as possible the quantity of dots present in the display by choosing from this set of responses without counting. Either density of the dot display (half the stimuli) or dot size (half the stimuli) was held constant (randomization across trials). Data was collected over three testing sessions, each starting with calibration, as in the previous experiment, but for all test numerosities (i.e. numerosities 10 through 80). Overall, the patient completed a total of 240 test trials, estimating each numerosity between 28 and 33 times. During test trials, the dots remained on the screen for 3 seconds or until the patient gave a response. After the dots disappeared, the patient could still give an answer before the next trial began. The dots were black (mean visual angle of 0.2°) and appeared in a white disc (mean visual angle of 6°) which remained empty for 2 seconds before each trial. RTs were collected using a vocal key, and the patient's answers were entered directly onto the computer keyboard by the experimenter. During the second session, the patient wore a new pair of glasses which corrected for far sight, and which she did not wear during the other sessions.

4.3.6.3.2 RESULTS[23]

Data did not vary much from one session to another and was therefore collapsed across the three testing sessions.

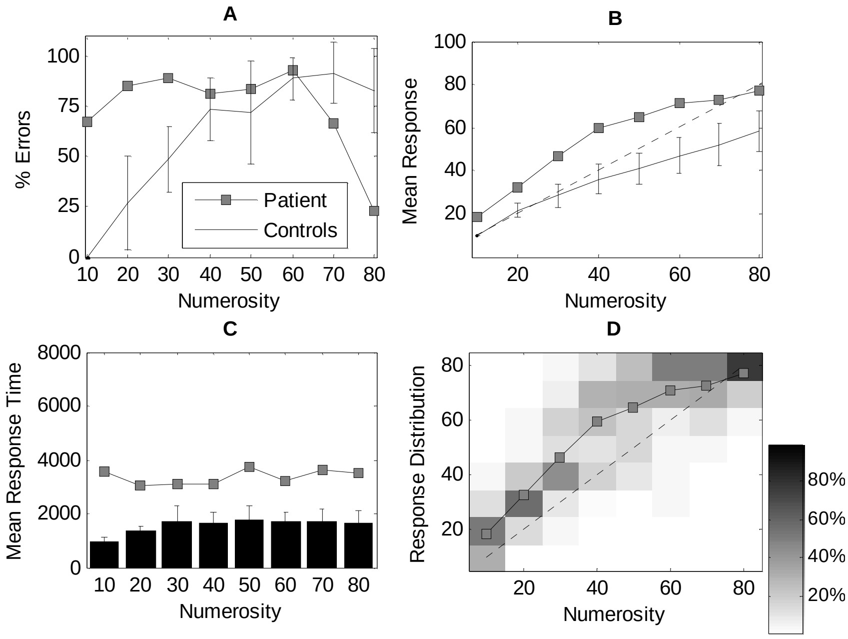


Figure 4-6 Patient's vs. controls' performance in forced-choice estimation of large sets of dots. (**A**) Percentage of errors. (**B**) Mean response. (**C**) Response times. (**D**) Response distribution. (Error bars represent ±1 standard deviation; in graph D, only the patient data is depicted, and the bar at right indicates response frequency in relation to total number of responses).

Our patient showed a reduced overall percentage of errors compared to her performance in the previous estimation task (*M* = 83%, vs. 100% in the previous task; see Figure 4-6.A for error rate in this task). RTs (*M* = 3319 ms, *SD* = 1173 ms) were fairly stable across

[23] Unless specified otherwise, we report results and analyses excluding data from the extremes numerosities (10 and 80) to avoid noise from anchoring effects.

numerosities, although there was a slight significant increase with numerosity ($R = 4.41$, $p < .05$; intercept = 2807, slope = 11; Figure 4-6.C), suggesting use of a same parallel process across stimuli. Responses were tightly related to the presented numerosity ($r = .73$, $p < .01$; Figure 4-6.B), increasing as numerosity increased ($R = 200.87$, $p < .01$). As in the previous estimation task, response distribution also reflected a tendency to overestimate, mean response being again consistently superior to the correct response across numerosities, except of course for the maximum numerosity (80, for which it is not possible to overestimate in this forced-choice paradigm). Again, the response distribution (Figure 4-6.D) indicated scalar variability, although it was "contaminated" by an expected anchoring effect of the maximum numerosity (reduced variation in responses to the two largest numerosities). The patient's mean variation coefficient (.22; *SD* = .07) was much lower than in the previous task (.44) and again showed only a slight linear decrease across numerosities ($R = 37.65$, $p < .01$; intercept = .37, slope = -.003). The patient made use of all the possible responses, without showing predominant use of a particular subset of responses. She also showed an overall reduction in the variability of responses for each numerosity compared to the previous task. Finally, several additional analyses suggested that our patient's responses were based on numerical information and not on information derived from other non-numerical continuous parameters. Indeed, there was no statistical difference between trials of constant dot density and trials of constant dot size as concerns error rate, numerosity-response correlation or mean variation coefficient.

4.3.6.3.3 COMPARISON TO CONTROLS[24,25]

The patient did not differ from controls regarding overall error rate, although she was significantly slower (see Table 4-3; see also Figure 4-6 for graph of controls' data).

[24] Controls performed this task in exactly the same conditions as the patient, except that they performed a total of 160 trials.

[25] Unless specified otherwise, we report results and analyses conducted after excluding data from the extremes numerosities (10 and 80) to avoid noise from anchoring effects.

	Patient	**Controls**		**t-value**	**p-value**
		mean	SD	(df = 4)	(two-tailed)
Errors (%)					
Overall	83	67	9	1.62	0.18
Constant density	*82*	*67*	*8*	*1.71*	*0.16*
Constant dot size	*85*	*69*	*10*	*1.46*	*0.22*
RTs (ms)					
Overall *	3319	1656	387	3.92	< 0.05
Regression of RT against numerosity					
*Intercept ** *	*2807*	*1416*	*228*	*5.58*	*< 0.01*
Slope	*11*	*5*	*5*	*NA*	*within 2 SDs*
Response					
Regression of response against numerosity					
Intercept	*22.27*	*10.32*	*4.36*	*2.50*	*0.07*
Slope	*0.80*	*0.61*	*0.15*	*NA*	*within 2 SDs*
Numerosity-response correlation coefficient	0.73	0.76	0.04	0.00	1.00
Constant density	*0.76*	*0.84*	*0.03*	*0.00*	*1.00*
Constant dot size	*0.70*	*0.72*	*0.08*	*0.00*	*1.00*
Mean variation coefficient	0.22	0.21	0.04	0.21	0.85
Constant density	*0.22*	*0.18*	*0.05*	*0.73*	*0.51*
Constant dot size	*0.21*	*0.21*	*0.05*	*0.00*	*1.00*
Regression of variation coefficient against numerosity					
Intercept	*0.37*	*0.17*	*0.13*	*1.40*	*0.23*
Slope	*-0.003*	*0.001*	*0.002*	*-1.49*	*0.21*

* Patient significantly differs from controls' at p < .05; ** at p < .01
NA: statistical analysis was not possible due to differences among the controls' error variances

Table 4-3 Comparison of patient's vs. controls' statistical results in the forced-choice estimation task.

Concerning the regression of RTs against numerosity, the intercept was significantly higher than the controls' but the slope was similar (Table 4-3). Linear regression of response against numerosity, numerosity-response correlation, variation coefficient and linear regression of variation coefficient against numerosity did not statistically differ from controls' (Table 4-3). Concerning non-numerical continuous parameters, the patient did not statistically differ from controls on error rate, numerosity-response correlation and mean variation coefficient when looking separately at the two types of trials (see Table 4-3); also, similarly to the patient, controls did not present a significant difference in numerosity-response correlation nor in mean variation coefficient between the two types of trials.

4.3.6.3.4 COMMENT

In sum, our patient was able to improve her estimation performance in this task which contains a smaller set of numerosities, provides calibration for all numerosities, and constrains responses through a forced-choice paradigm. RTs were fairly stable across numerosities, and response distribution suggested scalar variability, which leads us to think estimation was preserved and that it reflected use of a parallel process. The patient still showed a tendency to overestimate in comparison to controls, but did not significantly differ from the controls on all measures. In particular, in contrast to the free estimation task, the patient no longer presented differences in performance in relation to non-numerical parameters, and additionally, her variation coefficient, which is a measure of the precision of the estimates was not longer different from controls in this task. These results suggest that the difficulties in the free estimation task might not have been due to a deficit at the numerical representation level, but perhaps to difficulties in focusing on numerosity and in selecting and using the appropriate verbal labels. To address this last issue more directly, we presented our patient with two tasks in which she had to compare and add non-symbolic stimuli, with no requirement to use verbal labels.

4.3.6.4 Comparison of large sets of dots

4.3.6.4.1 METHOD

The patient was presented with two large sets of dots one after the other, which she was to compare by indicating which one contained the most dots as accurately and as fast as possible[26]. Each set could contain a numerosity ranging from 15 to 128. The ratio between the two sets was manipulated to form four ratio categories: ratio ~1.3, ~1.5, 2 or 4. The first set of dots was always yellow and the second blue, so that the patient answered “yellow” or “blue” to indicate the most numerous set. At the viewing distance of 82 cm, dots subtended a mean visual angle of 0.2°, and mean occupied area a visual angle of 5.1° (width) and 4.7° (height). The session began with five training trials with feedback (“correct” or “incorrect”). She performed a total of 72 test trials (18 trials for each ratio category in randomized order). The background was black and a small white central fixation dot appeared (600 ms) before each set of dots, which also appeared centrally (1 second). The second set of each comparison pair was followed by a black screen which remained until the patient gave a response. The largest set of dots was presented first in half the trials (order was randomized across trials). Data was gathered in one session.

[26] As the patient was unable to use the response box, RTs were measured by experimenter keypress and must therefore be interpreted with caution.

4.3.6.4.2 RESULTS

Accuracy was quite high (*M* = 81%) and increased in a linear fashion as ratio between the two numbers became larger (see Figure 4-7.A).

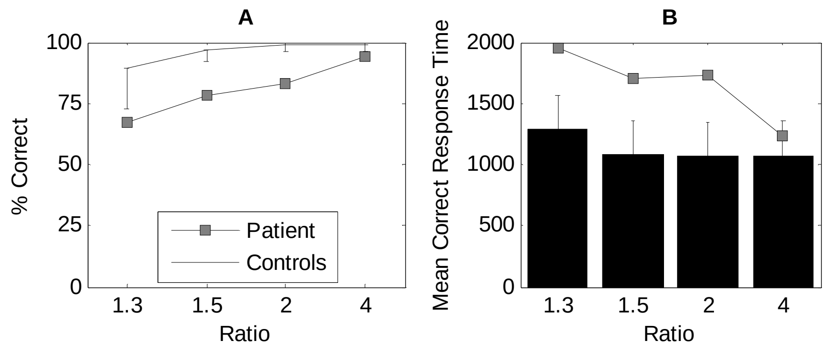


Figure 4-7 Patient's vs. controls' performance in comparison of large sets of dots. (**A**) Percentage of correct responses. (**B**) Mean response time. (Error bars represent ±1 standard deviation).

This distance effect was not statistically significant when taking into account all ratios, however, direct comparison between accuracy with ratio 1.3 vs. 4 was significant ($\chi^2(1) = 4.4$, $p < .05$, accuracy difference = 27%). Accuracy statistically differed from chance for all ratios except the smallest (for ratio 1.5, $\chi^2(1) = 5.6$, $p < .05$; for ratio 2, $\chi^2(1) = 8$, $p < .01$; for ratio 4, $\chi^2(1) = 14.2$, $p < .001$). The behavioural Weber Fraction was of 0.54. Correct RTs (*M* = 1621 ms, *SD* = 486 ms) varied across ratios and also followed a distance effect pattern (faster RTs for larger ratios), as was confirmed by a linear regression ($R = 21.50$, $p < .01$) (Figure 4-7.B), with a large difference between the smallest and largest ratio (718 ms faster with the largest ratio).

4.3.6.4.3 COMPARISON TO CONTROLS[27]

The patient significantly differed from controls on overall mean accuracy and accuracy with ratios 1.5 and 2, but not with ratios 1.3 and 4, nor concerning the difference in accuracy between the largest and smallest ratio (Table 4-4; see also Figure 4-7 for graph of controls' data).

[27] Controls performed this task in exactly the same conditions as the patient, except that they responded themselves using the response box.

	Patient	Controls		t-value	p-value
		mean	SD	(df = 4)	(two-tailed)
Accuracy (%)					
Overall *	81	96	4	-3.42	< 0.05
Ratio 1.3	67	89	16	-1.26	0.28
Ratio 1.5 *	78	97	5	-3.47	< 0.05
Ratio 2 **	83	99	3	-4.87	< 0.01
Ratio 4	94	99	3	-1.52	0.20
Difference ratio 4 - ratio 1.3	27	10	16	0.97	0.39
Weber Fraction	0.54	0.13	0.13	2.88	0.05
RTs (ms)					
Overall	1621	1131	258	1.73	0.16
Ratio 1.3	1946	1285	279	2.16	0.10
Ratio 1.5	1705	1088	268	2.10	0.10
Ratio 2	1735	1073	274	2.21	0.09
Ratio 4	1228	1073	284	0.50	0.64
Difference ratio 4 - ratio 1.3	-718	-212	186	2.48	0.07
Regression of RT against ratio					
Intercept **	*2166*	*1229*	*261*	*3.27*	*< 0.05*
Slope [a]	*-234*	*-44*	*50*	*NA*	*over 2 SDs*

* Patient significantly differs from controls' at p < .05; ** at p < .01
NA: statistical analysis was not possible due to differences among the controls' error variances
[a] Patient's result is lower/higher than 2 SDs of the controls' result

Table 4-4 Comparison of patient's vs. controls' results in the dots comparison task.

The patient's behavioural Weber Fraction did not significantly differ from controls'. The patient's overall mean correct RT, correct RT for each ratio category and the difference in RT between the largest and smallest ratio did not significantly differ from controls' (Table 4-4). However, the patient significantly differed from controls on measures of the linear regression of correct RTs against numerosity, presenting a higher intercept and a steeper slope (Table 4-4).

4.3.6.4.4 COMMENT

These results suggest overall spared ability in comparison of large sets of dots, with above chance performance for most ratio categories and a pattern that followed a distance effect. However, performance was overall not as accurate as controls, indicating that the process might be slightly impaired. Having established that estimation as well as comparison of large sets of dots was possible within certain limits, we were interested to find out if basic arithmetical manipulation of these non-symbolic quantities was also relatively spared. This was investigated in an addition task.

4.3.6.5 Addition and comparison of large sets of dots

4.3.6.5.1 METHOD

In each trial, the patient was presented with three large sets of dots one after the other, the first two being yellow and the third blue (See Figure 4-8 for an example of the stimuli).

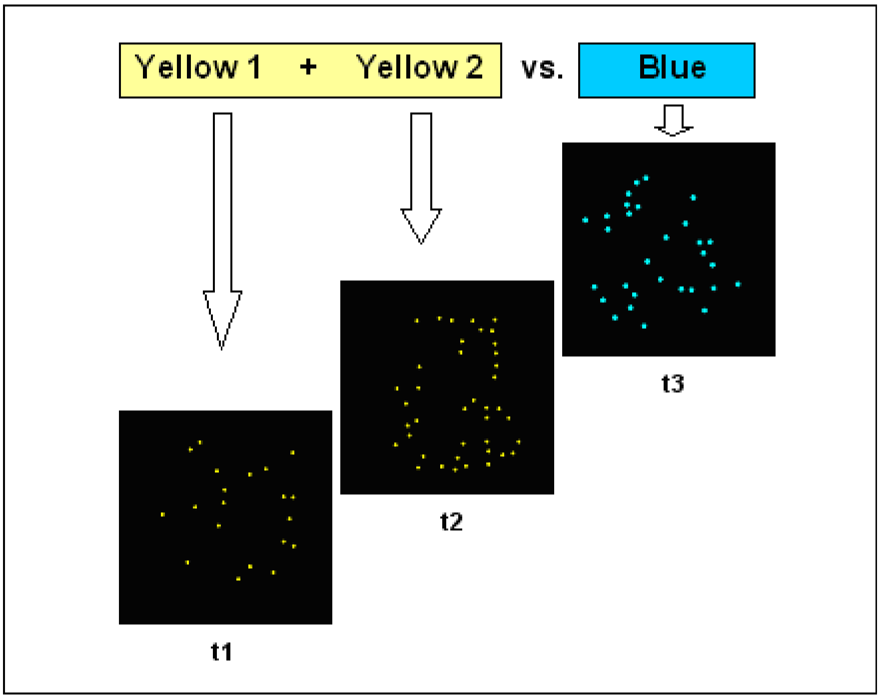


Figure 4-8 Example of the stimuli used in the addition and comparison of large sets of dots.

She was required to mentally "add" the two yellow sets and compare this result to the blue set, in order to determine whether there were more yellow dots altogether or more blue dots. She was asked not to count, but to estimate as accurately and as fast as possible the number of dots in each set and respond by saying "yellow" or "blue" in reference to the largest quantity[28]. The ratio between the two numerosities that constituted each comparison pair (i.e. between the result of the addition of the yellow sets, and the blue set) was manipulated to form three ratio categories, from which stimuli were selected randomly across trials: ~1.3, ~1.5, 2. Each session began with 10 training trials with feedback ("correct" or "incorrect"). The background was black and stayed empty (700 ms) before each set of dots appeared centrally (700 ms). The third set of dots was followed by a black screen (6 seconds) before the following trial began. Half the sets was of constant dot size (mean visual angle of

[28] As the patient was unable to use the microphone/response box, RTs were measured by experimenter keypress and must therefore be interpreted with caution.

0.2°), and the other half of constant total occupied area (about 5.7°; randomisation of this variable across trials). Data was gathered over two sessions with a total of 96 trials. In half the trials the yellow quantity was larger than the blue quantity (randomization across trials).

4.3.6.5.2 RESULTS

Results collected from two different testing sessions were similar and data was therefore collapsed across sessions.

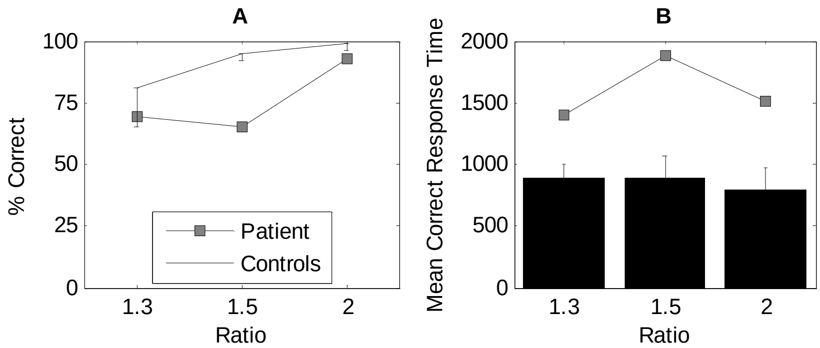


Figure 4-9 Patient's vs. controls' performance in addition and comparison of large sets of dots. (**A**) Percentage of correct responses. (**B**) Mean response time. (Error bars represent ±1 standard deviation).

Overall accuracy was good (*M* = 76%; see Figure 4-9.A). Accuracy varied a lot between the smallest (1.3) and largest ratio (2), increasing from 69% to 93% (accuracy difference = 24%), reflecting a distance effect confirmed by statistical analysis ($\chi^2(2) = 7$, $p < .05$), even though it was the lowest for ratio 1.5 (65% correct). Accuracy differed significantly from chance for all ratios except the smallest (for ratio 1.5, $\chi^2(1) = 4.9$, $p < .05$; for ratio 2, $\chi^2(1) = 19.6$, $p < .001$). Concerning the effect of non-numerical parameters, overall accuracy did not vary across conditions. The patient's behavioural Weber Fraction was 0.55. Correct RTs (Figure 4-9.B; *M* = 1682 ms, *SD* = 595 ms) were analysed in a 2x3 independent ANOVA with non-numerical parameter (constant dot size or constant total occupied area) and ratio (1.3, 1.5 or 2) as independent variables, and showed no significant effect.

4.3.6.5.3 COMPARISON TO CONTROLS[29]

The patient did not significantly differ from controls concerning overall mean accuracy, accuracy with ratios 1.3 and 2, and difference in accuracy between the largest and smallest

[29] Controls performed this task in exactly the same conditions as the patient, except that they performed a total of 48 trials (16 trials with each ratio category) and responded themselves using the response box.

ratio, whereas her accuracy was significantly lower with ratio 1.5 (Table 4-5; see also Figure 4-9 for graph of controls' data).

	Patient	**Controls**		**t-value**	**p-value**
		mean	SD	(df = 4)	(two-tailed)
Accuracy (%)					
Overall	76	92	6	-2.43	0.07
Constant dot size	*73*	*91*	*6*	*-2.74*	*0.05*
Constant area	*78*	*93*	*8*	*-1.71*	*0.16*
Ratio 1.3	69	81	16	-0.69	0.53
Constant dot size	*75*	*80*	*17*	*-0.27*	*0.80*
Constant area	*63*	*83*	*21*	*-0.87*	*0.43*
Ratio 1.5 **	65	95	3	-9.13	< 0.01
*Constant dot size ** *	*55*	*95*	*7*	*-5.22*	*< 0.01*
*Constant area **	*72*	*95*	*7*	*-3.00*	*< 0.05*
Ratio 2	93	99	3	-1.83	0.14
Constant dot size	*90*	*98*	*5*	*-1.46*	*0.22*
Constant area	*100*	*100*	*0*	-	-
Difference ratio 2 - ratio 1.3	24	18	13	0.42	0.70
Constant dot size	*15*	*17*	*14*	*-0.13*	*0.90*
Constant area	*37*	*17*	*21*	*0.87*	*0.43*
Weber Fraction *	0.55	0.21	0.10	3.1	< 0.05
RTs (ms)					
Overall *	1682	858	158	4.76	< 0.05
Ratio 1.3 *	1397	885	120	3.90	< 0.05
Ratio 1.5 **	1885	890	180	5.05	< 0.01
Ratio 2 *	1516	798	179	3.66	< 0.05
Difference ratio 2 - ratio 1.3	119	-88	118	-1.60	0.19
Regression of RT against ratio					
*Intercept ** *	*2126*	*1089*	*167*	*5.66*	*< 0.01*
Slope	*-271*	*-144*	*123*	*NA*	*within 2 SDs*

* Patient significantly differs from controls' at p < .05; ** at p < .01
NA: statistical analysis was not possible due to differences among the controls' error variances

Table 4-5 Comparison of patient's vs. controls' results in the dots addition and comparison task.

The patient's overall mean correct RT and correct RT for each ratio category were significantly slower than controls', and the intercept of her linear regression of correct RTs against numerosity was significantly higher (Table 4-5). However, the slope of the linear regression was similar to controls', and the difference in RTs between the largest and smallest ratio did not significantly differ from controls' (Table 4-5). Concerning non-numerical parameters, the patient did not significantly differ from controls' in both trials controlled for dot size and trials controlled for area as concerns the different accuracy measures (Table 4-5) except accuracy with ratio 1.5 for which she was worse than controls on both types of trials (Table 4-5). Also, the patient's behavioural Weber Fraction was significantly higher than controls'. Finally, controls' correct RTs were also analysed in a 2x3 independent ANOVA with non-numerical parameter (constant dot size or constant total occupied area) and ratio (1.3, 1.5 or 2) as independent variables; similarly to the patient, none of the main or interaction effects were significant.

4.3.6.5.4 COMMENT

These results indicate that our patient was overall able to perform addition of large sets of dots, and that her performance followed a distance effect (accuracy). However, precision was lower than controls. Regarding RTs, the controls' faster RTs could be due to the fact that they used the response box themselves, whereas the experimentator was pressing the key for the patient after she verbalized the response; yet this was also the case in the dots comparison task, in which the patient's RTs were nevertheless globally similar to the controls'.

4.3.6.6 Comment on performance in tasks involving non-symbolic stimuli

We have shown that our patient presents partial preservation of subitizing, estimation, comparison and addition of sets of dots. We have also observed that her performance at counting, although very poor, indicates that she may in fact be performing the task by using an estimation strategy, as suggested by her response distribution. These observations suggest that she relied, in all these tasks, on a parallel process which allowed her to apprehend numerosity in an approximate fashion. Preservation of this type of fast, parallel process contrasts with alteration in a slower, serial process (essential for exact counting). This dissociation is further supported by the data of the feature and conjunction search tasks.

4.4 DISCUSSION

We report the numerical performance of a patient presenting massive simultanagnosia, a disorder causing difficulties in the coherent perception of several elements in a visual scene, whereas individually presented objects can be perceived correctly (e.g. Balint, 1909, cited by Rizzo & Vecera, 2002). These difficulties were present in several neuropsychological tasks, as well as in everyday life. In particular, the patient presented marked difficulties in serial search, whereas parallel (pop-out) search was preserved, a dissociation which has been demonstrated in other simultanagnosic patients (Coslett & Saffran, 1991; Dehaene & Cohen, 1994). In addition to basic neuropsychological and numerical evaluation, we administered a task that required exact counting and several tasks requiring approximate evaluation of large numerical quantities. In sum, the results showed a dissociation between exact counting, which was severely impaired (outside the subitizing range), and approximate extraction and manipulation of quantity, which were largely preserved. Indeed, counting of small quantities (3-8) was severely disrupted, whereas the enumeration of 1 and 2 items was possible. Although counting was error-prone, errors were not random and reflected use of an approximate estimation process (in addition to that of a faulty counting process). This estimation process was directly evaluated with much larger quantities in free as well as forced-choice estimation tasks. In these tasks, the patient's performance suggested general sparing of an approximate quantification process: the patient's estimation responses were not random but correlated with presented numerosity, moreover in a pattern that suggested scalar variability, a typical signature of estimation processes (Gallistel & Gelman, 1992; Whalen et al., 1999; Izard, 2006; Dehaene & Marques, 2002). However, some measures in the free estimation task (variation coefficient and its pattern in relation to numerosities) indicated that the precision of this process was altered in comparison to controls. The patient's performance in comparison of large sets of items, and in addition and comparison of large sets of items was consistent with the estimation data, indicating general sparing of a however less precise quantification process. In the estimation tasks, imprecision was reflected not only by overestimation in comparison to controls (mean response was overall about twice as high as controls'), but especially by a much greater variation in response (overall 3 to 4 times higher than controls'). In the comparison tasks, the patient was more imprecise than controls as she needed a greater difference in the quantities to be compared in order to reach the same level of accuracy as controls. Finally, in contrast to controls, the patient was influenced to some extend by non-numerical parameters in the first estimation task and tended to give extreme or repetitive answers, especially to large quantities (for e.g. responding "one thousand" for a numerosity smaller than 200). However these differences were no longer present in the forced-choice estimation paradigm with complete calibration to the presented numerosities. We will discuss this below, and present a tentative explanation in terms of executive demands.

The subitizing-counting dissociation that the patient presents is comparable to that reported in Dehaene and Cohen's (Dehaene & Cohen, 1994) group of patients. Whereas Gallistel and Gelman (Gallistel & Gelman, 1991; Gallistel & Gelman, 1992) consider subitizing as fast preverbal serial counting, Dehaene and Changeux (Dehaene & Changeux, 1993; see also van Oeffelen & Vos, 1982) have proposed that it reflects use of parallel numerical estimation. Although estimation is an approximate process, precision is higher with smaller quantities, in accord with Weber's law (Izard, 2006; Whalen et al., 1999), and could therefore result in a flawless performance for small subitizable numbers. Others have suggested that subitizing relies on visual mechanisms which are non numerical in nature but can occur in parallel, such as attentional indexing of objects (Trick & Pylyshyn, 1994). Since simultanagnosic patients do not have access to serial exploration processes, their reported ability to quantify small sets of items (Dehaene & Cohen, 1994) strongly argues in favor of a parallel numerosity extraction process.

In the same vein, subitizing has also been shown to be preserved in neglect patients, who present difficulties in orienting to and taking into account items situated in the space contralateral to their cerebral lesion (usually left space following right parietal damage) (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000). Both these findings argue in favor of a parallel view of subitizing. However, one cannot conclude from the neuropsychological studies (Dehaene & Cohen, 1994; Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000) that the patients in question used numerical estimation rather than a more general visual process to subitize. Moreover, different studies have shown that infants and non-human animals have distinct systems for very small quantities (visual indexing) and larger quantities (numerical approximate system), but this is less clear in adults (review: Feigenson et al., 2004a). Therefore the question remains open as to whether adults' fast enumeration of small quantities of visually presented dots relies on visual indexing, numerical estimation, both of these processes or another parallel process.

Here we further extended the counting-subitizing dissociation and probed the general preservation of approximate judgments of larger non-symbolic quantities. We show, for the first time, that a severely simultanagnosic patient can remain able, to some extent, to estimate, compare and manipulate large sets of dots. Furthermore, our patient's performance in the visual search tasks suggests that counting was disrupted because of difficulties in serial processes, whereas the approximate apprehension of numerosity (whether small or large) might be explained by the preservation of a parallel process (preserved pop-out effect). These results therefore suggest that approximate numerical judgments rely on a parallel process (as suggested by Dehaene & Changeux, 1993). Alternatively, they might rely on a serial preverbal counting process (as suggested by Gallistel & Gelman, 1992), but this process would then have to be fairly independent from visual attention, in contrast with verbal counting. In sum, the serial processing of visual stimuli and the various sub-processes that it may call upon and that may be impaired in simultanagnosia (feature location and identity binding, Coslett & Saffran, 1991; location coding, McCrea et al., 2006; explicit access to spatial maps, Kim & Robertson, 2001; disengagement of attention, Pavese et al., 2002, see also Darlymple et al., 2007), do not seem to be indispensable to estimate large quantities of visual stimuli.

However, as mentioned above, the patient's performance indicated a lesser precision in the approximate quantification process. One possibility is that the core numerical process is also slightly impaired. This core numerical capacity, *number sense*, which is shared with babies (Xu & Spelke, 2000), non-human animals (for a review, see Gallistel & Gelman, 1992), and indigenous populations with a restricted numerical lexicon (Pica et al., 2004; Gordon, 2004), is thought to be subserved by the parietal lobe, more specifically the horizontal segment of the intraparietal sulcus (hIPS; for a review, see Dehaene et al., 2003). It is possible that part of the patient's hIPS may already be affected by the degenerative disease. Another or additional possibility is that the spatial attention deficit interfered slightly with the perception of the stimuli, for instance by preventing the normal attentional amplification and grouping of a dispersed set of dots. This would explain that performance with symbolic numerical judgments requiring number sense was less affected (verbal subtraction, Arabic digit comparison), as these other tasks either did not involve visual perception (subtraction problems were read out loud) or only involved symbol identification which was clearly spared (Arabic digits were easily identified).

Finally, as mentioned above, the patient performance in the free estimation task was influenced by non-numerical parameters, and showed repetitive use of extreme answers. These difficulties disappeared when calibration was complete and when response selection was more controlled and less demanding (select a response among 8 possibilities, rather than a potentially infinite list of possible answers as in the first estimation task). Although speculative, we hypothesize that the difficulties in the free estimation task could be due to executive difficulties in the selection of response labels, in the calibration process, or in the capacity to focus on numerosity and not be distracted by other non-numerical parameters such as total occupied area or density of the cloud of dots. Data in support of this hypothesis comes from a recent study of a frontal patient with discrete executive disorders who presented intact numerical processing in several tasks involving non-symbolic stimuli, but significant difficulties in estimation without any prior calibration (overestimation, more marked in trials in which area co-varied with numerosity) whereas his performance was improved (and was less influenced by non-numerical parameters) after calibration (Revkin *et al.*, 2007). Indeed, the present patient also presented some executive difficulties in addition to her main visuo-spatial impairments, and her performance was significantly improved in conditions which might require less executive functions (forced-choice estimation paradigm with complete calibration).

The present data further document the cognitive pattern of performance of posterior cortical atrophy patients, showing that preservation of some approximate numerical processes is possible. Another study of numerical processing in a posterior cortical atrophy patient has recently been reported by Delazer and collaborators (Delazer et al., 2006), and contrasts greatly with the present case. Indeed, their patient presented deficits in approximate numerical tasks (including numerosity estimation) while counting was relatively spared (she was able to count up to 9 dots, whether arranged in curved lines, circles or unstructured patterns). It is not known whether subitizing was preserved (response time was not measured in this counting task). Although this patient presented simultanagnosia, it seems it was not important enough to disrupt counting (the authors suggest spatial attention was thus partially preserved). In contrast, a clear impairment in number sense is suggested (difficulties in estimation of numerosities and of the result of subtraction operations, poor verbal subtraction and division, pronounced distance effect on an Arabic digit comparison task). Taken together with preserved multiplication and addition arithmetic facts, this pattern of results was interpreted as reflecting a major deficit in number sense, a partial deficit in the visual attention component of numerical processing, and a sparing of the verbal component of numerical capacities. In the case of our patient, the results point to a general sparing of number sense, important deficits in visual attention, and a slight disruption of the verbal component of numerical processing (difficulties with multiplication).

The partial double dissociation exhibited by these two patients can be tentatively explained by the pattern of cerebral dysfunction. Indeed, Delazer and collaborators' patient (Delazer et al., 2006) had a bilateral parietal hypometabolism, more severe on the right, whereas our patient's posterior hypoperfusion was more marked on the left, thus perhaps explaining the difference in verbal and numerical performance. Indeed, the triple-code model (Dehaene et al., 2003) proposes a left-lateralized verbal component for rote arithmetic facts such as multiplication and sometimes addition, whereas subtraction problems would be resolved more often by quantity processing (bilateral parietal cerebral substrate). Moreover, the dissociation between counting and estimation could perhaps also be linked to the asymmetry in the cerebral dysfunction, in accord with the two neural systems reported by Piazza and collaborators (Piazza et al., 2006) imaging study (strictly right lateralized circuit for numerical quantity estimation, whereas counting activates additional left parietal regions).

Altogether, such cases indicate that subitizing, estimation, counting and attention orienting are partially dissociable functions, although all related to the parietal lobe. In the future, multiple single-case studies, followed by a fine correlation of the deficits with the extent of the lesions, could contribute to clarify their anatomical and functional relations.

Acknowledgments We warmly thank the patient and the control subjects for participating in this study. This study was supported by INSERM, CEA, a Marie Curie Research Training Networks of the European Community (MRTN-CT-2003-504927, Numbra project), a Marie Curie fellowship of the European Community (QLK6-CT-2002-51635), and a McDonnell Foundation centennial fellowship.

5 CHAPTER 5: THE ROLE OF EXECUTIVE FUNCTIONS IN NUMERICAL ESTIMATION: A NEUROPSYCHOLOGICAL CASE STUDY[30]

Susannah K. Revkin[1,2,3*], Manuela Piazza[4], Véronique Izard[5], Laura Zamarian[6], Elfriede Karner[6], & Margarete Delazer[6]

[1] INSERM, U562, Cognitive Neuroimaging Unit, F-91191 Gif/Yvette, France

[2] CEA, DSV/I2BM, NeuroSpin Center, F-91191 Gif/Yvette, France

[3] Univ Paris-Sud, IFR49, F-91191 Gif/Yvette, France

[4] Functional NeuroImaging Laboratory, Center for Mind Brain Sciences, University of Trento, Italy

[5] Department of Psychology, Harvard University, Cambridge, U.S.A.

[6] Innsbruck Medical University, Austria

* Corresponding author

[30] This chapter is an article currently in revision for *Neuropsychologia*

5.1 ABSTRACT

Patients with frontal lobe damage have been shown to produce implausible answers in cognitive estimation, a task requiring approximate answers to quantity-related questions of general knowledge. We investigated a patient with frontal damage who presented executive deficits and difficulties in cognitive estimation, to determine whether they could extend to perceptual numerical estimation (approximately evaluating the quantity of visually presented sets of items) and if so, whether they emerged from impairments to the internal representation of quantities or to strategic processes of response selection and plausibility checking. The patient produced extreme answers in the perceptual numerical estimation task, well outside of controls' range of answers (overestimation); however, other numerical measures showed a globally intact internal representation of numerical quantities. This suggests that this patient's cognitive and perceptual estimation deficits are due to executive dysfunction likely to interfere at the level of translation from an intact internal representation to output.

5.2 INTRODUCTION

It has long been known that focal frontal lobe damage can sometimes cause relatively isolated cognitive deficits, which almost go unnoticed, as general intellectual capacities can be spared. One striking finding revealed that some patients with frontal lobe damage, whose general intellectual abilities were intact, presented specific difficulties in cognitive estimation, the capacity to give approximate answers to questions of general knowledge for which no precise answer is readily known (Shallice & Evans, 1978). Indeed, these patients' performance, when presented with questions pertaining for example to the size, height, or weight of objects, was characterized by extremely implausible answers (example of an answer in response to the question "what is the length of an average man's spine?": "between 4 and 5 feet"). As intellectual capacities were spared, this type of deficit was interpreted as resulting from selective and regulative processes attributed to the frontal lobes (selecting possible answers; checking for the plausibility of each answer, etc.), rather than degradation of general knowledge.

On the other hand, other patient studies (Taylor & O'Carroll, 1995; Mendez, Doss, & Cherrier, 1998; Brand, Kalbe, & Kessler, 2002a; Della Sala, MacPherson, Phillips, Sacco, & Spinnler, 2004, Experiment 3) have brought evidence that cognitive estimation deficits may not be specific to patients with focal frontal lobe damage. Indeed, cognitive estimation can also be impaired in patients with posterior lesions, in these cases supposedly reflecting impairment of general knowledge itself (semantic memory). In the same vein, performance on the Cognitive Estimation Task (CET; Shallice & Evans, 1978) has been found to correlate with a test of semantic memory (in patients with Alzheimer's disease: Della Sala et al., 2004, Experiment 3; in healthy subjects: Della Sala et al., 2004, Experiment 2). Also, cognitive estimation as measured by the CET and by another task (Luria Memory Test) has been shown to correlate in patients having suffered traumatic brain injury not only with tests of intelligence, but also with tests of memory (Freeman, Ryan, Lopez, & Mittenberg, 1995). These findings suggest that cognitive estimation relies partly on long-term memory functions (in particular semantic memory) known to be mainly sub-served by the temporal lobe.

Importantly, most tasks used to evaluate *cognitive* estimation do not require a perceptual judgement of quantity (as would, for example, judging the length of the experimenter's spine). What happens in the case of *perceptual* estimation, of numerical quantity for example? Could this type of estimation, which calls upon processes implicated in the extraction and representation of numerosity, also involve executive strategic processes (selection in a context of uncertainty), like cognitive estimation does? If so, could perceptual estimation also be impaired following frontal lobe damage?

Perceptual numerical estimation, that is, explicit naming of an estimate of a quantity (in a task in which subjects are to give a verbal estimate of the quantity of a set of items) is different from implicit numerosity apprehension or comparison of numerical quantity for example, which have been more frequently studied (e.g. Piazza et al., 2004; Cantlon et al., 2006; Piazza et al., 2007). One important aspect of perceptual numerical estimation, which is not present in numerical comparison, is calibration, involved in the mapping from approximate numerical representation to a verbal response grid. Izard & Dehaene (Izard & Dehaene, in press) recently studied calibration in young healthy subjects, and found that there was a spontaneous tendency to underestimate, which could be countered by externally calibrating subjects (showing an example of a set concurrently to the correct verbal response). They suggested that this external calibration process was probably a mix between strategic and automatic adjustment of verbal responses to an internal numerical representation. Indeed, subjects reported trying to keep in mind the example and correct their estimation accordingly (strategic component), but also had the impression of not making a very big adjustment, which contrasts with the relatively large adjustment objectively made (automatic component). Could external calibration rely on executive processes sub-served by the frontal lobe, as it possibly calls upon a strategic component?

Not many studies have specifically investigated the cerebral bases of perceptual numerical estimation. Three neuropsychological studies (Warrington & James, 1967; Delazer et al., 2006; Pesenti et al., 2000) suggest a role of the parietal structures, in particular the right parietal lobe, in perceptual numerical estimation. Whereas cognitive estimation relies on semantic knowledge sub-served by temporal structures, these studies suggest that perceptual numerical estimation relies on more general numerical processing abilities sub-served by the parietal structures (for a review on numerical processing and the parietal lobes, see Dehaene et al., 2003). Therefore, a deficit in perceptual numerical estimation in patients with focal frontal lesions would have to have another source than dysfunction of numerosity extraction and representation, as parietal lobes are spared in such patients.

To our knowledge, no controlled study has been conducted on perceptual numerical estimation in patients presenting executive deficits following focal frontal lobe damage. Similarly to studies pertaining to cognitive estimation (Shallice & Evans, 1978, Smith & Milner, 1984, Smith & Milner, 1988; Della Sala et al., 2004, Experiment 1) one could expect impairments in perceptual numerical estimation in patients with frontal lobe damage, as it also represents a task in which no exact answer is readily available (in contrast to counting), and calls upon selection of a response among a theoretically infinite range of possibilities. In the present study, we therefore aimed to replicate the finding of impaired cognitive estimation in a patient presenting focal frontal lobe damage, and to specifically investigate perceptual numerical estimation, and to decompose the estimation process, with the help of different tasks tapping into different levels of the numerical estimation procedure.

We defined three main levels at which perceptual numerical estimation deficits could occur. A first level is the representation of numerical quantity, that is, the core quantity system itself. Considering the evidence that we discussed above concerning the link between numerical representation and parietal structures, we reasoned that this level should be intact in a patient with focal frontal damage. To test it, we used tasks known to recruit representation of numerical quantity, and which do not require a verbal output: comparison of large sets of dots, addition and comparison of large sets of dots, digit comparison, and number-size Stroop digit comparison. A second level concerns the external calibration process. As it has been suggested that this process might involve executive functions, such as the capacity to draw inferences from an external reference, we hypothesized that it could be impaired following frontal lobe damage, as a deficit in adjusting one's output after being given examples of correct output. Therefore we tested perceptual numerical estimation with external calibration. The translation from representation to output constitutes the third level that we wished to investigate. A deficit at this level would reflect a faulty procedure, or link, from intact representation to output. Again, as for calibration, we hypothesized that frontal lobe damage could lead to an impairment at this level of selecting the appropriate output and/or checking the output for plausibility, similarly to reported impairments at this level in cognitive estimation. Moreover, if a deficit should occur at this level, we wished to investigate whether it was general or modality-specific, by testing different output modalities. We therefore used a forced-choice paradigm first to test the level of translation to output (forced-choice estimation "from dots to digits"), and second to test another output modality (forced-choice estimation "from digits to dots").

5.3 METHODS AND RESULTS

5.3.1 Case description

The patient we examined was a 28 year old right-handed native German speaking man who had accomplished polytechnical studies and trained as an engines fitter. He was at the benefit of an incapacity pension following a car accident about 8 years prior to testing, which had caused left frontal substance defect. About 2 years prior testing, the patient had suffered a second accident (a fall down some stairs), causing right cerebral contusions. A computed tomography (CT) scan taken during the testing period showed left fronto-polar to fronto-basal damage (see Figure 5-1).

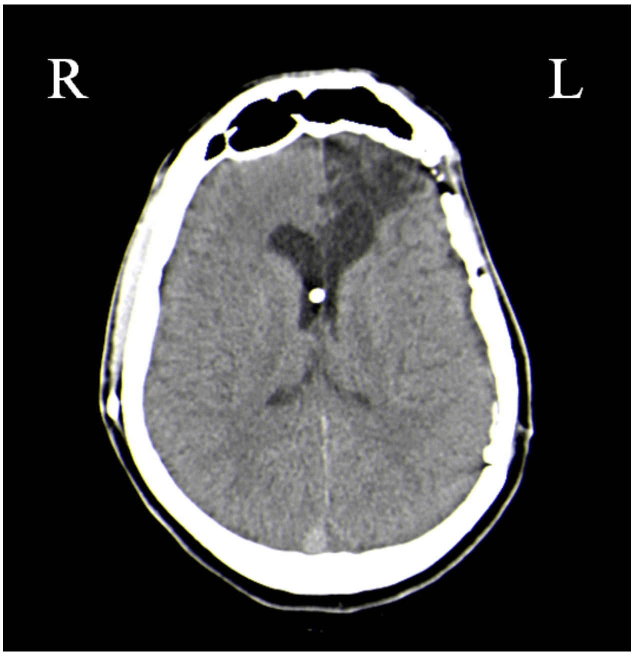


Figure 5-1 CT-scan showing left fronto-basal to fronto-polar damage.

Because of the recent occurrence of epileptic Grand Mal seizures, he underwent routine neuropsychological testing and at this occasion was proposed to participate in this study. The patient gave his informed written consent prior to his inclusion in the study.

5.3.2 Healthy participants

A first group of 15 healthy unpaid volunteers (5 men) was used as a comparison of the patient's results on most tasks. They were aged 21 to 43 years (mean age = 26.87 years). For one task (forced-choice estimation "from digits to dots", see section 2.9.), data was collected from a second group of 15 healthy participants (10 men), 5 of which were participants from the first group. Participants of this second group were aged 24 to 37 years (mean = 28.00 years) Participants of both groups were all native German speakers. Finally, for one other task (comparison of large sets of dots, see section 2.6.1) we used control data collected from 18 healthy French-speaking paid volunteers (8 men; mean age = 24.94 years, ranging from 18 to 38), participating in another study. We used this data even though it had been collected from French speakers, because the task did not call for verbal responses. Participants from all three groups were right-handed and of similar educational level (all university students or graduates) and gave their informed consent prior to their inclusion in the study.

5.3.3 Neuropsychological examination

A neuropsychological evaluation of the patient was carried out two days before numerical testing began (all results are reported in Table 5-1).

	Patient	Max. score
Verbal Intelligence		
Premorbid IQ (Lehrl, Merz, Burkard, & Fischer, 1991)	91	
Memory		
Verbal memory (VLMT-A; Helmstaedter & Durwen, 1990)		
Verbal learning (tot.) *	38	75
Free recall, short delay *	7	15
Free recall, long delay *	7	15
Recognition	15	15
Figural memory (RCFT; Rey, 1941; Spreen & Strauss, 1998)		
Free recall, short delay **	14.5	36
Free recall, long delay	21	36
Recognition	21	24
Attention		
Digit span forward (WMS-R; Wechsler, 1987)	6	12
Alertness (TAP; Zimmermann & Fimm, 2002)		
Alertness without warning (median, msec)	227	
(SD, msec)	33	
Alertness with warning (median, msec)	199	
(SD, sec) **	138	
Phasic alertness (score)	0.13	
Divided attention (TAP)		
Median (msec) *	769	

(Table 5-1 continued)

	Patient	Max. score
Attention		
Divided attention (TAP)		
SD (msec) **	385	
Errors	0	
Executive functions		
Digit span backward (WMS-R, Wechsler, 1987)	5	12
Complex mental calculation (GDAE; Jackson & Warrington, 1986) (scaled score)	8	17
Verbal fluency (RWT; Aschenbrenner, Tucha, & Lange, 2001)		
Categorical verbal fluency (animals/min) *	15	
Phonological verbal fluency (s-words/min) *	8	
Alternated verbal fluency (alternation sports-fruits/min)	12	
Alternated verbal fluency (alternation h-words vs. t-words/min) *	6	
Planning and problem-solving (TOL, German version; Kohler & Beck, 2004; Kohler, Beck, & Hohnecker, 2003) (trials)		
Solved trials	6	6
Errors **	7	
Cognitive flexibility (OMO; Flowers & Robertson, 1985) (errors)	0	
Inhibitory control (Go-NoGo task, computerised version; adapted from Fox, Michie, Wynne, & Maybery, 2000)		
Go correct %	98.9	
NoGo correct % **	63.3	
FAB (Dubois, Slachevsky, Litvan, & Pillon, 2000) (tot. score)	17	18
Conceptualisation	3	3
Mental flexibility	3	3
Motor programming	3	3
Sensitivity to interference	3	3
Inhibitory control	2	3
Environmental flexibility	3	3
IOWA gambling task (Bechara, Damasio, Damasio, & Anderson, 1994; Bechara, Tranel, & Damasio, 2000)		
Bloc 1-5 (tot. draws from favourable decks) **	34	100
Constructive abilities		
Copying a complex geometrical figure (RCFT; Rey, 1941; Spreen & Strauss, 1998)		
Score	34	36
Duration (sec) **	487	

(Table 5-1 continued)

	Patient	Max. score
Sensation seeking		
Intensity (AISS-D; Roth, Schumacher, & Arnett, 2003)	28	
Novelty (AISS-D) *	26	

Legend: (*) = patient's result below 1.5 SD from the mean of standardised norms; (**) = patient's result below 2 SD from the mean of standardised norms.

Table 5-1 Neuropsychological background tests' results.

The patient presented a slight deficit in verbal long-term memory (learning and recall difficulties, consolidation and recognition being intact), in verbal production (categorical, phonological and alternating phonological fluency tests), and a deficit in decision making (IOWA gambling task). The patient also presented inhibition difficulties in a go-no-go task, attention fluctuations in a phasic alertness test, and slow (although sufficiently accurate) performance in different tasks (divided attention test; complex mental calculation test; copy of a complex geometrical figure). He also presented extreme positive scores on the novelty component of a sensation-seeking scale, and occasional behaviour which was contextually inadequate or impulsive. There was no deficit in verbal span and working memory (digit spans forward and backward), figural long term memory, planning, cognitive flexibility, and in all subtests of a short battery investigating executive functions (FAB). Finally, verbal IQ was estimated at 91, a score that was in the normal range. In sum, the patient presented executive impairments compatible with and typical of focal frontal lobe damage. The experimental testing reported in the next section was carried out over 4 sessions which covered a period of 2 months. All computerized tasks were programmed and administered using e-prime software (Schneider et al., 2002).

5.3.4 Cognitive estimation

The "Test zum kognitiven Schätzen" was administered (TKS, Brand, Kalbe, & Kessler, 2002b), and showed a marked impairment (6 correct/16), visible in all four categories (size: 2/4; weight: 1/4; numerosity: 1/4; time: 2/4), half the time due to under-estimation and the other half to over-estimation. For example, when shown a picture of a pair of glasses and asked to estimate its weight, he replied "2 grams" (acceptable range = 24 to 130 grams). Or, when shown a picture of several flowers, and asked how many there were, he gave the answer "50 to 60", a response well above the acceptable range (15 to 31). Although results from this numerosity sub-section of the TKS suggest impaired estimation of quantity, this is based on only 4 items, and does not allow to situate at what level the deficit might occur (representation of numerical quantity, or translation from representation of numerical quantity to output). We further investigated this with the help of a set of different numerical tasks, after first re-testing perceptual numerical estimation in a more controlled task with more items.

5.3.5 Perceptual numerical estimation without calibration

5.3.5.1 Method

The patient was presented with sets of dots which represented the following 11 numerosities: 10, 13, 17, 22, 29, 37, 48, 63, 82, 106, and 138. He was instructed to estimate as accurately as possible the quantity of dots present in the display without counting. In order to prevent him from using non-numerical parameters that usually co-vary with numerosity (e.g. density of the dots or the size of the area of the envelope of the cloud of dots), half the stimuli consisted of groups of constant density across numerosities, and for the other half, constant area of the envelope of the clouds of dots (with randomization of this variable of control of non-numerical parameters across trials). The test was administered in one session of 3 blocs (each bloc containing 22 test trials). Numerosities were each presented 6 times in random order, amounting to a total of 66 test trials. During trials, the dots remained on the screen for 700 ms. The dots were black (mean visual angle of 0.2°) and appeared in a white disc (mean visual angle of 8.4°) which remained on the screen throughout the experiment. The patient entered his response using the computer keyboard. After each response was entered, the white disc remained empty for 1400 ms before the next set of dots appeared. We recorded responses in order to detect extreme answers, but also to obtain quantitative estimates of the precision of numerical estimation. The variation coefficient (standard deviation of responses divided by mean response) is expected to be stable across numerosities in the case of estimation judgments. Indeed, estimation judgments are known to become less precise as numerosity increases in such a way that the variability in responses increases *proportionally* to the increase in mean response. This characteristic is referred to as “scalar variability” (Gallistel & Gelman, 1992; Whalen et al., 1999; Izard & Dehaene, in press). We examined whether the patient’s responses also respected scalar variability. Also, mean variation coefficient across numerosities gives an indication of the precision of the estimation process, so we also tested if the patient’s values were higher than those of healthy participants, which would indicate a reduced precision of numerical estimates.

5.3.5.2 Patient's results[31]

Response times (RTs, computed after having removed outliers which were defined as RTs above or below two standard deviations of the mean; M = 5661 ms, SD = 1928 ms) were analysed in an independent 9x2 ANOVA, with numerosity (13 to 106) and type of control (area or density of dots) as variables. None of the main or interaction effects were significant, indicating that RTs were stable across numerosities and not influenced by non-numerical parameters. The patient's responses (M = 88.19, SD = 74.81; see Figure 5-2.A. for mean response and Figures 5-2.B. and 5-2.C for response distribution), which correlated positively with numerosity ($r = .74$, $p < .01$), were however consistently superior to the correct response across numerosities (and ranged from 9 to 500, or even 700 for numerosity 138), reflecting a clear tendency to overestimate.

[31]Unless specified otherwise, we report results and analyses excluding data from the extremes numerosities (10 and 138) to avoid noise from anchoring effects.

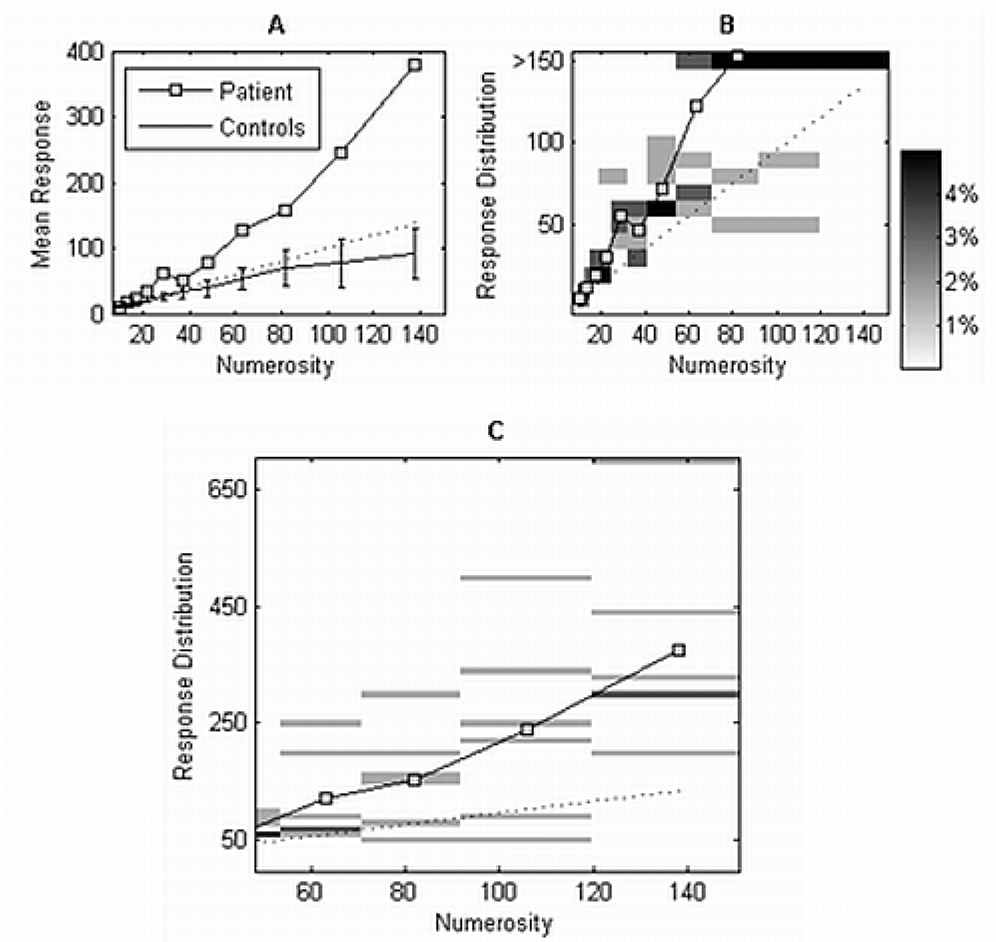


Figure 5-2 Patient's vs. healthy participants' (Controls) performance in perceptual numerical estimation without calibration. (**A**) Mean response. (**B**) Response distribution. (**C**) Zoom on response distribution with numerosities above 50. (Error bars represent ±1 standard deviation; in graphs B and C, only the patient data is depicted, and the bar at right of graph B indicates response frequency in relation to total number of responses; note the differences in scale of the three graphs).

Responses were further analysed in an independent 9x2 ANOVA, with numerosity (13 to 106) and type of control (area or density of dots) as variables. Results showed that responses increased with numerosity ($F(8, 36) = 12.10$, $p < 01$), and that they were larger in trials of constant density ($M = 114.26$, SD = 113.08) in comparison with trials of constant area ($M = 62.11$, SD = 38.39) ($F(1, 36) = 13.23$, $p < 01$). There was also an interaction effect ($F(8, 36) = 3.32$, $p < 01$), as this effect of non-numerical parameters was present only over larger numerosities (63 to 106). The larger estimates of larger numerosities did not seem to reflect a categorical judgement (for example, using label "700" repeatedly to mean "a lot"), as responses were varied and covered a large range (see Figure 5-2.C.). The spread of the patient's responses (Figure 5-2.B. and 5-2.C.) tended to increase as numerosity increased, suggesting scalar variability. Indeed, the patient's mean variation coefficient (*M* = .43, *SD* = .19) was constant across numerosities (*R* = 2.78, *p* = .12; intercept = .25, slope = .002). Finally, there was no significant difference in correlation between numerosity and response in trials of constant area (*r* = .73, *p* < .01) compared to trials of constant density (*r* = .88, *p* < .01) (test to compare independent correlations, Crawford et al., 2003: *z* = 1.73, *p* = .08). There was also no significant difference between these two types of trials as regards mean variation coefficient (constant area = 0.33; constant density = 0.38; *t*(16) = -0.61, *p* = .51).

5.3.5.3 Comparison to healthy participants

The patient's mean RT was significantly slower than healthy participants' (see Table 5-2 for all results of this section).

	Patient	**Healthy participants**		**t-value**	**p-value**
		mean	SD	(df = 14)	(two-tailed)
RT (ms)					
Overall *	5661	3509	888	2.35	< 0.05
Response					
Mean **	88.19	38.47	11.91	4.04	< 0.01
Constant area *	62.11	35.50	10.81	2.38	< 0.05
Constant density **	114.26	37.6	11.32	6.56	< 0.01
Numerosity-response correlation coefficient*	0.74	0.88	0.04	-2.33	< 0.05
Constant area	0.73	0.87	0.06	-1.70	0.11
Constant density	0.88	0.91	0.04	-0.70	0.50
Mean variation coefficient **	0.43	0.21	0.05	4.26	< 0.01
Constant area *	0.33	0.20	0.05	2.52	< 0.05
Constant density **	0.38	0.19	0.05	3.68	< 0.01

Legend: (*) = patient significantly differs from healthy participants' at p < .05; (**) at p < .01

Table 5-2 Comparison of patient's vs. healthy participants' results in perceptual numerical estimation without calibration.

Similarly to the patient, the results of the independent 9x2 ANOVA on healthy participants' RTs, with numerosity (13 to 106) and type of control (area or density of dots) as variables, revealed no significant effects. Overall, the patient's numerosity-response correlation was significantly lower than healthy participants'. However, similarly to the patient, healthy participants' correlation did no vary significantly with regards to type of control (area or density of dots) (z = 0.75, p = .45). Also, the patient's correlations calculated separately for each type of control did not significantly differ from healthy participants'. The patient's mean response was statistically higher than healthy participants' (for both trials controlled for area and density), and was over 2 standard deviations of healthy participants' mean response for each numerosity (see Figure 5-2.A.). Healthy participants' responses were also analysed in a 9x2 ANOVA (numerosity and type of control as variables). Response increased significantly with numerosity (F(8, 252) = 49.11, p < .0001). There was no main effect of type of control or interaction with numerosity, in contrast with the patient's results. The patient's mean variation coefficient across numerosities was statistically higher than healthy participants'. Regarding effects of non-numerical parameters, the patient statistically differed from healthy participants on mean variation coefficient for both trials controlled for area and those controlled for density. Similarly to the patient, healthy participants' mean variation coefficient in trials of constant area was not significantly different in comparison to trials of constant density (t(28) = 0.43, p = .67).

In sum, although the patient's responses correlated with numerosity, and although they respected scalar variability (stable variation coefficient across numerosities), his results differed from healthy participants' on most measures, and showed in particular a clear pattern of overestimation, as well as a larger variation coefficient, indicative of a lesser precision. Moreover, overestimation occurred mainly with larger numerosities in trials controlled for dot density, indicating that the patient may have been influenced by non-numerical parameters. There is in fact a known effect of density on estimation in healthy subjects, such that the denser the array of dots is, the more it is underestimated (Krueger, 1972; Hollingsworth et al., 1991). The patient's larger estimates in trials of constant density (increasing area as numerosity increases) compared to trials of constant area (increasing density as numerosity increases) could perhaps be explained as an exaggeration of a normal tendency. However, the patient's over-estimation in both types of trials remains to be explained. In order to better understand the origin of the patient's estimation deficit, we administered several tests tapping into the representation of numerical quantity, to rule out a deficit at this level.

5.3.6 Representation of numerical quantity

We administered several tasks tapping into numerical representation but not requiring the production or selection of a symbolic output, in order to determine whether the estimation deficit was due to a core numerical deficit.

5.3.6.1 Comparison of large sets of dots

5.3.6.1.1 METHOD

The patient was presented with two clouds of dots, and was asked to judge as accurately and as fast as possible which one contained the most dots. Discrimination difficulty was manipulated by having a reference numerosity (16 for half the trials, 32 for the other half) from which the deviant could differ by one of 4 possible ratios: 1.06, 1.13, 1.24, and 1.33. These variables were randomized across blocs. The patient responded by pressing on the mouse button on the same side as the cloud judged to contain the larger quantity of dots (using his left and right indexes). The dots, present on the screen until the patient responded, were black (visual angle varying from 0.2-0.5° of height and width) and appeared after a delay of 1400 ms in two white discs (visual angle of 7.2° of height and width; distance between circles subtended 1.8°) on a black background on either side of a central white fixation spot (visual angle of 0.2° of height and width). On half the trials, dot size of deviant clouds was held constant, and on the other half, the area of the envelope of the deviant clouds was held constant, whereas the reference stimuli varied on both parameters at once. This was designed in order to prevent the patient from basing his performance on these non-numerical parameters. First 16 training trials were performed, for which the patient received accuracy feedback. He performed a total of 128 trials (4 blocs of 32 trials) in one session, that is, 32 trials per ratio category. Accuracy was measured, and was used to compute another measure, the Weber Fraction, which was used to apprehend the precision of the numerical comparison process. Indeed, performance in non-symbolic numerical comparison typically improves with the ratio of the numbers to be compared (distance effect), and this relation between ratio and accuracy improvement is captured by the Weber Fraction. We tested if the patient’s Weber Fraction value was higher than those of healthy participants, which would indicate a reduced discrimination precision.

5.3.6.1.2 PATIENT'S RESULTS

Overall accuracy was good (87% correct). Data from both reference numerosities was collapsed, and analysed in relation to deviants.

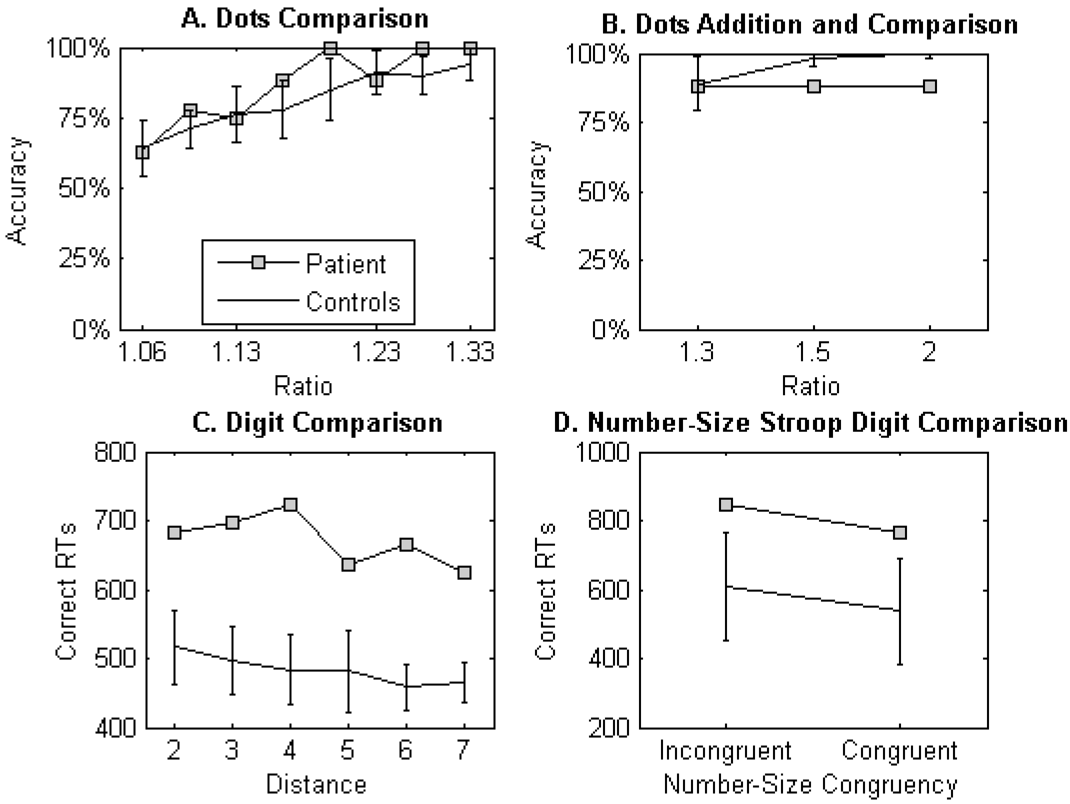


Figure 5-3 Comparison of patient's vs. healthy participants' (Controls) performance in the 4 tasks tapping into representation of numerical quantity. (**A**) Dots Comparison: ratio effect on accuracy. (**B**) Dots Addition and Comparison: ratio effect on accuracy. (**C**) Digit Comparison: distance effect on correct response times (RTs). (**D**) Number-Size Stroop Digit Comparison: number-size congruency effect on correct RTs.

Results (see Figure 5-3.A.) showed a distance effect, as expected, accuracy being lower for pairs where the deviant differed from the reference by a smaller ratio, and gradually increasing as ratio increased (R = 14.17, p = .009; intercept = -.58; slope = 1.23). This was also apparent as a correlation between ratio and accuracy (r = .84, p = .009). Accuracy scores were also used to calculate the Weber Fraction, using a method previously described (maximum likelihood decision model, Supplemental Data from Piazza et al., 2004). This basically estimates the standard deviation of the theoretical Gaussian distribution of underlying numerosity on a log scale. The subject's estimated Weber Fraction was of 0.14.

5.3.6.1.3 COMPARISON TO HEALTHY PARTICIPANTS[32]

The patient did not differ from healthy participants on all measures (see Table 5-3 for all results of this section, and also Figure 5-3.A.).

	Patient	**Healthy participants**		**t-value**	**p-value**
Dots Comparison (df = 17)		mean	SD	(df = 14)	(two-tailed)
Accuracy (%)					
Overall	87	81	11	0.53	0.60
Regression of accuracy against ratio					
Intercept	-0.58	-0.48	0.29	-0.34	0.74
Slope	1.23	1.10	0.24	NA	within 2 SDs
Correlation with ratio	0.84	0.83	0.11	-0.11	0.91
Weber Fraction	0.14	0.17	0.05	-0.58	0.57
Dots Addition and Comparison					
Accuracy (%)					
Overall *	88	95	3	-2.26	< 0.05
Constant area	96	95	3	0.32	0.75
Constant density **	79	96	5	-3.29	< 0.01
Ratio 1.3	88	89	10	-0.10	0.92
Constant area	88	89	9	-0.11	0.92
Constant density	88	88	13	0	1.00
Ratio 1.5 **	88	98	3	-3.23	< 0.01
Constant area	100	98	5	0.39	0.70
Constant density **	75	98	4	-5.57	< 0.01
Ratio 2 **	88	100	2	-5.81	< 0.01
Constant area	100	99	3	0.32	0.75
Constant density **	75	100	0	-	-
Difference ratio 2 - ratio 1.3	0	11	10	-1.07	0.31
Constant area	12	10	11	0.18	0.86
Constant density	-4	12	13	-1.19	0.25
RTs (ms)					
Overall	1104	896	222	0.91	0.38

[32] Controls performed the task in the same conditions as the patient except that they performed twice as many trials over two sessions

(Table 5-3 continued)

	Patient	Healthy participants		t-value	p-value
Digit Comparison		mean	SD	(df = 14)	(two-tailed)
Accuracy (%)					
Overall	98	99	1	-0.97	0.35
RT (ms)					
Overall **	681	484	43	4.46	< 0.01
Distance 2 **	684	507	56	3.06	< 0.01
Distance 7 **	624	467	30	5.07	< 0.01
Difference distance 2-7	60	40	47	0.41	0.69
Regression of RTs against ratio					
Intercept *	726	524	70	2.80	< 0.05
Slope	-12	-10	8.24	NA	within 2 SDs
Correlation of RT with ratio	-0.22	-0.23	0.19	0.08	0.94
Number-size stroop digit comparison					
Accuracy (%)					
Overall	93	96	3	-0.97	0.35
Congruent	100	98	4	0.48	0.64
Incongruent	86	93	5	-1.36	0.20
Incongruent - Congruent	-14	-5	7	1.25	0.23
RT (ms)					
Overall	802	574	201	1.10	0.29
Congruent	768	537	154	1.45	0.17
Incongruent	846	609	156	1.47	0.16
Incongruent - Congruent	78	72	69	0.09	0.93

Legend: (*) = patient significantly differs from healthy participants' at p < .05; (**) at p < .01

NA: statistical analysis was not possible due to differences among the healthy participants’ error variances

Table 5-3 Comparison of patient’s vs. healthy participants’ results in the 4 tasks tapping into representation of numerical quantity.

Overall accuracy in the healthy participants group was slightly lower than the patient’s although this difference was not significant. The patient’s distance effect, as measured by the slope of the regression of accuracy against ratio, and as the correlation between ratio and accuracy, was not significantly different from healthy participants’[33]. The patient’s Weber

[33] Following Crawford & Garthwaite, 2004), we wished to statistically compare the slope of the patient’s regression to that of controls’. Given that there were differences among the controls’ error variances, this test was not applicable and we instead determined whether the patient’s slope was within 2 SD of controls’ slopes. However, we also computed correlations as a measure of the distance effect, to statistically compare the patient’s measure with controls’ (see Crawford et al., 2003).

Fraction was slightly lower than healthy participants, indicating a slightly higher discrimination precision, although this difference was not significant.

5.3.6.2 Addition and comparison of large sets of dots

5.3.6.2.1 METHOD

In each trial, the patient was presented with three large sets of dots one after the other, the first two being yellow and the third blue (see Figure 5-4 for an example of the stimuli).

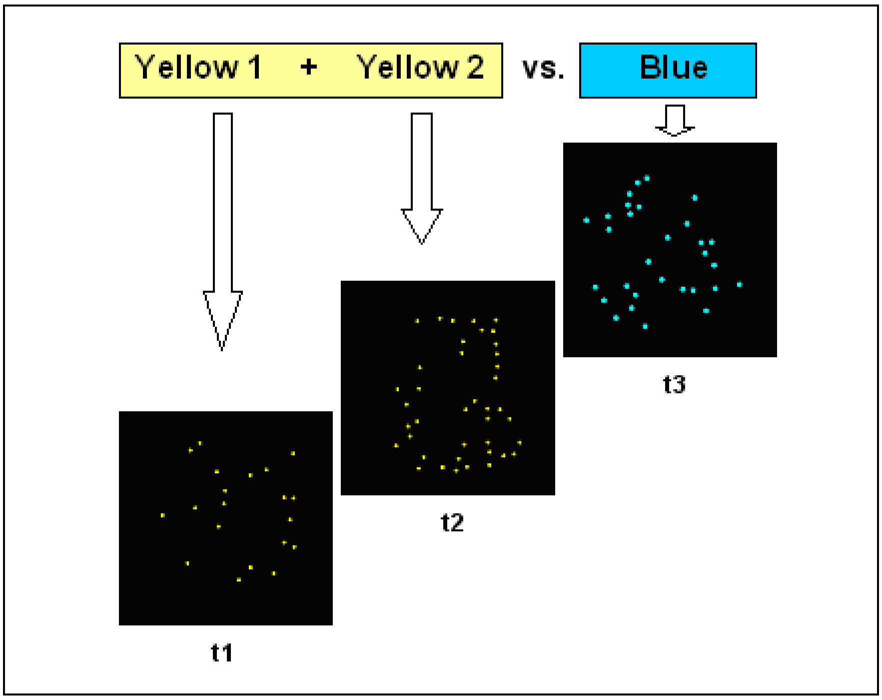


Figure 5-4 Example of the stimuli used in the addition and comparison of large sets of dots.

He was required to mentally “add” the two yellow sets and compare this result to the blue set, in order to determine whether there were more yellow dots altogether or more blue dots. He was asked not to count, but to estimate as accurately and as fast as possible the number of dots in each set and respond by pressing the left mouse button with his left index for a larger quantity of yellow dots, and the right mouse button with his right index for a larger quantity of blue dots. The ratio between the two numerosities that constituted each comparison pair (i.e. between the result of the addition of the yellow sets, and the blue set) was manipulated to form three ratio categories, from which stimuli were selected randomly across trials: ~1.3, ~1.5, 2. Each session began with 10 training trials with feedback (“correct” or “incorrect”). The background was black and stayed empty (600 ms) before each set of dots appeared centrally (400 ms). If the patient had not responded during the presentation of the last cloud of dots, it was followed by a black screen which remained until he responded. Half the sets was of constant density and dot size (mean visual angle of each dot = 0.2°), and the other half of constant total occupied area (area of about 5.7°; randomisation of this variable across trials). Data was gathered in one session of 48 trials, amounting to 16 presentations per ratio category. In half the trials the yellow quantity was larger than the blue quantity (randomization across trials). Accuracy and reaction times were measured.

5.3.6.2.2 PATIENT'S RESULTS

Overall accuracy was of 88% and did not vary at all in the different ratio conditions (difference ratio 2 minus ratio 1.3 = 0) (see Figure 5-3.B.). There was no significant effect of non-numerical parameters on accuracy ($\chi^2(2) = 3.05$, $p = .08$), but accuracy tended to be higher in the condition with constant area (96%) compared to constant density (79%). Correct RTs (computed after having removed outliers; M = 1104 ms, SD = 418 ms) were analysed in a 2x3 independent ANOVA with non-numerical parameter (constant area or constant density) and ratio (1.3, 1.5 or 2) as independent variables, and showed no significant effect.

5.3.6.2.3 COMPARISON TO HEALTHY PARTICIPANTS

The patient was significantly worse than healthy participants concerning overall mean accuracy, and accuracy with ratios 1.5 and 2 (see Table 5-3 for all results of this section, and also Figure 5-3.B.). There was however no difference in accuracy for the most difficult condition (ratio 1.3), and in difference in accuracy between the smallest and largest ratio. Healthy participants' accuracy was analysed in a 2x3 independent ANOVA with non-numerical parameter (constant area or constant density) and ratio (1.3, 1.5 or 2) as independent variables; unlike the patient, there was a significant main effect of ratio ($F(2, 84) = 19.88$, $p < .0001$), as accuracy increased concurrently with ratio increase. Similarly to the patient, there was no effect of non-numerical parameters, nor did they interact significantly with ratio. However, when comparing the patient's scores with the healthy participants' separately for trials of constant area and trials of constant density, there were differences: indeed, the patient was worse than healthy participants only with trials of constant density (for overall accuracy and accuracy with ratios 1.5 and 2). The patient's overall correct RTs did not significantly differ from healthy participants'. These were also analysed in a 2x3 independent ANOVA with non-numerical parameter (constant area or constant density) and ratio (1.3, 1.5

or 2) as independent variables; similarly to the patient, none of the main or interaction effects were significant.

5.3.6.3 Digit comparison

5.3.6.3.1 METHOD

We tested underlying numerical quantity representation through digit comparison which does not involve non-symbolic stimuli, therefore testing the quantity system through another entry. Typically, responses become faster as the distance between the digits to be compared increases; this is thought to reflect decrease of overlap of underlying numerical representations, similarly to ratio distance effect on accuracy scores in the previous tasks. In this task, all possible combinations of digits 1 to 9 were used to create 36 pairs of digits. The distance between the digits constituting different pairs therefore varied (from 1 to 8). The patient was instructed to respond as accurately and as fast as possible, pressing the left mouse button with his left index if the left digit represented the larger quantity, the right mouse button with his right index if the right digit was bigger. Before the test began, 10 training trials with feedback were administered[34]. Each test trial started with the presentation of the pair of digits (each digit subtended a maximum visual angle of 1.3° of height and 1° of width; they were separated by a distance of 2.4°), each digit on either side of a fixation circle (white on a black background, subtending 2°, for a duration of 700 ms). If the patient had not responded during the presentation of the digits, the fixation remained until he responded. The patient performed the test trials over 2 blocs of 36 trials (total of 72 trials). The pairs of digits were each presented twice (larger quantity presented once left and once right of fixation for each pair, randomized across trials and across blocs).

5.3.6.3.2 PATIENT'S RESULTS[35]

Overall accuracy was good (98% correct). Mean correct RT (computed after having discarded outliers) was 681 ms (*SD* = 84) (see Figure 5-3.C.). Correct RTs tended to decrease across distance, although this effect did not reach significance ($R = -1.62$, $p = .11$; intercept = 726; slope = -12; difference in RTs between the smallest and largest distances = 60 ms). Correct RTs also tended to correlate negatively with distance ($r = -.22$, $p = .11$).

34 Control subjects only performed 5 training trials

35 Extremes were excluded before computing the distance effect on correct RTs, because of anchoring effects.

5.3.6.3.3 COMPARISON TO HEALTHY PARTICIPANTS

Patient's overall accuracy did not significantly differ from healthy participants' (see Table 5-3 for all results of this section, and also Figure 5-3.C.). The patient's overall correct RT was significantly slower than healthy participants', and the intercept of regression of correct RT against distance was higher than healthy participants', also indicating a slower performance. However, importantly, the patient's distance effect did not significantly differ from healthy participants', either when measured as the difference in RTs between the smallest and largest distance, the slope of the regression of correct RT against distance, or by the correlation between correct RT and distance.

5.3.6.4 Number-size Stroop digit comparison

5.3.6.4.1 METHOD

In this task we tested whether Arabic digits elicited an automatic access to numerical quantity in the patient. Pairs of digits (1-7, 1-8, 2-7, 2-9, 3-8 and 3-9, distance of 5, 6 or 7) were presented and the patient had to judge the physical size of the digits (which differed by either 8, 16, 22, 30 or 38 units of character size, visual angle varying from 0.8° to 2.1° of height and from 0.4° to 1.3° of width), indicating as accurately and as fast as possible which digit was physically bigger, by pressing on the corresponding mouse button (using his left and right indexes). Numerical size of digits was to be ignored, and was congruent with physical size on half the trials, and incongruent on the other half (randomization across trials). Typically, RTs are slower in the incongruent condition if numerical quantity is automatically accessed by the perception of the digit. In half the trials the physically larger digit was on the left. The numerically bigger digit was also on the left on half the trials. Before the test began, 6 training trials with feedback were administered. Each trial started with the presentation of a pair of digits (700 ms; digits separated by a distance varying from 4.5° to 5°), each digit on either side of a fixation circle (white on a black background, visual angle of 2°). The fixation remained for 300 ms after the digits disappeared, and more (1500 ms) if no response had been detected. The patient performed 56 test trials in one bloc.

5.3.6.4.2 PATIENT'S RESULTS

Overall accuracy was good (93% correct), and was lower in the incongruent condition (86%) than in the congruent condition (100%), although this difference did not reach significance (difference = -14%; $\chi^2(1) = 2.42$, $p = .12$). Mean correct RT (computed after having discarded outliers) was 802 ms (*SD* = 147 ms). Correct RTs were slower in the incongruent condition (846 ms, vs. 768 ms in the congruent condition; difference incongruent – congruent = 78 ms); this effect approached statistical significance ($t(48) = 1.93$, $p = .06$) (see Figure 5-3.D.).

5.3.6.4.3 COMPARISON TO HEALTHY PARTICIPANTS

The patient did not differ from healthy participants on overall accuracy, accuracy for the congruent and incongruent conditions separately, or difference in accuracy between the incongruent and congruent conditions (see Table 5-3 for all results from this section, and also Figure 5-3.D.). This was also the case for the same comparisons on RTs. These results suggest intact automatic access to numerical quantity.

In a mirror task in which the patient was to judge digits on their numerical size, and ignore physical size, the patient's effect of interference from physical size was also comparable to healthy participants' on both accuracy and RT scores (although the patient's overall RTs, and RTs for each condition were slower than healthy participants').

5.3.6.5 Comment on tasks tapping into representation of numerical quantity

In sum, the patient's performance was not significantly different from healthy participants' on all measures of two out of the four tests, suggesting intact underlying numerical representation (dots comparison), and automatic access to numerical representation from Arabic digits (number-size Stroop digit comparison). However, performance was excessively slow during digit comparison (although the distance effect itself, importantly, was intact), and was disrupted in the dots addition and comparison task for trials of constant density only. This latter result might suggest, as in the first estimation task, difficulties in focusing on numerosity and not being influenced by other continuous non-numerical parameters.

We next tested the level of external calibration by administering the first estimation task *with* calibration, which means showing examples of correct responses, to see if the patient was able to take these into account to adjust his responses.

5.3.7 Perceptual numerical estimation with calibration

5.3.7.1 Method

The stimuli and test procedure were exactly the same as in the perceptual numerical estimation without calibration test (see section 2.5.1), except that each bloc was preceded by calibration, which consisted of examples of stimuli other than those tested, but sampling the same range (numerosities 15, 60 and 140). Two examples of each calibration numerosity were presented, one from a set of constant total occupied area, and one from a set of constant density, while the patient was informed of the exact numerosity (e.g.: “Here are 15 dots”). Calibration dots remained on the screen for 10 seconds or less if the patient was ready sooner to see the next set.

5.3.7.2 Patient’s results[36]

RTs (computed after having removed outliers; M = 4396 ms, SD = 564 ms) were analysed in an independent 9x2 ANOVA, with numerosity (13 to 106) and type of control (area or density of dots) as variables. None of the effects were significant, indicating that RTs were stable across numerosities and not influenced by non-numerical parameters. The patient’s responses (M = 61.67, SD = 34.66; see Figure 5-5.A for mean response and Figures 5-5.B. and 5-5.C. for response distribution), which correlated positively with numerosity (r = .74, $p < .01$), were still consistently superior to the correct response across numerosities although much less than in the same task without calibration (and ranged from 13 to 160, at the most 170 for numerosity 138).

[36]Unless specified otherwise, we report results and analyses excluding data from the extremes numerosities (10 and 138) to avoid noise from anchoring effects.

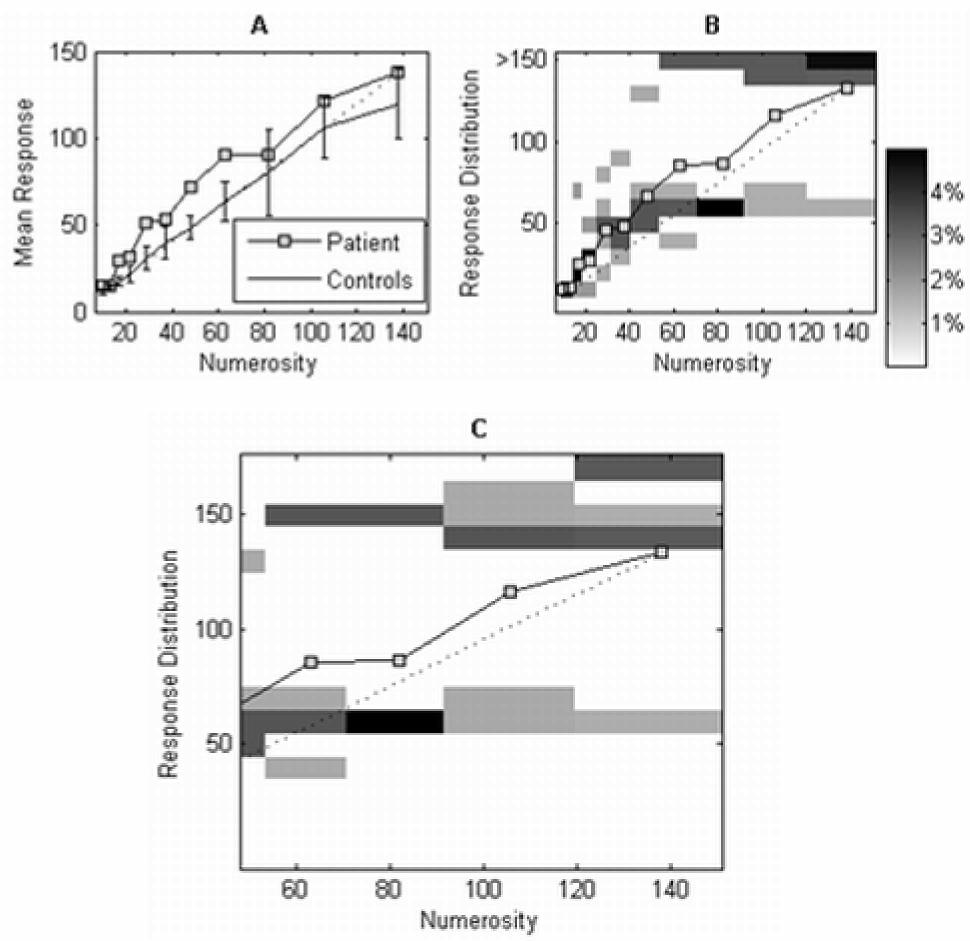


Figure 5-5 Patient's vs. healthy participants' (Controls) performance in perceptual numerical estimation with calibration. (**A**) Mean response. (**B**) Response distribution. (**C**) Zoom on response distribution with numerosities above 50. (Error bars represent ±1 standard deviation; in graphs B and C, only the patient data is depicted, and the bar at right indicates response frequency in relation to total number of responses; note the difference in scale for graph C).

Responses were further analysed in an independent 9x2 ANOVA, with numerosity (13 to 106) and type of control (area or density of dots) as variables. Results showed that responses increased with numerosity ($F(8, 36) = 6.80$, $p < 01$), and that there was no significant difference between trials of constant area ($M = 63.96$, $SD = 34.42$) and trials of constant dot density ($M = 59.37$, $SD = 37.04$). There was also no interaction effect. The spread of the patient's responses (Figure 5-5.B. and Figure 5-5.C.) tended to increase as numerosity increased, suggesting scalar variability. Indeed, the patient's mean variation coefficient ($M = .43$, $SD = .15$) was constant across numerosities ($R = 1.71$, $p = .21$; intercept = .32, slope = .002). Finally, additional analyses suggest that our patient's responses were not influenced by non-numerical parameters: there were no significant differences between conditions as regards numerosity-response correlation (constant area: r = .69, constant density: r = .79; z = 0.87, p = .39) or mean variation coefficient (constant area = .45, constant density = .34; t(16) = 1.41, p = .18).

5.3.7.3 Comparison to healthy participants

The patient did not statistically differ from healthy participants' regarding mean RT or numerosity-response correlation (see Table 5-4 for all results of this section).

	Patient	Healthy participants		t-value	p-value
		mean	SD	(df = 14)	(two-tailed)
RT (ms)					
Overall	4396	2773	794	1.98	0.07
Response					
Mean	61.67	46.91	7.02	2.04	0.06
Constant area *	63.96	45.20	8.08	2.25	< 0.05
Constant density	59.37	48.62	7.00	1.49	0.16
Numerosity-response correlation coefficient	0.74	0.88	0.05	-1.64	0.13
Constant area	0.69	0.86	0.07	-1.47	0.16
Constant density *	0.79	0.92	0.03	-2.77	< 0.05
Mean variation coefficient **	0.43	0.23	0.05	3.87	< 0.01
Constant area **	0.45	0.20	0.05	4.84	< 0.01
Constant density *	0.34	0.2	0.06	2.26	< 0.05

Legend: (*) = patient significantly differs from healthy participants' at p < .05; (**) at p < .01

Table 5-4 Comparison of patient's vs. healthy participants' results in perceptual numerical estimation with calibration.

This held for trials of constant area but not for those of constant density, in which the patient's numerosity-response correlation was significantly lower than healthy participants'. Similarly to the patient, the results of the independent 9x2 ANOVA on healthy participants' RTs, with numerosity (13 to 106) and type of control (area or density of dots), revealed no main effect of type of control and no interaction with numerosity; however, in contrast to the patient, RTs increased significantly with numerosity (F(8, 252) = 3.09, p = .002). The patient's mean response was no longer statistically higher than healthy participants, and was over 2 standard deviations of healthy participants' mean response for some numerosities only (5 out of 9; see Figure 5-5.A.). However, the patient's mean response with trials of constant area was significantly higher than healthy participants' (and not for trials of constant density).

Healthy participants' responses were also analysed in a 9x2 ANOVA (numerosity and type of control as variable). Response increased significantly with numerosity ($F(8, 252) = 138.20$, $p < .0001$). There was a trend towards a main effect of type of control ($F(1, 252) = 3.78$, $p = .05$), and the interaction with numerosity was significant ($F(8, 252) = 3.82$, $p < .0001$). Indeed, similarly to (but much less marked than) the patient in the estimation task without calibration, subjects tended to give larger responses in trials of constant density for larger numerosities only (82 and 106). Similarly to the patient, healthy participants' correlation did no vary significantly with regards to type of control ($z = 1.15$, $p = .25$). The patient's mean variation coefficient across numerosities was statistically higher than healthy participants'. This held for both trials of constant area and those of constant density. Similarly to the patient, healthy participants' mean variation coefficient in trials of constant area was not significantly different in comparison to trials of constant density ($t(28) = 0.03$, $p = .97$).

In comparison to the same task without calibration, the patient's responses again correlated with numerosity and respected scalar variability; also the patient's performance improved, as he presented less over-estimation. Results therefore suggest that the patient had difficulties calibrating himself in the first task, and somewhat benefited from external calibration to counter over-estimation in this task. However, the patient still seemed influenced to some degree by non-numerical parameters, as he differed from healthy participants on some measures when looking separately at the two types of trials. Also, estimation precision, as measured by the variation coefficient, was still lower than healthy participants, probably due mostly to a greater variation in response, and also to mean response still being somewhat higher than healthy participants'.

In order to counter excessive variability in response, we designed two forced-choice estimation tasks. These allowed testing of the level of translation from representation to output. The first forced-choice task was similar to the main estimation task, in that the stimuli were the same clouds of dots; it mainly explored the effect of preventing variability in response by presenting a choice of two Arabic numerals. The second forced-choice task probed the possibility that the estimation deficit may be modality-specific, by presenting Arabic numerals as stimuli, and clouds of dots as responses to choose from.

5.3.8 Forced-choice estimation "from dots to digits"

5.3.8.1 Method

We presented the same stimuli as in the first estimation task (see section 2.5.1), and asked the patient to choose, as accurately and as fast as possible, the corresponding Arabic numeral among two choices (the correct response and a distractor). Distractor was smaller on half the trials, and larger on the other half. The ratio between correct response and distractor was maintained constant (~2.24), and was picked to match the degree of overestimation in the first task. Smaller distractors comprised Arabic numerals ranging from 4 to 62, and larger ones from 22 to 309. The patient was to indicate the correct numeral by pressing on the corresponding mouse button (left with his left index if the correct numeral was left, and vice-versa). Dots were presented as in the first experiment, but were followed by an empty white central circle under which two white numerals appeared (height of each numeral of 0.5°, width of each numeral varying from 0.3° to 1.1°, distance between the two numerals was of 5.1°), one on the left and the other on the right, until the patient responded. The numerals then disappeared and the white circle remained empty for 700 ms before the presentation of the next set of dots. The patient performed a total of 132 trials divided into 3 blocs. On half the trials, the correct response was presented on the left, and vice-versa for the other half. Each numerosity (cloud of dots) was presented 12 times, 6 times with a smaller distractor, and 6 times with a larger one. We compared accuracy scores from each condition (smaller/larger distractor) to detect consistent over- or under-estimation.

5.3.8.2 Patient's results

The patient's overall accuracy was of 72% correct, and was significantly lower in the condition with a larger distractor (59%) compared to the condition with a smaller distractor (85%) (difference = 26%; $\chi^2(1) = 9.61$, $p = .002$) (see Figure 5-6.A.).

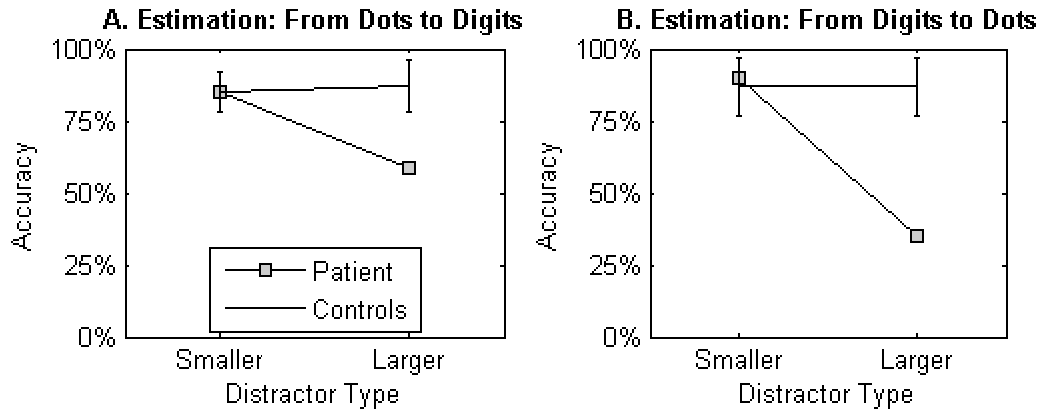


Figure 5-6 Comparison of the patient's vs. healthy participants' (Controls) performance in the 2 forced-choice estimation tasks. (**A**) Distractor effect on accuracy in the "Dots to digits" task. (**B**) Distractor effect on accuracy in the "Digits to dots" task.

His performance was significantly above chance in the condition with a smaller distractor ($\chi^2(1) = 32.06$, $p < .0001$), but not in the condition with a larger distractor ($\chi^2(1) = 2.18$, $p = .14$). There was no effect of non-numerical parameters on overall accuracy ($\chi^2(1) = 1.35$, $p = .25$), accuracy with a smaller distractor ($\chi^2(1) = 1.06$, $p = .30$), or with a larger one ($\chi^2(1) = 0.25$, $p = .62$).

5.3.8.3 Comparison to healthy participants

The patient significantly differed from healthy participants on overall accuracy, accuracy being significantly lower than healthy participants' only in the condition with larger distractors and not with smaller ones (see Table 5-5 for all results of this section, and also Figure 5-6.A.).

	Patient	Healthy participants		t-value	p-value
		mean	SD	(df = 14)	(two-tailed)
From dots to digits					
Accuracy (%)					
Overall **	72	86	4	-3.39	< 0.01
Smaller Distractor	85	85	7	-	-
Larger Distractor **	59	87	9	-3.01	< 0.01
Smaller - Larger Distractor	26	-0.02	0.14	1.94	0.07

(Table 5-5 continued)

	Patient	Healthy participants		t-value	p-value
		mean	SD	(df = 14)	(two-tailed)
From digits to dots					
Accuracy (%)					
Overall **	63	87	6	-3.87	< 0.01
Smaller Distractor	90	87	10	0.29	0.78
Larger Distractor **	35	87	10	-5.04	< 0.01
Smaller - Larger Distractor **	55	1	17	3.08	< 0.01

Legend: (*) = patient significantly differs from healthy participants' at p < .05; (**) at p < .01

Table 5-5 Comparison of patient’s vs. healthy participants’ results in the forced-choice estimation tasks.

Finally, the difference in accuracy between the two conditions was higher in the patient compared to healthy participants, but this did not reach significance.

In sum, the results point to a deficit which is not limited to excessive response variability, but also persists in a forced-choice paradigm, and only with larger distractors, in line with the overestimation found in the main estimation task. This suggests a deficit at the level of translation from numerical representation to output, affecting response selection but also the phase of checking response plausibility.

5.3.9 Forced-choice estimation “from digits to dots”

5.3.9.1 Method

In order to find out whether the patient’s estimation deficit was limited to symbolic output, we administered a forced-choice estimation task which mirrors the previous one, presenting an Arabic numeral and asking the patient to choose as accurately and as fast as possible the corresponding cloud of dots among two choices (the correct response and a distractor). Procedure was the same as in the previous task. However, we used less stimuli as in the previous task, presenting only 4 numerals (29, 48, 82 and 138) and their corresponding distractors (chosen as described for the previous task). Dots subtended a visual angle varying from 0.1 (height and width) to 0.3° (height and width) and the white discs a visual angle of 14° (distance between the discs of 0.4°). Each numeral (height of 0.6°, width varying from 1° to 1.5°) was presented 24 times, half the time with a smaller distractor. On half the trials the correct response appeared on the left. Half the sets of clouds were of constant dot size, and for the other half, the envelope of the area covered by the dots was held constant. Again, we compared accuracy scores from each condition (smaller/larger distractor) to detect consistent over- or under-estimation.

5.3.9.2 Patient's results

The patient's overall accuracy was of 63% correct, and was significantly lower in the condition with a larger distractor (35%) compared to the condition with a smaller distractor (90%) (difference = 55%; $\chi^2(1) = 27.78$, $p < .0001$) (see Figure 5-6.B.). His performance was significantly above chance in the condition with a smaller distractor ($\chi^2(1) = 30.08$, $p < .0001$), but was significantly worse than chance in the condition with a larger distractor ($\chi^2(1) = 4.08$, $p = .04$), indicating a clear bias to select the larger set of dots. There was no effect of non-numerical parameters on overall accuracy ($\chi^2(1) = 0.04$, $p = .83$), accuracy with a smaller distractor ($\chi^2(1) = 0$, $p = 1$), or with a larger one ($\chi^2(1) = 0$, $p = 1$).

5.3.9.3 Comparison to healthy participants

The patient significantly differed from healthy participants on overall accuracy, accuracy being significantly lower than healthy participants' only in the condition with larger distractors and not with smaller ones (see Table 5-5 for all results of this section, and also Figure 5-6.B.). Also, the difference in accuracy between the two conditions was significantly higher in the patient compared to healthy participants.

In sum, these results show that the deficit was not limited to symbolic output, but extended to non-symbolic output, and indicate a bias to select the larger response. Indeed, the patient consistently picked the larger set of dots, therefore matching large sets to smaller Arabic numerals. If given quantities of dots were consistently linked to larger numerals, as suggested by the overestimation in tasks with dots as stimuli and number words (see section 2.5. "Perceptual numerical estimation without calibration") or numerals (see section 2.8. "Forced-choice estimation "from dots to digits"") as output, the patient would have systematically picked the smaller set of dots in this last task. This argues against a deficit at the numerical representation level, and for an impairment at the level of translation from representation to output, which generalizes to different types of output.

5.4 DISCUSSION

This study reports impairment of both cognitive estimation and perceptual numerical estimation in a patient with frontal lobe damage. Indeed, not only did this patient present extreme answers in a test of cognitive estimation, in line with previous reports of such deficits in frontal patients (Shallice & Evans, 1978; Smith & Milner, 1984; Della Sala et al., 2004, Experiment 1), but he also showed extreme answers in a controlled test of perceptual numerical estimation. In this test, the patient's performance was not only characterized by overestimation, but also by a larger variability in response, and a tendency to be influenced by non-numerical continuous parameters that co-varied with numerosity (such as the size of the area occupied by the set of stimuli, or the density of the set of stimuli). However, his perceptual numerical estimation process was not completely impaired, as the patient's responses correlated positively with numerosity, and respected scalar variability, a signature of estimation processes (Gallistel & Gelman, 1992; Whalen et al., 1999; Izard & Dehaene, in press; Dehaene & Marques, 2002).

In accord with our prediction, the patient's perceptual numerical estimation deficit did not seem to reflect impairment at the level of extraction and representation of numerosity. Indeed, this patient's performance on tests tapping into numerical representation suggested general sparing of numerical abilities, consistent with the sparing at the anatomical level of parietal lobes which are known to play an important role in numerical representation (for a review, see Dehaene et al., 2003). However, the patient's performance was impaired compared to healthy participants on some measures of two of the tasks tapping into numerical representation. Firstly, the patient was generally slower in the digit comparison task. This could perhaps be interpreted in the context of attention fluctuations, which were present in the neuropsychological examination, especially since the patient's response times did not differ from healthy participants' in other numerical tasks. It has indeed been shown that slowing and excessive variation of RTs can reflect frequent lapses of attention and an instability of attention performance (Benke, Delazer, Bartha, & Auer, 2003). In any case, importantly, the distance effect, which pertains to numerical representation, was not statistically different from healthy participants' in the digit comparison task. Secondly, the patient was less accurate in the dots addition and comparison tasks, but only for trials of constant density. As the patient did not present systematic deficits with trials of constant density in all tasks, it seems plausible that the deficit in the dots comparison and addition task is not due to a specific deficit in apprehension of area which co-varies with numerosity on such trials. It probably also does not reflect impairment of extraction of numerical quantity, as the patient's performance on the dots comparison task was intact, although stimuli were again controlled for non-numerical parameters. It could be interpreted as reflecting difficulties in focusing on numerosity and not being distracted by other non-numerical parameters, in the more general context of attention and inhibition difficulties exhibited in the neuropsychological background testing. Alternatively, it could reflect a domain-specific deficit; indeed, some studies have shown implication of frontal structures in numerical tasks in monkeys (Nieder & Miller, 2004; Nieder et al., 2002; for a review, see Nieder, 2005) and in human healthy adults (e.g. Piazza et al., 2006). It has been suggested that in the monkey, numerosity extraction takes place in parietal structures but is amplified and maintained in working memory in the prefrontal cortex (Nieder & Miller, 2004). If this were also the case in humans, this later stage could perhaps be affected in this patient. However, given the attention and inhibition difficulties that this patient presents in several non-numerical tasks, the interpretation that dysfunction of these general executive processes affects numerical performance seems more parsimonious. Further studies of numerical performance in patients with focal frontal lobe damage might shed light on this issue.

We had also predicted that external calibration could be impaired, as a recent study has suggested possible involvement of strategic processes in calibration (Izard & Dehaene, in press). When externally calibrated, the patient was able to adjust his responses to some extent (less over-estimation), suggesting some sparing of capacity to draw inferences from external reference. In fact, quite impressively, this adjustment was visible over the whole range of numerosities, not just over numerosities closest to those which had been used for calibration, similarly to what has been shown in healthy subjects (Izard & Dehaene, in press). He still presented some overestimation and a large variability in response, as well as still being somewhat influenced by non-numerical parameters. We do not rule out the hypothesis that another patient with more pronounced executive difficulties may not benefit at all from calibration.

Finally, in accord with our last hypothesis, results suggested that the patient presented a deficit at the level of translation from representation to output, in relation to executive deficits. Indeed, as numerical representation was globally intact, this level of the estimation process cannot account for the estimation deficit. And as the deficit was not specific to one type of output, the output level cannot either be the level at which the estimation deficit occurs. Indeed, we established that the estimation deficit was not limited to excessive variability in response, as it persisted in a forced-choice paradigm. Also, we determined that it was not specific to the verbal output modality, as the patient also presented marked difficulties in a forced-choice paradigm with non-symbolic output. Interestingly, this last paradigm also brought evidence that the patient's estimation deficit was not a consistent erroneous link between representation and response, which might have suggested an impairment at the representation level. Indeed, although the patient linked clouds of dots to larger numerals in the other estimation tasks, in this last estimation paradigm, he consistently linked numerals to the larger set of dots, rather than the smaller one, thus breaking the overestimation pattern. It therefore seems that the patient presented a bias toward selecting large quantities, whether number words, numerals, or sets of dots.

Similarly to the conclusion drawn from other cases of frontal lobe patients suffering cognitive estimation deficits (Shallice & Evans, 1978; Smith & Milner, 1984; Della Sala et al., 2004, Experiment 1), or frequency estimation deficits (Smith & Milner, 1988), we conclude that executive deficits can contribute to impairment of cognitive estimation, and additionally extend their involvement to perceptual numerical estimation.

Acknowledgments We warmly thank the patient and the control subjects for participating in this study, as well as Sandra Lehmann-Barcellona for useful comments and suggestions on a previous version of this manuscript. This study was supported by INSERM, CEA, two Marie Curie fellowship of the European Community (MRTN-CT-2003-504927; QLK6-CT-2002-51635), and an Austrian FWF grant (P18896-B05).

6 CHAPTER 6: GENERAL DISCUSSION

Human adults are thought to possess three main processes to quantify objects that surround them. When dealing with a set of dots for example, they can rapidly and accurately enumerate up to 3 or 4 items (subitizing) (e.g. Trick & Pylyshyn, 1994; Mandler & Shebo, 1982; Chi & Klahr, 1975). For larger quantities, they will rely on exact counting, or approximate estimation. Different studies have suggested that non-human animals and pre-verbal infants may possess precursors to both exact (subitizing) and approximate numerical capacities displayed by humans (estimation, but also comparison, addition or subtraction of non-symbolic quantities). Indeed, both non-human animals and pre-verbal infants show capacities to keep track of, and manipulate (compare, add, subtract) sets of objects in an exact way, as long as there are no more than 3 or 4 (e.g. non-human animals: Hauser et al., 2000; Hauser & Carey, 2003; pre-verbal infants: Feigenson et al., 2002; Wynn, 1992). This applies not only to visual objects, but also in some cases to sounds, or actions, suggesting use of an abstract representation of quantity (e.g. non-human animals: Hauser et al., 2002; pre-verbal infants: Wynn, 1996). Additionally, they also show approximate numerical apprehension and manipulation (comparison, addition, subtraction) of large quantities, presenting performance which follows Weber's law, with different types of stimuli, suggesting use of another abstract quantity system (for a review, see Feigenson et al., 2004a). Adults' basic approximate quantity extraction process also shows signatures of Weber's law (reflecting increasingly overlapping underlying numerical representation) when comparing sets of dots (distance and size effects, indicating effect of ratio; e.g. Buckley & Gillman, 1974; Barth *et al.*, 2006), or when estimating (scalar variability: responses become increasingly less precise as numerosity increases; e.g. Whalen et al., 1999; Izard & Dehaene, in press).

In our different studies of adults' numerical performance, we aimed to better understand the process(s) involved in subitizing, in particular by investigating its possible link to numerical estimation, and by determining whether it is really independent of spatial attention. We were also interested in improving our understanding of some of the mechanisms operating during estimation. We investigated whether estimation was tightly linked to numerosity discrimination. We also sought to determine whether it (and other approximate numerical processes) could occur independently of spatial attention and serial visual attention. Finally, we also investigated whether adults' estimation called onto executive processes, to link underlying approximate numerical representation to exact symbols.

6.1 SUBITIZING: WHAT PROCESS IS INVOLVED?

6.1.1 Numerical estimation

Subitizing has been extensively investigated, but its underlying process still remains debated. It has been proposed that subitizing in adults might be linked to numerical estimation, rather than constitute a separate process: estimation of very small numerosities might be precise enough to allow exact verbal labeling (Dehaene & Cohen, 1994; Dehaene & Changeux, 1993; van Oeffelen & Vos, 1982; Gallistel & Gelman, 1991). In contrast, larger numerosities would be less easily discriminated, and thus require counting to ensure exact responses. The subitizing range would thus be directly related to an increase in numerical discrimination difficulty as numerosity increases and to the resulting increase in variability in estimation responses. We tested this hypothesis in our 2nd chapter (Revkin et al., in press) by using a new paradigm, which allowed directly comparing performance over the subitizing range to performance with larger quantities matched for discrimination difficulty. Our results strongly suggest that subitizing is not linked to numerical estimation or discrimination difficulty. These results provide evidence for the idea that adults possess two separate numerical systems, one devoted to small numerosities (1-4), and another for larger quantities. This converges with the data from non-human animals and pre-verbal infants, which also suggests two core quantity systems in these populations (Feigenson et al., 2004a).

6.1.2 Subitizing without spatial attention

A study of subitizing in patients with visual extinction reported preservation of this capacity (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000), suggesting that dots that could not be localised in the presence of competing stimuli could nonetheless be taken into account when the task was to enumerate items. However, this was based on use of displays of two or four dots, which could be interpreted as forming lines (numerosity two) or a square (numerosity four was presented as a pattern of a square). Canonical pattern recognition, which was proposed as a possible explanation for the occurrence of subitizing (Mandler & Shebo, 1982), has been discarded as it cannot account for the fact that lines of three dots can be subitized (Trick & Pylyshyn, 1994; Atkinson et al., 1976a; Atkinson et al., 1976b; Starkey & Cooper, 1995), proving that the triangle pattern is not a prerequisite for subitizing of this quantity. However, this does not mean that pattern recognition may not be used through Gestalt grouping which reduces extinction to subitize arrays disposed in canonical patterns. In our 3rd chapter, we tested two patients presenting visual extinction with random, line, and canonical shape patterns, with numerosities two, three and four, to make sure subitizing was preserved and not canonical shape pattern recognition. Our results support the idea that subitizing is indeed preserved in patients with visual extinction, and thus, that it does not require spatial attention to operate.

6.1.3 Visual indexing

Although the results from our 2nd chapter strongly suggest that subitizing does not rely on numerical estimation, and therefore support ruling out this hypothesis, the question still remains as to which process is involved. Visual indexing (Trick & Pylyshyn, 1994; Pylyshyn, 2000) represents a plausible candidate, and deserves further investigation. This theory proposes that a limited number of objects can be tagged in parallel, and that multiple object tracking performance can be used to measure the visual indexing range in adults. However, the use of this task involves many other processes which are not needed in subitizing (such as movement processing for example, or working memory), and might therefore not be the best measure of visual indexing capacity. For example, although subitizing is thought to be preserved in patients with visual extinction (Vuilleumier & Rafal, 1999; Vuilleumier & Rafal, 2000; chapter 3), a study reported impaired multiple object tracking in such patients (Battelli *et al.*, 2001); this does not necessarily mean that visual indexing is impaired, and that it is therefore not linked to subitizing. Rather, visual indexing may be preserved, although multiple object tracking is impaired due to a deficit in movement perception. Similarly, a recent study (Green & Bavelier, 2006) showed a differential influence of action video game playing on visual indexing (measured by the multiple object tracking task) and subitizing: multiple object tracking was improved but not the subitizing range. This could mean that subitizing and visual indexing are not related; alternatively, it could just reflect the fact that multiple object tracking can be improved through processes which are not involved in subitizing, without meaning that there is no link between visual indexing and subitizing. A task of visual short term memory, which has been shown to have a capacity limit of four (Luck & Vogel, 1997), and which has also been shown to present similar properties to multiple object tracking (same capacity superiority across visual fields as compared to within visual fields; in spatial location short term memory: Delvenne, 2005; in multiple object tracking: Alvarez & Cavanagh, 2004), might prove useful in future investigations of visual indexing as a possible source for subitizing.

6.1.4 Subitizing: an amodal process?

Subitizing has recently been reported with tactile stimuli (Riggs *et al.*, 2006; but see Gallace, Tan, & Spence, 2006), and might also occur with auditory stimuli (Repp, 2007). A cross-modal study has also been conducted recently, to try to provide evidence for amodal subitizing. However, although its results support the idea of a shared pool of resources across tactile and visual modalities for numerical processing of 1-6 items, it reports continuous performance over this range, suggesting use of an approximate quantity system rather than subitizing (Gallace, Tan, & Spence, 2007). Strong evidence for subitizing in auditory or tactile modalities, and in cross-modal paradigms, would suggest a similar process to the amodal core quantity system dedicated to small numerosities found in non-human animals and pre-verbal infants (Feigenson et al., 2004a).

Visual indexing only applies to the visual modality (as suggested by its name), providing no explanation for subitizing with auditory or tactile stimuli. However, a recent study mentions a cross-modal indexing capacity, in relation to interference from sequential finger tapping (tapping fingers in a specific sequence, for example, index, ring finger, middle finger) during multiple object tracking (Trick, Guindon, & Vallis, 2006), suggesting that both finger tapping and multiple object tracking may rely on the same indexing capacity. Further investigation of such tasks in relation to subitizing range might be of interest.

6.2 ESTIMATION: A CHARACTERIZATION OF ITS UNDERLYING PROCESSES

6.2.1 A direct link to numerical discrimination

Weber's law is thought to govern adults', animals', and pre-verbal infants' discrimination of numerical quantities. Is has also been linked to adults' verbal estimation process, during which a verbal label is mapped onto the underlying quantity, although approximately, as response variability increases concurrently to numerosity (scalar variability; e.g. Izard & Dehaene, in press). The Log-Gaussian model of numerosity representation postulates that a single parameter, the internal Weber fraction (which estimates the precision of underlying numerosity representation), should determine subjects' precision not only in discrimination of large quantities, but also in estimation (Dehaene, 2007). We tested this hypothesis in our 2nd chapter, for which both discrimination and estimation precision was measured. Indeed, these precision measures correlated, suggesting a direct link between discrimination and estimation, and supporting the Log-Gaussian model (Dehaene, 2007).

Future studies should however be conducted to clearly establish the causality of this link, for example, by intensively training subjects in dots comparison (discrimination precision), and seeing if it influences their estimation precision in a naming task. Also, in such a training study, an absence of increase in the subitizing range after dots comparison training would provide another argument against a link between approximate numerical processes and subitizing, as discussed previously.

6.2.2 Estimation without spatial attention

Numerical estimation is thought to rely on a basic approximate numerosity system, which has been shown to be sub-served by the intra-parietal sulcus (for a review, see Dehaene et al., 2003). Does this approximate numerical extraction process require spatial attention? To address this question (in our 3rd chapter), we tested numerical estimation in a patient presenting left visual extinction, that is, a patient who failed to attend to items in the left visual field, when a competing right stimulus was present, and when stimuli had to be localised. During the estimation task, two arrays were presented (one in each field) which were either close enough to each other to form one object, or separated by a distance which lead to the perception of two objects. Interestingly, results suggested that dots in the extinguished field were only taken into account when forming one central object with the right-sided dots. This suggests that an area might need to be delineated (through spatial attention) before estimation can operate over it.

Future studies involving patients presenting either within-object neglect or between-object neglect would be of interest. A modification in the presentation of the “one object” condition would also be useful, for example by using the same distance between hemi-clouds as in the “two objects” condition, but linking them with a fine horizontal line of dots, to control better for possible extinction in this condition and see the effect of grouping by connectedness.

A recent study reported spared ability to unconsciously process underlying numerical information in extinguished Arabic numerals (Cappelletti & Cipolotti, 2006). It would be interesting, in future studies, to compare access to numerical quantity through extinguished symbols (Arabic numerals) and through non-symbolic stimuli (dots, as in our study), within the same patients.

Finally, the fact that estimation might depend on spatial attention, but not subitizing, constitutes another argument to believe that they represent separate processes. However, it remains to be explained why subitizing can occur without spatial attention, but not estimation.

Perhaps the dots in the subitizing task were more salient (as they were much larger than the dots used for estimation). It might be interesting to test subitizing of sets of small clouds of dots; if this were preserved, it might argue against a difference in stimulus saliency.

6.2.3 A serial or parallel numerosity extraction process?

Two prominent models of extraction of numerosity can be contrasted: the pre-verbal counting model, which proposes a serial extraction process (Gallistel & Gelman, 1992), and the Log-Gaussian model, which is based on a parallel numerosity detector (Dehaene, 2007; Dehaene & Changeux, 1993). In our 4th chapter, we wished to confront these two models by testing a patient with impairment in serial visual attention (simultanagnosia). We showed that although this patient was unable to count sets of items presented visually, subitizing was preserved, and estimation was also mostly spared. Other approximate operations thought to rely on a general numerosity extraction process were also mostly spared (comparison, but also addition of large sets of dots). Also, non-numerical search tasks provided evidence for a sparing of parallel processing and impairment of serial processing. These results suggest that numerical extraction can take place without serial visual attention, therefore supporting the Log-Gaussian model (Dehaene, 2007; Dehaene & Changeux, 1993), and weakening the hypothesis of a serial pre-verbal counting process (Gallistel & Gelman, 1992).

Future studies should aim to replicate this finding, perhaps in patients presenting simultanagnosia without gaze apraxia, to constitute a more controlled demonstration that serial attention, and not a deficit in serial refocusing of attention, causes this pattern of results.

6.2.4 Does estimation require executive functions?

Although adults' estimation presents characteristics that link it to the approximate non-verbal quantification system (scalar variability), it goes beyond this system in the sense that it requires language to give labels to the quantities that are extracted. This labeling requires calibration, that is, correct correspondence from the underlying quantity to the verbal symbol. Adults' spontaneous calibration is somewhat poor, as they show under- or over-estimation for larger quantities, even though their responses correlate with numerosity (correct ordering) and respect scalar variability (Minturn & Reese, 1951; Izard & Dehaene, in press). However, when presented with an example of a correct estimate (external calibration), adults' whole range of answers is improved to approach correct mean estimates (Izard & Dehaene, in press). In our 5th chapter, we asked ourselves whether spontaneous and/or external calibration required executive functions, as strategic or regulative processes might be needed to find a plausible corresponding label to a given quantity. Contrary to counting, for which there is a precise procedure which leads to the cardinality of a set, estimation is a process for which no given strategy is available and whose outcome is given in a context of uncertainty (approximate answer required). These task conditions and demands are somewhat similar to those required in cognitive estimation which has been shown to involve executive functions (disrupted after frontal lobe damage: Shallice & Evans, 1978). By studying estimation without external calibration in a patient with focal frontal lobe damage who presented executive deficits and cognitive estimation deficits, we showed that numerical estimation performance was indeed disrupted, showing a pattern of over-estimation which however correlated with numerosity and respected scalar variability. After external calibration, performance improved, although there was still some over-estimation and excessive variability in responses. We further showed, with the help of different numerical tasks, that the numerical estimation deficit was not linked to impairment at the level of non-verbal extraction and representation of numerosity. Moreover, the deficit did not seem to be specific to a given output, as it persisted when the patient had to match Arabic digits to sets of dots. We conclude that executive functions indeed play a role in spontaneous calibration (translation from numerical representation to output). We suggest that they probably also contribute to performance involving external calibration, although this might be more clearly demonstrated with a patient presenting more marked executive deficits.

Future studies of patients presenting executive deficits following frontal lobe damage might be of interest, to determine whether a deficit in numerical estimation can occur independently from one in cognitive estimation. This would help determine whether calibration in numerical estimation is related to a process specific to the numerical domain or to a more general process. Moreover, the role of non-numerical parameters could be further investigated (are difficulties in calibration always linked to influence of non-numerical parameters, or can they arise independently?). The patient that we examined presented lesions both to the left and right frontal lobes. It would be interesting to determine whether lateralization of the lesion plays an important role, especially since Piazza and collaborators found right frontal activation in (non-verbal) estimation of numerical quantity (Piazza et al., 2006). It would also be of interest to test several patients with frontal lobe lesions to determine more precisely which part of the frontal lobe plays a role in calibration.

7 FIGURE INDEX

8 TABLE INDEX

9 REFERENCES

Alvarez, G.A., & Cavanagh, P. (2004). Independent attention resources for the left and right visual hemifields [Abstract]. *Journal of Vision, 4*, 29, 29a, http://journalofvision.org/24/28/29/, doi:10.1167/1164.1168.1129.

Ansari, D., Garcia, N., Lucas, E., Hamon, K., & Dhital, B. (2005). Neural correlates of symbolic number processing in children and adults. *Neuroreport, 16*, 1769-1773.

Aschenbrenner, S., Tucha, O., & Lange, K.W. (2001). *Regensburger Wortflüssigkeits-Test*. Göttingen Bern Toronto Seattle: Hogrefe Verlag für Psychologie.

Ashcraft, M.H. (1992). Cognitive arithmetic: A review of data and theory. *Cognition, 44*, 75-106.

Atkinson, J., Campbell, F.W., & Francis, M.R. (1976a). The magic number 4 +/- 0: A new look at visual numerosity judgments. *Perception, 5*, 327-334.

Atkinson, J., Francis, M.R., & Campbell, F.W. (1976b). The dependence of the visual numerosity limit on orientation colour and grouping in the stimulus. *Perception, 5*, 335-342.

Balakrishnan, J.D., & Ashby, F.G. (1991). Is subitizing a unique numerical ability. *Perception & Psychophysics, 50*, 555-564.

Balakrishnan, J.D., & Ashby, F.G. (1992). Subitizing: Magical numbers or mere superstition. *Psychological Research, 54*, 80-90.

Barnea-Goraly, N., Eliez, S., Menon, V., Bammer, R., & Reiss, A.L. (2005). Arithmetic ability and parietal alterations: a diffusion tensor imaging study in velocardiofacial syndrome. *Cognitive Brain Research, 25*, 735-740.

Barth, H., Kanwisher, N., & Spelke, E. (2003). The construction of large number representations in adults. *Cognition, 86*, 201-221.

Barth, H., La Mont, K., Lipton, J., Dehaene, S., Kanwisher, N., & Spelke, E. (2006). Non-symbolic arithmetic in adults and young children. *Cognition, 98*, 199-222.

Barth, H., La Mont, K., Lipton, J., & Spelke, E.S. (2005). Abstract number and arithmetic in preschool children. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 14116-14121.

Battelli, L., Cavanagh, P., Intriligator, J., Tramo, M.J., Hnaff, M.A., Michl, F., et al. (2001). Unilateral right parietal damage leads to bilateral deficit for high-level motion. *Neuron, 32*, 985-995.

Bechara, A., Damasio, A.R., Damasio, H., & Anderson, S.W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition, 50*, 7-15.

Bechara, A., Tranel, D., & Damasio, H. (2000). Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. *Brain, 123 (Pt 11)*, 2189-2202.

Benke, T., Delazer, M., Bartha, L., & Auer, A. (2003). Basal ganglia lesions and the theory of fronto-subcortical loops: neuropsychological findings in two patients with left caudate lesions. *Neurocase, 9*, 70-85.

Benson, D.F., Davis, R.J., & Snyder, B.D. (1988). Posterior cortical atrophy. *Archives of Neurology, 45*, 789-793.

Bijeljac-Babic, R., Bertoncini, J., & Mehler, J. (1991). How do four-day-old infants categorize multisyllabic utterances. *Developmental Psychology, 29*, 711-721.

Blaser, E., Pylyshyn, Z.W., & Holcombe, A.O. (2000). Tracking an object through feature space. *Nature, 408*, 196-199.

Bourdon, B. (1908). Sur le temps nécessaire pour nommer les nombres. *Revue philosophique de la France et de l'étranger, 65*, 426-431.

Brand, M., Kalbe, E., & Kessler, J. (2002a). Qualitative and quantitative differences in cognitive estimation of patients with probable Alzheimer's disease from healthy controls – what are the differences? In P. Calabrese & A. Neugebauer (Eds.), *Memory and emotion* (pp. 425-429). New Jersey: World Scientific.

Brand, M., Kalbe, E., & Kessler, J. (2002b). *Test zum kognitiven Schätzen (TKS)*. Göttingen: Hogrefe.

Bruandet, M., Molko, N., Cohen, L., & Dehaene, S. (2004). A cognitive characterization of dyscalculia in Turner syndrome. *Neuropsychologia, 42*, 288-298.

Buckley, P.B., & Gillman, C.B. (1974). Comparison of digits and dot patterns. *Journal of Experimental Psychology, 103*, 1131-1136.

Butterworth, B. (1999). *The Mathematical Brain*. London: Macmillan.

Butterworth, B., Cappelletti, M., & Kopelman, M. (2001). Category specificity in reading and writing: the case of number words. *Nature Neuroscience, 4*, 784-786.

Cantlon, J.F., Brannon, E.M., Carter, E.J., & Pelphrey, K.A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *Public Library of Science Biology, 4*, e125.

Cappelletti, M., Butterworth, B., & Kopelman, M. (2001). Spared numerical abilities in a case of semantic dementia. *Neuropsychologia, 39*, 1224-1239.

Cappelletti, M., & Cipolotti, L. (2006). Unconscious processing of Arabic numerals in unilateral neglect. *Neuropsychologia, 44*, 1999-2006.

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

Chochon, F., Cohen, L., van de Moortele, P.F., & Dehaene, S. (1999). Differential contributions of the left and right inferior parietal lobules to number processing. *Journal of Cognitive Neuroscience, 11*, 617-630.

Cipolotti, L., Butterworth, B., & Denes, G. (1991). A specific deficit for numbers in a case of dense acalculia. *Brain, 114*, 2619-2637.

Cohen Kadosh, R., Kadosh, K.C., & Henik, A. (2007). When Brightness Counts: The Neuronal Correlate of Numerical-Luminance Interference. *Cerebral Cortex*.

Cohen, L., & Dehaene, S. (2000). Calculating without reading: Unsuspected residual abilities in pure alexia. *Cognitive Neuropsychology, 17*, 563-583.

Cohen, L., Wilson, A.J., Izard, V., & Dehaene, S. (2007). Acalculia and Gerstmann's syndrome. In O. Godefroy & J. Bogousslavsky (Eds.), *Cognitive and Behavioral Neurology of Stroke* (pp. 126-147). Cambridge: Cambridge University Press.

Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., & Shulman, G.L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci, 3*, 292-297.

Cordes, S., Gelman, R., Gallistel, C.R., & Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychonomic Bulletin & Review, 8*, 698-707.

Coslett, H.B., & Saffran, E. (1991). Simultanagnosia: to see but not two see. *Brain, 114*, 1523-1545.

Crawford, J.R., Bryan, J., Luszcz, M.A., Obonsawin, M.C., & Stewart, L. (2000). The executive decline hypothesis of cognitive aging: do executive deficits qualify as differential deficits and do they mediate age-related memory decline? *Aging, Neuropsychology, and Cognition, 7*, 9-31.

Crawford, J.R., & Garthwaite, P.H. (2002). Investigation of the single case in neuropsychology: confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia, 40*, 1196-1208.

Crawford, J.R., & Garthwaite, P.H. (2004). Statistical methods for single-case studies in neuropsychology: comparing the slope of a patient s regression line with those of a control sample. *Cortex, 40*, 533-548.

Crawford, J.R., Garthwaite, P.H., Howell, D.C., & Venneri, A. (2003). Intra-individual measures of association in neuropsychology: Inferential methods for comparing a single case with a control or normative sample. *Journal of the International Neuropsychological Society, 9,* 989-1000.

Crawford, J.R., & Howell, D.C. (1998). Comparing an individual's test score against norms derived from small samples. *The Clinical Neuropsychologist, 12,* 482-486.

Dagenbach, D., & McCloskey, M. (1992). The organization of arithmetic facts in memory: Evidence from a brain-damaged patient. *Brain and Cognition, 20,* 345-366.

Darlymple, K.A., Kingstone, A., & Barton, J.J.S. (2007). Seeing trees OR seeing forests in simultanagnosia: Attentional capture can be local or global. *Neuropsychologia, 45,* 871-875.

De Renzi, E. (1996). Balint-Holmes' syndrome. In C. Code, Y., C.-W. Wallesch, Y. Joanette & A. Roch Lecours (Eds.), *Classic Cases in Neuropsychology* (pp. 123-143). Hove, East Sussex: Psychology Press.

Dehaene, S. (1997). *La bosse des maths.* Paris: Odile Jacob.

Dehaene, S. (2007). Symbols and quantities in parietal cortex: Elements of a mathematical theory of number representation and manipulation. In P. Haggard & Y. Rossetti (Eds.), *Attention & Performance XXII. Sensori-motor foundations of higher cognition*. Cambridge, Mass.: Harvard University Press.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and numerical magnitude. *Journal of Experimental Psychology: General, 122,* 371-396.

Dehaene, S., & Changeux, J.-P. (1993). Development of elementary numerical abilities: A neuronal model. *Journal of Cognitive Neuroscience, 5,* 390-407.

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

Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex*, *33*, 219-250.

Dehaene, S., Dupoux, E., & Mehler, J. (1990). Is numerical comparison digital: Analogical and Symbolic effects in two-digit number comparison. *Journal of Experimental Psychology: Human Perception and Performance, 16,* 626-641.

Dehaene, S., Izard, V., Pica, P., & Spelke, E. (2006). Core knowledge of geometry in an Amazonian indigene group. *Science, 311,* 381-384.

Dehaene, S., & Marques, J.F. (2002). Cognitive euroscience: scalar variability in price estimation and the cognitive consequences of switching to the euro. *The Quarterly Journal of Experimental Psychology, 55*, 705-731.

Dehaene, S., & Mehler, J. (1992). Cross-linguistic regularities in the frequency of number words. *Cognition, 43*, 1-29.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology, 20*, 487-506.

Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., & Tsivkin, S. (1999). Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science, 284,* 970-974.

Delazer, M., & Benke, T. (1997). Arithmetic facts without meaning. *Cortex, 33*, 697-710.

Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., et al. (2003). Learning complex arithmetic--an fMRI study. *Brain Research. Cognitive Brain Research, 18*, 76-88.

Delazer, M., Karner, E., Zamarian, L., Donnemiller, E., & Benke, T. (2006). Number processing in posterior cortical atrophy--a neuropsycholgical case study. *Neuropsychologia, 44*, 36-51.

Della Sala, S., MacPherson, S.E., Phillips, L.H., Sacco, L., & Spinnler, H. (2004). The role of semantic knowledge on the cognitive estimation task--evidence from Alzheimer s disease and healthy adult aging. *Journal of Neurology, 251*, 156-164.

Delvenne, J.F. (2005). The capacity of visual short-term memory within and between hemifields. *Cognition, 96*, B79-88.

Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition, 79*, 39-88.

Dubois, B., Slachevsky, A., Litvan, I., & Pillon, B. (2000). The FAB: a Frontal Assessment Battery at bedside. *Neurology, 55*, 1621-1626.

Eliez, S., Blasey, C.M., Menon, V., White, C.D., Schmitt, J.E., & Reiss, A.L. (2001). Functional brain imaging study of mathematical reasoning abilities in velocardiofacial syndrome (del22q11.2). *Genetics in medicine: official journal of the American College of Medical Genetics, 3*, 49-55.

Emmerton, J., & Renner, J.C. (2006). Scalar effects in the visual discrimination of numerosity by pigeons. *Learning & behavior: a Psychonomic Society publication, 34*, 176-192.

Feigenson, L., Carey, S., & Hauser, M. (2002). The representations underlying infants' choice of more: object files versus analog magnitudes. *Psychological Science, 13*, 150-156.

Feigenson, L., Dehaene, S., & Spelke, E. (2004a). Core systems of number. *Trends in Cognitive Sciences, 8*, 307-314.

Feigenson, L., Dehaene, S., & Spelke, E. (2004b). Origins and endpoints of the core systems of number. *Trends in Cognitive Sciences, 8*, 448-449.

Fias, W., & Verguts, T. (2004). The mental number line: exact and approximate. *Trends in Cognitive Sciences, 8*, 447-448; author reply 448-449.

Flowers, K.A., & Robertson, C. (1985). The effect of Parkinson s disease on the ability to maintain a mental set. *Journal of Neurology, Neurosurgery, and Psychiatry, 48*, 517-529.

Fox, A.M., Michie, P.T., Wynne, C.D., & Maybery, M.T. (2000). ERP correlates of response inhibition to elemental and configural stimuli in a negative patterning task. *Clinical neurophysiology: official journal of the International Federation of Clinical Neurophysiology, 111*, 1045-1053.

Freeman, M.R., Ryan, J.J., Lopez, S.J., & Mittenberg, W. (1995). Cognitive estimation in traumatic brain injury: relationships with measures of intelligence, memory, and affect. *International Journal of Neuroscience, 83*, 269-273.

Gainotti, G., D'Erme, P., & Bartolomeo, P. (1991). Early orientation of attention toward the half space ipsilateral to the lesion in patients with unilateral brain damage. *Journal of Neurology, Neurosurgery and Psychiatry, 54*, 1082-1089.

Gallace, A., Tan, H.Z., & Spence, C. (2006). Numerosity judgments for tactile stimuli distributed over the body surface. *Perception, 35*, 247-266.

Gallace, A., Tan, H.Z., & Spence, C. (2007). Multisensory numerosity judgments for visual and tactile stimuli. *Perception & Psychophysics, 69*, 487-501.

Gallistel, C.R., & Gelman, I. (2000). Non-verbal numerical cognition: from reals to integers. *Trends in Cognitive Science, 4*, 59-65.

Gallistel, C.R., & Gelman, R. (1991). The preverbal counting process. In W. Kessen, A. Ortony & F. I. M. Craik (Eds.), *Thoughts memories and emotions: Essays in honor of George Mandler* (pp. 65-81). Hillsdale N.J.: Lawrence Erlbaum Associates.

Gallistel, C.R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition, 44*, 43-74.

Gallistel, C.R., & Gelman, R. (2005). Mathematical cognition. In K. Holyoak & R. Morrison (Eds.), *The Cambridge Handbook of thinking and reasoning* (pp. 559-588). New York: Cambridge University Press.

Gauthier, L., Dehaut, F., & Joanette, Y. (1989). The Bells test: a quantitative and qualitative test for visual neglect. *International Journal of Clinical Neuropsychology, 11*, 49-54.

Gelman, R., & Gallistel, C.R. (1978). *The child's understanding of number*. Cambridge Mass.: Harvard University Press.

Gerstmann, J. (1940). Syndrome of finger agnosia, disorientation for right and left, agraphia, and acalculia. *Archives of Neurology and Psychiatry, 44*, 398-408.

Ginsburg, N. (1976). Effect of item arrangement on perceived numerosity: Randomness vs regularity. *Perceptual and Motor Skills, 43*, 663-668.

Ginsburg, N. (1978). Perceived numerosity item arrangement and expectancy. *American Journal of Psychology, 91*, 267-273.

Ginsburg, N. (1991). Numerosity estimation as a function of stimulus organization. *Perception, 20*, 681-686.

Gordon, P. (2004). Numerical cognition without words: evidence from Amazonia. *Science, 306*, 496-499.

Green, C.S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature, 423*, 534-537.

Green, C.S., & Bavelier, D. (2006). Enumeration versus multiple object tracking: the case of action video game players. *Cognition, 101*, 217-245.

Gross-Tsur, V., Manor, O., & Shalev, R.S. (1996). Developmental dyscalculia: prevalence and demographic features. *Developmental Medicine and Child Neurology, 38*, 25-33.

Hauser, M.D., & Carey, S. (2003). Spontaneous representations of small numbers of objects by rhesus macaques: examinations of content and format. *Cognitive Psychology, 47*, 367-401.

Hauser, M.D., Carey, S., & Hauser, L.B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 267*, 829-833.

Hauser, M.D., Dehaene, S., Dehaene-Lambertz, G., & Patalano, A.L. (2002). Spontaneous number discrimination of multi-format auditory stimuli in cotton-top tamarins (Saguinus oedipus). *Cognition, 86*, B23-32.

Helmstaedter, C., & Durwen, H.F. (1990). VLMT: Verbaler Lern- und Merkfähigkeitstest: Ein praktikables und differenziertes Instrumentarium zur Prüfung der verbalen Gedächtnisleistungen. *Schweizer Archiv für Neurologie und Psychiatrie, 141*, 21-30.

Henik, A., & Tzelgov, J. (1982). Is three greater than five: The relation between physical and semantic size in comparison tasks. *Memory and Cognition, 10*, 389-395.

Hollingsworth, W.H., Simmons, J.P., Coates, T., & Cross, H.A. (1991). Perceived numerosity as a function of array number, speed of array development, and density of array items. *Bulletin of the Psychonomic Society, 29*, 448-450.

Howe, E., & Jung, K. (1987). Judgment of numerosity: effects of symmetry and goodness in dot pattern arrays. *Acta Psychologica, 64,* 3-11.

Hubbard, E.M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience, 6*, 435-448.

Humphreys, G.W. (1998). Neural representation of objects in space: a dual coding account. *Philosophical Transactions of the Royal Society of London, Series B, 353*, 1341-1351.

Humphreys, G.W., & Heinke, D. (1998). Spatial representation and selection in the brain: neuropsychological and computational constraints. *Visual Cognition, 5*, 9-47.

Huntley-Fenner, G. (2001). Children s understanding of number is similar to adults and rats: numerical estimation by 5--7-year-olds. *Cognition, 78*, B27-40.

Isaacs, E.B., Edmonds, C.J., Lucas, A., & Gadian, D.G. (2001). Calculation difficulties in children of very low birthweight: A neural correlate. *Brain, 124,* 1701-1707.

Ischebeck, A., Zamarian, L., Siedentopf, C., Koppelstaetter, F., Benke, T., Felber, S., et al. (2006). How specifically do we learn? Imaging the learning of multiplication and subtraction. *Neuroimage, 30*, 1365-1375.

Izard, V. (2006). *Interactions entre les représentations numériques verbales et non-verbales: étude théorique et expérimentale.* Université Paris 6, Paris.

Izard, V., & Dehaene, S. (in press). Calibrating the mental number line. *Cognition (2007),* doi:10.1016/j.cognition.2007.1006.1004.

Jackson, M., & Warrington, E.K. (1986). Arithmetic skills in patients with unilateral cerebral lesions. *Cortex, 22*, 611-620.

Jordan, K.E., Brannon, E.M., Logothetis, N.K., & Ghazanfar, A.A. (2005). Monkeys match the number of voices they hear to the number of faces they see. *Current Biology, 15,* 1034-1038.

Kahneman, D., Treisman, A., & Gibbs, B.J. (1992). The reviewing of object files: object-specific integration of information. *Cognitive Psychology, 24*, 175-219.

Karnath, H.O. (1988). Deficits of attention in acute and recovered hemineglect. *Neuropsychologia, 26,* 27-43.

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

Kim, M.-S., & Robertson, L.C. (2001). Implicit representations of space after bilateral parietal lobe damage. *Journal of Cognitive Neuroscience, 13,* 1080-1087.

Kohler, J., & Beck, U. (2004). Der Planungstest - Softwareprogramm zur Diagnostik von Planungsstörungen. EnJoiME Software (Beck & Kohler GbR). 78467 Konstanz.

Kohler, J., Beck, U., & Hohnecker, B. (2003). Neuropsychological assessment of basic planning competence. *Journal of the International Neuropsychological Society, 9*, 519.

Koontz, K.L., & Berch, D.B. (1996). Identifying simple numerical stimuli: Processing inefficiencies exhibited by arithmetic learning disabled children. *Mathematical Cognition, 2,* 1–23.

Krishna, A., & Raghubir, P. (1997). The effect of line configuration on perceived numerosity of dotted lines. *Memory & Cognition, 25*, 492-507.

Krueger, L.E. (1972). Perceived numerosity. *Perception and Psychophysics, 11,* 5-9.

Kucian, K., Loenneker, T., Dietrich, T., Dosch, M., Martin, E., & von Aster, M. (2006). Impaired neural networks for approximate calculation in dyscalculic children: a functional MRI study. *Behavioral and brain functions: BBF, 2,* 31.

Landerl, K., Bevan, A., & Butterworth, B. (2004). Developmental dyscalculia and basic numerical capacities: a study of 8-9-year-old students. *Cognition, 93*, 99-125.

Lee, K.M. (2000). Cortical areas differentially involved in multiplication and subtraction: A functional magnetic resonance imaging study and correlation with a case of selective acalculia. *Annals of Neurology, 48,* 657-661.

Lehrl, S., Merz, J., Burkard, G., & Fischer, B. (1991). *Mehrfachwahl-Wortschatz Intelligenz Test*. Erlangen: Peri-Med Fachbuch.

Lemer, C., Dehaene, S., Spelke, E., & Cohen, L. (2003). Approximate quantities and exact number words: Dissociable systems. *Neuropsychologia, 41*, 1942-1958.

Lewis, C., Hitch, G.J., & Walker, P. (1994). The prevalence of specific arithmetic difficulties and specific reading difficulties in 9- and 10-year-old boys and girls. *Journal of Child Psychology and Psychiatry, 35*, 283-292.

Lipton, J.S., & Spelke, E.S. (2003). Origins of number sense. Large-number discrimination in human infants. *Psychological Science, 14*, 396-401.

Logie, R.H., & Baddeley, A.D. (1987). Cognitive processes in counting. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 13*, 310-326.

Luck, S.J., & Vogel, E.K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279-281.

Mandler, G., & Shebo, B.J. (1982). Subitizing: An analysis of its component processes. *Journal of Experimental Psychology: General, 111*, 1-21.

McCrea, S.M., Buxbaum, L.J., & Coslett, H.B. (2006). Illusory conjunctions in simultanagnosia: Coarse coding of visual feature location? *Neuropsychologia, 44*, 1724-1736.

McCrink, K., & Wynn, K. (2004). Large-number addition and subtraction by 9-month-old infants. *Psychological Science, 15*, 776-781.

Meck, W.H., & Church, R.M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology. Animal Behavior Processes, 9*, 320-334.

Mendez, M.F., Doss, R.C., & Cherrier, M.M. (1998). Use of the cognitive estimations test to discriminate frontotemporal dementia from Alzheimer s disease. *Journal of Geriatric Psychiatry and Neurology, 11*, 2-6.

Minturn, A.L., & Reese, T.W. (1951). The effect of differential reinforcement on the discrimination of visual number. *Journal of Psychology, 31*, 201-231.

Molko, N., Cachia, A., Riviere, D., Mangin, J.F., Bruandet, M., Le Bihan, D., et al. (2003). Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. *Neuron, 40*, 847-858.

Mort, D.J., Malhotra, P., Mannan, S.K., Rorden, C., Pambakian, A., Kennard, C., et al. (2003). The anatomy of visual neglect. *Brain, 126*, 1986-1997.

Moyer, R., & Landauer, T. (1967). Time required for judgements of numerical inequality. *Nature, 215*, 1519-1520.

Nestor, P.J., Caine, D., Fryer, T.D., Clarke, J., & Hodges, J.R. (2003). The topography of metabolic deficits in posterior cortical atrophy (the visual variant of Alzheimer s disease) with FDG-PET. *Journal of Neurology, Neurosurgery and Psychiatry, 74*, 1521-1529.

Nieder, A. (2005). Counting on neurons: the neurobiology of numerical competence. *Nature Reviews Neuroscience, 6*, 177-190.

Nieder, A., Diester, I., & Tudusciuc, O. (2006). Temporal and spatial enumeration processes in the primate parietal cortex. *Science, 313*, 1431-1435.

Nieder, A., Freedman, D.J., & Miller, E.K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. *Science, 297*, 1708-1711.

Nieder, A., & Miller, E.K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 7457-7462.

Nuerk, H.C., Wood, G., & Willmes, K. (2005). The universal SNARC effect: the association between number magnitude and space is amodal. *Experimental Psychology, 52*, 187-194.

Ota, H., Fujii, T., Suzuki, K., Fukatsu, R., & Yamadori, A. (2001). Dissociation of body-centered and stimulus-centered representations in unilateral neglect. *Neurology, 57*, 2064-2069.

Oyama, T., Kikuchi, T., & Ichihara, S. (1981). Span of attention backward masking and reaction time. *Perception & Psychophysics, 29*, 106-112.

Pavese, A., Coslett, H.B., Saffran, E., & Buxbaum, L. (2002). Limitations of attentional orienting. Effects of abrupt visual onsets and offsets on naming two objects in a patient with simultanagnosia. *Neuropsychologia, 40*, 1097-1103.

Pesenti, M., Seron, X., & van der Linden, M. (1994). Selective impairment as evidence for mental organisation of arithmetical facts: BB, a case of preserved subtraction? *Cortex, 30*, 661-671.

Pesenti, M., Thioux, M., Samson, D., Bruyer, R., & Seron, X. (2000). Number processing and calculation in a case of visual agnosia. *Cortex, 36*, 377-400.

Peterson, S.A., & Simon, T.J. (2000). Computational evidence for the subitizing phenomenon as an emergent property of the human cognitive architecture. *Cognitive Science, 24*, 93-122.

Piazza, M. (2003). *The quantifying brain: a functional imaging approach to subitizing, counting, and numerosity estimation (thesis).* University College London, London.

Piazza, M., Giacomini, E., Le Bihan, D., & Dehaene, S. (2003). Single-trial classification of parallel pre-attentive and serial attentive processes using functional magnetic resonance imaging. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 270*, 1237-1245.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron, 44*, 547-555.

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

Piazza, M., Mechelli, A., Price, C.J., & Butterworth, B. (2006). Exact and approximate judgements of visual and auditory numerosity: an fMRI study. *Brain Research, 1106*, 177-188.

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron, 53*, 293-305.

Pica, P., Lemer, C., Izard, V., & Dehaene, S. (2004). Exact and approximate arithmetic in an Amazonian indigene group. *Science, 306*, 499-503.

Pinel, P., Dehaene, S., Riviere, D., & LeBihan, D. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *Neuroimage, 14*, 1013-1026.

Pinel, P., Piazza, M., Le Bihan, D., & Dehaene, S. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron, 41*, 983-993.

Pylyshyn, Z.W. (2000). Situating vision in the world. *Trends in Cognitive Science, 4*, 197-207.

Pylyshyn, Z.W., & Storm, R. (1988). Tracking multiple independent targets: Evidence for both serial and parallel stages. *Spatial Vision, 3*, 179-197.

Repp, B.H. (2007). Perceiving the numerosity of rapidly occurring auditory events in metrical and nonmetrical contexts. *Perception & Psychophysics, 69*, 529-543.

Revkin, S., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (in press). Does subitizing reflect numerical estimation? *Psychological Science*.

Revkin, S., Piazza, M., Izard, V., Zamarian, L., Karner, E., Dehaene, S., et al. (2007). *The role of executive functions in numerical estimation: A neuropsychological case study*: Poster presented at the 25th European Workshop on Cognitive Neuropsychology, Bressanone.

Rey, A. (1941). L'examen psychologique dans les cas d'encéphalopathie traumatique. *Archives de Psychologie, 28*, 286-340.

Riggs, K.J., Ferrand, L., Lancelin, D., Fryziel, L., Dumur, G., & Simpson, A. (2006). Subitizing in tactile perception. *Psychological Science, 17*, 271-272.

Rivera, S.M., Menon, V., White, C.D., Glaser, B., & Reiss, A.L. (2002). Functional brain activation during arithmetic processing in females with fragile X Syndrome is related to FMR1 protein expression. *Human Brain Mapping, 16*, 206-218.

Rivera, S.M., Reiss, A.L., Eckert, M.A., & Menon, V. (2005). Developmental changes in mental arithmetic: evidence for increased functional specialization in the left inferior parietal cortex. *Cerebral Cortex, 15*, 1779-1790.

Rizzo, M., & Vecera, S.P. (2002). Psychoanatomical substrates of Balint's syndrome. *Journal of Neurology, Neurosurgery, and Psychiatry, 72*, 162-178.

Roth, M., Schumacher, J., & Arnett, J. (2003). Die deutsche Version des Arnett Inventory of Sensation Seeking (AISS-D). In M. Roth & P. Hammelstein (Eds.), *Sensation Seeking: Konzeption, Diagnostik und Anwendung* (pp. 100-121). Göttingen: Hogrefe.

Rourke, B.P. (1993). Arithmetic disabilities, specific and otherwise: A neuropsychological perspective. *Journal of Learning Disabilities, 26*, 214-226.

Rourke, B.P., & Conway, J.A. (1997). Disabilities of arithmetic and mathematical reasonning. Perspectives from neurology and neuropsychology. *Journal of Learning Disabilities, 30*, 34-46.

Rousselle, L., & Noël, M.P. (2007). Basic numerical skills in children with mathematics learning disabilities: a comparison of symbolic vs non-symbolic number magnitude processing. *Cognition, 102*, 361-395.

Rumbaugh, D.M., Savage-Rumbaugh, S., & Hegel, M.T. (1987). Summation in the chimpanzee (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 13*, 107-115.

Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-Prime Users Guide*. Pittsburgh: Psychology Software Tools Inc.

Scholl, B.J., & Pylyshyn, Z.W. (1999). Tracking multiple items through occlusion: clues to visual objecthood. *Cognitive Psychology, 38*, 259-290.

Sears, C.R., & Pylyshyn, Z.W. (2000). Multiple object tracking and attentional processing. *Canadian Journal of Experimental Psychology, 54*, 1-14.

Shalev, R.S., Auerbach, J., Manor, O., & Gross-Tsur, V. (2000). Developmental dyscalculia: prevalence and prognosis. *European Child and Adolescent Psychiatry, 9,* II58-64.

Shallice, T., & Evans, M.E. (1978). The involvement of the frontal lobes in cognitive estimation. *Cortex, 14*, 294-303.

Shuman, M., & Kanwisher, N. (2004). Numerical magnitude in the human parietal lobe; tests of representational generality and domain specificity. *Neuron, 44*, 557-569.

Siegler, R.S., & Opfer, J.E. (2003). The development of numerical estimation: evidence for multiple representations of numerical quantity. *Psychological Science, 14*, 237-243.

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

Smith, M.L., & Milner, B. (1984). Differential effects of frontal-lobe lesions on cognitive estimation and spatial memory. *Neuropsychologia, 22*, 697-705.

Smith, M.L., & Milner, B. (1988). Estimation of frequency of occurrence of abstract designs after frontal or temporal lobectomy. *Neuropsychologia, 26*, 297-306.

Soltész, F., Szucs, D., Dékany, J., Markus, A., & Csépe, V. (2007). A combined event-related potential and neuropsychological investigation of developmental dyscalculia. *Neuroscience Letters*, doi:10.1016/j.neulet.2007.1002.1067.

Spreen, O., & Strauss, E. (1998). *A compendium of neuropsychological tests: Administration, norms, and commentary* (2nd ed.). New York: Oxford University Press.

Starkey, P., & Cooper, R.G. (1980). Perception of numbers by human infants. *Science, 210*, 1033-1035.

Starkey, P., & Cooper, R.G. (1995). The development of subitizing in young children. *British Journal of Developmental Psychology, 13*, 399-420.

Sulkowski, G.M., & Hauser, M.D. (2001). Can rhesus monkeys spontaneously subtract? *Cognition, 79*, 239-262.

Taylor, R., & O'Carroll, R. (1995). Cognitive estimation in neurological disorders. *British Journal of Clinical Psychology, 34 (Pt 2)*, 223-228.

Thiebaut de Schotten, M., Urbanski, M., Duffau, H., Volle, E., Levy, R., Dubois, B., et al. (2005). Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. *Science, 309*, 2226-2228.

Thioux, M., Pillon, A., Samson, D., De Partz, M.P., Noel, M.-P., & Seron, X. (1998). The isolation of numerals at the semantic level. *Neurocase, 4*, 371-389.

Thompson, R.F., Mayers, K.S., Robertson, R.T., & Patterson, C.J. (1970). Number coding in association cortex of the cat. *Science*, *168*, 271-273.

Treisman, A., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*, 97-136.

Trick, L.M., Guindon, J., & Vallis, L.A. (2006). Sequential tapping interferes selectively with multiple-object tracking: do finger-tapping and tracking share a common resource? *Quarterly Journal of Experimental Psychology (2006), 59*, 1188-1195.

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

Trick, L.M., & Pylyshyn, Z.W. (1994). Why are small and large numbers enumerated differently? a limited capacity preattentive stage in vision. *Psychological Review, 100*, 80-102.

Vallar, G., & Perani, D. (1986). The anatomy of unilateral neglect after right-hemisphere stroke lesions. A clinical/CT-scan correlation study in man. *Neuropsychologia, 24*, 609-622.

van Oeffelen, M.P., & Vos, P.G. (1982). A probabilistic model for the discrimination of visual number. *Perception & Psychophysics, 32*, 163-170.

VanMarle, K., & Scholl, B.J. (2003). Attentive tracking of objects versus substances. *Psychological Science, 14*, 498-504.

Venkatraman, V., Ansari, D., & Chee, M.W. (2005). Neural correlates of symbolic and non-symbolic arithmetic. *Neuropsychologia, 43*, 744-753.

Verguts, T., & Fias, W. (2004). Representation of number in animals and humans: a neural model. *Journal of Cognitive Neuroscience, 16*, 1493-1504.

Verguts, T., Fias, W., & Stevens, M. (2005). A model of exact small-number representation. *Psychonomic Bulletin & Review, 12*, 66-80.

Vuilleumier, P., & Rafal, R. (1999). "Both" means more than "two": localizing and counting in patients with visuospatial neglect. *Nature Neuroscience, 2*, 783-784.

Vuilleumier, P.O., & Rafal, R.D. (2000). A systematic study of visual extinction. Between- and within-field deficits of attention in hemispatial neglect. *Brain, 123 (Pt 6)*, 1263-1279.

Warrington, E.K., & James, M. (1967). Tachistoscopic number estimation in patients with unilateral cerebral lesions. *Journal of Neurology, Neurosurgery, and Psychiatry, 30*, 468-474.

Warrington, E.K., & James, M. (1991). *VOSP: Visual Object and Space Perception Battery*. Burry St Edmunds: Thames Valley Test Company.

Wechsler, D. (1987). *WMS-R Wechlser Memory Scale-Revised*. San Antonio: Psychological Corporation.

Whalen, J., Gallistel, C.R., & Gelman, R. (1999). Non-verbal counting in humans: The psychophysics of number representation. *Psychological Science, 10*, 130-137.

Wilson, A., & Dehaene, S. (2007). Number sense and developmental dyscalculia. In D. Coch, G. Dawson & K. Fischer (Eds.), *Human Behavior and the Developing Brain* (2nd ed., pp. 212-238): Guilford Press.

Wilson, A.J., Dehaene, S., Dubois, O., & Fayol, M. (submitted). “The Number Race”: Using adaptive game technology to improve early number sense.

Wilson, A.J., Dehaene, S., Pinel, P., Revkin, S.K., Cohen, L., & Cohen, D. (2006a). Principles underlying the design of "The Number Race", an adaptive computer game for remediation of dyscalculia. *Behavioral and brain functions: BBF, 2*, 19.

Wilson, A.J., Revkin, S.K., Cohen, D., Cohen, L., & Dehaene, S. (2006b). An open trial assessment of "The Number Race", an adaptive computer game for remediation of dyscalculia. *Behavioral and brain functions: BBF, 2*, 20.

Wynn, K. (1992). Addition and subtraction by human infants. *Nature, 358*, 749-750.

Wynn, K. (1996). Infants' individuation and enumeration of actions. *Psychological Science, 7*, 164-169.

Xu, F., & Spelke, E.S. (2000). Large number discrimination in 6-month-old infants. *Cognition, 74*, B1-B11.

Zamarian, L., Karner, E., Benke, T., Donnemiller, E., & Delazer, M. (2006). Knowing 7 x 8, but not the meaning of elephant: evidence for the dissociation between numerical and non-numerical semantic knowledge. *Neuropsychologia*, *44*, 1708-1723.

Zimmermann, P., & Fimm, B. (2002). *Testbatterie zur Aufmerksamkeitsprüfung (TAP)*. Herzogenrath, Germany: Psychologische Testsysteme.

Zorzi, M., & Butterworth, B. (1999). A computational model of numerical comparison. In M. Hahn & S. C. Stoness (Eds.), *Proceedings of the Twenty First Annual Conference of the Cognitive Science Society* (pp. 778-783). Mahwah (NJ): Erlbaum.

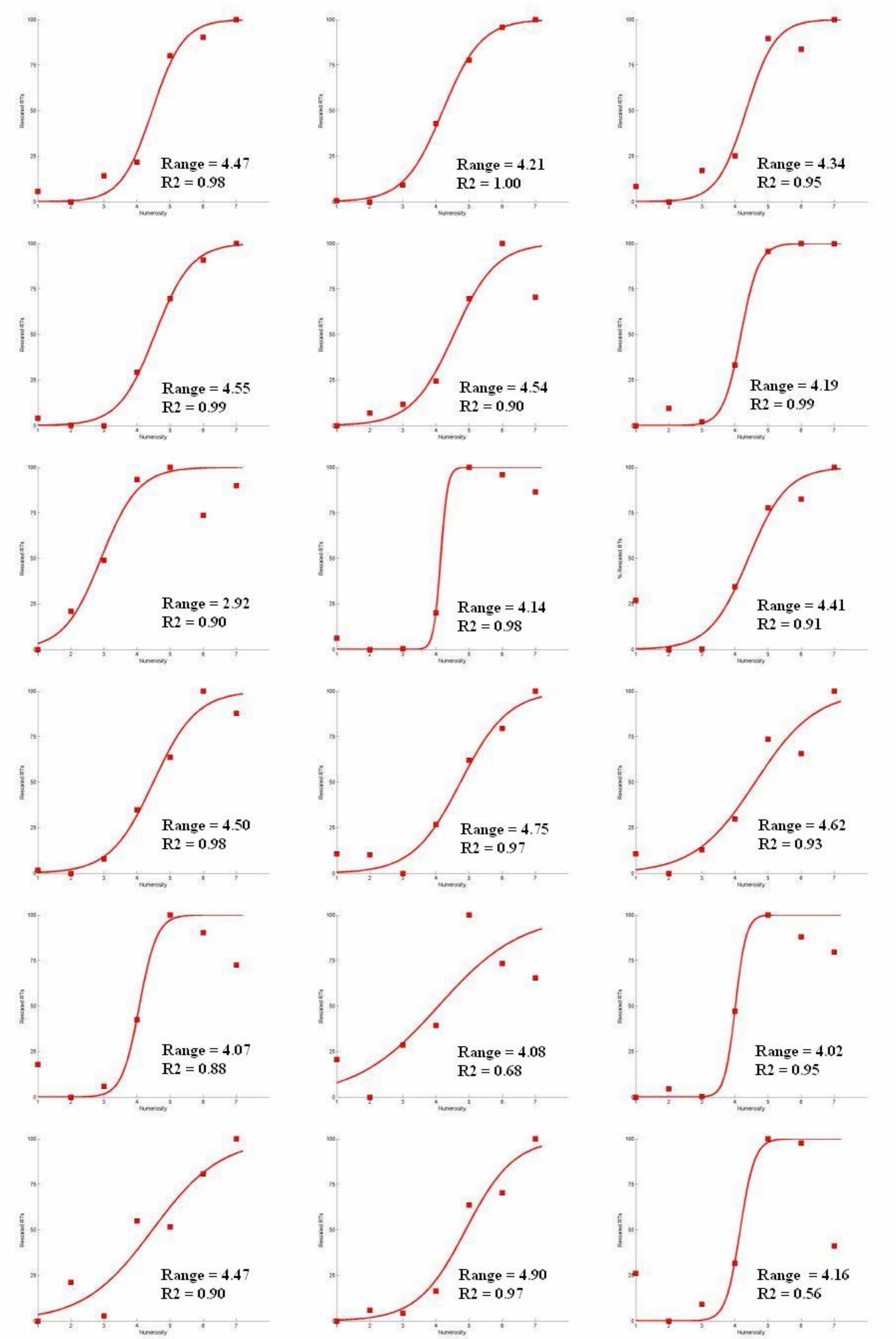
Zorzi, M., Priftis, K., & Umilta, C. (2002). Brain damage: neglect disrupts the mental number line. *Nature*, *417*, 138-139.

Zorzi, M., Stoianov, I., & Umiltà, C. (2005). Computational modeling of numerical cognition. In J. Campbell (Ed.), *Handbook of Mathematical Cognition* (pp. 67-84). New York: Psychology Press.

10 APPENDIX

10.1 APPENDIX 1: RESPONSE TIME FITS FROM THE 1-8 NAMING TASK (CHAPTER 2)

The 18 following graphs correspond to the normalized response times (0-100) for each of the 18 subjects plotted against numerosity (1-7), as well as the sigmoid fit. In each graph, the range derived from this fit (inflexion point of the sigmoid) is indicated as well as the goodness of fit (R2). The last subject was excluded from analyses because of a poor fit (R2 = 0.56).


Range = 4.47
R2 = 0.98
Range = 4.21
R2 = 1.00
Range = 4.34
R2 = 0.95
Range = 4.55
R2 = 0.99
Range = 4.54
R2 = 0.90
Range = 4.19
R2 = 0.99
Range = 2.92
R2 = 0.90
Range = 4.14
R2 = 0.98
Range = 4.41
R2 = 0.91
Range = 4.50
R2 = 0.98
Range = 4.75
R2 = 0.97
Range = 4.62
R2 = 0.93
Range = 4.07
R2 = 0.88
Range = 4.08
R2 = 0.68
Range = 4.02
R2 = 0.95
Range = 4.47
R2 = 0.90
Range = 4.90
R2 = 0.97
Range = 4.16
R2 = 0.56

10.2 APPENDIX 2: SMALL NUMEROSITY PROCESSING AND NON-NUMERICAL CONTINUOUS PARAMETERS (CHAPTER 3)

A shorter and modified version of the enumeration task was administered to ensure that non-numerical parameters did not influence the patients' performance, that is, to make sure that their responses were based on numerosity, and not on other continuous variables which usually co-vary with numerosity (such as the area covered by the dots, or the total area of black if black dots are presented on a white background). Indeed, in the main localisation and enumeration tasks, stimuli were not controlled for non-numerical parameters. Thus, we intermixed trials where dot size was held constant (and total occupied area co-varied with numerosity) with trials where total occupied area was held constant (and dots size co-varied negatively with numerosity), using the same numerosities and presentation duration as in the main enumeration task. Stimuli consisted in random patterns of dots, and were presented only in the left visual field; we reasoned that if performance was equally good across the different types of controls in this field, this would argue for responses based on numerosity in the main enumeration task as well (whether in the left, bilateral, or right field). The patients performed a total of 48 trials in one session (8 trials per condition: 3 numerosities x 2 types of controls x 8 trials). Accuracy results were analysed using χ^2 tests to compare performance across control type (constant area vs. constant dot size) for each numerosity.

10.2.1 Patient JM

Accuracy differences across types of control were non-significant for numerosities 2 ($\chi^2(1) = 1.07$, p (Fisher's exact test) = .61) and 3 ($\chi^2(1) = 1.07$, p (Fisher's exact test) = 1.00), whereas constant area lead to a significantly better performance with numerosity 4 ($\chi^2(1) = 7.27$, $p < .05$). However, as exposed in the main results section, numerosity 4 did not lead to an advantage of enumeration over localisation. Enumeration was quite poor with numerosity 2 (constant dot size: 50% correct; constant area: 25%), perhaps reflecting within-field extinction or neglect, but higher with numerosity 3 (constant dot size: 88% correct; constant area: 100%). We therefore conclude that these results suggest that the patient's advantage of enumeration over localisation (at least with numerosities 2 and 3) in the main tests was indeed related to numerosity processing and not based on non-numerical parameters.

10.2.2 Patient FC

Accuracy differences across types of control were non-significant for numerosities 2 ($\chi^2(1) = 1.07$, *p* (Fisher's exact test) = 1.00) and 3 ($\chi^2(1) = 1.33$, *p* (Fisher's exact test) = 0.57); accuracy was strictly equal across types of control for numerosity 4. Accuracy was quite high with all three numerosities (2: constant dot size: 88% correct, constant area: 100%; 3: constant dot size: 63%, constant area: 88%; 4: 100% in both conditions). We therefore conclude that these results suggest that the patient's advantage of enumeration over localisation in the main tests was indeed related to numerosity processing and not based on non-numerical parameters.

10.3 APPENDIX 3: TRANSCRIPTION OF THE COOKIE THEFT PICTURE DESCRIPTION (CHAPTER 4)

(translated from French by S.K. Revkin)

“It’s a little girl who is throwing a ball. She has a skirt on. There are two pictures in fact, one here and one here [the patient shows the left side and the right side of the picture]. There’s the mother cooking… or ironing. [What does the whole picture represent?] I don’t know. [What else do you see?] There’s a doorknob here, isn’t there? That’s the little girl. And here is the mother. [What else do you see?] There’s a cupboard here perhaps. The little girl… she’s playing with a ball perhaps… [Do you see anything else?] This is some salt, isn’t it? And isn’t this a pan?”

11 SHORT SUMMARY

11.1 IN ENGLISH

Human adults are thought to possess three processes to quantify visual objects: *subitizing* (the rapid and accurate enumeration of up to 3 or 4 items), *counting* and *estimation*. We investigated the underlying process involved in subitizing, the parallel or serial nature of approximate numerical processes (such as estimation) and the processes involved in estimation.

First, we directly tested the hypothesis that subitizing might represent estimation at a high level of precision. A unique advantage for quantities 1-4 was found, suggesting that human adults possess separate numerical systems for small and large numerosities. We further established that subitizing could occur independently of spatial attention (in patients with visual extinction).

Second, we showed that approximate numerical processes were globally spared in a patient presenting a deficit in serial visual attention, supporting the hypothesis of a parallel extraction of numerosity. We also found that estimation could not occur independently of spatial attention (in a patient with visual extinction), unless stimuli formed a single object. Finally, we investigated the hypothesis that executive processes might be needed in estimation. Results of a patient presenting executive deficits supported this hypothesis, as he presented extreme over-estimation. Different tests suggested a sparing of underlying quantity and an extension of the deficit to a non-verbal output, pointing to impairment in mapping from underlying quantity to output.

These findings argue for the existence of separate numerical systems for small and large numerosities in adults, and inform us on some of the characteristics of these systems.

11.2 IN FRENCH

L’adulte possède trois processus de quantification d’objets visuels : la *subitisation* (énumération rapide et exacte de 1-3 ou 4 items), le *comptage* et l’*estimation*. Nous avons investigué l’origine de la subitisation, le caractère sériel ou parallèle des processus numériques approximatifs (tels que l’estimation) ainsi que les processus impliqués dans l’estimation.

Nous avons testé l’hypothèse que la subitisation est de l’estimation à un degré élevé de précision. Un unique avantage pour les quantités 1-4 a été trouvé suggérant que les adultes possèdent des systèmes séparés pour les petites et les grandes quantités. Nous avons aussi montré que la subitisation peut survenir sans attention spatiale (patients avec extinction visuelle).

Nous avons montré que les processus numériques approximatifs étaient globalement préservés chez une patiente présentant un déficit de l’attention visuelle sérielle, soutenant l’hypothèse d’un mécanisme parallèle. Nous avons aussi montré que l’estimation ne peut opérer sans attention spatiale (patient avec extinction visuelle) à moins que les stimuli ne forment un seul objet. Enfin, nous avons testé l’hypothèse que l’estimation fait appel à des processus exécutifs. Cette idée est soutenue par les résultats d’un patient dysexécutif qui a présenté une surestimation extrême. La préservation de la quantité sous-jacente et l’extension du déficit à une réponse non verbale indiquent un déficit à l’étape de mise en correspondance entre quantité sous-jacente et réponse.

Ces résultats suggèrent l’existence chez l’adulte de systèmes numériques distincts pour les petites et les grandes quantités et nous éclairent sur les caractéristiques de ces systèmes.

12 SUBSTANTIAL SUMMARY IN FRENCH

L'adulte humain possède trois processus pour quantifier les objets de son environnement. Lorsqu'il a à faire à un ensemble de points par exemple, il peut rapidement et correctement énumérer jusqu'à 3 ou 4 items (subitisation). Pour des quantités plus larges, il utilise le comptage exact ou l'estimation approximative. Différentes études suggèrent que les animaux non-humains et les enfants pré-verbaux possèdent des précurseurs des capacités numériques exactes (subitisation) et approximatives (estimation, mais aussi comparaison, addition ou soustraction de quantités non-symboliques) de l'adulte. En effet, les animaux et les enfants pré-verbaux sont capables de discriminer et de mentalement manipuler (additionner, soustraire) des ensembles d'objets de manière exacte, du moment que leur quantité n'excède pas 3 ou 4. Ces capacités s'appliquent non seulement à des objets perçus visuellement, mais également à des sons ou des actions, suggérant l'utilisation d'une représentation abstraite de la quantité. Ils présentent également une appréhension et une manipulation approximative des grandes quantités qui suivent la loi de Weber, et ce, avec différents types de stimuli, suggérant l'utilisation d'un deuxième système de quantité abstraite, approximatif en contraste au premier. Les performances numériques approximatives de l'adulte obéissent également à la loi de Weber (reflétant des représentations numériques sous-jacentes dont le recouvrement augmente au fur et à mesure que les numérosités augmentent), lors de la comparaison de groupes de points (effets de distance et de taille, indiquant un effet du ratio entre les deux numérosités à comparer), ou lors de leur estimation (variabilité scalaire : augmentation de la variabilité des réponses qui est proportionnelle à l'augmentation de la réponse moyenne).

Au cours de nos différentes études de sujets adultes, nous avons eu pour but d'améliorer notre compréhension des processus impliqués dans la subitisation, en particulier en investiguant un possible lien avec l'estimation numérique, et en déterminant si la subitisation peut vraiment opérer en l'absence d'attention spatiale, comme le suggère une étude précédente. Nous avons aussi cherché à comprendre certains des mécanismes impliqués dans l'estimation. Nous avons investigué l'idée que la précision de l'estimation puisse être étroitement liée à la discrimination des numérosités. Nous avons également cherché à déterminer si l'estimation (et d'autres processus numériques approximatifs) pouvait survenir en l'absence d'attention spatiale et d'attention visuelle sérielle. Enfin, nous avons investigué la possibilité que l'estimation puisse faire appel à des processus exécutifs, lors de la mise en correspondance entre représentation numérique sous-jacente et symbole exact dans un contexte d'incertitude.

Dans notre premier chapitre expérimental (**chapitre 2**), nous rapportons les résultats d'une étude au cours de laquelle nous avons testé des volontaires sains en utilisant un nouveau paradigme pour investiguer leurs performances en subitisation et en estimation. Plusieurs auteurs proposent que la subitisation pourrait représenter de l'estimation numérique à un niveau élevé de précision. Nous avons testé cette hypothèse en comparant la performance de nos sujets à dénommer des petites quantités (dont celles qui mènent à la subitisation) en contraste avec des grandes (contrôlées pour leur difficulté de discrimination). Un unique avantage a été trouvé pour les quantités menant à la subitisation. Les grandes quantités dont la difficulté de discrimination était appariée à celle des quantités menant la subitisation n'étaient pas plus faciles à dénommer que les autres grandes quantités. Ces résultats suggèrent que l'adulte humain possède, tout comme les animaux et les enfants pré-verbaux, deux systèmes numériques distincts pour les petites et les grandes quantités. Cette étude nous a également apporté des réponses par rapport à un autre de nos questionnements : nous avons trouvé, chez ces sujets, que la précision de leurs performance en discrimination de grandes quantités corrélait avec leur précision de dénomination de quantités (en dehors des quantités menant à la subitisation). Ces résultats soutiennent l'idée d'un lien entre discrimination de numérosités et précision de l'estimation.

Dans une deuxième étude expérimentale (**chapitre 3**), nous avons testé deux patients cérébro-lésés présentant une extinction visuelle pour investiguer leurs capacités de subitisation. Nous avons répliqué une étude précédente montrant que l'énumération de petites quantités (2 et 4) disposées en patterns canoniques (respectivement en ligne et en carré) est globalement préservée même lorsqu'une partie des quantités ne peut être correctement localisée (dans une tâche de localisation). Nous avons étendu ces résultats à des patterns non-canoniques (quantités formant des patterns aléatoires) et à la numérosité 3 (formant un triangle, une ligne, ou un pattern aléatoire). Ces résultats suggèrent que la subitisation (par opposition à la reconnaissance de patterns canoniques) peut effectivement opérer en l'absence d'attention spatiale dirigée vers les éléments à quantifier. Nous avons également investigué la quantification de grandes quantités chez un de ces patients. Nous lui avons présenté des nuages de points et avons constaté que l'estimation ne peut opérer dans l'hémi-champ négligé lorsque les nuages sont nettement séparés (un à gauche, et un à droite) et entrent en compétition pour l'attention visuelle. Ceci implique que l'attention visuelle est peut-être nécessaire pour délimiter une zone dans laquelle l'estimation va ensuite pouvoir opérer. Nos résultats suggèrent qu'il est peut-être possible que l'estimation puisse opérer en l'absence d'attention spatiale lorsqu'un seul objet (nuage) central est présenté, mais de futures investigations sont nécessaires pour l'affirmer. Ces résultats convergent avec ceux de la première étude chez des volontaires sains (chapitre 2), puisqu'ils suggèrent aussi une différence entre traitement des petites et des grandes quantités chez l'adulte.

Dans une troisième étude expérimentale (**chapitre 4**), nous avons étudié les performances d'une patiente cérébro-lésée présentant un trouble de l'attention sérielle (simultanagnosie). En effet, deux modèles des processus numériques approximatifs conduisent à des prédictions opposées quant aux performances d'une telle patiente. Un modèle propose que les processus numériques approximatifs reposent sur un mécanisme sériel d'extraction de la numérosité, chaque élément à quantifier étant pris en compte un par un, à la suite ; un autre propose un mécanisme parallèle par lequel tous les éléments seraient pris en compte en une fois. Les résultats de cette patiente soutiennent le deuxième modèle, puisque ses performances en estimation, en comparaison, et en addition de nuages de points étaient globalement préservées, alors qu'elle présentait un déficit marqué en comptage, qui requiert un déplacement sériel de l'attention entre les éléments à dénombrer. Par ailleurs, ses résultats à des tâches non-numériques de recherche visuelle suggèrent également un déficit d'attention sérielle et une préservation de processus d'extraction parallèle de l'information.

Dans une dernière étude (**chapitre 5**), nous avons investigué un patient cérébro-lésé présentant des troubles exécutifs, pour explorer la possibilité que l'estimation puisse requérir des processus stratégiques, généralement atteints chez de tels patients. En effet, l'estimation requiert une calibration, pour assurer une correspondance correcte (ou du moins plausible) entre la représentation numérique sous-jacente et la réponse verbale. Les performances du patient dysexécutif à un test d'estimation furent marquées par une sur-estimation extrême en comparaison aux sujets de contrôle. Par ailleurs, différents tests numériques suggérèrent une préservation globale de la représentation de la quantité ; un autre test montra que le déficit d'estimation s'étendait à une réponse non-symbolique ; ces résultats suggèrent que le déficit de ce patient se situe au niveau de la calibration, c'est à dire de la mise en correspondance, et non au niveau de la représentation numérique sous-jacente ou de la sortie (réponse). Nos résultats suggèrent également que la calibration externe (prise en compte d'exemples de réponses correctes) puisse être légèrement atteinte chez ce patient ; d'autres études sont nécessaires pour confirmer un rôle des processus stratégiques dans la calibration externe.

En résumé, nos études suggèrent l'existence chez l'adulte de deux processus numériques distincts pour les petites et les grandes quantités, en concordance avec les données chez l'animal et l'enfant pré-verbal. Elles nous renseignent également sur certaines caractéristiques de ces systèmes, en suggérant que le traitement numérique des petites quantités peut opérer en l'absence d'attention spatiale, contrairement à l'estimation des grandes quantités. Nos recherches suggèrent également que le deuxième système (dédié aux grandes quantités) peut opérer de manière parallèle, comme cela a été démontré précédemment pour le premier. Enfin, elles suggèrent un rôle des processus stratégiques dans l'estimation des grandes quantités.