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Processing of quantitative information, investigated with fMRI.

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Processing of quantitative information, investigated with fMRI.

This thesis is about numbers.

The hitchhiker's guide to the galaxy says the following about numbers:

"There is a revolutionary new way of understanding the behaviour of numbers, which is called bistromathics. Just as Einstein observed that time was not an absolute but depended on the observer's movement in space, and that space was not an absolute, but depended on the observer's movement in time, so it is now realized that numbers are not absolute, but depend on the observer's movement in restaurants.

The baffling discrepancies which used to occur between the number of items on the bill, the cost of each item, the number of people at the table, and what they are each prepared to pay for, remained uninvestigated for centuries simply because no one took them seriously. They were at the time put down to such things as politeness, rudeness, meanness, flashness, tiredness, emotionality, or the lateness of the hour, and completely forgotten about on the following morning. They were never tested under laboratory conditions, of course, because they never occurred in laboratories - not in reputable laboratories at least.

And so it was only with the advent of pocket computers that the startling truth became finally apparent, and it was this:

Numbers written on restaurant bills within the confines of restaurants do not follow the same mathematical laws as numbers written on any other pieces of paper in any other parts of the Universe."

Douglas Adams– Life, the universe and everything, p42

I would like to stress that, although non-negligible parts of the experimental design were invented on numerous bar paths, this thesis is not written on a restaurant bill.

…

Well, at least not entirely.

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The fellowship of the number sense

Chantal Roggeman

In the beginning was the Number Sense, and the Number Sense was with Dehaene, and the Number Sense was Dehaene (adapted from Johannes, 1, 1). And the Number Sense became a Number Line, and dwelt among us (adapted from Johannes, 1, 14) cause Dehaene would have dominion over the Number Line, even to the end of numerical cognition (adapted from Lord of the Rings, 4, 24).

And Stan the Man said: ‘the number line is logarithmic, and place coding will be the principle!’ But faith would not have it so. And somewhere far away, in a very idyllic corner of a beautiful office in an extremely ugly building, the Master of Numbers and Master of Models joined their forces and made a Model of Numbers. And the nodes in the Model cuddled nicely together and so Summation coding was born.

‘Now let's buy a three-tea machine and stuff it in Dehaene's a… IPS!’ chuckled the Master of Numbers. Christophe perceived his chance and asked the Master of Numbers for a new coffee machine as well. ‘Hiphoi’, mumbled the Master of Numbers, according to the newest method to quit smoking.

And so Bernie was appointed as scan-man. ‘Piece of cake’, said the scan-man, and in no time half the department had been scanned as “naïve” subject. Unfortunately, it was a three-tea machine, which did not work with a piece of cake at all. The Master of Numbers tried to save the day and persuaded the scan-man to stuff the other half of the department in the scanner as well, but the scan-man would not hear of it and went working with Cochlear. ‘Hiphoi’, said the Master of Numbers, and promptly started smoking again.

Meanwhile, Chantal had had enough of monkeys in Leuven and she asked Michael in Ghent to teach her how to draw dots on a screen. ‘Beautiful’, she said, and had 100 students look at it just to know what they thought. By this time, Mister Hippocampus had discovered the secret of the PhD life: each new analysis could be turned into a poster which is a ticket for a congress. 3 posters and 6 congresses later however, Lies said there was no money left for congresses because she had to buy a new supply of cookies, and she held an email referendum on which cookies were the favourites. ‘How come makes no sense?’ asked Mister Hippocampus, and he decided after all to dump his data in the dustbin. The dustbin said it was okay but needed some extra analyses.

Following this example, Chantal threw herself in the fMRI. ‘If I can scan monkeys, I can scan students’, she thought, and she tossed the Master of Numbers into the scanner just to practice. Professor 8& came to have a look, which was exactly three too much, cause we only scanned numbers till 5. The Master of Numbers’ brains were boiling and he tried to communicate with very complicated movements of his feet that he had a suspicion his microphone didn’t work. Professor 8& explained that in order for the microphone to work, the bleu lights of the Visuastim system have to be on, but not the red, and the purple and the pink must chase each other, while the green must flicker. ‘And it is a high tech system from Iran’, he added proudly. The all-wise-Pieter explained that if it doesn’t work after 7 reboots, you just have to drop it to the floor and then pray that it works again.

‘Never again!’ thought the Master of Numbers when his brains had cooled down again, and he called the PhD committee to keep Chantal under control. The scan-man, the Mauro-man and the BrainVoyager-man were asked for a tea party and agreed to everything, as long as they were given the cookies of the referendum. The Mauro-man did 90% of the talking and gave Chantal a big hug, something which caused Freja in the next office to look very much forward to her own PhD committee. The scan-man said ‘Thy shall listen!’ and tried to curse her with auditory experiments in hopes of finding a number line in the ear. The BV-man said ‘Thy shall go to Pisa for a course on BV!’ and Chantal listened mostly to the BV-man.

Down the corridor, Liliane had taken all office chairs out in order to clean the offices. Isabel, Jolien, WimG, Ineke, JP en Liesbeth couldn’t help themselves and started a musical office chairs. Isabel went of to a pub and Jolien took her place with Ineke, which made a vacancy for JP in WimG’s office who could however not stand his talking and therefore went talking himself to everybody. Liesbeth had enough of the numbers in the number club and joined the Club. Seppe was supposed to take over her brains but preferred to scan his own brains. Jan, the Grey Computer Wizard, had much joy with a lovely new plaything called

PP02MRI2, and everybody stood so much in awe that nobody noticed that the Master of Models had smuggled a secret weapon from China with the codename 'Qi' in an empty office.

The Grey Computer Wizard in the mean time was the first to activate his IPS. Profoundly impressed by the magical abilities of the Grey Computer Wizard and as profoundly drunk from the party afterwards in the rowing club, Chantal returned to the scanner. 'Nie deur het nat lupen'! cried Liliane after her. Together with Seppe, she tossed the Master of Models in this time, because the Master of Numbers had fallen asleep. The Visuastim was now extended with an eye-track device, but even the all-wise-Pieter could not make it work properly, and said it was all the fault of the Trio-Troll. Finally, Pascal was called in, who managed with help of the soldering bolt of Antoine to get the Trio-Troll under control. Mister Hippocampus proposed to publish it in Eta Evolutiva. Benedicte asked Chantal how to analyze a Trio-Troll with Brainvoyager and made a poster of it.

The Grey Computer Wizard finally had enough and left the care of his dear PP02MRI2 to the White Computer Wizard Christophe. The White Computer Wizard grumbled a lot and said he had trouble enough already with Curios, and then sneaked back into the office to steal some more cookies out of the cupboard from Lies. Chantal and Mister Hippocampus had in the mean time finished their first fMRI and went very proudly to Chicago to celebrate their 30th birthday, just to escape the obligatory treat in the department. Ineke considered it a lovely strategy and went a year to Canada in search of a Canadian article.

Ruth decided to join the fMRI forces, and was immediately taken in by WimG to join his hunt for the SNARC. Simone and Dura(Mar)cel (performs 3 times as much research!) also joined the force, but in the end they were more interested in doing nothing, a paradigm which also stirred great interest in WimG.

Down the corridor, the Master of Numbers and Dura(Mar)cel were comparing their trousers. 'Mine is finer' said the Master of Numbers. 'But my gown is longer' said Dura(Mar)cel. 'And I have the most beautiful tie', said the Master of Models, not noticing that he was the only one to have a tie, and he started to draw a model on the whiteboard to prove it, smearing ink all over his tie in the process. 'My model will be greater', said Dura(Mar)cel, 'cause I have a larger drawing board!' That was too much for the Master of Models. He produced a red TL light from under his desk and cried to Dura(Mar)cel: 'Prepare to die! But wait a moment because I have a phone call’, and 5 seconds later he threw his phone into the air, threw his arms around Dura(Mar)cel’s neck and sung 'We have the GOA!! We have the GOA!!' (Later he wanted to phone Chantal to ask where his phone was but since he couldn't find his phone this was kind of a problem.)

Almost to the end of his tether, the Master of Numbers again invited the PhD committee for a tea party, and since Chantal baked a cake this time, they all agreed she had now finally proven to be worthy of the doctoral status. The end-thesis-stress brigade burst in to eat the rest of the cake and Mister Hippocampus took the opportunity to explain the Jos-line to all present.

‘That was fun!’ said Chantal, and she submitted a postdoc project for three years more of the same.

<u>End credits</u> (every resemblance with existing persons is 100% on purpose)

I'd like to thank everybody to play a part in my story:

Master of Numbers	Prof. Dr. Wim Fias
Master of Models	Prof. Dr. Tom Verguts
PhD committee: The scan-man The Mauro-man & the BV-man	Dr. Bernie Caessens, Prof. Dr. Mauro Pesenti & Prof. Dr. Guy Vingerhoets
Mister Hippocampus & Seppe	Filip & Seppe, partners in crime in fMRI
Grey Computer Wizard & Simone	Jan & Simone, roommates
White Computer Wizard	Christophe
Lies, Pascal & Antoine	technical assistance
The all wise Pieter	Pieter Vandemaele
Professor 8&	Prof. Dr. Rik Achten
Liliane	floor assistant
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The end thesis stress brigade	Els, Filip & Sarah
Delivery of Canadian articles	Ineke
Layout	Wouter

Thanks are extended to:

Svetlana	teached me the all there is about scanning
Stijntje Stoer & broer Klaas	delivery of hugs and comfort
Karen, Philippe Cara, Hiromasa, Olivier, Fjo, Theresa	the circle of friends
IUAP & GOA	producers of the project
Mom & dad	producers of me
Chaslik	kotkat

Chapter 1:

General introduction

Chantal Roggeman[1]

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[1] I would like to thank Wim Fias and Tom Verguts for helpful remarks on previous versions of this chapter.

1.1 Numerical representations

Numbers constitute a large part of daily life for organized human beings. Allow me to illustrate this by taking you through a part of my daily routine. In the morning, I take the train at 7.00 am, at platform 9. This train has a 90% chance of being 5 minutes late. The train has 12 carriages and I take a seat in the 2nd. I take out my book and recall I was on page 54. Arriving in Ghent at 8.06 am, I remember I have now reached page 82 (I will need this information tonight). I take tram 21 or 22 which brings me close to the office building I work in, at Henri Dunantlaan 2. I take the elevator to the 4th floor, and enter office 140-020. Then I start my research about how people think about numbers.

Even from this short snapshot, it is clear that numbers have many different meanings (Jacob & Nieder, in press). First, numbers denote numerical quantities, or cardinalities, which provide an answer to the question ‘how many’ (12 carriages). Second, a number can denote an item’s position in an ordered sequence, its rank, which provides an answer to the question ‘which one’ (platform 9, 4th floor). This exploits the ordinal meaning of numbers. Finally, numbers can also be used to indicate the identity of something, drawing on the fact that numbers are unequivocally defined, as in ‘tram 21’ (this does not mean that I let the first 20 trams pass by, for example). In this thesis, I concentrated on the first meaning of numbers, as denoting quantities or cardinalities, and I focused on how numbers in this respect are represented in our thoughts and brains.

Set the stage for numerical research

Numbers can be presented in many different formats: as an Arabic digit (“5”), as a written number word (“five”), as a sound (the spoken word “five”), or literally as a number of objects (e.g. dots “ :∴ ”) or events, which can be seen simultaneously or sequentially. Quantity and magnitude are general terms, which refer to a numerical stimulus in whichever format. Quantity and magnitude can also refer to a more abstract idea, the semantic meaning of the quantity that the numbers represent, irrespective of the format in which it is given. Arabic digits and written or spoken number words are symbolic numbers; they are symbols for the hidden abstract meaning. A number of objects or events is non-symbolic; there are as many objects or events as the number denotes. In numerical experiments, non-symbolic numbers are mostly presented as a pattern of dots, which are also called numerosities.

When processing numerical stimuli, two classical effects are omnipresent (Dehaene, Dehaene-Lambertz & Cohen, 1998). The distance effect refers to the phenomenon that it is more difficult to discriminate two numbers as the numerical distance between them decreases (e.g. 8 and 9 are more difficult to discriminate than 2 and 9; Moyer & Landauer, 1967). The size effect refers to the phenomenon that for an equal numerical distance, discrimination is more difficult as their numerical size increases (e.g. 8 and 9 are more difficult to discriminate than 2 and 3; Parkman, 1971). The distance and size effects are present in various formats: when presented as Arabic digits (Dehaene, Dupoux & Mehler, 1990), as verbal number words (Koechlin, Naccache, Block & Dehaene, 1999) and as non-symbolic numerosities (Buckley & Gilman, 1974). Several models of numerical representation have been proposed to explain the distance and size effect. These models can be categorized in two main coding models: place coding and summation coding.

1.2 Place coding representation

The distance and size effect were combined by Dehaene (1992) in a very influential model of numerical representation. Dehaene proposed analogue magnitudes to be represented on a mental number line, with small numbers represented at the left and large numbers at the right end of the line (Dehaene, Bossini & Giraux, 1993). It is important to stress here that the 'number line' is merely a metaphor for an ordered group of input neurons, where each neuron activates for a particular number. Magnitudes are thus represented in the brain by activating the corresponding neuron, or as a pattern of activation over the group of neurons which constitute the number line.

In Dehaene's model (1992), the representation of a specific number is implemented as the activation of a specific position along the number line. This activation pattern is referred to as 'place coding' because it activates a 'place' along the number line. In order to explain the distance effect, it was further assumed that the place coding is not precise, but subject to variability. While the activation peaks at the target position, neighbouring numbers are also activated with decreasing strength, so 5 is represented as the activation of the neuron labelled "5" plus activation of "4" and "6". In other words, the activation associated with one magnitude partially overlaps the activation associated with neighbouring magnitudes. This overlap decreases for magnitudes further apart and hence the distance effect emerges. See Figure 1.

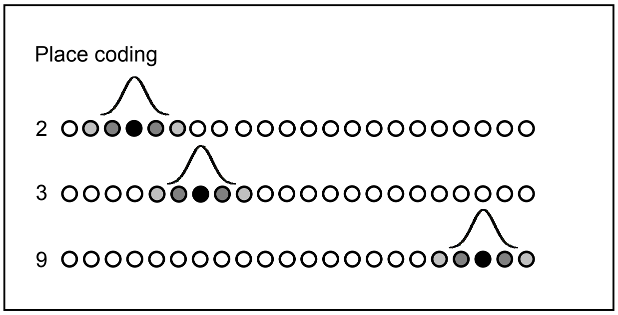

Figure 1. Illustration of place coding activation of the number line. Numbers which are numerically close have overlapping activation patterns (e.g. 2 and 3), and are more difficult to discriminate than numbers which are numerically far (e.g. 2 and 9); hence the distance effect emerges (adapted from Verguts, Fias & Stevens, 2005).

In order to explain the size effect, the number line was assumed to be logarithmically compressed for large numbers. Compressed scaling can explain the size effect because small numbers are represented as being further apart from each other than larger numbers (for a fixed numerical distance), and the overlap between neighbouring numbers will thus be less than between larger numbers. Another explanation for the size effect was proposed by Verguts, Fias & Stevens (2005), in a model similar to that of Dehaene (1992), Verguts et al. (2005)

however implemented a strictly linear number line, instead of the compressed number line of Dehaene's model. The size effect in this model was explained as emerging from non-linearities in the mapping from number line to output mechanisms.

Behavioural evidence

Empirical evidence for the place coding principle is abundant. Behavioural evidence can be found in the distance effect, which is also a very robust phenomenon in behavioural priming experiments. In these experiments, two stimuli are presented one after another, and the processing of the second stimulus (target) is analyzed as a function of the first stimulus (prime). The first authors to investigate the processing of numbers with this paradigm were den Heyer and Briand (1986). These authors showed that, in a letter-digit classification task, digits were processed faster when they were preceded by a prime with a numerically close value than when they were preceded by a prime with a numerically more distant value.

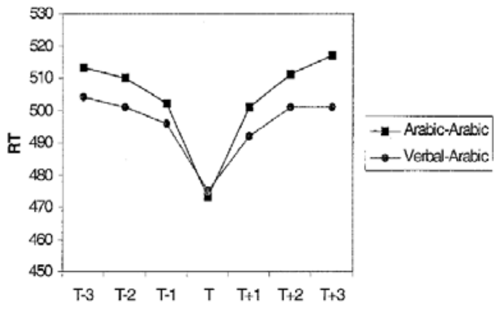

Figure 2. Reaction times of a number naming task in a priming experiment. Numerical distance between prime and target value is indicated on the X-axis as the value of the prime in relation to the value of the target. Reaction time increases when distance between the prime and target value increases (reproduced from Reynvoet, Brysbaert & Fias, 2002).

The effect was subsequently replicated with a naming task (Brysbaert 1995; Reynvoet, Brysbaert & Fias, 2002), a comparison task (Koechlin et al., 1999; Naccache & Dehaene, 2001a) and a parity judgment task (Reynvoet & Brysbaert, 1999, 2004), both within and across notations (Arabic digits and verbal number words). In all studies, it was repeatedly shown that the target magnitudes were processed faster when preceded by a prime of close magnitude. See Figure 2. These results are interpreted as evidence of the hypothesis that the prime activates its corresponding magnitude on the number line, thereby also activating the neighbouring magnitudes, which will consequently be processed faster.

Neural evidence: single cell recordings

Neural evidence for a place coding based representation of numbers is available from single cell recordings in macaque monkeys. In a classic experiment, Nieder, Freedman & Miller (2002) measured neuronal response in the prefrontal and parietal cortex while monkeys were performing a delayed match-to-sample task. In this task, monkeys were presented with 2 consecutive dot patterns, containing 1 to 5 dots, and were asked to indicate if the second display contained the same number of dots as the first one. The neuronal response showed peak activity to a specific quantity and a systematic decrease of activity as the number of dots deviated from the preferred values (see Figure 3). This is in line with the models of Dehaene (1992) and Verguts et al. (2005) and provides direct evidence for a place coding representation of numbers.

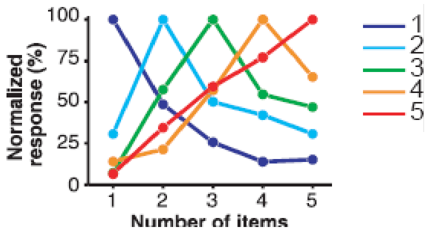

Figure 3. Neuronal response of quantity neurons, tuned to different preferred values (reproduced from Nieder, Freedman & Miller, 2002).

Neural evidence: fMRI experiments

Finally, neural evidence for a place coding mechanism has also been found in humans. These studies draw mostly on the 'repetition suppression' or adaptation method in fMRI. This method is based on the fact that, when the same visual stimulus is repeated, the neuronal activity in neurons responsive to the stimulus is reduced. Therefore, the activity of neurons responsive for a specific quantity should decrease when this quantity is repeatedly presented. This is known as adaptation of the neuronal response. In a clever adaptation experiment, Naccache and Dehaene (2001b) performed the behavioural priming paradigm while measuring the neuronal response. They showed that the neuronal response to the target in the intraparietal sulcus was suppressed when it was the same number as the prime, but not when it was a different number, thus providing evidence that different numbers were coded by different populations of neurons. Taking this a step further, Piazza, Izard, Pinel, LeBihan & Dehaene (2004), Piazza, Pinel & Dehaene (2007) and Cantlon, Brannon, Carter & Pelphrey (2006) performed an fMRI adaptation study in which they showed adaptation of the neuronal response in the intraparietal sulcus after repeated presentation of the same numerosity. The response recovered from adaptation when a deviant numerosity was occasionally presented, but not when the same numerosity was shown with deviant shapes, thus providing evidence for an adaptation of number-coding neurons. Moreover, Piazza et al. (2004) showed that the recovery of the response increased as the distance between the adaptation and the deviant numerosity increased. See Figure 4.

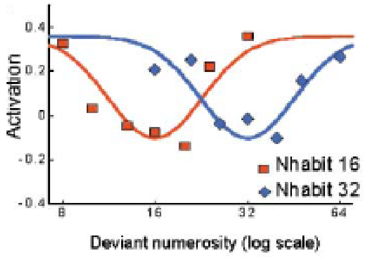

Figure 4. Neuronal response to different numerosities, after adaptation of the response to the habituation number (Nhabit), showing the distance related recovery from adaptation (reproduced from Piazza, Izard, Pinel, LeBihan & Dehaene, 2004).

This pattern of results provides evidence for an activation profile of the underlying quantity neurons in terms of place coding. Indeed, the variability of the activation in this coding scheme predicts that neighbouring numbers will also be activated, and thus also adapted. In a follow up study, the adaptation numbers were presented as numerosities and Arabic digits, and a distance dependent recovery of adaptation was found, independent of notation change (Piazza et al., 2007).

1.3 Summation coding representation

An alternative way to code quantities among a population of quantity neurons is referred to as summation coding. In this coding scheme, the coding is analogous to the number it represents. This can be implemented as the same neurons activating more strongly for larger numbers, or as more neurons activating for larger numbers. This means that the activation pattern for smaller numbers is included in the activation pattern of a larger number. Using the number line metaphor, it can be thought of as the activation of a line segment defined from the origin all the way up to the represented number, whereas place coding would be a line segment centred on a point.

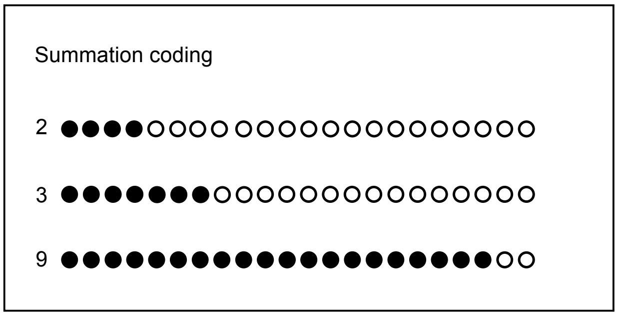

Figure 5. Illustration of summation coding activation of the number line. The activation for a number includes the activation pattern for all smaller numbers (adapted from Verguts, Fias & Stevens, 2005).

Origin and models of summation coding

The idea of summation coding was first introduced to explain certain characteristics of animal behaviour. The behaviour of animals in numerosity discrimination tasks was investigated in a series of experiments conducted by Mechner (Mechner, 1958; Mechner & Guevrekian, 1962) and Platt (Platt & Johnson, 1971). These authors required rats to make a certain number of lever presses (N) in order to receive a reward. Figure 6 shows the probability of the number of lever presses the animals actually made for various values of N.

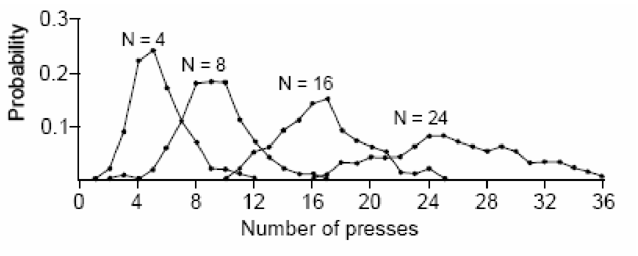

Figure 6. Probability distributions for conditions in which different numbers of presses were required for reward (reproduced from Platt & Johnson, 1971).

The data in Figure 6 show clearly that the rats were only able to estimate the approximate number of lever presses, even for numbers as small as 4. More importantly, the trial-to-trial variability of the number of presses produced by the rats increased as the target number increased. The ability of the rats to discriminate numerosities therefore obeys Weber's law (Stevens, 1957, 1961): the discriminability of two perceived magnitudes (in this case number of lever presses) is determined by the ratio of the objective magnitudes. This property of number discrimination was termed 'scalar variability' by Gallistel and Gelman (1992, see also Gibbon, 1977): the standard deviation of the probability curve of estimations for a certain target number scales with the target number itself.

The experiments with rats were carried one step further by Meck and Church (1983), by showing that the characteristics of animal discrimination of numerosities (countable magnitude) and duration (continuous and uncountable magnitude) are strikingly similar, with the same constant ratio between the standard deviation and the represented magnitude (Meck & Church, 1983; Meck, Church & Gibbon, 1985). Based on these findings, Meck and Church (1983, Meck et al., 1985) proposed a model for numerical representations in animals, which is depicted in Figure 7. The model assumes that, in case a continuous magnitude such as duration has to be estimated, a steady signal is generated throughout the interval being timed. In the case where discrete items have to be counted, the steady signal is gated through a pulse former, which pulses once for each item or event to be counted. In both cases, this activation is then added to an accumulator. One way to visualize this is to imagine that, in the counting case, the accumulator is filled one cupful for each item, but in the timing case, the accumulator is filled by a hose, the flow from which is terminated at the end of an interval to be timed. The magnitude of the accumulator at the end of the count is read into memory, where it represents the number of the counted set. This representation is an implementation of the summation coding representation of quantity, since it is an inherent property of the accumulator that the representation for a smaller number is always included in the representation of a larger number, which is the basic idea of summation coding. The scalar variability property of the model, which is the origin of the size effect, stems from the memory representation of the magnitude, as it has been shown that memory, rather than the process of accumulation, is the dominant source of trial-to-trial variability (Gibbon, 1992).

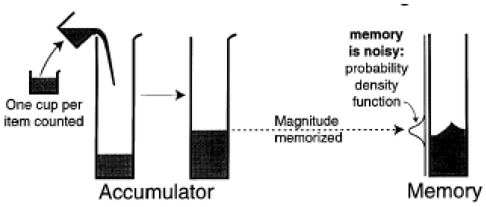

Figure 7. Cartoon of cognitive processes underlying nonverbal number abilities (reproduced from Whalen, Gallistel & Gelman, 1999).

The model was taken a step further by Gallistel and Gelman (1991, 1992). These authors assumed that human verbal competence with numbers is actually built on a similar preverbal numerical competence. They proposed that, when children learn to count, they also learn a bidirectional mapping between the preverbal magnitudes that represent numerosity and the number words they represent (Figure 8).

The distance and size effects which are characteristic for numerical processing, can be explained by this model in the following way. The distance effect arises from the fact that numbers numerically close together, have a similar activation pattern. The size effect emerges from the scalar variability property: since the variability increases with increasing number, the numbers are more difficult to discriminate.

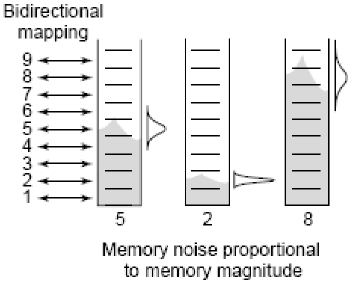

Figure 8. Humans learn a bidirectional mapping which enables them to map from a magnitude to a numeral and from a numeral to a corresponding magnitude (reproduced from Gallistel & Gelman, 2000).

Another model which is based on a summation coding representation of quantity is the numerosity code model of Zorzi and Butterworth (1999, 2005). This model builds upon the constraint that magnitude information should encode cardinal meaning. These authors proposed to represent numerosity magnitude straightforwardly as the number of units activated. In this sense, the numerosity code is also a summation code, since the units activated for a smaller number will also be included in the activation pattern for all larger numbers.

Contrary to the model of Gallistel and Gelman (1992, 2000), the numerosity code displays no scalar variability; instead, the noise in the number representation (leading to distance and size effects) originates from the specific task being performed.

Behavioural evidence

Behavioural evidence for a summation coding representation in humans was found by Whalen, Gallistel and Gelman (1999). In an experiment conducted by Whalen et al. (1999, see also Cordes, Gelman, Gallistel & Whalen, 2001), human participants were asked to produce a given number by pressing a key an approximate number of times. Subjects were specifically instructed not to verbally count the number of presses they made, but rather to arrive at the appropriate number of presses 'by feel'. The results were strikingly similar to animal data. The average number of presses for a particular target number was approximately correct, and the standard deviation in the number of key presses produced varied in direct proportion to the target magnitude. It was therefore concluded that adult humans and animals have comparable nonverbal representations of number magnitude.

Neural evidence

Neural evidence for a summation coding based representation of numbers is also found in single cell recordings in macaque monkeys. Roitman, Brannon & Platt (2007) recorded from neurons in the lateral intraparietal area (LIP) while monkeys performed an implicit numerical discrimination task. While numerical displays up to 32 dots were presented, monkeys were asked to plan an eye movement to a different target, located distal to the numerical stimulus. The numerosity of the array merely predicted the amount of reward the monkey would receive when he performed the eye movement. Nevertheless, neurons showed graded modulation by the numerosity of the stimulus: a significant positive or negative relationship between numerosity and neural response was found. This is in line with the models of Gallistel and Gelman (1991, 1992) and Zorzi and Butterworth (1999, 2005) and provides direct evidence for a summation coding representation of numbers.

1.4 Summation coding as a precursor of place coding

An important question is the difference between symbolic and non-symbolic number formats. Several of the studies mentioned thus far provide evidence for a notation independent numerical representation of the place coding type (e.g. Reynvoet et al., 2002; Reynvoet & Brysbaert, 2004; Koechlin et al., 1999; Naccache & Dehaene, 2001a, 2001b; Piazza et al., 2007), but so far nothing has been said about how these different numerical notations are transformed into this single numerical place coding representation. This is most challenging for the transformation from a non-symbolic number, consisting of a number of objects, into an activation of a specific number neuron.

Two computational modelling studies have tried to model this conversion (Dehaene & Changeux 1993; Verguts & Fias 2004). The models start from an object location map, which is a map of the visual input of the presented numerosity. The object location map is a spatial neuronal map, in which each neuron corresponds to one location. If an object is presented at this location, the neuron detects it and is activated. This object location map results from earlier processing in the primary visual cortex, necessary to represent objects independent of the physical appearance of that object: each object is represented as 'one' by only one location neuron, independent of the size and form of the object.

When the object location map has been obtained from visual input, the information in this object location map must be further converted into a specific pattern of activation among the place coding number neurons. For example, the number neuron coding for "1", should be activated if only 1 object is presented in the object location map; the neuron coding for "2" should be activated if 2 objects are present in the object location map, and so on. However, it is impossible to obtain this through a direct connection between the two neuronal systems. The reason is that, if an object location neuron is activated because it represents an object, it should for example make a connection and activate number neuron 3, but only if exactly 2 other neurons in the object location map are activated. Unfortunately, the neuron in the object location map has no possible way of knowing this. It does not know how many other objects are represented, and hence does not know to which number neuron it should send its activation. In fact, this can be viewed as a generalization of the exclusive OR-problem in logic (Minsky & Papert, 1969). The fact that these problems are not linearly separable makes it impossible to solve them with a direct linear mapping from input to output. Therefore, an intermediate step is necessary.

In Verguts and Fias (2004), this intermediate step was computationally investigated. A neural network was provided with an object location map as input and was given an intermediate layer between input and output. The network was then trained with backpropagation to map the object location representation of the numerosity at input via the intermediate layer to a place coding representation at output. After training, it was found that neurons in this intermediate layer exhibited a monotonously varying activation (i.e., monotonously stronger or weaker) when more objects were presented. Hence, the intermediate step between visual input and a place coding system consisted of neurons accumulating or summating (in a positive or negative way) the number of objects that was represented in the object location map. In other words, the neurons in the intermediate step displayed summation coding.

The implication of this is straightforward: rather than two alternative coding principles, the model predicted that summation coding is actually a necessary preceding step in the transformation from numbers presented in a non-symbolic format to an abstract, notation independent place coding representation. The investigation of this hypothesis was the focus of the present thesis.

1.5 Overview of the experiments

We tested the existence of a summation coding system for non-symbolic numerosities in humans with 2 different experimental paradigms. First, we employed a behavioural priming paradigm. Priming has been shown to be a useful technique to uncover characteristics of mental representations, as it was formerly used to show evidence for a place coding system using Arabic digits and number words (Reynvoet et al., 2002). The same technique however, had never been adopted to investigate the processing of non-symbolic numerical stimuli. In view of the model of Verguts and Fias (2004), we predicted a different priming effect with these stimuli. This was the focus of chapters 1 (using small numbers) and 3 (using larger numbers). Second, using event-related fMRI, we aimed at detecting and locating brain regions which show a neural signal in line with a summation coding system. We reasoned that a summation coding system would give rise to neural activity that is positively correlated with numerosity because the visual presentation of more dots will activate more neurons in the object location map, which in turn will lead to enhanced neural activity due to a summation coding system. We therefore presented dot displays containing different numbers of dots and measured neural activity for each numerosity. We then searched for brain areas showing increasing activity when presented with an increasing number of dots. This was the focus of chapter 2 (using small numbers) and 4 (using large numbers).

The first two chapters were concerned with a small number range: we used only dot patterns containing 1 to 5 dots. This range was chosen for several reasons. First, people can only estimate the number of dots in a visual pattern reliably up to 4 or 5 items. Estimates of larger numbers are imprecise (Mandler & Shebo, 1982); hence larger numbers cannot adequately be named and recognised when presented as a number of dots. Second, the computational modelling study which pointed to summation coding as a plausible coding for the processing of non-symbolic displays, was chiefly concerned with this number range (Verguts & Fias, 2004). We therefore restricted our first studies to this small number range. In the next two chapters, we extended our experiments to larger numbers, using dot patterns containing 4 to 64 dots.

1.6 Enumeration of non-symbolic quantities

Since the research presented in this thesis is mainly concerned with numbers presented in a non-symbolic format, more specifically as patterns of dots, it is important to summarize how people enumerate or quantify such patterns. Enumeration consists in grasping the numerosity of a perceived set and accessing the corresponding (possibly approximate) mental representation (Dehaene, 1992).

Three quantification processes have been postulated: counting, estimation and subitizing (Klahr, 1973).

Counting

Counting is an enumeration process which is used for larger numbers, to find the exact number of items in the set. Counting as such is a difficult concept to grasp, as is evidenced by the fact that children after language acquisition need several more years to grasp the full abstractness of counting (Bloom & Wynn, 1997; Butterworth, 1999). For example, a child that does not yet understand that the number of items remains the same when the position of two elements is changed can hardly be said to understand the abstract principles of counting. On the other hand, counting does not require a correct knowledge of the verbal number word sequence. Any fixed sequence of tokens will do, as long as they are ordered and always recited in the same order. The Yupno people in Papua New Guinea, for example, have no special words for numbers, but use a fixed series of body parts as the counting sequence, and can therefore said to be a counting people (Butterworth, 1999). In this sense, it is not a priori excluded that animals and preverbal infants can count.

Estimation

Estimation is the process used to enumerate larger numbers of objects, when not enough time is available to pass through the counting process, or when the exact result is not important and an approximate one will do. Estimation is also the process used in situations involving large numbers or continuous quantities (Klahr, 1973).

Estimating the number of a large array of dots is an instantaneous process. The reaction time is constant and does not depend on the estimated numerosity (Kaufmann, Lord, Reese & Volkman, 1949; Klahr, 1973). Estimation is also an inaccurate process. The variability of responses on the other hand is not constant, and depends on the estimated numerosity. More particularly, estimates become less accurate for larger numerosities (Krueger, 1982). This has also been termed 'scalar variability', which means that the mean responses and the standard deviation of the responses are proportional to each other as the numerosity to be estimated varies (Krueger, 1982, Whalen et al., 1999).

Remarkably, numerosities are mostly severely underestimated (Krueger, 1982, 1984). Minturn & Reese (1951), for example, reported responses diverging from the true numerosity with a factor 4 (e.g. response 50-70 for a stimulus containing 200 dots). Moreover, estimation does not improve with training. Wolters, van Kempen & Wijlhuizen (1987) trained their subjects for 5 consecutive days to estimate random dot patterns, but could not find a significant difference in accuracy over the 5 days. However, estimation can be substantially improved by calibration: Izard and Dehaene (2008) showed recently that if one 'example' numerosity is shown, others are estimated quite well. This shows that numerosity estimations are relative, and that we are not endowed with an innate calibration for accurate estimation of large numbers, although calibration with an external stimulus is possible.

Furthermore, the estimation of large numerosities is influenced by a number of properties from the display. First, dense displays appear less numerous than the same dots spaced more loosely (Krueger, 1972; Hollingsworth, Simmons, Coates & Cross, 1991). Second, irregular displays are estimated to be less numerous than regularly positioned dots (Ginsburg, 1978). Finally, estimation depends on the total area spanned: a larger total area is judged as more numerous (Sophian & Chu, in press). It should also be noted that the influence of these parameters depends on the numerosity. For example, Durgin (1995) showed that the influence of density on the estimate is different for small and large numbers. This led Allik and Tuulmets (1991) to postulate that the perceptual system does not abstract the number per se from all the other stimulus attributes, but that the impression of numerosity depends on the spatial arrangement. In other words, the visual attribute used for making decisions about numerosities contains geometrical information – that is, information about spatial distances between the objects (Allik & Tuulmets, 1991, Allik, Tuulmets & Vos, 1991). On the other hand, this stimulus attribute is not specified in terms of absolute retinal distance. Indeed, when the size of a dot pattern is increased or reduced, so that the dot pattern is magnified or scaled but all inter-dot distances are changed accordingly, there is no difference in estimation (Allik et al., 1991). Based on these results, Allik and Tuulmets (1991) proposed an occupancy model for estimation, which states that clusters of dots are surrounded with a contour, and the filled area within this contour is used as an index for a relative judgment of numerosity.

Subitizing

When enumerating the number of items in a visual array, it is generally known that the performance for arrays up to three or four items is fast, effortless, and flawless. Although this performance pattern has been known for more than a century (Cattell, 1886; Warren, 1897), it was only given a name as a distinctive process by Kaufmann et al. (1949). It was called subitizing and it stands for the phenomenon whereby subjects can immediately perceive the number of objects in a visual display up till about 4 items. But despite its having been given a name, it still lacks an accurate definition. Beckwith and Restle (1966), attempted a definition by describing subitizing as 'a somewhat mysterious but very rapid and accurate 'perceptual' method'.

The most common working definition of subitizing originates from the distinction between subitizing and counting. When enumerating a number of objects in a visual display, reaction times increase very little, less then 50 ms per item, for one to four items, from which point on the reaction time starts to increase with 250 ms per item as subjects count each additional item (Atkinson, Campbell & Francis 1974, Mandler & Shebo 1982, Balakrishnan & Ashby 1991, 1992). The same pattern is found in the error data: performance is almost flawless for up to 4 items, from which point on the error rate starts to increase. These changes in the linear increase in the reaction time and error curves are usually taken as the very definition of the subitizing process: 'subitizing is the process that produces the results up to the discontinuity' (Kaufmann et al., 1949, see also Klahr, 1973). This working definition was, however, proved to be incorrect by Balakrishnan and Ashby (1991, 1992). These authors subjected the performance parameters to several statistical tests, and found that they did not change abruptly at around 4, but changed more gradually over the whole range from 1 to 6. They proposed that there is no such thing as a performance limit, and that subitizing defined as such does not exist.

The only option remaining is to define subitizing as 'not counting' and 'not estimating'. Several lines of evidence distinguish subitizing from counting. First, it is simply too fast. Second, double dissociations have been found between subitizing and counting in brain-lesioned patients, clearly indicating two separate underlying processes. A patient with impaired subitizing and intact counting was described by Cipolotti, Butterworth, & Denes (1991) and Butterworth (1999). Halpern, Clark, Moore, Cross & Grossman (2007) also described patients with corticobasal degeneration who showed a 'counting like' slope in reaction time starting from 1 item: the reaction time for enumeration in these patients increased with 250 ms per item even in the subitizing range, whereas in normal subjects this is the typical increase in the counting range. These authors concluded that the patients could not subitize the displays, but counted them 1 item at the time. Similar results were found for patients with Turner syndrome (Bruandet, Molko, Cohen & Dehaene, 2004). On the other hand, Dehaene and Cohen (1994) described 5 simultanagnostic patients who could subitize but were severely impaired in counting larger displays. These patients have problems shifting attention from one item to the next: they have trouble scanning the display and tend to miss some of the elements. The patients also have problems in keeping track of already counted items: one patient counted the same items over and over again without recognizing the errors. Despite this, all patients had a preserved subitizing performance up to two or three items, showing clearly that subitizing must be a different mechanism than counting.

The distinction between subitizing and estimation is less clear-cut. Some authors propose that subitizing reflects the use of a numerical estimation procedure shared for small and large numbers (Gallistel & Gelman, 1991, Whalen et al., 1999, Balakrishnan & Asby, 1991, 1992). The accurate performance in the subitizing range is then viewed as a floor effect of estimation: it is correct for this range because the variability is low in this range. A recent study by Revkin, Piazza, Izard, Cohen & Dehaene (in press) put this hypothesis to the test by comparing the performance for numerosities 1 to 8 with the performance for the decades 10 to 80. Since the ratio of these two number ranges is the same, the estimation of the range should yield similar performance. Revkin et al. (in press) found large differences in both comparison tasks and naming for the two number ranges, providing convincing evidence for the distinction between subitizing and estimation.

1.7 Enumeration skills in preverbal infants

The next question is how place and summation coding representations develops. The model of Verguts and Fias (2004) for example showed that a numerical representation is easily achieved, even in a priori unspecified neurons. Dehaene (1992), however, claimed that the number sense must be innate. Several studies have therefore tried to investigate whether preverbal infants have an understanding of an abstract meaning of quantity.

Infants' perception of number is usually determined using the habituation-dishabituation paradigm (Wynn, 1995). In this paradigm, each infant is repeatedly presented with arrays containing a certain number of items, until the infant's looking time to the arrays decreases. At this point, the infant is considered to be habituated to the stimuli. The infant is then presented with new displays, some containing the original number of items and some containing a new number of items. Infants tend to look longer at things that are new or unexpected to them; therefore, if infants can distinguish between the two numbers, they should look longer at the displays containing the new number of items (Wynn, 1995).

Using this paradigm, it has been shown that 6-month-old infants perceive the difference between numerosities 8 and 16 when numerosities were presented as visual dot patterns which were controlled for continuous variables (dot size, brightness, contour length, density and total occupied area) (Xu & Spelke, 2000). Brannon, Abbott & Lutz (2004) even showed that 6-month-old infants succeeded in distinguishing these particular numerosities when they were controlled for total area, whereas the same infants failed in perceiving a twofold increase or decrease in total area, when controlled for number. This provided unequivocal evidence that infants attend to number but not to continuous quantities such as total area. Under the same control conditions, 6-month-olds also succeed in distinguishing 16 from 32 (Xu, Spelke & Goddard, 2005) and 4 from 8 (Xu, 2003). On the other hand, 6-month-old infants fail in distinguishing 16 from 24 (Xu et al., 2005); and 8 from 12 (Xu & Spelke, 2000). These findings show that infants are sensitive to large numerosities, but that the representation is imprecise and that numerical discrimination depends on the ratio of the set sizes (Spelke, 2000; Lipton & Spelke, 2003).

Despite these successes, infants fail systematically in discriminating small numbers. Although earlier research did find evidence for small number discrimination (Antell & Keating, 1983; Starkey & Cooper, 1980; Starkey, Spelke & Gelman, 1983, 1990), recent experiments, which were controlled in the same way as the above experiments in the large number range, failed to replicate these findings. Indeed, 6-month-old infants failed systematically to discriminate 2 from 4 dots (Xu, 2003) and even 1 from 2 dots (Xu et al., 2005).

Nevertheless, infants have succeeded in small number tasks in different experiment settings. Feigenson, Carey & Hauser (2002) tested 10- to 12-month-olds with a completely different paradigm. Different numbers of crackers were sequentially placed in opaque containers in view of the infants, and at the end the infants were allowed to crawl to one of the containers. It was expected that, if the infants could discriminate between the different numbers of crackers, they would choose the container with the largest number. Infants succeeded for 1 versus 2 and 2 versus 3 crackers. They failed, however, for 3 versus 4; 2 versus 4 and 3 versus 6 crackers, showing that they failed to keep track of more than three items. In a subsequent control experiment, Feigenson et al. (2002) presented the infants with crackers which were twice as large, and were able to show that infants in these experiments based their judgments on the continuous total amount of cracker, rather than on number.

These results led Spelke (2000, see also Xu, 2003 and Feigenson, Dehaene & Spelke, 2004) to the conclusion that there are two different systems at work in these experiments. This conclusion was supported by at least 2 findings. First, performance with small and large numbers is subject to different limits: small-number tasks show a set size limit of three (Feigenson et al., 2002) whereas large-number tasks show a set size ratio limit of 2:1. Second, performance with large numbers of items is robust over variations in continuous quantities including item size, total surface area, density, and array size, but performance with small numbers of items is not: infants fail to discriminate one from two dots or objects when continuous quantities are strictly equated across the arrays (Xu et al., 2005).

These two different systems are recognized as a system in the small number range for representing objects and their persisting identity over time; and a system in the large number range for representing sets and their approximate numerical values. These systems are domain specific (one applies to objects, the other to sets), task specific (one allows for addition of one, the other allows for comparisons of sets), and independent (the situations that evoke one are different from the situations that evoke the other) (Spelke, 2000). The system used in the small number range is an object tracking system. It operates on a small number of objects (3 or 4) and keeps track of individual objects, but it does not represent groups of objects as sets. More precisely, small numbers of dots would induce infants to see the items as individual objects, but not as a set with a specific cardinal value, hence the failure of infants to perceive the numerosity of small numerosities. On the other hand, in the experiment of Feigenson et al. (2002), viewing the crackers as individual objects helps the infants to choose the container with the largest number. The fact that infants based their judgments on the continuous total amount of cracker rather than on number when larger crackers were used, supports the fact that the infants were representing the crackers as individual objects with individual properties (in this case size). The system used in the large number range is a number estimation system. This system represents approximate large numbers as sets, and it has no inherent set size limit. The representations however are imprecise, and discrimination accords with Weber's law: successful discrimination is determined by the ratio between two numbers, and not by the absolute difference. Whether these two systems give rise to the distinction in adults between different enumeration processes used for small and large numbers (subitizing or estimation) is not yet known.

1.8 Localization of numbers in the brain

It is also important in this introduction to recognize studies that have tried to determine the neural locus of numerical cognition in the brain using imaging techniques. A meta-analysis of studies using positron emission tomography (PET) studies, or functional magnetic resonance imaging (fMRI) to study the neural substrate of a number representation revealed that there are three key parietal areas for the processing of number knowledge (Dehaene, Piazza, Pinel, & Cohen, 2003). The first area of the network included the bilateral horizontal segment of the intraparietal sulcus (hIPS), which is supposed to reflect number specific processing, and to be associated with the abstract representation of numerical information. A second area is situated in the left angular gyrus, which is involved in the manipulation of numbers in verbal form. A third area is the bilateral posterior superior parietal region, responsible for spatial and non-spatial attention and general support mechanisms.

The hIPS as the seat for abstract numerical knowledge

A major site of activation in neuroimaging studies of number processing is the bilateral horizontal segment of the intraparietal sulcus (hIPS; Dehaene et al., 2003). These regions seem to be activated whenever subjects are engaged in number processing, such as calculation (Pesenti, Thioux, Seron & De Volder, 2000; Chochon, Cohen, van de Moortele & Dehaene, 1999; Kawashima et al., 2004; Zago, Pesenti, Mellet, Crivello, Mazoyer & Tzourio-Mazoyer, 2001; Venkatraman, Ansari & Chee, 2005) and comparison (Fias, Lammertyn, Reynvoet, Dupont & Orban, 2003; Fulbright, Manson, Skudiarski, Lacadie & Gore, 2003; Thioux, Pesenti, De Volder & Seron, 2001; Le Clec'H et al., 2000; Pinel, Piazza, LeBihan & Dehaene, 2004; Cohen Kadosh et al., 2005; Fias, Lammertyn, Caessens & Orban, 2007). Although some studies failed to find number specific IPS activation (Shuman & Kanwisher, 2004), or attributed IPS activation to response selection (Göbel, Johansen-Berg, Behrens & Rushworth, 2004), other studies found an increasing hIPS activation even following the display of Arabic numbers or number words, when the display duration was subliminal (Naccache & Dehaene, 2001b) or when the task instructions did not require explicit magnitude processing (Eger, Sterzer, Russ, Giraud & Kleinschmidt, 2003). Furthermore, this region is also more involved when numbers are approximately processed than when they are exactly processed (Dehaene, Spelke, Stanescu & Tsivkin, 1999; Stanescu-Cosson, Pinel, van de Moortele, Le Bihan, Cohen & Dehaene, 2000), which shows that it is the abstract numerical meaning which activates hIPS, while the exact interpretation relies more on language areas (angular gyrus). This is also evidenced by the fact that the hIPS is activated for numbers independent of the modality in which they are presented: the hIPS is not only activated by Arabic digits, but also by number words (Ansari, Fugelsang, Dhital & Venkatraman, 2006; Naccache & Dehaene, 2001b; Pinel, Le Clec'H, van de Moortele, Le Bihan & Dehaene, 1999; Pinel, Dehaene, Riviere & Le Bihan, 2001; Dehaene et al., 1998; Cohen Kadosh, Cohen Kadosh, Kaas, Henik & Goebel, 2007) and dot patterns (Ansari, Dhital &

Siong, 2006; Piazza et al., 2004, 2007; Venkatraman et al., 2005; Piazza, Giacomini, Le Bihan & Dehaene, 2003).

Most importantly for this thesis, the hIPS has been identified as the seat of a place coding representation of numbers. Place coding neurons tuned for quantity were found in the fundus of the IPS in monkey parietal cortex (Nieder & Miller, 2004), although it is not certain that it is the same homologue region in monkeys and humans. In humans, however, activation according to a place coding representation was found in the bilateral IPS by Piazza et al. (2004, 2007) and Cantlon et al. (2006).

Localization of enumeration processes

A number of studies have tried to localize the process of enumerating non-symbolic numerosities, with conflicting results. Boles (1986) found a left visual field superiority for the numerical processing of non-symbolic stimuli (dot patterns, bar graphs and dials), whereas a right visual field advantage was found for number words. No lateralization effect was found for digits. Kosslyn, Koenig, Barrett, Cave, Tang, & Gabrieli (1989) found a right hemisphere superiority for numerosity estimation, whereas Jackson and Coney (2004) also found a similar right hemisphere advantage for enumeration of dot patterns in the subitizing range. Pasini and Tessari (2001) also found an advantage for the subitizing of dot patterns which were flashed in the right hemisphere, but they also found that the left hemisphere is more specialized in counting. This is in contrast to Seron, Deloche, Ferrand, Cornet, Frederix & Hirsbrunner (1991), who found that right-brain lesioned subjects were more impaired with the spatial correspondence components of a counting task (correct pointing to the dots). Contrary to all these findings, a study with a split-brain patient (Colvin, Funnell & Gazzaniga, 2005) showed that both hemispheres were equally proficient for subitizing 1 to 4 dots.

Counting activates a network in the occipital, bilateral dorsolateral prefrontal cortex and inferior frontal gyrus, and in the bilateral intraparietal areas, most notably the posterior part of the IPS (Piazza, Mechelli, Butterworth & Price, 2002; Piazza et al., 2003; Sathian, Simon, Peterson, Patel, Hoffman & Grafton. 1999, Fink et al., 2001, Venkatraman et al., 2005). Interestingly, Piazza et al. (2002, 2003) found an increasing activation with increasing number in this last region, which was interpreted as an activation due to spatial attention shifts. This region is generally involved in attention shifts and eye movements (Corbetta & Shulman, 2002) and is therefore activated by counting as a serial process.

A study contrasting counting versus estimation was conducted by Piazza, Mechelli, Price & Butterworth (2006). These authors found a right lateralized network involved in estimation, whereas counting activated the same areas and additional areas in the left hemisphere. Interestingly, the right hIPS was activated more during estimation, while the left hIPS was activated more during counting. These findings agree with the studies by Dehaene et al. (1999) and Stanescu-Cosson et al. (2000) which contrasted exact versus approximate processing of numbers. These studies both found that approximate judgments correlated with stronger activation in the right than in the left IPS, while exact judgments correlated with more activation in the left versus right IPS. This confirms the earlier findings of a right hemispheric advantage during non-symbolic number processing (see also Venkatraman et al., 2005).

Studies that tried to find the locus of subitizing in the brain have mostly contrasted subitizing versus counting (Piazza et al., 2002, 2003, Sathian et al., 1999). None of these studies could find a region which activates more for subitizing than counting. In fact, all studies found that subitizing and counting activated the same network, but the activations found during the counting tasks were generally more extensive and stronger.

Finally, only one study has contrasted subitizing with estimation (Ansari, Lyons, van Eimeren & Xu, 2007). These authors found more activation for subitizing than estimation in the temporoparietal junction, which has been identified as a part of a stimulus-driven attention network (Corbetta & Shulman, 2002). Ansari et al. (2007) interpreted these findings in light of differential attentional processing during subitizing and estimation: whereas subitizing would rely on a stimulus-driven attentional network, estimation would draw upon a goal-directed attentional network located in the posterior parietal cortex.

Chapter 2:

Priming reveals differential coding of symbolic and non-symbolic quantities

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Cognition, 2007

Number processing is characterized by the distance and the size effect, but symbolic numbers exhibit smaller effects than non-symbolic numerosities. The difference between symbolic and non-symbolic processing can either be explained by a different kind of underlying representation or by parametric differences within the same type of underlying representation. We performed a primed naming study to investigate this issue. Prime and target format were manipulated (digits or collections of dots) as well as the numerical distance between prime and target value. Qualitatively different priming patterns were observed for the two formats, showing that the underlying representations differed in kind: Digits activated mental number representations of the place coding type, while collections of dots activated number representations of the summation coding type.

2.1 Introduction

Not only adult humans but also young infants and various non-human animal species are able to mentally represent and process numerosity (for a review see Dehaene, Dehaene-Lambertz & Cohen, 1998; Feigenson, Dehaene & Spelke, 2004). The processing of numerical stimuli shows highly similar behavioural characteristics between species, including human adults (Dehaene et al., 1998). A first signature is the omnipresence of a distance effect: Two quantities are more difficult to discriminate if they are closer to each other. A second signature is the size effect: For a fixed distance between two numbers, discrimination is more difficult with larger size (e.g. 2 and 3 are compared more easily than 8 and 9).

Different explanations for the distance and size effects have been provided, arising from different models of numerical representation (for review see Verguts, Fias & Stevens, 2005). These different models can be categorized in two classes: place coding and summation coding. The characteristics of these two types of number representation can best be understood using the mental number line metaphor, with small numbers being represented at one end of the line and larger numbers at the other end (Dehaene, 1992).

Place coding refers to the idea that a number activates a specific position on the number line. This activation peaks at the target position but also neighbouring numbers are activated with decreasing strength. In this way, number representation acts like a band pass filter (see Figure 1A). The amount of overlap between two number representations determines the distance effect. The size effect can be explained with additional assumptions: a compressed number line (Dehaene, 1992), scalar variability in the mapping to the number line (Gallistel & Gelman, 1992) or non-linearities in the mapping from number line to output mechanisms (Verguts et al., 2005). It is interesting to note that neurons exhibiting this type of band pass filter property exist in monkey parietal and prefrontal cortex (Nieder, Freedman & Miller, 2002; Nieder & Miller, 2004).

An alternative way to code number is summation coding (which is called numerosity coding by Zorzi & Butterworth, 1999; Zorzi, Stoianov & Umiltà, 2005). A number activates a segment of the number line but, unlike place coding, this segment is not a restricted region around the target number but includes the complete range of numbers up to the target number (see Figure 1B), much like a thermometer or an accumulator (Meck & Church, 1983; Zorzi & Butterworth, 1999; Zorzi, Stoianov, & Umiltà, 2005, chap. 5). Summation coding can account for the distance effect because the closer the to-be-compared numbers are to each other, the more similar their internal representations. The size effect emerges because, for a given distance between two numbers, a larger number pair has more units in common than a smaller number pair.

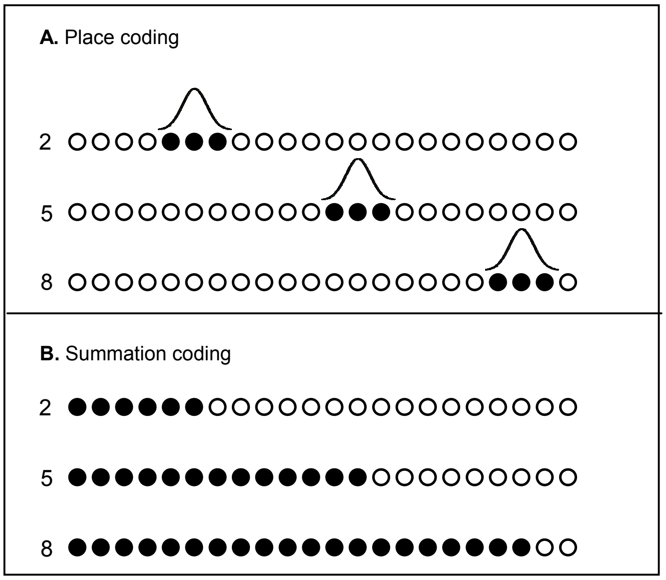

Figure 1: Schematic representation of **A.** place coding and **B.** summation coding

An important observation is that the numerical ability of adult humans is enhanced relative to non-human animal species, an effect for which symbol use is obviously at least partially responsible (Verguts & Fias, 2004). Symbols allow representation of numerical values with much higher precision than non-symbolic stimuli (such as collections of dots). This is evidenced by smaller distance and size effects for symbolic as compared to non-symbolic stimulus formats (Buckley & Gilman, 1974) and by the inability of exact calculation in cultures without symbolic number (Gordon, 2004; Pica, Lemer, Izard & Dehaene, 2004).

Following this, one can ask whether there are merely parametric differences between the representation of numerical information conveyed by symbolic and non-symbolic stimuli, or whether there are differences in kind (qualitative differences) between symbolic and non-symbolic number representation. In principle, each of the two qualitatively different kinds of representations described above could explain by itself the difference between symbolic and non-symbolic number processing. Hence, a single representational mechanism could underlie both. Another possibility is that a different kind of representation underlies symbolic and non-symbolic processing. Empirical arguments are necessary to distinguish between these possibilities. This is the focus of the present paper.

Priming is a useful technique to uncover characteristics of mental representations. In the case of number processing, numerical distance between prime value and target value has been used as a marker for number line access (Koechlin, Naccache, Block & Dehaene, 1999; Reynvoet, Brysbaert & Fias, 2002). In the present study, we manipulate prime format (symbolic versus non-symbolic), target format, and numerical distance between prime and target value to see if there are qualitative or quantitative differences between how symbolically and non-symbolically presented number is mentally coded.

Although number comparison is a widely used task to investigate number representations, we decided not to use the number comparison task because it prevents a pure measurement of the prime-target distance effect. One problem is that in primed number comparison, three distance relations are involved: The distances between the prime value and each of the to-be-compared numbers and the distance between the two to-be-compared numbers itself. Another problem is that the number line representations may not be linearly related to the obtained effects in comparison tasks because non-linearities may occur in the mapping from the number line to the number comparison decision mechanism (cf. Verguts et al., 2005). Rather, we opted for a naming task because it avoids the above problems. Moreover, the observed distance-dependent priming effects (Reynvoet & Brysbaert, 1999, 2004; Reynvoet et al., 2002) indicate that primed number naming is a valid way to obtain insight in the mental representation of numerical magnitudes.

2.2 Experiment 1

2.2.1 Materials & Methods

Participants

Participants were 25 students at Ghent University (8 male, 17 female). Average age was 21.7 years. Three participants were left-handed.

Apparatus

Timing routines used the method described by MacInnes and Taylor (2001). Stimuli were presented on a 15 inch colour screen, connected to a Pentium III computer. Reaction times (RTs) were measured with a voice key connected to the game port.

Stimuli

We restricted the number range from 1 to 5, for two reasons. First, participants cannot reliably process the quantity of larger numbers of dots when presented briefly. The subitizing range, in which subjects can immediately determine the numerosity of a display, is thought to be limited at around 4 or 5 elements (Mandler & Shebo, 1982). In case of larger numbers, subjects are likely to resort to a counting strategy and consequently RTs would not reflect the pure characteristics of number representations. Second, Nieder et al. (2002, 2004) demonstrated number-selective neurons for numerosities up to 5; therefore we chose to use 1-5 as the number range.

Primes and targets were Arabic digits or collections of dots, presented in black against a grey background. Each dot pattern was randomly generated: Dots were positioned randomly (within a visual circle of 12.3 deg), and dot radius varied randomly between 2.0 and 4.0 deg, in order to eliminate the role of cues other than quantity. All dots were separated by at least 2.5 deg. Arabic digits were presented in courier font with a size comparable to the dot patterns.

Procedure

Two stimulus formats were tested. In the first stimulus format, prime and target were presented as Arabic digits while in the second stimulus format, prime and target were presented as dot patterns. All participants completed both formats, order was counterbalanced between participants. For each stimulus format there were 5 × 5 = 25 possible combinations of prime – target value, which were randomly presented. Participants completed 3 blocks of 100 trials per stimulus format (6 blocks in total), separated by a brief pause. Before each format, 15 practice trials were given for familiarization with the procedure.

Each trial began with the presentation of a fixation cross for 515 ms followed by a forward mask for 49 ms. Then the prime was presented for 83 ms, so that the prime was clearly visible but participants had no time to react to it. The prime was followed by a backward mask for another 49 ms. Each mask was different and consisted of a pattern of random lines, which filled a square (17.4 deg). Finally, the target was presented for 182 ms, after which participants named aloud the indicated quantity. When either the voice key triggered an answer or 1500 ms were passed, the response was typed in by the experimenter, who also noted whether the time registration had been successful.

2.2.2 Results

Error rate was too low (1.17%) for further analysis. Another 5.92% of the trials were excluded due to voice key failure. RTs below 200 ms or above 1000 ms were also excluded from analysis (0.25%).

First, a 2 (stimulus format) × 5 (prime value) × 5 (target value) ANOVA was run on mean RTs. This revealed significant main effects of stimulus format [dot format: 525 ms, digit format: 466 ms; $F(1, 24) = 42.2$, $MSE = 25852$, $p < 0.0001$], prime value [501, 501, 498, 489, and 487 ms for primes from 1 to 5 respectively; $F(4, 96) = 12.5$, $MSE = 926$, $p < 0.0001$], and target value [463, 464, 482, 532 and 537 ms for targets 1 to 5 respectively; $F(4, 96) = 74.6$, $MSE = 4492$, $p < 0.0001$]. All interactions were significant [format × target value: $F(4, 96) = 150.0$, $MSE = 1423$, $p < 0.0001$; format × prime value: $F(4, 96) = 15.0$, $MSE = 884$, $p < 0.0001$; prime value × target value: $F(16, 384) = 30.0$, $MSE = 575$, $p < 0.0001$ and format × prime value × target value: $F(16, 384) = 3.3$, $MSE = 558$, $p < 0.0001$, see Figure 2A, B]. The format × target value interaction originates from a size effect (slower RTs with increasing target size) in the dot format [mean RT for targets 1 to 5 respectively 462, 468, 507, 588, 600 ms; regression slope = 39.8 ms] which is not present in the digit format [mean RT for targets 1 to 5 respectively 463, 459, 456, 476, 474 ms; regression slope = 3.8 ms]. This size effect in the dot format reflects the subitizing slope, which is about 40 ms per item (contrary to the counting slope, which is about 270 ms per item; Mandler & Shebo, 1982). The format × prime value interaction is due to a decrease of RT as a function of prime value in the dot format [538, 536, 529, 515, 506 ms for primes 1 to 5 respectively; regression slope = -8.6 ms], which is not found in the digit format [465, 466, 467, 463, 468 ms for primes 1 to 5 respectively; regression slope = 0.41 ms].

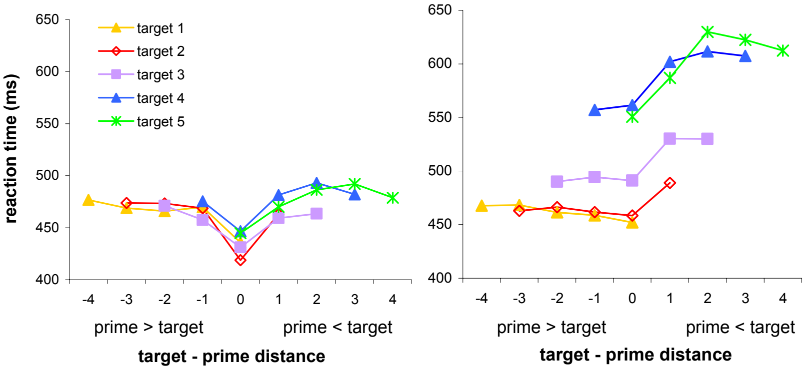

Figure 2: RTs for all prime-target combinations for the two different prime-target formats in Experiment 1: **A.** digit format; **B.** dot format

The most important finding for the present purposes was the modulation of the prime value × target value interaction by format. As can be seen in Figure 2A and B, the priming effect in the two stimulus formats differs considerably. In the digit format condition, the priming curve is V-shaped, indicating that a digit primes smaller and larger numbers as a function of numerical distance. This type of priming has been found before (Reynvoet & Brysbaert, 1999, 2004; Reynvoet et al., 2002). In the dot format condition the priming curve is stepwise, indicating that a dot pattern primes all targets values that are smaller than or equal to the prime value.

In order to establish the difference in the priming-curve shapes statistically, we fitted regression equations with two predictors that coded for a step-function and a V-function, respectively. The step-function predictor had a coefficient equal to -1 if prime value ≥ target value and a coefficient +1 if prime value < target value. The V-function predictor had coefficients equal to |target value – prime value|. A positive regression coefficient for the step-function predictor indicates that the shape of the priming curve can be described by a step-function in which prime values larger than or equal to the target value lead to faster RTs; on the other hand, a positive coefficient for the V-function predictor means that larger |prime value – target value| distances lead to higher RTs and in this way this predictor codes for the presence of a V-shape. In addition to these two predictors, an intercept and the target value were included in the regression. The analysis was restricted to distances zero up to 3, to eliminate distortions from the low number of prime-target combinations for larger distances. The regression was run for each participant separately (Lorch & Myers, 1990) and the pattern of coefficients over the two stimulus formats was compared with a 2 (stimulus format) × 2 (shape of function) ANOVA. This analysis revealed a significant main effect of stimulus format [$F(1, 24) = 9.5$, $MSE = 56$, $p = 0.0052$] and, most importantly, an interaction between stimulus format and function [$F(1, 24) = 38.0$, $MSE = 80$, $p < 0.0001$]. This interaction is clearly illustrated in Figure 3, where we plotted the regression coefficients for both formats.

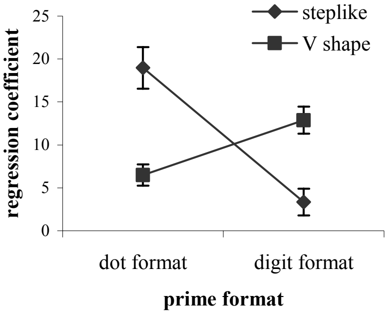

Figure 3: Regression coefficients for the predictors describing step-like and V-shape priming functions as a function of prime format in Experiment 1 (from analysis including distance 0). Error bars denote ± 1 standard error of measurement.

For the dot format, the step-function predictor was clearly the best predictor [paired t-test over the two regression coefficients, t(24) = 4.16, p = 0.0004, 2-tailed], while for the digit format, the V-function predictor had a higher value [t(24) = -4.32, p = 0.0002, 2-tailed]. Moreover, t-tests showed that these best predictors differed significantly from zero, see Table 1. These results provide quantitative evidence of the striking difference between the priming curves.

To verify that the V-shape curve was not completely determined by identity priming but also reflects distance-related priming (and hence semantic access), we ran the same regression on the same data where trials with zero distance were omitted. In this regression, the V-function predictor codes for distance related priming only, since the identity effect is omitted by excluding the distance 0.

Table 1: Results of the multiple regression analyses in Experiment 1

condition	digit			dot		
predictor	size	Step	V shape	size	Step	V shape
Regression with distance 0 included						
mean R^2 (SE)	0.32 (0.04)			0.73 (0.03)		
mean β (SE)	3.17 (1.99)	3.35 (1.55)	12.87 (1.57)	33.27 (2.65)	18.97 (2.43)	6.49 (1.24)
t(24)	1.59	2.17	8.20	12.54	7.81	5.25
p-value	0.13	0.041	<0.0001	<0.0001	<0.0001	<0.0001
Regression with distance 0 excluded						
mean R^2 (SE)	0.75 (0.03)			0.19 (0.05)		
mean β (SE)	4.61 (2.03)	-0.40 (1.81)	5.74 (1.34)	34.29 (2.80)	18.85 (2.80)	8.88 (1.81)
t(24)	2.27	-0.22	4.30	12.26	6.73	4.91
p-value	0.03	0.83	0.00025	<0.0001	<0.0001	<0.0001

Upper part of the Table: distance zero included; **lower part of the Table:** distance zero excluded. Adjusted R^2 of the general fit of the regression was calculated for every participant separately and was averaged over participants (mean and standard error provided). Mean and standard error of obtained regression coefficients β (regressions were run for each participant separately; Lorch & Myers, 1990); t-tests (2-tailed) over regression coefficients against zero, for the two prime-target format conditions of Experiment 1.

Regression coefficients of the V-function predictor were indeed significant for the digit format [t(24) = 4.30, p < 0.0003, 2-tailed], indicating that the distance-related priming was not solely an effect of repetition priming, and was therefore semantically mediated. Without distance 0, the step-function predictor in the digit format uniquely codes for asymmetries on both sides of the identity, therefore the non-significance of this predictor in the digit format [t(24) = -0.22, p = 0.83, 2-tailed] shows that the V-curve in this condition was symmetrical. Note that none of the effects is attributable to the size effect (see ANOVA) because size was partialled out in all regression analyses by including target value as a predictor.

2.2.3 Discussion

The results from the digit format replicate the findings of Reynvoet et al. (2002), although the number range was 1 to 5 instead of 4 to 9. Similar to this experiment, an identity and an additional distance related priming effect were found. In view of our research question, the priming pattern induced by digit primes is in line with what would be expected from place coded representations: A digit prime activates a delineated segment around the prime value, thereby facilitating the processing of targets smaller and larger than but close to the prime value. The priming pattern in the dot format was clearly of a qualitatively different type. The priming pattern observed for dots is compatible with the properties of summation coding: The prime did not only facilitate the processing of that particular number but also of all smaller numbers.

Whereas the V-shaped pattern of priming is well established and generally accepted to reflect the nature of the number representation (Koechlin et al., 1999; Naccache & Dehaene, 2001a; Reynvoet et al., 2002), it is possible that the step-like priming function in the dot format is due to the interaction of the processes involved in enumerating the prime and the target rather than to the underlying representation itself. In order to exclude this possibility we ran a mixed design study in which primes and targets could be either dots or digits. If it is the underlying representation that causes the step-like priming function when dots are used both as primes and targets, then the priming function should also be step-like when dots are used as primes and digits as targets.

2.3 Experiment 2

2.3.1 Materials & Methods

Participants

Participants were 20 students at Ghent University (6 male, 14 female). Average age was 19.9 years. Two participants were left-handed.

Apparatus & stimuli

These were the same as in Experiment 1.

Procedure

In this experiment, the 2 stimulus formats were randomly intermixed, so that all four combinations of prime and target format occurred within the same block. We will refer to a condition by stating the format of the prime and target, respectively. There were 25 combinations of prime – target values in each of the four format conditions, yielding 100 different trials. These trials were randomly presented in one block. Subjects completed 10 blocks, separated by a brief pause. Before the first block, 50 practice trials were given. Otherwise, the procedure was the same as in Experiment 1.

2.3.2 Results

Error rate was too low (1.72%) for further analysis. 5.77% of trials were excluded because of voice-key failure and 0.49% because RT was below 200 ms or above 1000 ms.

A 2 (format of prime) × 2 (format of target) × 5 (prime value) × 5 (target value) ANOVA on mean correct RTs revealed significant main effects of prime format [dot format: 511 ms, digit format: 524 ms; $F(1, 19) = 67.6$, $MSE = 1408$, $p < 0.0001$]; target format [dot format: 552 ms, digit format: 483 ms; $F(1, 19) = 402.1$, $MSE = 5976$, $p < 0.0001$]; prime value [523, 523, 516, 514, and 512 ms for primes 1 to 5 respectively; $F(4, 76) = 12.2$, $MSE = 889$, $p < 0.0001$] and target value [468, 500, 503, 557 and 559 ms for targets 1 to 5 respectively; $F(4, 76) = 51.4$, $MSE = 12255$, $p < 0.0001$]. As in experiment 1, a size effect is reflected in the main effect of target value (regression slope = 24.0 ms) but not in the main effect of prime value [regression slope = -3.2 ms]. There is a also a target format × target value interaction [F(4, 76) = 126.9, MSE = 1551, $p < 0.0001$, see Figure 4] because the size effect is restricted to the dot targets (and is probably due to the subitizing mechanism involved in the enumeration of collections of objects) [mean RT for dot targets 1 to 5 respectively 482, 515, 532, 608, 624 ms, regression slope = 37.6 ms; mean RT for digit targets 1 to 5 respectively 454, 484, 474, 506, 494 ms, regression slope = 10.9 ms]. All other interactions, except the target format × prime value interaction, the prime format × target format × target value interaction, and the target format × prime value × target value interaction were significant [all $p < 0.0001$].

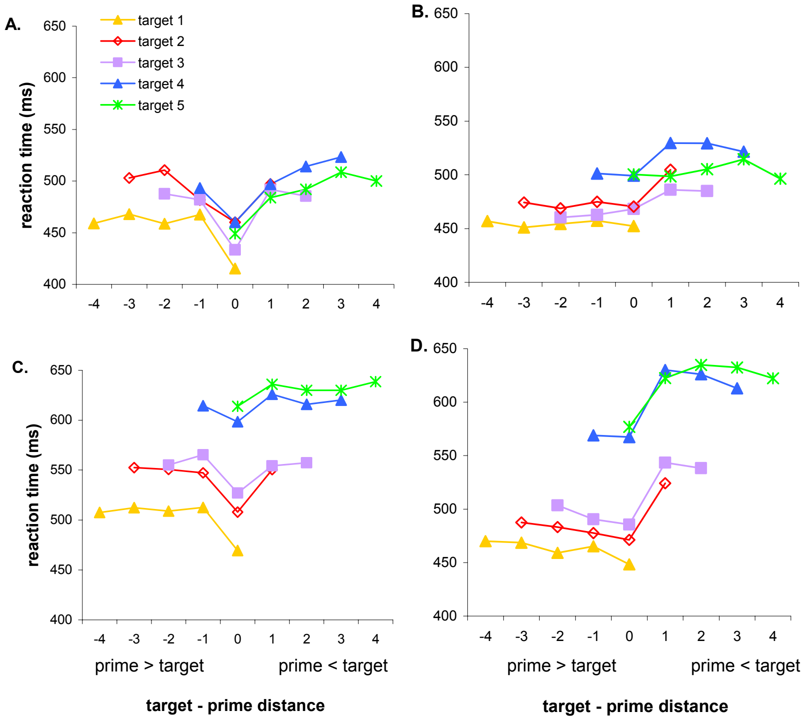

Figure 4: RTs for all prime-target combinations for the four different prime – target format conditions in Experiment 2: **A.** digit – digit; **B.** dot – digit, **C.** digit – dot; **D.** dot – dot.

This complex pattern of interactions becomes more interpretable by applying the multiple regression approach which was introduced for Experiment 1. As before, we conducted the same regressions with a step-function predictor and a V-function predictor, both with and without distance 0 trials included, to quantify the shapes of the priming curves. The pattern of coefficients over the four conditions (regression with distance 0 trials included) was compared with a 2 (prime format) × 2 (target format) × 2 (shape of function) ANOVA. This analysis revealed a significant main effect of shape of function [$F(1, 19) = 7.0$, $MSE = 89$, $p < 0.016$], a significant prime format × target format interaction [$F(1, 19) = 54.9$, $MSE = 37$, $p < 0.0001$] and, most informatively for the present purposes, a significant interaction between prime format and shape of function [$F(1, 19) = 66.9$, $MSE = 75$, $p < 0.0001$], see Figure 5. The mean regression coefficients and the results of the t-tests over regression coefficients against zero are summarized in Table 2.

In the digit-digit condition (Figure 4A), we obtained a significant contribution of the V-function predictor, which was a significantly better predictor than the step-function predictor [paired t-test: $t(19) = -3.94$, $p = 0.00087$, 2-tailed, see Figure 5]. The regression without distance 0 trials also revealed a significant contribution of the V-function predictor, which replicates Experiment 1 by providing evidence for a distance related priming effect on top of the identity effect. The contribution of the step-function predictor was also significant, indicating a small deviation from symmetry in the V-shape. To test the origin of this asymmetry we conducted t-tests between distance -1 and +1 for targets 2 to 4. Only for target 2 the difference between distance -1 and +1 was significant [target 2: $t(19) = 2.66$, $p = 0.015$; target 3: $t(19) = 1.12$, $p = 0.27$; target 4: $t(19) = 0.64$, $p = 0.53$; all p-values 2-tailed]. A paired t-test between distance 2 and -2 for target 3 was also not significant [$t(19) = -0.27$, $p = 0.79$, 2-tailed].This confirms that the asymmetry was not a general phenomenon, but was due to some local deviations (see Figure 4A), presumably due to noise.

In the dot-dot condition (Figure 4D), we could also replicate the findings of Experiment 1: There was a significant contribution of the step-function predictor, both with and without distance 0 included in the regression. The step-function predictor was also a significantly better predictor than the V-function predictor, as can be seen in Figure 5 [paired t-test: $t(19) = 5.99$, $p < 0.0001$, 2-

	digit - digit			digit - dot			dot - digit			dot - dot		
predictor	size	Step	V shape	size	Step	V shape	Size	Step	V shape	size	Step	V shape
Regression with distance 0 included												
mean R^2 (SE)	0.28 (0.05)			0.62 (0.03)			0.30 (0.04)			0.71 (0.03)		
mean β	3.98	7.22	15.17	31.98	2.23	8.82	9.71	11.72	-0.75	34.40	22.97	5.07
(SE)	(1.69)	(1.64)	(1.63)	(2.35)	(1.74)	(1.62)	(1.46)	(1.43)	(1.08)	(3.22)	(2.39)	(1.12)
t(19)	2.36	4.41	9.28	13.60	1.28	5.45	6.67	8.17	4.82	10.68	9.61	4.52
p-value	0.029	0.0003	<0.0001	<0.0001	0.28	<0.0001	<0.0001	<0.0001	0.50	<0.0001	<0.0001	0.0002
Regression with distance 0 excluded												
mean R^2 (SE)	0.07 (0.04)			0.60 (0.04)			0.29 (0.05)			0.71 (0.03)		
mean β	5.09	3.28	6.66	31.18	0.075	0.58	7.98	13.44	-0.23	34.07	23.08	4.51
(SE)	(1.72)	(1.54)	(1.57)	(2.66)	(2.26)	(2.20)	(1.57)	(1.51)	(1.64)	(2.84)	(2.43)	(1.96)
t(19)	2.97	2.13	4.24	11.74	0.03	0.26	5.09	8.92	-0.14	12.01	9.48	2.31
p-value	0.0079	0.047	0.0004	<0.0001	0.97	0.796	0.00007	<0.0001	0.89	<0.0001	<0.0001	0.033

Table 2: Results of the multiple regression analyses in Experiment 2. **Upper part of the Table:** distance zero included; **lower part of the Table:** distance zero excluded. Adjusted R^2 of the general fit of the regression was calculated for every participant separately and was averaged over participants (mean and standard error provided). Mean and standard error of obtained regression coefficients β (regressions were run for each participant separately; Lorch & Myers, 1990); t-tests (2-tailed) over regression coefficients against zero, for the four prime-target format conditions of Experiment 2.

tailed]. The V-function predictor also contributed slightly in the dot-dot condition, revealing a trace of a distance related priming effect. The reason for this can be found in the small decrease on the right-hand side of some of the dot-dot curves (when prime value > target value), especially the curves for target 2 and target 3. This increase however is much smaller than the step, as can be seen in Figure 4D.

The most important finding is that the step-like priming function was replicated in the dot-digit condition. A t-test over the regression coefficients of the step-function predictor was significant for the dot-digit condition (Figure 4C) in both regressions, showing that the dot primes induced the same priming pattern as in the dot-dot condition. Figure 5 clearly illustrates that the step-curve indeed accounts best for the data in this condition.

In the digit-dot condition, the t-test over the regression coefficients of the V-shape function predictor was significant in the regression with distance 0 included but not in the regression without distance 0. This indicates that in the digit-dot condition there was an identity effect but no distance related priming effect, which can also be seen in Figure 4B. However, the contribution of the step-function predictor for the digit-dot condition was far from significant, pointing to the symmetry of the curve.

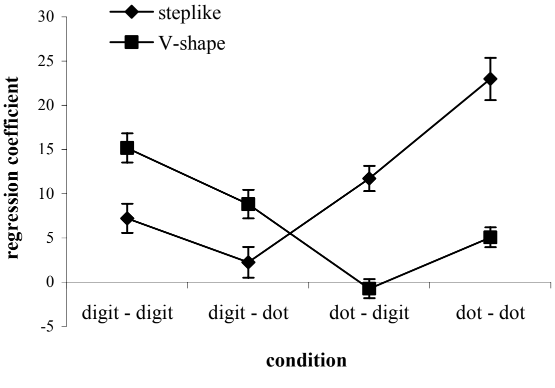

Figure 5: Regression coefficients for the predictors describing step-like and V-shape priming functions as a function of prime and target format in Experiment 2 (from analysis including distance 0). Error bars denote ± 1 standard error of measurement.

2.3.3 Discussion

The results of the digit-digit and dot-dot condition of Experiment 1 were largely replicated in Experiment 2. Only one difference was observed: the small contribution of the V-function predictor in the dot-dot condition, revealing a trace of a distance-related priming effect, which was not observed in the blocked design of Experiment 1. A possible explanation is that the mixed design may have fostered some cross-activations between the place and summation coding systems. Another possibility is that both stimulus formats activate the two representational systems but that one of them is strategically suppressed in the blocked design of Experiment 1.

Apart from replicating the results from Experiment 1 in the digit-digit and dot-dot conditions, the results of Experiment 2 clearly demonstrate that the step-like priming function with dot primes was not due to the blocked design of Experiment 1. The fact that the step-like priming function induced by dots generalizes to digit targets convincingly demonstrates that the step-like priming function derives from the properties of the numerical representations evoked by the dot primes. The possibility that the step-like priming function would be a consequence of the enumeration processes, possibly interacting between dot primes and dot targets, can be safely ruled out.

The distance-related V-shaped priming effect elicited by digit primes did not manifest itself in the digit-dot condition as it did in the digit-digit condition. Given that dot targets are named significantly slower than digits, a possible account for the relative weakness of V-shaped distance priming in the digit-dot condition compared to the digit-digit condition is that the place code activations induced by the digit primes have largely decayed by the time the dots reach the place coding system. This explanation is not incompatible with robust (step-like) priming in the dot-dot condition, if one assumes that summation coding representations are more robust.

In sum, Experiment 2 strengthens our conclusion that there are qualitative differences in the coding of number as conveyed by symbolic versus non-symbolic formats: Numerical values of non-symbolic numerosities are represented with summation codes, whereas numerical values of digits are represented with place codes.

2.4 Conclusion

The observation of summation coding has important theoretical implications. It highlights the fact that the representational coding of symbolic numbers differs considerably from the coding of non-symbolic numerosities. Recently a number of explicit models have been proposed trying to explain the internal organization of number knowledge. The present findings clearly indicate that such models need to allow for both place and summation coding (as in Dehaene & Changeux, 1993 and in Verguts & Fias, 2004). Models which focus on one of these types of coding are clearly applicable to only one numerical format. Models extended to explain both types of coding should also provide a rationale explaining which code is used in which situation.

An issue deserving further attention is Nieder et al.'s (2002, 2004) observation that neurons in parietal and prefrontal cortex code non-symbolic numerosities following a place-coding scheme. Our results suggest that in addition to these band-pass filtering (number-selective) neurons, the number processing system is also equipped with low- (or high-) pass filtering (number-sensitive) neurons. In fact, the neurons that were categorized as band-pass filtering neurons selective to the most extreme numerosities (1 and 5) by Nieder et al. could actually be low-pass or high-pass filters.

For non-symbolic formats, we (Verguts & Fias, 2004) have predicted number-sensitive neurons to precede the number-selective neurons in the processing stream. For a number of other quantitative features, this has been empirically observed (e.g., velocity; Orban, Kennedy & Bullier, 1986). Further empirical research and theory formation in the area of numerical cognition would clearly benefit from an explicit demonstration and detailed description of summation coding neural structures.

In conclusion, the present work shows at a behavioural level that the representation of small numbers is not supported by a single representational type. In addition to a place coding mechanism, a summation coding mechanism has now been shown to exist. The two mechanisms cause different priming characteristics. These observations raise questions to be addressed in future research. A first question is how the representation of larger numerical values, both in symbolic and non-symbolic modality, relates to the place and summation coding representations. In a recent review, Feigenson et al. (2004) proposed distinct representations for small and large numbers, the first being precise and the second approximate. The priming paradigm adopted in the present manuscript may prove a useful tool to investigate the characteristics of large number representations in relation to small number representations. A particularly interesting question to be addressed is whether the summation code representations are specifically related to the subitizing mechanism employed during the enumeration of small numbers of objects. Another unsolved issue is how exactly these representations are organized in a functional architecture of the human numerical cognitive system.

Chapter 3:

Number-sensitive preprocessing of visual numerosity in human parietal cortex

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manuscript submitted for publication

Numerous studies have identified the intraparietal sulcus as an area critically involved in numerical processing. Intraparietal sulcus neurons in macaques have been shown to be tuned to a preferred numerosity, hence neurally coding numerosity in a number-selective way. Recent fMRI studies in humans have demonstrated number-selective neural processing in the anterior parts of the IPS. Nevertheless, the characteristics of the neural processes that convert visual input into a number-selective neural code remain largely unknown. Computational studies have suggested that a stage of neural coding that is sensitive, but not selective to number, precedes number-selective coding. We used event-related fMRI to test this prediction. Dot patterns with a numerosity ranging from 1 to 5, carefully controlled for non-numerical parameters, were presented to the subjects. Because of a recent demonstration of number-sensitive processing in macaque LIP, we used a localizer task to identify the human homologue of LIP. In this region, located posterior to the anterior IPS regions engaged in number-selective processing, the BOLD signal increased with increasing numerosity of the dot patterns. This shows that also in humans number-sensitive processing steps precede number-selective coding.

3.1 Introduction

Many animal species, from salamanders to humans, are able to process number when presented in a nonsymbolic format. This suggests that number processing is biologically highly relevant and evolutionarily advantageous. Furthermore, the behavioural markers of this ability show striking correspondences between humans and non-human animals (e.g., distance and size effects, Dehaene, Dehaene-Lambertz & Cohen, 1998). This close correspondence suggests that there are common species-independent constraints on the development of this ability, and that the higher numerical skills in humans are rooted in this nonsymbolic numerosity system (Feigenson, Dehaene & Spelke, 2004), the characteristics of which have recently begun to become uncovered.

Recent neuroscientific studies have described how neurons in the intraparietal sulcus of human and non-human primates encode numerosity in a way that is consistent with the behavioural markers of numerical processing (Nieder & Miller, 2004). Using single-cell recording in monkeys, trained in a match-to-numerosity task, Nieder and colleagues (Nieder, Freedman & Miller, 2002; Nieder & Miller, 2003) found neurons in the intraparietal sulcus and in the prefrontal cortex which responded to numerosity in a number-selective way. In particular, these neurons' firing rates were selectively tuned to a specific numerosity: it was maximal for its preferred numerosity; and the neural response decreased when the value of the presented numerosity was numerically more distant from the preferred numerosity.

Recent fMRI studies have confirmed the existence of a number-selective coding system in humans by means of the fMRI adaptation paradigm. Piazza and colleagues (Piazza, Izard, Pinel, LeBihan & Dehaene, 2004; Piazza, Pinel & Dehaene, 2007) and Cantlon, Brannon, Carter & Pelphrey (2006) showed neural adaptation for repeated numerosities and rebound of adaptation for deviant (i.e., numerically different) values, in the anterior part of the intraparietal sulcus. In line with the tuning characteristics of the number-selective neurons described by Nieder et al. (Nieder et al., 2002; Nieder & Miller, 2003), this rebound effect increased as the distance between the adaptation numerosity and the deviant numerosity increased. These adaptation effects were observed for numerosities (dot patterns) (Piazza et al., 2004; Cantlon et al., 2006) as well as for symbolic numbers (Piazza et al., 2007).

The characteristics of the number-selective neurons can readily explain many aspects of overt behaviour (Nieder & Miller, 2004). In contrast, not much is known about the neural processes leading up to number-selective neurons; that is, the neural mechanisms that convert visual input, consisting of a number of objects, into a number-selective coding system. In an attempt to bridge this gap, the systems that are required for this conversion have been investigated by computational modelling studies (Dehaene & Changeux, 1993; Verguts & Fias, 2004). These models proposed that two intermediate number-sensitive preprocessing steps are necessary between visual input and a number-selective coding system.

The first step is the creation of an object location map: a spatial neuronal map where each neuron signals the presence of an object at a given location, independent of the physical appearance of that object. Behavioural evidence for the contribution of such an object location map to the enumeration process derives from the fact that rapid enumeration of a small number of objects (i.e., subitizing) is only possible when the objects occupy different positions in space. When the to-be-enumerated objects are presented concentrically (i.e. objects at the same position in the object location map), subitizing is impossible and a counting procedure is required (Trick & Pylyshyn, 1994). The object location map is number-sensitive in the sense that when more objects are presented, more neurons will signal the presence of an object in its receptive field and consequently there is more neural activity in the map considered as a whole. Note that the object location map, despite being number-sensitive, is not number-selective as it is not tuned to a specific numerosity. Note also that processing steps preceding the object location map, such as the primary visual processing necessary to individuate objects regardless of appearance, are not number-sensitive (or number-selective), as they also respond to non-numerical features of the display (e.g. respond more for a single larger object).

After the object location map has been obtained from visual input, the information in this object location map must be further converted into a number-selective coding system. This conversion of the object location map into a number-selective coding system entails a nonlinear transformation (Verguts & Fias, 2004). Such a non-linear transformation cannot be achieved in a single step.

The most straightforward way to accomplish a nonlinear transformation in neural networks is to implement an intermediate preprocessing step between input and output. In Verguts and Fias (2004), the nature of this intermediate step was computationally investigated. A neural network with an object location map as input was trained to construct a number-selective coding system at output. The network was equipped with an intermediate layer between input and output (for more details, see Verguts & Fias, 2004). After training, it was found that neurons in this intermediate layer responded monotonously (i.e., monotonously stronger or weaker) when more objects were presented. Hence, the second preprocessing step between visual input and a number-selective coding system consisted of nodes accumulating or summating (in a positive or negative way) the number of objects that are activated in the first preprocessing step (the object location map). Therefore this second preprocessing step was termed a summation coding system. The nodes in the summation coding system are number-sensitive but, importantly, are not number-selective, since they do not selectively respond to a specific number.

Very recently, the biological reality of a summation coding system has been demonstrated by means of single cell recording. Summation-type neurons have been discovered in the lateral intraparietal area (LIP) of the macaque monkey (Roitman, Brannon & Platt, 2007). The responses of LIP neurons were recorded after presentation of a task-irrelevant visual array of 2, 4, 8, 16, or 32 elements. More than half of the recorded LIP neurons showed a monotonic relationship between firing rate and the number of elements presented to the neuron's receptive field, indicating that these neurons summated (in a positive or negative way) the number of elements displayed.

At a behavioural level, evidence demonstrating a summation coding system in humans has been found by Roggeman, Verguts & Fias (2007). A priming study was conducted, in which the effect of a briefly presented prime (Arabic digit or dot display) on the naming of a subsequently presented target number (Arabic digit or dot display) was evaluated. When primes were Arabic digits, a classic distance-dependent priming effect (faster naming of the target when the numerical distance between the prime and the target is small, see Reynvoet, Brysbaert & Fias, 2002) was found. This distance-dependent priming effect provides evidence for an underlying number-selective coding system. Indeed, since the tuning of number-selective neurons is not perfect, a prime number will not only activate neurons that are tuned to the prime's numerical value but also neurons that are tuned to numerically close values, thereby facilitating the naming of subsequently presented numerically close numbers. In contrast, when primes were dot displays instead of numerical symbols, it was found that naming the target value was faster whenever the value of the prime was larger than or equal to the value of the target. These results point to an underlying representation of numerosities in accordance with a summation coding system. In particular, if neurons respond more strongly with more objects, the neural code of the target will be sufficiently pre-activated when the prime is larger then the target, which allows fast naming of the target. On the other hand, when the prime is smaller than the target, not all target neurons will be activated and additional neurons will have to be activated to name the target, increasing response time.

The present study aimed at detecting and locating brain regions that perform the number-sensitive preprocessing steps (object location map and summation coding system) which precede a number-selective coding system. We predicted these numerical preprocessing steps to occur, at least partly, in the human homologue of macaque monkey area LIP (human LIP), because neurons in monkey LIP have some characteristics that point towards an object location map and a summation coding system. First, LIP neurons in the monkey have retinotopically organized receptive fields and can therefore serve to create an eye-centered object location map (Colby & Goldberg, 1999). A recent fMRI study confirmed the retinotopic organization of human LIP (Sereno, Pitzalis & Martinez, 2001). Second, neurons in LIP integrate and accumulate information over relatively large areas of the visual field (Shadlen & Newsome, 2001). This property makes LIP neurons well suited to perform the integrative processes that are required for a summation coding system. This is confirmed by the number-sensitive neurons detected in area LIP by Roitman et al. (2007).

We used event-related fMRI to localize the areas involved in the number-sensitive preprocessing steps. We presented dot displays containing one to five dots and measured neural activity for each numerosity. We restricted the numerosities to this range for several reasons. We wanted the range of numbers to match the range that we used in our earlier studies (Verguts & Fias, 2004; Roggeman et al., 2007) because these studies provided behavioural evidence for summation coding. Moreover, the processes involved in the enumeration of small numerosities (i.e. up to around 4 elements) are qualitatively different from those involved in the enumeration of larger numerosities (Revkin, Piazza, Izard, Cohen & Dehaene, in press). In order to test the prediction that number-sensitive preprocessing steps would occur in human LIP, we localized this region by means of a separate localizer run. This block-design localizer run consisted of a saccade task and a fixation task, following Baker, Patel, Corbetta & Snyder (2006).

In order to be sure that we actually detect areas involved in numerical preprocessing steps (object location map and summation coding system) rather than areas that are sensitive to physical parameters that correlate with numerosity (such as total luminance or object size), stimuli were constructed such that confounds of these non-numerical parameters were eliminated (see Materials and Methods).

3.2 Materials & Methods

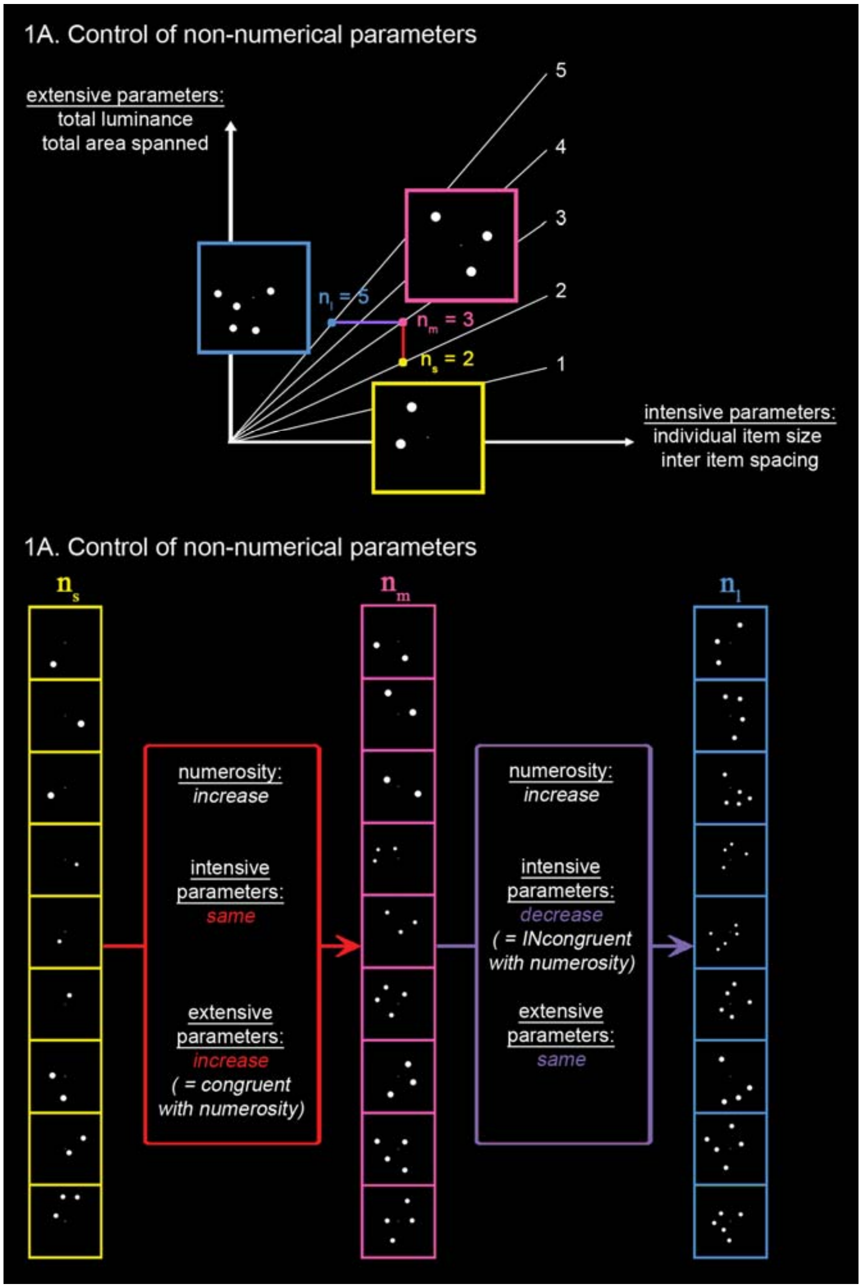
Participants

Twenty-one adult volunteers were recruited from Ghent University, and were paid for participation. Four subjects were excluded from analysis due to poor performance (see results). One other subject was excluded because of self-reported drowsiness. The remaining sixteen subjects (13 male, 1 left-handed male), were on average 22.2 years old (range 19-26y). All subjects had normal or corrected-to-normal vision. All reported to have no neurological or psychiatric history. The study was approved by the ethical committee of the Medical Department of Ghent University. All subjects gave written informed consent prior to scanning.

Stimuli

Stimuli were dot displays with a numerosity ranging from 1 to 5. The procedure to remove confounding effects of non-numerical parameters was based on Piazza et al. (2004) and Dehaene, Izard & Piazza (2005) (see Figure 1A).

Non-numerical parameters can be divided in intensive parameters (individual item size and inter item spacing) and extensive parameters (accumulated area of all dots in the display or total luminance, and total area spanned by the dot configuration). For a given numerosity, each intensive parameter is linearly related to one of the extensive parameters (Figure 1A, linear relationship is shown as white lines for numerosities 1, 2, 3, 4 and 5). For example, when the numerosity is fixed and the size of the individual dots increases, the accumulated area of all dots also increases. Consequently, it is impossible to control both parameters simultaneously within a single pair of numerosities. The only way out is to use two pairs of numerosities, one controlling for the intensive parameters, the other for the extensive parameters. For this purpose, we constructed triplets of dot displays with increasing numerosity $n_{small} < n_{medium} < n_{large}$ (from now on referred to as n_s, n_m and n_l, respectively). For the first pair of the triplet (n_s and n_m, yellow and magenta displays in Figure 1A, B), the intensive parameter (e.g., individual dot size) was constant (red line on the graph), but the extensive parameter (accumulated area of all dots) covaried congruently with numerosity: the accumulated area increased with increasing numerosity when individual dot size was constant. For the second pair (n_m and n_l, magenta and blue display in Figure 1A, B), the extensive parameter was constant (purple line in the graph) but the intensive parameter covaried with numerosity. In this case, the covariance relation was incongruent, because the individual dot size decreased with increasing numerosity when the accumulated area was fixed. Within the same triplet, the same logic was used for controlling the inter item spacing (intensive parameter) and total area spanned (extensive parameter). Thus, whereas both extensive parameters increase from n_s to n_m, the intensive parameters decrease from n_m to n_l, and numerosity is the sole parameter that monotonically increases from n_s to n_l. Therefore, brain areas that are found activated in the contrasts ($n_l > n_m$) and ($n_m > n_s$) (as measured by a conjunction analysis) can safely be regarded as areas responding solely to numerosity and not to the intensive or extensive confounding parameters. Note that the design is tailored to quantitatively distinguish neural responses to small, medium and large numerosities (i.e. the categories n_s, n_m, and n_l) but does not allow distinguishing between individual numerosities since they could belong to multiple categories. Category n_s could be numerosity 1, 2 or 3, n_m could be numerosity 2, 3, or 4, and n_l could be numerosity 3, 4 or 5 (Figure 1B).


1A. Control of non-numerical parameters
extensive parameters:
total luminance
total area spanned
5
4
3
2
1
n_l = 5
n_m = 3
n_s = 2
intensive parameters:
individual item size
inter item spacing
1A. Control of non-numerical parameters
n_s
n_m
n_l
numerosity:
increase
intensive
parameters:
same
extensive
parameters:
increase
(= congruent
with numerosity)
numerosity:
increase
intensive
parameters:
decrease
(= INcongruent
with numerosity)
extensive
parameters:
same

Dots were displayed in an area of approximately 10 × 10 visual degrees. The minimum and maximum item size varied between 0.2 and 0.63 visual degrees. Dot displays were generated randomly by an adapted version of a Matlab program (Matlab 7.0.4, The MathWorks, Inc.) described in Dehaene et al. (2005).

Experimental procedure

Stimuli were presented for 150 ms, white against a black background. A small yellow fixation cross remained on the screen throughout the total scan time. Stimuli were presented on average every 5 seconds, with a jittering factor (Burock, Buckner, Woldorff, Rosen & Dale, 1998; Dale, 1999; Miezin, Maccotta, Ollinger, Petersen & Buckner, 2000) varying between 0 and 1600 ms, so that the interstimulus interval between 2 consecutive events could vary between 3400 ms and 6600 ms. 20% of all events were null events. In order to make sure that subjects paid attention to the stimuli, occasionally (12 times per run) a task trial was introduced. In these task trials, 2 Arabic digits were presented left and right of fixation and subjects were asked to indicate the number that corresponded to the numerosity of the previous dot display by pressing a button with their left or right index finger. The experiment consisted of 5 runs with 102 events per run. Order of the 5 event types (n_s, n_m, n_l, null events and task trials) was pseudo-randomly intermixed with first order counterbalancing within runs (each trial type followed every other trial type equally often, Dale & Buckner 1997; Buckner et al., 1998). Order of numerosities 1, 2, 3, 4 and 5 was counterbalanced over all runs for each subject.

Figure 1 (left);. Control of non-numerical parameters, as based on Piazza et al. (2004) and Dehaene et al. (2005). **A.** Non-numerical parameters were divided in intensive parameters (X-axis) and extensive parameters (Y-axis). The linear relationship between these parameters for a given numerosity is schematically shown in the graph. Numbered lines specify this relationship for 1 to 5 dots. Colored lines provide an example of how stimuli were selected to remove the confounding influence of intensive or extensive parameter values. Starting from an medium numerosity (n_m), a smaller numerosity (n_s) is selected with the same intensive parameter and a larger numerosity (n_l) with the same extensive parameter. In this way, only numerosity increases from n_s over n_m to n_l (see text for details). **B.** Examples of stimuli with different numerical values in the categories n_s, n_m, and n_l.

At the end of the experiment, subjects were engaged in a block-design localizer run to determine human LIP (see above) based on the finding that LIP is involved in the execution of eye movements (Corbetta et al., 1998; Baker et al., 2006). Stimuli were the displays for numerosity 1 used in the main experiment. Every stimulus was presented for 1 second, and was immediately followed by another stimulus, yielding a dot which changed location and size every second. In the saccade condition, subjects were asked to make a saccade to the dot and back to the fixation cross every time the dot changed position. In the fixation condition subjects were asked to ignore the dots and keep fixating the fixation cross. The task was indicated by the colour of the fixation cross (red: make saccades, yellow: no saccades). Block duration was 16 s. The saccade and fixation block alternated and each block was repeated 8 times.

The experimental procedure was controlled with E-Prime 1.1 SP3 (www.pstnet.com/eprime; Psychology Software Tools), running on a Pentium IV laptop. Stimuli were presented through dual display MRI compatible LCD displays, mounted in a lightweight headset (VisuaStim XGA, Resonance technology Inc, http://www.mrivideo.com/; resolution 800 × 600, refresh rate 60 Hz).

Imaging procedure

Subjects were positioned head first and supine in the bore. Images were collected with a 3T Magnetom Trio MRI scanner system (Siemens Medical Systems, Erlangen, Germany), using an 8-channel radiofrequency head coil. First, 176 high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence (TR = 1550ms, TE = 2.89ms, image matrix = 256 × 256, FOV = 220mm, flip angle = 9°, slice thickness = 0.9mm, voxel size = 0.9 × 0.871 × 0.871 mm (resized to 1 × 1 × 1 mm), 176 sagittal slices). Whole brain functional images were collected using a T2*-weighted EPI sequence, sensitive to BOLD contrast (TR = 2000ms, TE = 30ms, image matrix = 64 × 64, FOV = 224mm, flip angle = 90°, slice thickness = 3.0mm, distance factor = 17%, voxel size 3.5 × 3.5 × 3 mm, 31 axial slices). During numerosity runs, 256 images were acquired per run. In the localizer run, 135 images were acquired with the same EPI sequence.

Image processing and statistical analysis

Data analysis was performed with BrainVoyager QX 1.8 software package (Brain Innovation, Maastricht, The Netherlands; Goebel, Esposito & Formisano, 2006). An unforeseen technical problem caused inaccurate timing of events in the first run. Therefore the first run was discarded from the analyses for all subjects. Functional volumes were corrected for slice timing, motion corrected to the first image of each run (trilinear/sinc interpolation), and high pass filtered (cutoff 0.0083 Hz) after linear trend removal. Anatomical data were corrected for inhomogeneities. Functional images were coregistered with the within-session anatomical volume for each run separately. Anatomical and functional volumes were then transformed into Talairach space. Functional images were smoothed with a Gaussian kernel of 8 mm FWHM prior to statistical analysis.

Functional data were subjected to GLM analyses with 5 predictors for the main experiment (n_s, n_m, n_l, response left, response right) or 2 predictors for the localizer run (saccade, no saccade) (protocol specified in milliseconds and convolved with a 2 Gamma haemodynamic response function, time to response peak = 5 s, time to undershoot peak = 15 s), for each run and each subject separately. For multi-subject GLM, runs of the same subject were implemented as fixed effects, between subjects as random effects. Activations are reported at a p-level of 0.005 with a cluster extent threshold which leads to a cluster-level corrected p-level of 0.05 (Forman, Cohen, Fitzgerald, Eddy, Mintun & Noll, 1995), unless stated differently. Conjunction of the 2 contrasts of interest ($n_l > n_m$) & ($n_m > n_s$) was calculated based on the minimum t-statistic compared against the conjunction null (Nichols, Brett, Andersson, Wager & Poline, 2005).

The definition of the ROIs corresponding to human LIP was based on the contrast saccade versus no saccade from the localizer run. ROIs were analyzed by averaging the time course over all voxels in the specified ROI. A random effects analysis was then performed on these averaged time courses for the conjunction of the 2 contrasts of interest ($n_l > n_m$) & ($n_m > n_s$). Event-related average curves were plotted by extracting this time course, averaged over all voxels in the specified ROI, for every event of the specified type in every run of every subject. The time courses were extracted from 2 seconds before until 16 seconds after the onset of the event. For this analysis, a time course for the null events was extracted in the same way as for numerosity events, that is, a time course for a fixation event of 150 ms with a jittered onset was extracted. This null event time course served as a baseline and was subtracted from the time courses of the events of interest (n_s, n_m and n_l events). Null events produced a reliable baseline because they were counterbalanced with numerosity events.

For viewing purposes, and to investigate the anatomical location of the ROIs with respect to the intraparietal sulcus, we visualized the functional ROIs on a reconstructed cortical surface of a group average of the subjects' brains. This was important because monkey LIP is situated in the lateral intraparietal sulcus, whereas the human equivalent is reported to be in the medial bank of the IPS. We wanted to check this organization in our sample of subjects. To this end, a cortical-based alignment algorithm was used as implemented in BrainVoyager (www.BrainVoyager.com).

3.3 Results

Behavioural results

Four subjects were excluded due to poor performance on the task trials, suggesting that they did not attentively process the stimuli. We excluded subjects when they made more than 20% errors over the 4 runs, or when they made more then 30% errors in a singe run. The remaining subjects made on average 6.25% errors (range: 0 to 7 errors on the total of 48 trials).

Whole-brain analysis

The whole brain random effects analysis of the conjunction ($n_l > n_m$) & ($n_m > n_s$) thresholded at $p < 0.005$ with a cluster extent threshold of 167 voxels, yielded a network of bilateral occipital and parietal areas and an area in the medial frontal gyrus (see Figure 2).

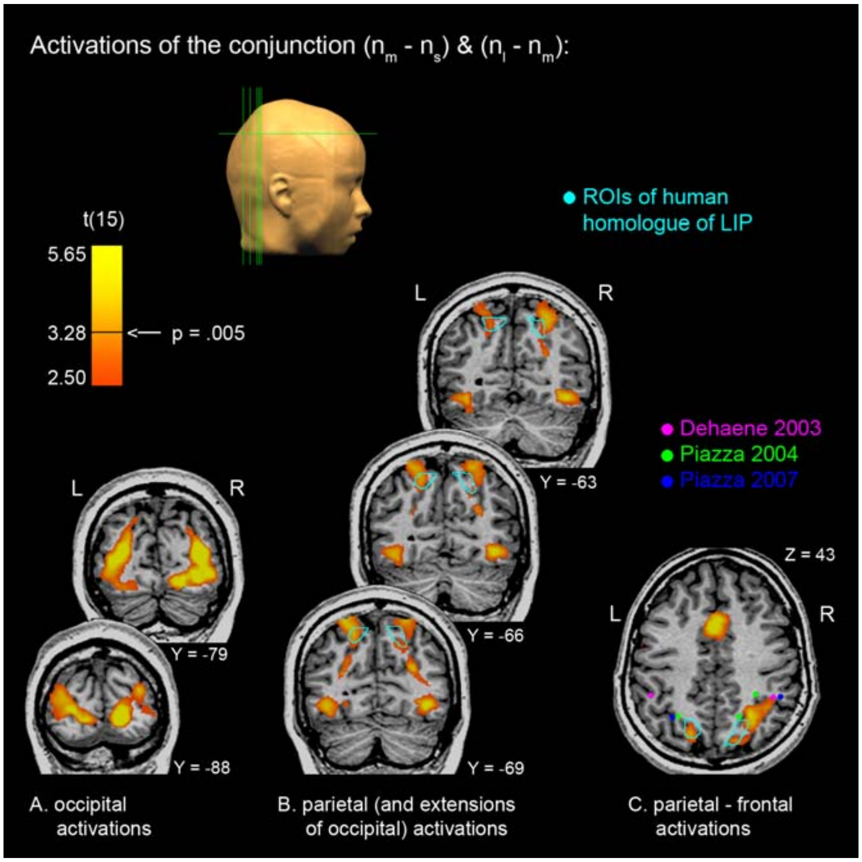


Figure 2. Results of the random effects analysis of the conjunction ($n_l > n_m$) & ($n_m > n_s$), thresholded at $p < 0.005$ with a cluster extent threshold of 167 voxels. See text for Talairach coordinates. **A.** Activations in bilateral lingual gyrus, right V8 and bilateral middle occipital gyrus (LOC). **B.** Activations in posterior part of the superior parietal lobe. The most anterior parts of the occipital activations are also visible. ROIs of human LIP are shown in blue outline, and are shown to be close to and overlapping with the parietal activations. **C.** Activations in intraparietal sulcus and pre-sMA. ROIs of human LIP are shown in blue outline. Centers of activations of previous studies (projected on Z = 43) focusing on number-selective coding are shown to be more anterior in intraparietal sulcus [magenta: barycentre of the meta-analysis by Dehaene et al. (2003); green: activations found in the study by Piazza et al. (2004); blue: activations found in the study by Piazza et al. (2007)].

The occipital activations comprised the lingual gyrus (Figure 2A) with coordinates previously associated with area VP [Talairach coordinates left: -15 -91 -5, 282 voxels (resized to 1 × 1 × 1 mm voxels); right: 15 -88 -5, 2243 voxels] and right V8 [Talairach coordinates 30 -76 -8, 2128 voxels] (Van Essen & Drury, 1997; Tootell & Hadjikhani, 2001). Activations in the middle occipital gyrus were centered left around -27 -79 10 [3146 voxels] and right around 30 -79 13 [2131 voxels], but extended in lateral and inferior directions, thus overlapping with regions identified as area LOC (Grill-Spector, Kushnir, Edelman, Itzchak & Malach, 1998; Tootell & Hadjikhani, 2001; Denys, Vanduffel, Fize, Nelissen, Peuskens, Van Essen & Orban, 2004).

The activation in the medial frontal gyrus [0 11 43, 1372 voxels] extended posterior and superior from the local maximum (Figure 2C), and was situated in an area generally recognized as pre-SMA (Behrens, Jenkinson, Robson, Smith & Johansen-Berg, 2006; Klein et al., 2007).

Significant clusters of activations [left: -24 -70 52, 182 voxels; right: 21 -67 55, 25 voxels] were found symmetrically in the posterior part of the superior parietal lobe, although the smallest cluster on the right side did not survive the cluster threshold correction (167 voxels for a corrected p-value of 0.05). The activations were close to, and extended bilaterally into areas that have been described as human LIP (see next paragraph and Figure 2B) (Corbetta et al., 1998; Sereno et al., 2001; Koyama, Hasegawa, Osada, Adachi, Nakahara & Miyashita, 2004). Another cluster of activation [24 -58 46, 850 voxels] was found in the right hemisphere only, and was situated more anteriorly then the other parietal clusters. This cluster was situated in the posterior part of the intraparietal sulcus (Figure 2C) (Swisher, Halko, Merabet, McMains & Somers, 2007).

ROI analysis

Subsequently we performed a ROI analysis to test the prediction that human LIP, functionally defined as a saccade-related parietal region, is involved in number-sensitive preprocessing. For this purpose, we computed the contrast saccade versus fixation on the images of the localizer run, thresholded at $p < 0.00001$. Within the resulting activation network, we selected in both hemispheres a region which corresponded best with coordinates of human LIP as reported in the literature (Sereno et al., 2001; Simon, Mangin, Cohen, Le Bihan & Dehaene, 2002;

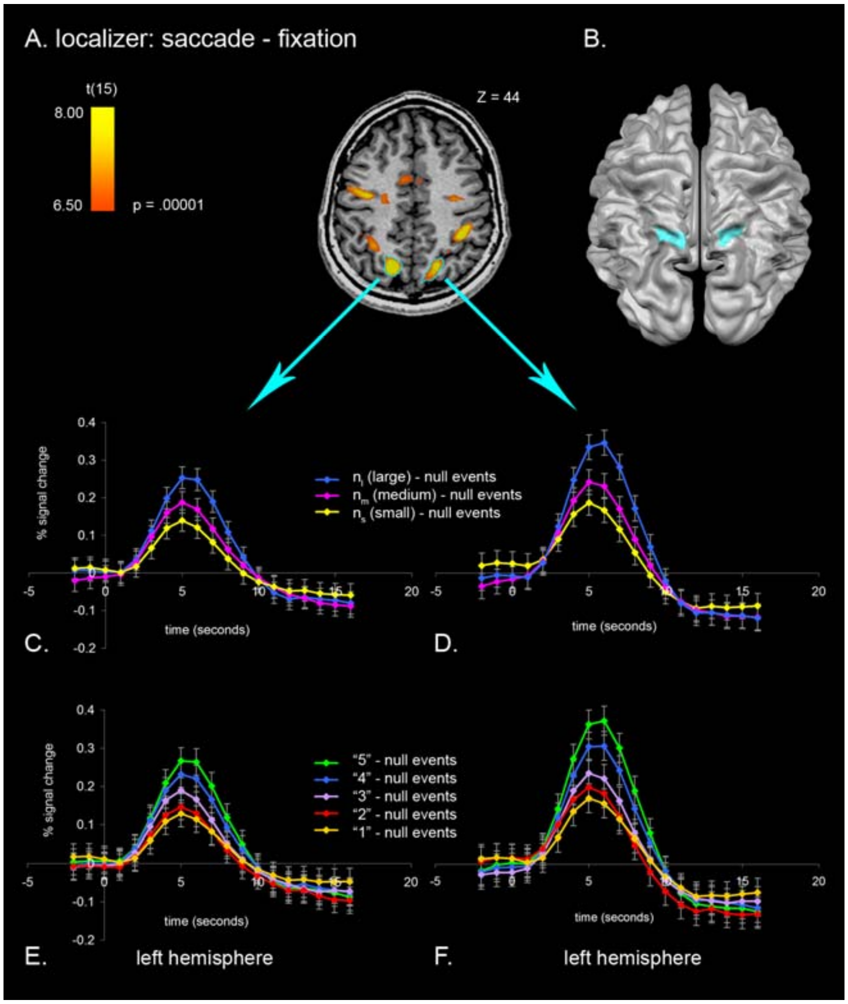
Koyama et al., 2004), which was then defined as a ROI for human LIP, see Figure 3A.

To specify the anatomical location of the ROIs within this specific sample of subjects, we mapped the ROIs to the average cortical surface of all subjects' brains as obtained by the cortex-based alignment algorithm implemented in BrainVoyager QX (see Methods). From Figure 3B it is clear that the ROIs are situated on the medial wall of the intraparietal sulcus. This is consistent with many earlier studies reporting that the saccade region, which is located in the lateral parts of the intraparietal sulcus in the monkey, has shifted to the medial wall in humans (Simon et al., 2002; Grefkes & Fink, 2005; Orban et al., 2006).

The left hemisphere human LIP ROI comprised 1927 voxels and was centered at -16 -64 46; the right hemisphere human LIP ROI comprised 1940 voxels and was centered at 15 -68 44. The ROIs of human LIP were adjacent to the local maxima of the areas found active in the whole brain analysis, but were situated slightly more medial, posterior and inferior. Overall they were very close to each other (mean distance 12 mm, see blue outlines in Figure 2B and C).

Given that the ROIs did not completely overlap with the whole brain activation for the conjunction, it was necessary to test if the ROIs were also number-sensitive. The random effects analysis on the average activation over all voxels in these ROIs showed that the conjunction ($n_l > n_m$) & ($n_m > n_s$) was significant for the ROI in both hemispheres [left: $t(15) = 2.8$, $p = 0.0065$; right: $t(15) = 2.7$, $p = 0.0076$]. Event-related averaging curves (Figure 3 C, D) for the ROI regions illustrate the pattern of increasing activation with increasing numerosity in human LIP, controlled for non-numerical parameters.

Figure 3 (next page): Number-related activation in the ROIs of human LIP as defined by the localizer task. **A.** Random effects analysis of the localizer run: contrast saccade – fixation, thresholded at $p < 0.00001$. ROIs were defined on these saccade activations as the regions which corresponded best with coordinates of human LIP as reported in literature, and are shown in blue outline. **B.** ROIs for human LIP projected on a segmented and inflated average brain after cortical based alignment. This projection clearly shows the position of the ROIs in the medial banks of the intraparietal sulcus. **C&D.** Mean time courses, after subtraction of the time course of the null events (see Methods), of the three stimulus categories, in the left and right hemisphere ROIs of human LIP (cf. Figure 3A). Stimulus categories n_s, n_m, and n_l



corresponded respectively to small, medium and large numerosities, where category n_s could be numerosity 1, 2 or 3, n_m could be numerosity 2, 3, or 4, and n_l could be numerosity 3, 4 or 5 (cf. Figure 1B). **E&F.** Mean time courses, after subtraction of the time course of the null-events (see Methods) of the 5 individual numerosities, in the left and right hemisphere ROIs of human LIP. Note that, although activation due to non-numerical parameters in these same ROIs is excluded for the time courses of the stimulus categories (cf Figure 3C, D), this cannot be excluded for the time courses of the individual numerosities, as the non-numerical parameters were controlled only between categories and individual numerosities could belong to multiple categories.

3.4 Discussion

The present study aimed at detecting number-sensitive preprocessing steps of visual numerosity in the human brain. In recent years, neuroimaging and patient work demonstrated that regions in and around the intraparietal sulcus play a crucial role in number processing (Dehaene, Piazza, Pinel & Cohen, 2003; Dehaene, Molko, Cohen & Wilson, 2004; Nieder & Miller, 2004; Nieder, 2005 for reviews). Whereas previous studies did not distinguish between number-sensitive and number-selective processing (e.g. Cohen Kadosh, Cohen Kadosh, Kaas, Henik & Goebel, 2007; Naccache & Dehaene, 2001b; Pinel, Dehaene, Riviere & LeBihan, 2001) or aimed specifically at detecting number-selective processing (Piazza et al., 2004, 2007), we could now demonstrate that also number-sensitive preprocessing steps are present in the numerical pathway. More specifically, our results show that number-sensitive preprocessing occurs in relatively posterior parts of the intraparietal sulcus, comprising the human homologue of monkey LIP in the medial wall of the intraparietal sulcus. This posterior intraparietal sulcus location of number-sensitive preprocessing proved to be a region complementary to the more anterior parts of the intraparietal sulcus observed in experiments that specifically investigated number-selective coding (Piazza et al., 2004, 2007; see Figure 2C). It might be argued that the dissociation between the posterior areas reported here and the more anterior intraparietal areas reported by Piazza et al. (2004, 2007) is caused by the different range of numbers used in these studies. Nevertheless, this cannot be the only reason for the dissociation, as the barycentre of a meta-analysis of Dehaene et al. (2003), which was based on studies including small and large numbers, was also situated more anteriorly. Moreover, the study of Roitman et al. (2007), which proved the existence of summation coding in monkey LIP, included large numbers, while the studies of Nieder et al. (2002, 2003), which proved the existence of number-sensitive coding in a more anterior area of IPS, included mainly small numbers. In monkey data, the difference is therefore reversed: evidence for large numbers (Roitman et al., 2007) is found more posterior than evidence for small numbers (Nieder et al., 2002; Nieder & Miller, 2003). We therefore conclude that the difference in the coordinates is not driven by the range of numbers, but by the underlying coding system. The anterior intraparietal region is also engaged in symbolic number processing, with the barycentre of the recent meta-analysis located at a Talairach coordinate of -41 along the Y-axis (Dehaene et al., 2003; see Figure 2C; see also Fias, Lammertyn, Caessens & Orban, 2007). This dissociation between the two areas is in line with the idea that symbolic number processing does not involve number-sensitive preprocessing, as evidenced by behavioural experiments (Reynvoet et al., 2002; Roggeman et al., 2007) and suggested by computational modelling (Verguts & Fias, 2004).

Such a posterior to anterior gradient along the intraparietal sulcus from number-sensitive to number-selective processing is consistent with the hypothesis that number-sensitive processing is a necessary intermediate processing step for nonsymbolic number processing between early visual sensory analysis and a more abstract number-selective coding system. This number-sensitive preprocessing of nonsymbolic number was hypothesized to consist of two steps: a topographically organized object location map and a summation coding system that summates the amount of objects. As outlined in the introduction, electrophysiological results in macaque monkeys have shown that relatively posterior parts of the intraparietal sulcus, specifically LIP, are equipped with neurons that are well suited for the task of creating an object location map. The fact that in our study number-sensitive preprocessing comprised human LIP strongly suggests that it is the object location map and the subsequent summation coding system that drives the posterior parietal activations, although the present design does not allow dissociating the two systems. Nevertheless, the hypothesis that the number-sensitive activations observed in human LIP and surrounding regions are at least partly caused by a summation coding system is supported by a recent report of summation neurons in macaques LIP region (Roitman et al., 2007). In this study, half of the number-sensitive neurons in LIP showed a positive linear relationship, while the other half showed a negative relationship between number and firing rate. At first sight, this is incompatible with our findings, as it would seem that the combined activity of the positively and negatively accumulating neurons must cancel each other out, so that activity at the population level would remain invariable with respect to numerosity. With regard to this argument it is interesting to mention that nothing was activated in the reversed contrast of the conjunction, that is, the conjunction of ($n_l < n_m$) & ($n_m < n_s$). It must be kept in mind though that the BOLD signal measured with fMRI does not directly reflect neuronal firing rate. Rather, it reflects metabolic aspects of synaptic activity of the underlying neuronal population (Logothetis, Pauls, Augath, Trinath & Oeltermann, 2001; Heeger & Ress, 2002; Visnawathan & Freeman, 2007; Nir et al., 2007). Because both positively and negatively accumulating neurons receive more input (leading to more synaptic activity) when numerosity increases (e.g., in the Verguts & Fias, 2004 model), it is not surprising that the BOLD signal exhibits a positive correlation with numerosity.

A number of alternative interpretations for the positive correlation between the number of dots and the BOLD signal must be considered. The number-sensitive activation observed in this study could not be due to response selection, since the task was only occasionally and unpredictably inserted after a dot pattern stimulus and was always to choose between two Arabic digits. Moreover, the task was implemented as separately defined task trials and was modelled separately, so number-sensitive activation cannot be confounded with activation due to response selection.

Since we determined human LIP on the basis of saccade-related neural activation, one could argue that the positive relation between number of dots and neural activity in human LIP merely reflects the fact that there was more saccade related processing when subjects were presented with displays containing more dots. Several arguments can be raised against this interpretation. Stimuli were presented for a duration of only 150 ms, which is too short to allow generating even one saccade, let alone a number of saccades as a function of numerosity. Still, one could maintain that not the actual execution of saccades but the mere intention to make a saccade is sufficient to activate human LIP. However, in a recent study, Connolly, Goodale, Menon & Munoz (2002) convincingly demonstrated that human LIP, contrary to the frontal eye fields (FEF), was not activated by saccadic intention alone. Indeed, whereas the FEF were activated during the planning period preceding a saccade, human LIP was only activated when the saccade target appeared and the saccade was actually executed. Similarly, Lee, Wade & Lee (2006) presented several possible saccade target stimuli, varying the number of potential saccade target locations. A positive correlation between the strength of the BOLD response and number of target locations was observed in the intraparietal sulcus only when an actual saccade target was selected and the saccade was effectively executed. Finally, Todd and Marois (2004) found neural activity in the intraparietal sulcus to be correlated with the number of elements in a visual display during encoding and active maintenance in visual short term memory. In a control condition without the need to maintain the visual objects in memory, parietal activity was not modulated by the number of objects displayed. The areas found by Todd and Marois (2004) could be the same area as the ones we found (mean distance between their and our local maxima was 8.7 mm). The task used by these authors would indeed activate an object location map, which may be involved in visuo-spatial working memory. Nevertheless, the Todd and Marois (2004) study does not allow the conclusion that the intraparietal sulcus activation is number-sensitive, since in their study non-numerical physical parameters were not controlled. Together, these studies rule out an interpretation in terms of the number of saccades that is planned for a particular stimulus.

Another possibility is that the numerosity-dependent increase of the BOLD signal is attributable to an increase of the number of covert attention shifts to enumerate the dots. Here it is important to note that the range of numerosities presented was in the subitizing range, which has been shown to be based on parallel, rather than serial processes (Trick & Pylyshyn, 1994; Dehaene & Cohen, 1994; Nan, Knosche & Luo, 2006; Vuilleumier & Rafal, 1999). This clearly refutes an account in terms of attention shifts.

An increase of neural activity as a function of numerosity was not only observed in parietal cortex, but also in occipital cortex. This is not surprising since displays containing more dots are visually more complex, even when intensive and extensive variables such as area, dot size, luminance and interdot spacing are controlled. Interestingly, the visual areas that were modulated by numerosity comprised the lateral occipital complex (LOC). This area plays a pivotal role in object perception and is activated by visual objects, independent of how object information is represented (contours, Kourtzi & Kanwisher, 2001; structure from motion, Grill-Spector et al., 1998). A number of studies have demonstrated the involvement of LOC during the perception of illusory contours (for a review, see Seghier & Vuilleumier, 2006). This suggests that the visual system tries to derive shape by connecting individual visual elements. This is consistent with Murray, Schrater & Kersten (2004) who found higher activation in LOC when visual perception involved grouping of individual elements into a coherent representation. The lingual gyrus, where we also observed a positive correlation between the BOLD signal and numerosity, has also been implied in the perception of illusory contours (Halgren, Mendola, Chong & Dale, 2003). It can therefore be argued that the involvement of lingual gyrus and LOC in our study reflects the mandatory tendency of the visual system to construct visual patterns. Indeed, within our range of low numerosities, the perceptual organization of two dots as a line, three dots as a triangle, and four dots as a quadrangle is quite salient. Importantly, earlier behavioural studies have ruled out the tendency to perceive shapes in visual dot displays as a critical factor for rapid enumeration (subitizing) of visual dot displays (Trick & Pylyshyn, 1994). We therefore conclude that the observed modulation of occipital areas by numerosity is not a critical numerical preprocessing step but is a mere side effect of the way the visual system operates. Importantly, the posterior parietal cortex is not consistently involved in perception of illusory contours (Seghier & Vuilleumier, 2006) nor in grouping of elements (Murray et al., 2004). This implies that the functions of LOC and IPS are dissociable, and that the number-sensitive activations in the IPS region must not be attributed to the complexity of the stimuli.

Beyond activations in the occipito-parietal stream, activation that positively correlated with numerosity was also observed in the pre-SMA. pre-SMA has been observed in other studies involving enumeration (Kansaku, Johnson, Grillon, Garraux, Sadato & Hallett, 2006; Piazza, Mechelli, Price & Butterworth, 2006; Sathian, Simon, Peterson, Patel, Hoffman & Grafton, 1999) or non-symbolic addition (Venkatraman, Ansari & Chee, 2005), although its contribution remained largely undiscussed. Pre-SMA is known to play an important role in the planning of sequentially structured motor plans (for review see Ashe, Lungu, Basford & Lu, 2006) but has also been observed in sequence perception (Schubotz & von Cramon, 2002). Both in motor planning and in perceptual sequence observation, pre-SMA has been observed to activate in relation to the length and complexity of the sequence (Boecker et al., 1998, Schubotz & von Cramon, 2002). Single cell electrophysiology has shown that a subset of neurons in this area selectively responds to ordinal sequence position (Isoda & Tanji, 2004; Shima & Tanji, 2000; Clower & Alexander, 1998). This property of pre-SMA neurons can explain the positive relation between number of elements of the sequence and the BOLD signal, since longer sequences cause more position-specific neurons to become activated. Although there is an obvious conceptual link between the processing of sequential information and enumeration (Nieder, 2005), it is not clear how sequential motor planning or perception can have contributed to the numerosity-dependent increase of pre-SMA activation in our study. First, the collections of dots were not presented sequentially but simultaneously. Second, the collections of dots were presented for such a brief duration (150 ms) that sequential scanning is prevented. And third, there was no overt response; hence no response selection or motor execution was required. One possibility is that during enumeration of a collection of dots, an implicit sequential motor program (possibly related to finger counting) is triggered without being overtly executed. Whatever the reason for pre-SMA activation, it is safe to assume that pre-SMA does not reflect the type of number-sensitive preprocessing that is required to convert visual numerosity into a number-selective coding system because it is not located in the occipito-parietal stream of visual information. It is more likely that pre-SMA receives numerical information that has been computed at earlier stages of the cortical hierarchy (see also Nieder, 2005, for a similar argument). The precise reasons for its involvement remain to be found out.

3.5 Conclusion

Many earlier studies have pinpointed the locus of numerical processing abilities to regions in and around the intraparietal sulcus. These studies did not distinguish number-sensitive from number-selective processing or were only concerned with number-selective processing. Number-sensitive preprocessing steps, which have been shown by computational modelling studies to be necessary to achieve a number-selective coding system, has not yet been observed directly. The present study was designed to close this gap. Evidence for number-sensitive preprocessing was found in the intraparietal sulcus, in areas posterior to the areas usually activated by a number-selective coding system. This is consistent with recent single-cell recording data of number-sensitive processing in the homologue area in the monkey brain (Roitman et al., 2007). Taken together, these results are consistent with the notion of intermediate number-sensitive preprocessing steps in the numerical pathway leading up to a number-selective coding system.

Chapter 4:

Priming reveals no evidence for summation coding of large non-symbolic quantities

Chantal Roggeman, Tom Verguts & Wim Fias

The implementation of a numerical representation in a neural code can be achieved in different ways. A fundamental distinction is whether the neural code is implemented by place coding or summation coding. Previous research has found evidence for both types of coding in the range of small numbers (1 to 5). Evidence for place coding using larger numbers has also been found. In the present study, we aimed at exploring evidence for a summation coding system for larger numbers. We conducted a primed naming study, using dot patterns of numerosities 2 to 64. Numerical distance between prime and target was manipulated. We could not find any evidence for summation coding for larger numbers.

4.1 Introduction

The ability of human adults to understand and work with numerical information is often thought of as one of the principal accomplishments of humanity. Nevertheless, the ability to process numerical quantities presented in non-symbolic format is shared with many animal species (Dehaene, Dehaene-Lambertz & Cohen, 1998; Feigenson, Dehaene & Spelke, 2004; Feigenson, Carey & Hauser, 2002; Whalen, Gallistel & Gelman, 1999; Cantlon & Brannon, 2006). Furthermore, we seem to share a similar underlying representational format for this non-symbolic numerical information, since many similar properties emerge when humans and animals are engaged in numerical tasks (Dehaene et al., 1998; Whalen et al., 1999; Cantlon & Brannon, 2006; Roitman, Brannon & Platt, 2007; Roggeman, Verguts & Fias, submitted). Despite this, the neural code of this shared system is not yet fully understood. Theoretical modelling has provided two plausible alternatives for the coding of quantity-responsive neurons: place coding and summation coding.

Place coding points to the idea that a neuron has a preferred quantity to which it responds most strongly. The neural response decreases as a function of the numerical distance between this preferred quantity and the presented quantity. Recent neuroscientific research has provided evidence for the existence of this type of neurons, both in monkeys (Nieder, Freedman & Miller, 2002; Nieder & Miller, 2004) and in humans (Piazza, Izard, Pinel, LeBihan & Dehaene, 2004; Piazza, Pinel & Dehaene, 2007; Cantlon, Brannon, Carter & Pelphrey, 2006). Behavioural evidence for the existence of this type of coding can be found in priming studies (Reynvoet & Brysbaert, 1999, 2004; Reynvoet, Brysbaert & Fias, 2002). In these studies, two numerical stimuli (prime and target) are presented successively, but only the second stimulus (the target) has to be named. By varying the numerical distance between the prime and target stimulus, the influence of the prime is investigated. The observed priming effects are distance-dependent, which means that the target is named faster when the numerical distance between the prime and the target is small. This provides evidence for an underlying place coding system. Indeed, when the prime activates a number in a place coding representation, neurons selective for numbers close to the prime number will also be somewhat pre-activated by the prime, thereby facilitating the naming of a subsequent numerically close target.

An alternative way to code quantities among a population of quantity neurons is referred to as summation coding (Zorzi & Butterworth, 1999; Meck & Church, 1983; Gallistel & Gelman, 1992, 2000). In this coding scheme, the coding is analogous to the number it represents. This can be implemented by neurons that respond monotonically to number (e.g., more strongly for larger numbers). This implies that the specific activation pattern for a smaller number is always included in the activation pattern of a larger number. Recently, neuroscientific research has also provided evidence for this type of coding, both in monkeys, by means of single cell recordings (Roitman et al., 2007) and in humans, by means of fMRI (Roggeman et al., submitted). Furthermore, behavioural evidence for this type of coding has recently been found in a priming study using non-symbolic stimuli (Roggeman, Verguts & Fias, 2007). In this study, both prime and target where presented as dot patterns or numerical symbols (Arabic digits). When primes were dot patterns, it was found that the target number was named faster whenever the prime numerosity was larger than or equal to the target. This provides evidence for an underlying summation coding system, since a larger prime numerosity will then pre-activate all smaller numerosities as well, hence facilitating the naming of all subsequent smaller targets.

Summation coding has also been pointed out by computational modelling studies as a necessary preceding step to obtain a place coding system (Verguts & Fias, 2004; Dehaene & Changeux, 1993). Importantly, it should be noted that these results were confined to small numbers only (1 to 5, or roughly the subitizing range). Empirical studies providing evidence for the existence of summation coding in humans were also restricted to small numbers (Roggeman et al., 2007, submitted; though see Roitman et al., 2007, for evidence of summation coding with larger numbers in monkeys). It is therefore tempting to speculate whether summation coding would also be plausible in human processing of larger numbers. This is the issue of the present study.

We adopted the priming method employed by Roggeman et al. (2007) that clearly demonstrated summation coding with numbers 1 to 5. We used the same method, but used dot patterns of numerosities in the range 2-64.

4.2 Experiment 1

4.2.1 Materials & Methods

Participants

Participants were 10 students from Ghent University (all female) who participated for course credits. All students gave informed consent prior to the experiment. Average age was 18.6 ± 0.5 years. Two participants were left-handed.

Apparatus

Stimuli were presented on a 17 inch color screen (resolution 1024 × 768; refresh rate 70 Hz), connected to a Pentium 4 computer, running under Windows XP. Reaction times (RTs) were measured with a voice key connected to the game port. Timing routines used the method described by MacInnes and Taylor (2001).

Stimuli

Stimuli were dot patterns containing 2, 4, 8, 16, 32 or 64 dots. In earlier studies it has been shown that participants underestimate numerosities by up to 50% when estimating larger numerosities (Mandler & Shebo, 1982; Lorinstein & Haber, 1975; Minturn & Reese, 1951; Krueger, 1982, 1984; Izard & Dehaene, 2008). We therefore choose numerosities which differed from each other by a factor 2 in order to allow reliable naming of the presented numerosities by the participants.

Dots were presented in white against a black background, and were randomly positioned within a visual circle of 11.2 deg. Non-numerical cues were controlled between the dot patterns for the prime and for the target of a single trial. Four different prime-target control types were used. In the first control condition, individual dot size and total area spanned (size of the pattern as a whole) was kept constant, so that for a smaller number of dots, the dots were situated further apart. In the second control condition, individual dot size was constant, and the distance between two adjacent dots was constant. In the third control condition, the accumulated area of all dots (total luminance) was kept constant, so that for a larger number of dots, the dots were smaller; and the total area spanned was constant. In the fourth control condition, the total luminance and the distance between two adjacent dots were held constant. All control conditions were randomly intermixed.

Procedure

Before the start of the experiment, participants were trained until they could reliably discriminate and name the number of the dot patterns. In a training block, each numerosity was presented 4 times, yielding training blocks of 24 trials. Participants completed at least 2 training blocks, and had to reach a performance of 95% before they were allowed to continue with the main experiment. A trial in the training phase consisted of the same screens as in the main experiment (see below), with the exception that no prime was shown. Feedback was given after every trial, and at the end of each training block.

In the main experiment, prime and target were both dot patterns. There were 6 × 6 = 36 possible combinations of prime – target value. Each combination was presented 16 times (4 times in each control condition). This yielded a total of 576 trials, divided in 8 blocks of 72 trials each, separated by a brief pause. All combinations and control conditions were randomly presented.

A small red fixation cross remained always in the middle of the screen. Each trial began with the presentation of the fixation cross for 500 ms. Then the prime was presented for 82 ms, so that the prime was clearly visible but participants had not sufficient time to react to it. The prime was followed by a backward mask for 49 ms. Masks consisted of a pattern of random lines which filled a square of 11.2 deg. Twenty different mask patterns were generated and for each trial one of these patterns was randomly chosen, with the restriction that the same mask could not be used in two consecutive trials. Finally, the target was presented for 149 ms, after which participants named aloud the perceived quantity. Either when the voice key was triggered or 2000 ms elapsed without an answer having been recorded, the response was recorded by the experimenter, who also noted whether the time registration had been successful. Feedback was only presented at the end of each block.

4.2.2 Results

Training phase

Participants required on average 6 training blocks (minimum: 2, one participant; maximum: 8, three participants) to reach a performance level of 95%. Performance in the first blocks was on average 81.7 ± 11.8% (range: 66.7% -

95.8%), while performance in the last blocks was on average 96.3 ± 2.4% (range: 95.8% - 100.0%).

Error data

0.43% of trials were discarded due to equipment failure (timing errors). Participants made 15.6% naming errors, mainly due to mislabeling of numerosities 32 and 64 (12.2%). A logistic regression was performed for each participant separately (Lorch & Myers, 1990) with accuracy (0/1) as the dependent variable and control condition, prime value and target value as independent variables. The parameter estimate of each factor was then tested over all participants with a t-test against zero. There was a significant effect of target value [percentage of errors was 0.65%, 0.65%, 6.28%, 12.88%, 23.59% and 49.03% for target 2, 4, 8, 16, 32 and 64 respectively, mean estimate -1.04 ± 0.34, $t(9) = -9.76$, $p < 0.00001$, 2-tailed] and a significant effect of prime value [percentage of errors was 14.94%, 11.69%, 14.29%, 16.88%, 15.26% and 20.02% for prime 2, 4, 8, 16, 32 and 64 respectively, mean estimate -0.12 ± 0.14, $t(9) = -2.72$, $p = 0.023$, 2-tailed]. There was also a main effect of control condition: participants made significantly more errors in the first control condition (constant individual dot size and constant area spanned) then in the fourth control condition (constant total luminance and constant distance between dots) [number of errors was 17.97%, 15.73%, 15.30% and 13.06% for control condition 1, 2, 3 and 4 respectively, comparison between control condition 1 and control condition 4: mean estimate -0.52 ± 0.61, $t(9) = -2.70$, $p = 0.024$, 2-tailed. No other comparison between control conditions reached significance]. The effects of prime and control condition are illustrated in Figure 1, where the number of errors over all target values was plotted as a function of prime value, for the 4 control conditions.

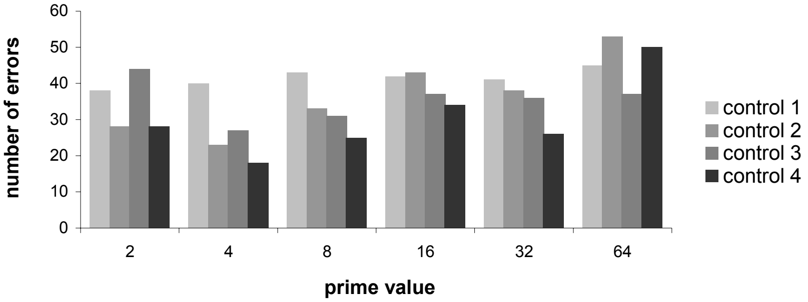


Figure 1. Number of errors made **for** all targets, as a function of prime value and control condition.

Average response

In order to explore the pattern of errors, we calculated the average response, for each combination of control condition, prime value and target value. For this analysis, we used the logarithm for prime and target values, in order to avoid distortions from the unequal distance between adjacent prime values and target values. A 4 (control condition) × 6 (log(prime value)) × 6 (log(target value)) repeated measures ANOVA was performed. There was a significant main effect of control condition [average response: 17.1, 17.6, 18.4 and 19.5 for control condition 1, 2, 3 and 4 respectively; $F(3, 24) = 9.07$, $MSE = 0.04$, $p = 0.0003$] and a significant main effect of target value [average response: 2.20, 4.02, 8.38, 16.58, 30.098 and 47.64 for target value 2, 4, 8, 16, 32 and 64 respectively; $F(5, 40) = 5100.8$, $MSE = 0.12$, $p < 0.00001$]. Note that the average response for target 64 is only 47.64, indicating the large number of errors (usually 32 instead of 64) participants made in naming this numerosity. More interestingly, there was also a significant main effect of prime value [average response: 19.45, 19.08, 18.08, 17.43, 17.55 and 17.34 for prime values 2, 4, 8, 16, 32 and 64 respectively; $F(5, 40) = 5.25$, $MSE = 0.06$, $p = 0.0008$; see Figure 2]. This means that participants made a different type of errors dependent on the prime. As can be seen in Figure 2, this priming pattern was the same for all target values: a decrease of average response as prime value increases. Closer inspection revealed that participants were more likely to make an overestimation when the prime value was small, and were more likely to make an underestimation if the prime value was large. There was a significant target value × prime value interaction [F(25, 200) = 3.05, MSE = 0.03, $p < 0.00001$] that was due to the fact that the priming effect was only present for larger target values, as almost no errors were made for smaller target values. In sum, no specific prime – target modulation was obtained. Put differently: small and large primes had the same influence on target naming, independent of the distance between prime and target.

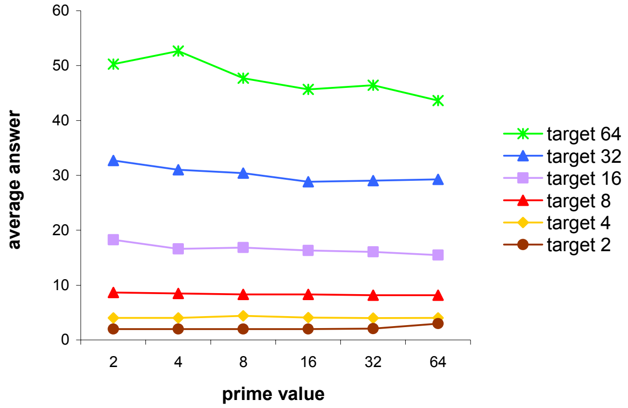


Figure 2. Average response for each target, as a function of prime value, collapsed over control conditions.

Because the effect of average response is determined by the type of errors made, and because most errors were made for the largest target values and almost none were made for the smallest target values, all effects of average response disappeared for the smallest target values, yielding all interactions with target value significant [target value × control condition: F(15, 120) = 6.12, MSE = 0.04, $p < 0.00001$, see Figure 2; control condition × target value × prime value: F(75, 600) = 1.31, MSE = 0.03, $p = 0.046$]. Finally, the interaction between prime value and control condition was also significant [F(15, 120) = 2.37, MSE = 0.04, $p = 0.005$], indicating that the effect of the control condition was annihilated, or even reversed, for larger prime values (see Figure 1).

Reaction times

One participant was excluded from the RT analysis because she did not complete the whole experiment. The RT analysis for the other participants was performed on the correct responses only. Another 8.8% of trials were discarded due to technical failure of the voice key, and RTs below 200 ms or above 2000 ms were also discarded from analysis (0.13%). We could not perform a general ANOVA analysis, due to the large number of errors made for target 64, which resulted in too many missing data points for this target value. We therefore fitted regression equations with control condition, prime value and target value as predictors. All predictors were mean centered at zero. In addition, we included a prime × target predictor in order to test for the prime × target interaction. The regression was run for each participant separately (Lorch & Myers, 1990). The contribution of each factor was then tested with a t-test against zero.

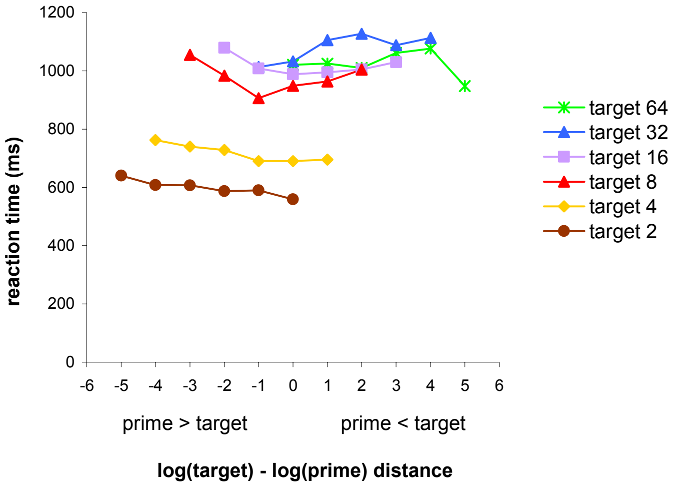


Figure 3. Reaction time for each target, as a function of prime value, collapsed over control conditions.

This analysis revealed a significant contribution of target value [598 ms, 713 ms, 952 ms, 995 ms, 1076 ms and 1020 ms for targets 2, 4, 8, 16, 32 and 64 respectively; t(8) = 9.82, p = 0.00001, 2-tailed] but not of prime value [882 ms, 889 ms, 890 ms, 881 ms, 890 ms and 922 ms for prime 2, 4, 8, 16, 32 and 64 respectively; t(8) = 1.99, p = 0.08, 2-tailed]. There was no significant contribution of control condition [879 ms, 889 ms, 888 ms, 889 ms for control condition 1, 2, 3 and 4 respectively; t(8) = 0.24, p = 0.81, 2-tailed]. There was a significant interaction between prime and target value [t(8) = -3.48, p = 0.008, 2-tailed], which is probably due to the noisy data for higher target values (see Figure 3, RTs collapsed over the four control conditions).

In order to analyze specific priming patterns in the data, we fitted regression equations with two predictors that coded for a step-function and a V-shape function, as reported earlier (Roggeman et al., 2007). The step-function predictor had a coefficient equal to -1 if prime value ≥ target value and a coefficient +1 if prime value < target value. The V-shape function predictor had coefficients equal to |log(target value) – log(prime value)|, and the regression was limited to data points were this predictor was smaller or equal to 4 in order to eliminate distortions from the low number of data points for the most distant prime - target combinations. The logarithm of the target value was also included in the regression to remove distortions from a size effect, and an intercept was also included. The regression was run for each participant separately (Lorch & Myers, 1990), and the regression coefficients for all participants were tested against zero. There was a significant contribution of size [t(8) = 9.38, p = 0.00001, 2-tailed]. None of the shape predictors were significant [step-function: t(8) = 0.61, p = 0.56, 2-tailed; V-shape: t(8) = 2.21, p = 0.06, 2-tailed].

4.2.3 Discussion

We did not find a distance related or prime specific effect on errors or on RTs. It may be surprising that we did not find an effect even for prime value and target value 2 and 4 given that we did find an effect for these numbers in our previous study. A possible explanation is that this effect disappeared because of the overall larger reaction times found in the present study.

A possible explanation for the general failure could be that the prime duration was too short. Whereas in the former study (Roggeman et al., 2007) we did find an effect with this prime duration, it should be noted that the numerosities used in that study were in the subitizing range, and it is well established that the naming of a numerosity is much faster in this range (Kaufmann, Lord, Reese & Volkman, 1949; Mandler & Shebo, 1982; Balakrishnan & Ashby, 1991, 1992; Trick & Pylyshyn, 1993, 1994). Hence, it could be that the short prime duration was not enough to evoke a sense of numerosity for the larger numbers used in this study. This possibility will be investigated in Experiment 2, where we repeated the study with longer prime and target durations.

Although we did not find a specific priming effect, a number of interesting conclusions can be drawn from the pattern of errors subjects made in this task. The training phase indicated that participants needed quite extensive training in order to reliably name dot patterns with numerosities 2, 4, 8, 16, 32 and 64 dots, and even then participants made on average as many as 50% errors on naming dot patterns of 64 dots in the main experiment. This is not in accordance with a number of studies which calculated Weber fractions around 0.2 for human discrimination of dot patterns (e.g. Izard & Dehaene, 2008, calculated a Weber fraction of 0.22 for the estimation of dot patterns, Piazza et al., 2004, found a Weber fraction of 0.17 for comparison of dot patterns, van Oeffelen & Vos, 1982, estimated a Weber fraction of 0.163 for the identification of a target numerosity (yes/no) each time it appeared in a series amongst a number of known possibilities). Van Oeffelen and Vos (1982) defined the Weber fraction as the 50% correct discrimination between the 2 stimuli. Based on the Weber fractions mentioned in literature therefore, participants should have no difficulty in discriminating 64 dots from 32 dots. Furthermore, in our results, participants made very few errors for the lower numerosities, and an increasing number of errors for higher numerosities, despite the fact that the ratio between adjacent numerosities remained the same. This is not in accordance with the very definition of a Weber fraction (Stevens, 1957, 1961). This definition states that the minimal numerical change that can be discriminated increases in direct proportion of the magnitude of the involved numerosities. Put differently, the definition intrinsically states that the numerosity discrimination only depends on the ratio, and not on the absolute value (Dehaene, 2007). This could perhaps be explained by the use of the enumeration task, which differs from the comparison task used in most discrimination experiments (although see Izard & Dehaene, 2008; van Oeffelen & Vos, 1982). Another possibility is that the small numerosities 2 and 4 were enumerated by a different mechanism; such as an object file system (Feigenson et al., 2002, 2004; Xu, 2003) which is characterized by a set size limit instead of a Weber ratio signature and which could explain the more reliable naming of the small numbers. Still, a Weber fraction signature should then be found for the larger numbers from numerosity 8 onwards, which was not the case.

Most errors in our study were underestimations. This is in line with previous data (Mandler & Shebo, 1982; Lorinstein & Haber, 1975; Minturn & Reese, 1951; Krueger, 1982, 1984; Izard & Dehaene, 2008). Izard & Dehaene (2008) argued that this underestimation is due to a miscalibration of the internal representation of numerosities. In their experiments, they provided subjects with a dot pattern of a known numerosity before proceeding with the experiment. They found that this calibration step was enough to make subjects quite accurate in an estimation task. It is therefore striking that our participants continued to underestimate the presented numerosities, since calibration was abundantly provided in the training phase by means of direct feedback after every trial.

The pattern of errors in the different control conditions is also interesting. This pattern was especially striking with larger target values (most errors made) which where preceded by small prime values. In these cases, participants made more errors in control condition 1, and less in control condition 4 (see Figure 1). This finding can be readily explained. Recall that in the first control condition, the individual dot size was constant between prime and target display, and the total area spanned of the pattern was kept constant. This means that, in the case of a small prime and a large target, these target numerosities were rather large dots, which were very close together (since they had to fit in the same total area spanned as the previous few dots of the small prime numerosity). Here we thus find that a smaller distance between the individual dots leads to more severe underestimations (Allik & Tuulmets, 1991; Vos, van Oeffelen, Tibosch & Allik, 1988; Hollingsworth, Simmons, Coates & Cross, 1991). In the fourth control condition, the total luminance and the distance between two adjacent dots were kept constant between prime and target display. This means that, again in the case of a small prime and a large target, these target patterns consisted of very small dots, since the total luminance of the large target numerosity had to be the same as the total luminance of the small prime numerosity, which were well spread apart. These findings are therefore in line with previous findings (Allik, Tuulmets & Vos, 1991; Vos et al., 1988; Ginsburg, 1978). In control conditions 2 and 3, dots were respectively rather large but widely spaced apart, or close together but very small. These two conditions had therefore the same ratios of non-numerical parameters, but control condition 3 can be seen as a scaled version of condition 2. It is therefore not surprising that we did not find a difference between these two conditions. Indeed, Allik et al. (1991) found that scaling of displays did not interact with numerosity processing, as long as all dimensions of the display are scaled with the same factor. Note also that, as the prime increased, the non-numerical parameters of a dot pattern for a large target value had to be less extreme to fit into the desired control, hence the effect of control condition diminished, and tended to even reverse, as the prime increases (see Figure 1).

A last finding in the error data is that the type of mistakes made by participants depended on the prime. Subjects were more inclined to make an overestimation when the prime value was small, while the reverse was true when prime value was large. This indicates that participants viewed the prime pattern, but tended to overcompensate when estimating the subsequent target. This overcompensation was a general effect of prime value, but was not dependent on the specific relation between the current prime and target value, hence indicated no specific prime-target effect.

4.3 Experiment 2

4.3.1 Materials & Methods

Participants

Participants were 13 students from Ghent University (all female) who participated for course credits. All students gave informed consent prior to the experiment. Average age was 19.4 ± 1.4 years. Two participants were left-handed.

Apparatus

The apparatus was the same as in Experiment 1.

Stimuli

Stimuli were dot patterns containing 4, 8, 16, 32 or 64 dots. The dot patterns were made and controlled in the same way as in Experiment 1. We omitted numerosity 2 to allow more repetitions of the other numerosities.

Procedure

The training phase in this experiment consisted of training blocks of 20 trials, in which each numerosity was presented 4 times. Participants again completed at least 2 training blocks, and had to reach a performance of 95% before they were allowed to continue with the main experiment. A trial in this training phase was the same as in the first experiment except that the numerosity was presented for 298 ms. Feedback was given after every trial, and at the end of each training block.

The main experiment was also the same as in the first experiment, with the exception that the prime was presented for 149 ms and the target was presented for 298 ms. Mask presentation was 49 ms. There were 5 × 5 = 25 possible combinations of prime – target value. Each combination was presented 24 times (6 times in each control condition). This yielded a total of 600 trials, divided in 8 blocks of 75 trials each, separated by a brief pause. All trials were randomly presented.

4.3.2 Results

Training phase

One participant did not reach a performance level of 95% after 12 training blocks, and was excluded from further analysis. Participants needed on average six training blocks (minimum: 5, five participants; maximum: 9, one participant) to reach a performance level of 95%. Performance in the first blocks was on average 80.0 ± 12.1% (range: 60.0% - 100.0%), while performance in the last blocks was on average 96.7 ± 2.5% (range: 95.0% - 100.0%).

Error data

0.54% of trails were discarded because of incorrect timing. Participants made 15.1% errors, of which 9.3% was due to a mislabeling of numerosity 64 and another 3.0% was due to a mislabeling of numerosity 32.

A logistic regression was again performed for each participant separately (Lorch & Myers, 1990) with accuracy (0/1) as the dependent variable and control condition, prime value and target value as independent variables. The contribution of each estimate was then tested over participants with a t-test against zero. There was a significant effect of target value [percentage of errors was 0.14%, 5.63%, 8.82%, 15.00% and 46.11% for target 4, 8, 16, 32 and 64 respectively; mean estimate -1.31 ± 0.65, t(11) = -6.94, p = 0.00003, 2-tailed] and a significant effect of prime value [percentage of errors was 13.06%, 13.89%, 15.83%, 15.90% and 17.01% for prime 4, 8, 16, 32 and 64 respectively; mean estimate -0.11 ± 0.17, t(11) = -2.33, p = 0.040, 2-tailed]. There were also main effects of control condition: participants made significantly less errors in the fourth control condition compared to all other control conditions [number of errors was 17.39%, 16.50%, 14.94% and 11.72% for control condition 1, 2, 3 and 4 respectively; comparison against control condition 4 for control condition 1, 2 and 3 respectively: mean estimate -0.59 ± 0.38, t(11) = -5.34, p = 0.0002; mean estimate -0.53 ± 0.26, t(11) = -7.21, p = 0.00002 and mean estimate -0.36 ± 0.33, t(11) = -3.70, p = 0.004; all t-tests 2-tailed. No other comparison between control conditions reached significance, see Figure 4].

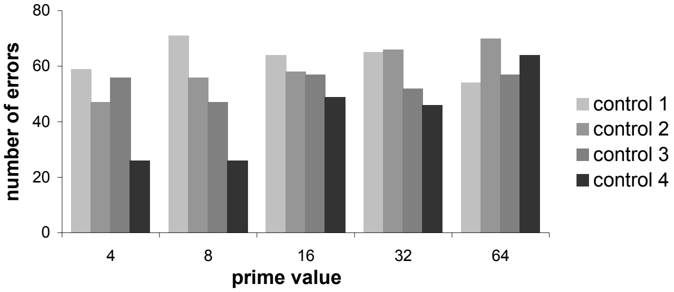


Figure 4. Number of errors made for all targets, as a function of prime value and control condition.

Average response

The pattern of errors was again explored with an analysis over the average response for each combination of control condition, prime value and target value. As in Experiment 1, we used the logarithm for prime and target values. A 4 (control condition) × 5 (log(prime value)) × 5 (log(target value)) repeated measures ANOVA was performed. There was a significant main effect of target value [average response: 4.01, 8.70, 16.80, 29.91 and 49.08 for target value 4, 8, 16, 32 and 64 respectively; $F(4, 44) = 3851.3$, $MSE = 0.12$, $p < 0.00001$] and a significant main effect of control condition [average response: 20.8, 21.4, 22.0 and 22.6 for control condition 1, 2, 3 and 4 respectively; $F(3, 33) = 10.95$, $MSE = 0.042$, $p = 0.00004$]. There was also a significant main effect of prime value [average response: 21.6, 21.8, 21.5, 21.2 and 21.3 for prime values 4, 8, 16, 32 and 64 respectively; $F(4, 44) = 8.76$, $MSE = 0.02$, $p = 0.00003$, see Figure 5].

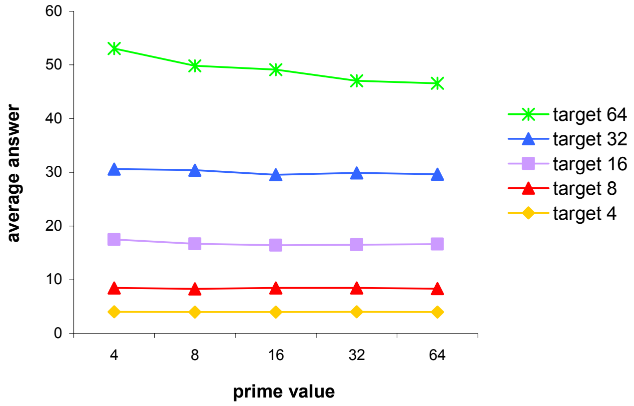


Figure 5. Average response for each target, as a function of prime value, collapsed over control conditions.

Nevertheless, the trend which was noticed in the first experiment for all larger numerosities (more underestimations for increasing prime value), was in this experiment present only for numerosity 64, yielding a target value × prime value interaction [$F(16, 176) = 3.0$, $MSE = 0.02$, $p = 0.0002$]. The number of times that numerosity 64 was erroneous labeled as 32 was 97, 126, 132, 148 and

152 times for prime values 4, 8, 16, 32 and 64 respectively. Moreover, in this experiment, almost all errors were underestimations (12.6% of 15.1% errors); whereas in the first experiment we found a tendency to make overestimations when prime value was small. All other interactions were also significant [control condition × prime: F(12, 132) = 4.64, MSE = 0.02, $p < 0.00001$; control condition × target: F(12, 132) = 6.48, MSE = 0.02, $p < 0.00001$; control condition × prime × target: F(48, 528) = 1.75, MSE = 0.02, $p = 0.002$].

Reaction times

The analysis of RTs included only RTs from correct trials. 15.2% of trials were excluded due to errors, and another 10.4% of trials were excluded due to incorrect working of the voice key. Finally, RTs below 200 ms and above 2000 ms were also excluded (0.57%). We fitted regression equations with control condition, prime value and target value as predictors for each participant separately (Lorch & Myers, 1990). All predictors were mean centered at zero. In addition, we included a predictor as prime value × target value, in order to test

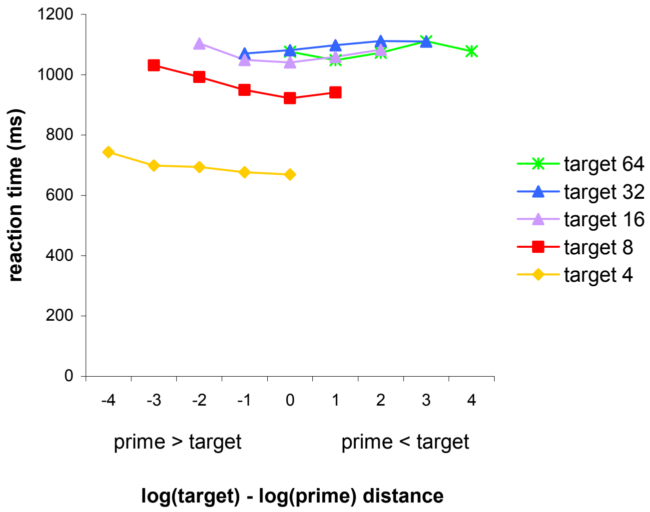


Figure 6. Reaction time for each target, as a function of prime value, collapsed over control conditions.

for an interaction between these two predictors. The significant contribution of each factor was then tested with a t-test against zero. There was no significant contribution of control condition [992 ms, 974 ms, 968 ms and 984 ms for control condition 1, 2, 3 and 4 respectively, t(11) = -1.55, p = 0.15, 2-tailed]. There was a significant contribution of target value [694 ms, 963 ms, 1063 ms, 1090 ms and 1075 ms for target values 4, 8, 16, 32 and 64 respectively, t(11) = 11.78, p < 0.00001, 2-tailed] and a significant contribution of prime value [975 ms, 975 ms, 971 ms, 974 ms and 1005 ms for prime value 4, 8, 16, 32 and 64 respectively, t(11) = 2.45, p = 0.03, 2-tailed]. There was no significant target value × prime value interaction [t(11) = -2.08, p = 0.06, 2-tailed, see Figure 6].

The shapes of the priming curves were again explored by a regression with a step-function predictor and a V-shape function predictor. The regression was run for each participant separately (Lorch & Myers, 1990), and the regression coefficients for all participants were tested against zero. Again, there was a significant contribution of size [t(11) = 9.09, p < 0.00001, 2-tailed]. The contribution of the step-function predictor was not significant [t(11) = 0.13, p = 0.89, 2-tailed], but the contribution of the V-shape function predictor was [t(11) = 3.28, p = 0.007, 2-tailed]. Some of the curves in the graph indeed show a flat V-shape, although not prominent (see Figure 6). Nevertheless, when we fitted the same regression on the data without logarithmic transformation of prime and target, we found the reverse pattern [step-function: t(11) = 5.37, p = 0.0002, 2-tailed; V-shape: t(11) = -0.50, p = 0.63, 2-tailed]. Since the shape of the priming curve for each target remains the same, but only the mutual relation changes by logarithmic transformation of the data, this is an indication that the finding of significant contribution of the shape-predictors is in this instance due to noise.

4.3.3 Discussion

Despite the longer prime and target durations, we again failed to find a specific priming effect on error data or on reaction times.

The patterns of errors subjects made in this experiment replicated almost all effects of Experiment 1. The substantial amount of training needed by participants again showed that it is not self-evident to reliable name numerosities which differ by a ratio of 2 (Weber fraction 0.5). Again, participants made more mistakes as target value increases, although the ratio between adjacent numbers remained the same. The tendency to underestimate numerosities was even more prominent then in Experiment 1. We also replicated the same pattern of errors with respect to the four control conditions.

The tendency to overestimate the numerosity of a target following a small prime value was not present in these data. This indicates that the effect of overcompensation is not evident with a longer prime duration.

4.4 General discussion

The present study was designed to test whether summation coding would also be found when participants are presented with larger numerosities. We could not find any evidence for this. In a previous study (Roggeman et al., 2007), evidence for summation coding has been found for non-symbolic numerosities, for numbers 1 to 5, by using the same method as employed in this study. Given this, two possibilities for the present failure can be adopted: the present method was not suitable to detect summation coding for larger numerosities, or there is no summation coding for larger numbers.

A reason why it is plausible that summation coding is not detectable with larger numerosities comes from the very models which predicted its presence in the small numerosity range. It is noteworthy that the computational modelling studies which point to summation coding as a necessary preprocessing step in the numerical pathway (Verguts & Fias, 2004; Dehaene & Changeux, 1993), are both concerned with small numbers (subitizing range) only. To find out how the models behave with larger numerosities is therefore difficult. The model of Verguts and Fias (2004) for example, takes as input an object location map, in which each object is represented by one node, regardless of its physical appearance. It is conceivable that each node in this map is activated with a certain level of noise, and hence that the total noise in the map increases with the number of activated nodes, and thus with increasing numerosity. This supposition could explain why the number of errors increased with increasing numerosity, despite the constant ratio between adjacent numerosities. In this view then, summation coding might still be engaged in the processing of larger numerosities, but it might be too noisy to be picked up by the priming technique. This might explain why summation coding was nevertheless found for larger numerosities in monkeys using single cell recording, as this method is more sensitive by nature (Roitman et al., 2007).

An alternative possibility is that there simply is no summation coding for larger numbers. Increasing noise in the system might give rise to a capacity limit, which renders summation coding as such inadequate for larger numerosities. This implies that there is a fundamental difference between the processing of small and large numerosities. This is in line with Feigenson et al. (2002, 2004) and Xu (2003), who also proposed distinct representations for small and large numbers; namely an object file system for a small number of objects and an approximate analogue representation for large numbers. This is also in line with the general idea that small numerosities are 'subitized', whereas larger numerosities are counted or, in case insufficient time is available for the counting procedure, estimated. In this sense, the capacity limit of summation coding could be an explanation of the subitizing limit.

If there are different processing mechanisms for small and large numbers, how are these then compatible with the data of our priming experiments? In particular, how is the summation coding system, which has been shown for small numbers (Roggeman et al., 2007, submitted) compatible with the subitizing and/or the objects file mechanism proposed for enumerating small numbers? Subitizing is the fast and effortless process which enables participants to immediately perceive the number of items in a visual display, and is usually thought to be limited at around 4 items (Kaufmann et al., 1949; Klahr, 1973). A theory proposed by Trick and Pylyshyn (1993, 1994) suggests that subitizing requires two stages. The first stage is a parallel, pre-attentive individuation stage. In this stage, the items are individuated on the basis of their pop-out characteristics from the background. The second stage is number recognition, or the choice of a numeric response. In our framework, the pre-attentive individuation stage could correspond with the formation of the object location map (Verguts & Fias, 2004). In this map, the objects are individuated regardless of their size and identity, as being 'one'. The formation of the object location map could also be interpreted as a part of the object file mechanism, as the 'spatial location' part of the information in the object file. Once the objects are individuated and localized and the object location map is generated, summation coding follows naturally and yields a total activation proportional to the total number of objects in a subsequent summation coding map (Verguts & Fias, 2004). The output of this summation map is then propagated to the number field, where a numerical label is assigned. This could correspond to the second step of the subitizing process in the theory of Trick and Pylyshyn (1993, 1994).

How is this subitizing framework compatible with the priming data found in the small number range (Roggeman et al., 2007)? .It is important to note that the first stage is pre-attentive, and therefore undeliberate. The prime stimulus would thus automatically activate a summation coding representation. The second stage would then follow easily because participants are asked to name numerosities and are bent on labelling the perceived dot patterns. This is evidenced by the results of another priming experiment (data not published), where the primes were dot patterns and the targets were Arabic digits. In this experiment however, contrary to Roggeman et al. (2007), the trials were blocked, and prime and target were always presented in the same format, instead of randomized over different notation conditions. In this case, the prime stimulus (dot pattern) is expected to pass automatically through the first stage and activate the summation coding representation, but is not expected to pass through the deliberate second stage to assign a numerical label, because subjects knew that the target would be an Arabic digit and that dot patterns were not relevant for the task. As expected, no priming effects were found. It is important to note that when modalities are mixed and participants do not know beforehand in which modality the target will be presented, as in the experiments in Roggeman et al. (2007), subjects cannot ignore the primes based on information about modality, and hence a summation coding priming effect is found.

If the summation coding system is valid in the subitizing range (for small numerosities), and if summation coding is indeed rendered inadequate for larger numerosities due to a capacity limit caused by noise in the system, which processes are then employed in the large number range to arrive at an estimate of the indicated number (for example the approximate analogue representation of Feigenson et al., 2002, 2004)? Several studies have shown that participants rely on a mixture of non-numerical cues (in case counting is not possible, as in our experiment) to extract an idea of numerosity in a visual display (Allik & Tuulmets, 1991; Durgin, 1995). This is evidenced in our data by the fact that participants made a different pattern of errors when the non-numerical cues were differently controlled. In this sense, the enumeration of a large dot pattern is a completely deliberate action, influenced by top-down decision mechanisms. It is therefore not surprising that this deliberate action is not applied to the prime numerosity, since participants are aware that there are 2 consecutive displays and that they only have to answer on the second display. On the contrary, the data of Experiment 1 seem even to imply that the processing of the prime pattern is actively suppressed, as we found traces of overcompensation in the error data. The difference with smaller numerosities in the earlier experiments is that the subitizing process is at least partially pre-attentive and automatic and thus the prime cannot be entirely ignored; whereas this is possible with larger numerosities because the pre-attentive parallel first stage reaches its capacity limit and hence yields no useful information.

If this account is true, the data of Roitman et al. (2007) remain to be explained. These authors did find summation coding neurons for larger numerosities. With respect to this finding, it is important to note that the task requirements in both studies differed considerably. In particular, whereas the monkeys of Roitman et al. (2007) were not required to pay attention to the numerical stimuli, which were only given as a cue but were not behaviourally relevant in the task, our subjects were required to extract the numerosity of the displays. It could be that, when numerosity is not behaviourally important, the summation coding system is less active, and that therefore a capacity limit is never reached. This summation coding would then be measurable by single cell, as this is a more sensitive technique (Roitman et al., 2007), but would be too low to foster a representation of number, and hence would be virtually nonexistent at a behavioural level.

Together, these data seem to imply that a different process is at work when participants enumerate small and large numerosities in visual displays. Whereas the enumeration of a small number of dots relies on pre-attentive and automatic summation preprocessing, the enumeration of a larger number of dots makes use of non-numerical cues rather than the summation coding system. This does not exclude that summation coding can exist with larger dot patterns, but merely that paradigms other than enumeration will have to be used to find its behavioural manifestations.

Chapter 5:

The rise and fall of summation coding

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manuscript in preparation

Traditionally, the neural coding of quantity in the brain is implemented in terms of a place coding system. In such a system, a quantity is represented in the brain by a specific population of neurons. Recently, computational modelling studies showed that summation coding (or more generally number-sensitive coding) is a relevant preceding step in the pathway leading up to such a system. Subsequent evidence for summation coding was found in behavioural studies, fMRI and single cell experiments. In the present study, we tested the existence of number-sensitive coding using fMRI, in a larger number range (dot patterns of numerosities 4 to 64). We did not find evidence for number-sensitive coding using larger numbers, but instead found that the number-sensitive coding system is liable to a capacity limit. We argue that the implementation of this limited capacity depends on the specific task set.

5.1 Introduction

Numerical cognition is the field of research which investigates how numerical or quantitative information is stored and manipulated, both in humans and other animal species. These manipulations must rely on neuronal quantity representations. In recent years we have witnessed an explosion in research investigating the neural coding of these quantity representations in the brain.

The present state of the field seems to favor the neural coding of quantity in terms of a place coding system. In such a system, neurons respond to a preferred quantity, and as such, each quantity is represented in the brain by a specific population of neurons. In addition, the quantity neurons also are activated when presented with quantities numerically close to their preferred quantity. This property is necessary for the place coding system in order to account for certain characteristics of number processing which emerge when both humans and other animal species are engaged in numerical tasks (e.g. the distance and size effects, Dehaene, Dehaene-Lambertz & Cohen, 1998). In this way, the neural response decreases as a function of the numerical distance between this preferred quantity and the presented quantity.

Evidence for this type of coding has been found in various species (monkeys: Nieder, Freedman & Miller, 2002; Nieder & Miller, 2004; Nieder & Merten, 2007; humans: Piazza, Izard, Pinel, LeBihan & Dehaene, 2004; Piazza, Pinel & Dehaene, 2007; Cantlon, Brannon, Carter & Pelphrey, 2006; Reynvoet, Brysbaert & Fias, 2002; Reynvoet & Brysbaert, 2004, 1999), in different task settings (numerical information needed for the task: Nieder et al., 2002, 2004, 2007; Reynvoet et al., 1999, 2002, 2004; passive viewing: Piazza et al., 2004, 2007; Cantlon et al., 2006) and in different number ranges (small numbers: Nieder et al., 2002, 2004; Reynvoet et al., 2002, 2004; large numbers: Nieder et al., 2007; Reynvoet et al., 1999; Piazza et al., 2004, 2007; Cantlon et al., 2006).

An alternative way to code quantities among a population of quantity neurons is summation coding. This type of coding was first brought forward as an explanative model for animal data (e.g. Meck & Church, 1983) but has since been more generally implemented as an abstract quantity representation in various models of numerical coding (Gallistel & Gelman, 2000; Zorzi & Butterworth, 1999). In this coding scheme, the coding is analogous to the number it represents.

This can be implemented by neurons that respond monotonically to number (e.g., more strongly for larger numbers). Importantly, computational modelling studies have shown that summation coding is a necessary intermediate step between an object location map (which represents objects independent of the physical appearance of the object) and a place coding system (Dehaene & Changeux, 1993; Verguts & Fias, 2004). The object location map and the subsequent summation coding system are collectively named number-sensitive coding. Evidence for this type of coding is more sparse, but has been found in monkeys, in a passive viewing task with a large number range (Roitman, Brannon & Platt, 2007), and in humans in an active numerosity encoding task with a small number range (Roggeman, Verguts & Fias, 2007, submitted). Therefore, more research is needed to establish the reality of summation coding in different species, using different task settings in different number ranges.

The present study was designed to close one of these gaps. We used fMRI to search for evidence of number-sensitive coding in humans, as it is impossible to make a distinction between the object location map and summation coding using the fMRI method. In particular, we used the same method as Roggeman et al. (submitted), but used dot patterns of numerosities in the range 4-64.

5.2 Materials & Methods

Participants

Twenty-one adult male volunteers participated in this study and were paid for participation. One participant was excluded from all analyses due to self-reported motion during scanning. Five other participants were excluded due to poor performance on the task (see below), which indicated that they did not attentively process the stimuli. The remaining 15 participants were on average 24.1 ± 3.1 years old (range 18 – 30y). All subjects were right-handed and had normal or corrected-to-normal vision. All subjects reported by means of a questionnaire having no neurological or psychiatric history, and gave written informed consent prior to scanning. The study was approved by the ethical committee of the Medical Department of Ghent University.

Stimuli

Stimuli were dot patterns with numerosities 4, 8, 16, 32 or 64. The procedure to remove confounding cues from non-numerical parameters was described in detail elsewhere (Roggeman et al., submitted). Non-numerical parameters were divided in intensive parameters (individual item size and inter item spacing) and extensive parameters (accumulated area of all dots in the display or total luminance, and total area spanned by the dot configuration) (Dehaene, Izard & Piazza, 2005). Stimuli were constructed as triplets of dot patterns with increasing numerosity ($n_{small} < n_{medium} < n_{large}$; from now on referred to as n_s, n_m and n_l, respectively). The extensive parameters were constant between n_s and n_m, and the intensive parameters were constant between n_m and n_l (see Figure 1A). Therefore the intensive parameters covaried incongruently with increasing numerosity between n_s and n_m, and the extensive parameters covaried congruently with increasing numerosity between n_m and n_l. In this way, numerosity is the sole parameter that monotonically increases from n_s to n_l, and brain areas that are found activated in a conjunction analysis over the contrasts ($n_l > n_m$) and ($n_m > n_s$) must be responding to numerosity, and not to intensive or extensive confounding parameters. The intensive and extensive parameters were controlled in a reversed order compared to Roggeman et al. (submitted). This was done because it allows a larger range of possible item sizes within the constraints of the control, especially for larger dot patterns (64 dots). Note that the numerosities were divided in three categories (n_s, n_m, and n_l) but that individual numerosities could belong to multiple categories. Category n_s could be numerosity 4, 8 or 16, n_m could be numerosity 8, 16, or 32, and n_l could be numerosity 16, 32 or 64. Therefore, although the design was optimized to quantitatively distinguish neural responses to small, intermediate and large numerosities, differences between individual numerosities could not be reliably distinguished since they were not controlled for non-numerical parameters at the level of the individual items.

Dot displays were generated randomly by an adapted version of a Matlab program (Matlab 7.0.4, The MathWorks, Inc.) described in Dehaene et al. (2005). Dots were displayed in an invisible circle which extended approximately 10 × 10 visual degrees around fixation point. The sample method for item size and total area spanned was the same as in Roggeman et al. (submitted).

Experimental procedure

Before going into the scanner, participants were trained until they could reliably name the number of the dot patterns. In a training block, each numerosity was presented 6 times, yielding training blocks of 30 trials. A trial in the training phase started with a fixation cross for 500 ms, followed by a dot pattern for 150 ms. Participants were asked to name the dot pattern, and the answer was typed in by the experimenter. Feedback was given after every trial and at the end of each training block. Participants completed at least 2 training blocks, and had to reach a performance of 93% before they were allowed to participate in the fMRI experiment.

In the fMRI experiment, stimuli were presented for 150 ms, white against a black background. A small yellow fixation cross remained on the screen throughout the whole experiment. Stimuli were presented on average every 5 seconds, with a jittering factor (Burock, Buckner, Woldorff, Rosen & Dale, 1998; Dale, 1999; Miezin, Maccotta, Ollinger, Petersen & Buckner, 2000) varying between 0 and 1600 ms, so that the interstimulus interval between 2 consecutive events could vary between 3400 ms and 6600 ms. 20% of all events were null events. In order to make sure that subjects paid attention to the stimuli, occasionally (12 times per run) a task trial was introduced. In these task trials, 2 Arabic numbers were presented left and right of fixation and subjects were asked to indicate the number that corresponded to the numerosity of the previous dot display by pressing a button with their left or right index finger. The experiment consisted of 5 runs with 103 events per run. The order of the 5 event types (n_s, n_m, n_l, null events and task trials) was pseudo-randomly intermixed with first order counterbalancing within runs (each trial type followed every other trial type equally often, Buckner et al., 1998). Order of numerosities 1, 2, 3, 4 and 5 was counterbalanced over all runs for each subject. The first trial was always a null event. This was done because it was found that it improved the timing accuracy of the stimulus presentation software. However, the event was regarded as baseline and was not included in the analysis of null events as necessary for the event-related average curves (see below).

At the end of the experiment, subjects were engaged in a short localizer experiment to determine human LIP, implemented as a block design run. This localizer was based on the finding that human LIP is involved in the preparation of eye movements (Corbetta et al., 1998; Baker, Patel, Corbetta & Snyder, 2006).

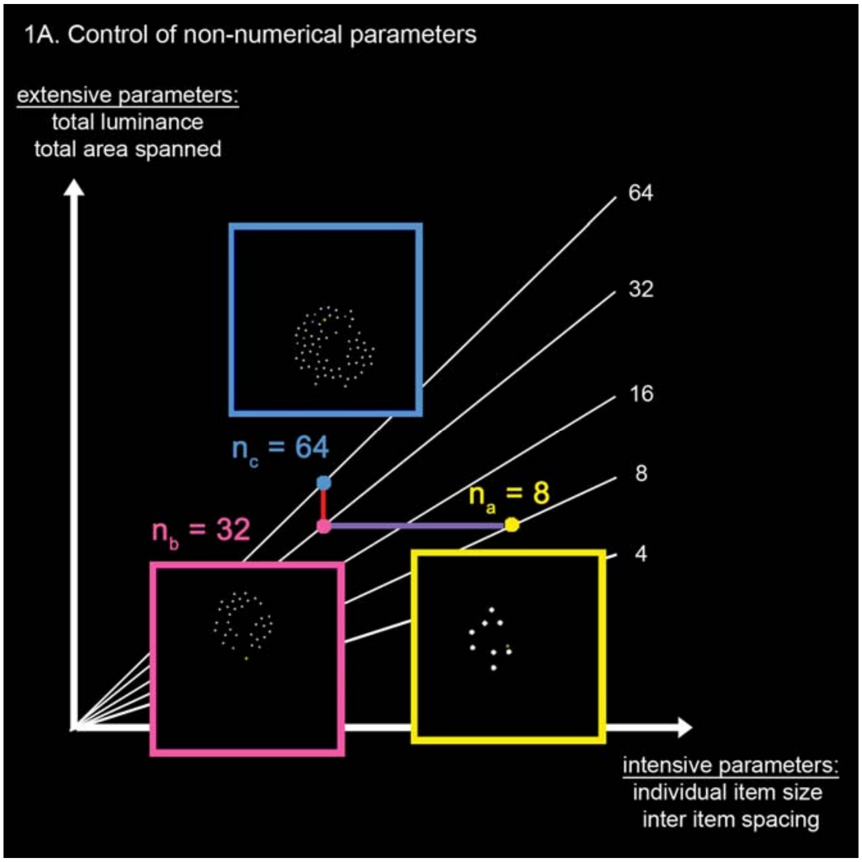
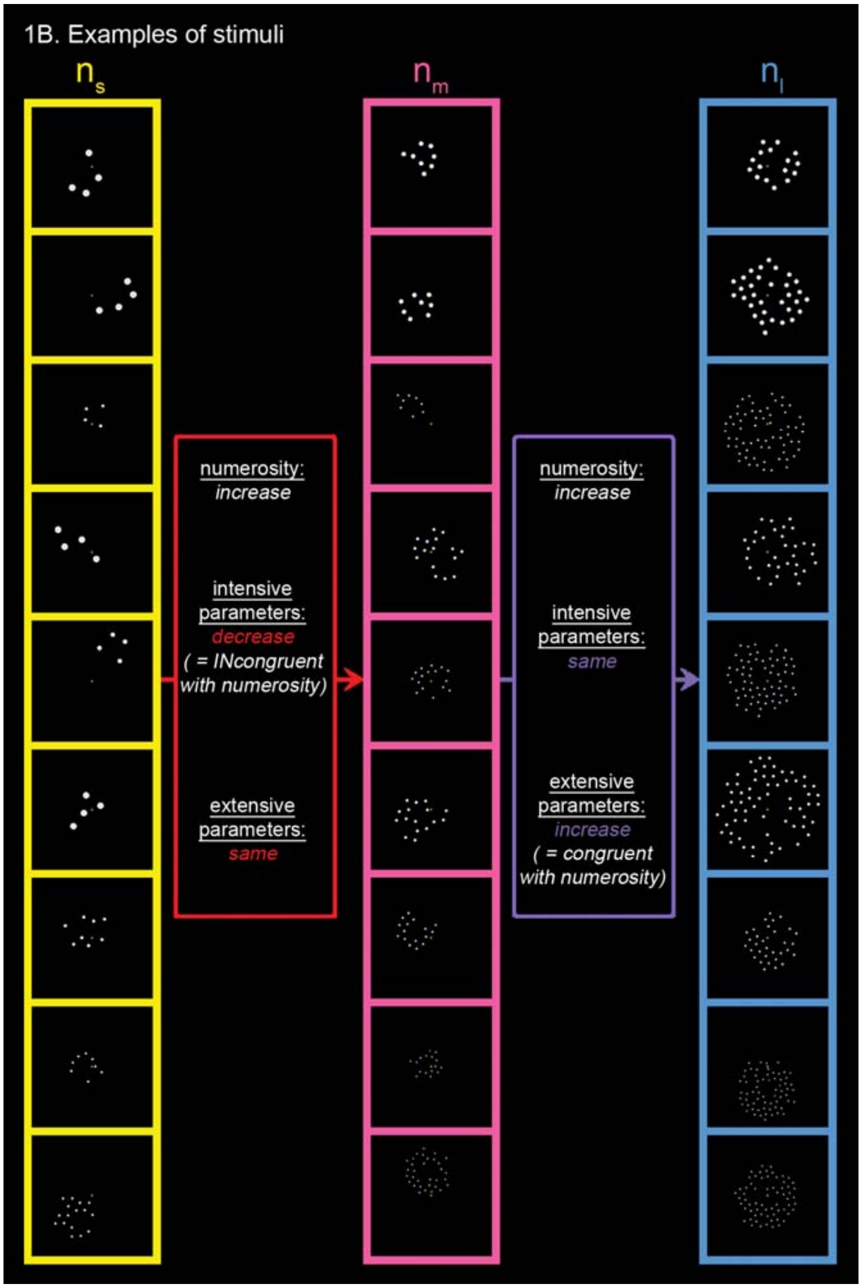


Figure 1A. Control of non-numerical parameters

Right: Figure 1B. Examples of stimuli with different numerical values in the categories n_s, n_m, and n_l.


1B. Examples of stimuli
n_s
n_m
n_l
numerosity:
increase
intensive parameters:
decrease
(= INcongruent with numerosity)
extensive parameters:
same
numerosity:
increase
intensive parameters:
same
extensive parameters:
increase
(= congruent with numerosity)

Stimuli were single dots with random position (within the invisible circle of 10 visual degrees) and random item size (between 0.2 and 0.63 visual degrees). Every stimulus was presented for 1 second, and immediately followed by another stimulus, yielding a dot which changed location and size every second. In the saccade condition, subjects were asked to make a saccade to the dot and back to the fixation cross every time the dot changed position. In the fixation condition subjects were asked to ignore the dots and keep fixating the fixation cross. The task was indicated by the color of the fixation cross (red: make saccades, yellow: no saccades). Block duration was 16s. The saccade and fixation blocks alternated and each block was repeated 8 times.

The experimental procedure was controlled with E-Prime 1.1 SP3 (www.pstnet.com/eprime; Psychology Software Tools), running on an AMD Athlon 64 Processor (2.41 GHz) under Windows XP. Stimuli were presented through dual display MRI compatible LCD displays, mounted in a lightweight headset (resolution 800 × 600, refresh rate 60 Hz; VisuaStim XGA, Resonance technology Inc, http://www.mrivideo.com/). An eye tracking system was mounted on the headset, and eye movements were monitored online by the experimenter. Eye movement data were also recorded but were not sufficiently reliable for further processing.

Imaging procedure

Subjects were positioned head first and supine in the bore. Images were collected with a 3T Magnetom Trio MRI scanner system (Siemens Medical Systems, Erlangen, Germany), using an 8-channel radiofrequency head coil. First, 176 high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence (TR = 2530ms, TE = 2.58ms, image matrix = 256 × 256, FOV = 220mm, flip angle = 7°, slice thickness = 0.90mm, voxel size = 0.9 × 0.86 × 0.86 mm (resized to 1 × 1 × 1 mm), 176 sagittal slices). Whole brain functional images were collected using a T2*-weighted EPI sequence, sensitive to BOLD contrast (TR = 2000ms, TE = 35ms, image matrix = 64 × 64, FOV = 224mm, flip angle = 80°, slice thickness = 3.0mm, distance factor = 17%, voxel size 3.5 × 3.5 × 3 mm, 30 axial slices). During numerosity runs, 262 images were acquired per run. In the localizer-saccade run, 135 images were acquired with the same EPI sequence.

Image processing and statistical analysis

Data analysis was performed with BrainVoyager QX 1.9 software package (Brain Innovation, Maastricht, The Netherlands; Goebel, Esposito & Formisano, 2006). Functional volumes were corrected for slice timing, motion corrected to the first image of each run (trilinear/sinc interpolation), and high pass filtered (cutoff 0.0083 Hz) after linear trend removal. Anatomical data were corrected for inhomogeneity. Functional images were coregistered with the within-session anatomical volume for each run separately. Anatomical and functional volumes were then transformed into Talairach space. Functional images were smoothed with a Gaussian kernel of 8 mm FWHM just prior to statistical analysis.

Functional data were subjected to GLM analyses with 5 predictors for the main experiment (n_s, n_m, n_l, response left, response right) or 2 predictors for the localizer run (saccade, no saccade) (protocol specified in milliseconds and convolved with a 2 Gamma haemodynamic response function, time to response peak = 5 s, time to undershoot peak = 15 s, response undershoot ratio = 6), for each run and each subject separately. For multi-subject GLM, runs of the same subject were implemented as fixed effects, between subjects as random effects. Activations are reported at the p-level stated in the text. Correction for multiple comparisons was implemented either as an FDR corrected p-level or as a cluster extent threshold which leads to a cluster-level corrected p-level of 0.05 (Forman, Cohen, Fitzgerald, Eddy, Mintun & Noll, 1995). Conjunction of the 2 contrasts of interest ($n_l > n_m$) & ($n_m > n_s$) was calculated based on the minimum t-statistic compared against the conjunction null (Nichols, Brett, Andersson, Wager & Poline, 2005).

Event-related average curves were plotted by extracting the mean time course of all voxels in the specified ROIs for every event of the specified type (in every run of every subject). The time courses were extracted from 2 seconds before until 16 seconds after the onset of the event. For this analysis, a time course for the null events was extracted in the same way as for numerosity events, that is, a time course for a fixation event of 150 ms with a jittered onset was extracted. The first null event at the start of each scan was not included in the average. This null event time course served as a baseline and was subtracted from the time courses of the events of interest (n_s, n_m and n_l events). Null events produced a reliable baseline because they were counterbalanced with numerosity events.

5.3 Results

Training phase

Participants required on average 2.5 training blocks (minimum: 2, ten participants; maximum: 5, one participant) to reach a performance level of 93%. Performance in the first blocks was on average 89.6 ± 7.9% (range: 73.3% - 100%), while performance in the last blocks was on average 95.8 ± 2.7% (range: 93.3% - 100.0%).

Region	X	Y	Z	# voxels	t(14)	p-value
$(n_l > n_m)$ & $(n_m > n_s)$						
occipital lobe, lingual gyrus	15	-88	-2	14869*	7.12	.0000005
	-18	-94	-11	13031*	5.08	0.00017
right fusiform gyrus	27	-37	-17	958	3.19	0.0066
limbic lobe, culmen	-30	-31	-20	47	2.70	0.018
right inferior parietal lobe	39	-52	40	5	2.51	0.03
left precentral gyrus	-51	-13	40	37	2.83	0.014
$(n_s > n_m)$ & $(n_m > n_l)$						
middle occipital gyrus	-39	-64	10	232	-2.77	0.015
middle temporal gyrus	60	-49	4	485	-2.78	0.015
	48	-70	16	129	-2.98	0.0099
	42	-58	10	51	-2.48	0.027
right medial frontal gyrus	12	44	25	34	-2.45	0.028
left superior frontal gyrus	-9	62	28	11	-2.51	0.025
left anterior cingulated	-3	32	7	305	-2.88	0.012
right parietal lobe, precuneus	21	-55	49	624	-3.06	0.0084
right postcentral gyrus	60	-28	25	1511*	-3.31	0.005

Table 1. Talairach coordinates, number of voxels (resized to 1 × 1 × 1 mm voxels) and statistical values of the local maxima from the whole brain random effects analysis of the conjunction $(n_l > n_m)$ & $(n_m > n_s)$ and the reverse conjunction $(n_s > n_m)$ & $(n_m > n_l)$. Clusters surviving the cluster extent threshold are indicated with *.

Behavioural results

Five subjects made a considerable number of errors (more than 13%) on the task trials, suggesting that they did not attentively process the stimuli. These subjects were excluded from further analysis. The remaining subjects made on average 7.1 ± 2.8 % errors.

Whole brain analysis

The whole brain random effects analysis of the conjunction $(n_l > n_m)$ & $(n_m > n_s)$ yielded no results at an FDR corrected threshold of $p < 0.05$. We therefore performed an analysis thresholded at $p < 0.05$, corrected with a cluster extent threshold which was estimated at 1361 voxels (resized to 1 × 1 × 1 mm voxels). This yielded a variety of clusters, of which only the occipital regions survived the cluster correction (see Table 1). The only surviving cluster in the reversed analysis $(n_s > n_m)$ & $(n_m > n_l)$ was a cluster in the right postcentral gyrus (see Table 1).

Next, we analyzed the two contrasts of interest separately, at an FDR corrected level of $p < 0.05$. This yielded substantial parietal and frontal activation (see Figure 2A). It is clear from this figure that the activation from the two contrasts of interest is almost reversed. Particularly in the parietal cortex, the same regions are activated in both contrasts, but in reversed directions. This

Region	X	Y	Z	# voxels	t(14)	p-value
frontal lobe	27	-1	25	1496	5.04	.00018
	30	29	16	1075	5.57	.00007
	-27	23	10	245	3.49	.0036
medial frontal gyrus	6	8	46	519	3.61	.0029
inferior frontal gyrus	-45	2	31	3270	5.98	.00003
parietal lobe	27	-52	28	554	3.94	.0015
	27	-67	34	1134	3.52	.0034
parietal lobe, angular gyrus	-30	-61	37	3615	5.86	.00004
parietal lobe, supramarginal gyrus	-39	-40	37	434	4.05	.0012

Table 2. Talairach coordinates, number of voxels (resized to 1 × 1 × 1mm voxels) and statistical values of the local maxima from the whole brain random effects analysis of the conjunction $(n_m > n_s)$ & $(n_m > {}_{nl})$. Only clusters larger than the cluster extend threshold are listed.

pattern of activation was tested by a conjunction of the contrasts ($n_m > n_s$) & ($n_m > n_l$) (in which the second term of the conjunction is reversed). The results of this analysis, thresholded at $p < 0.01$ with a cluster extent threshold of 239 voxels, are given in Table 2 and Figure 2B.

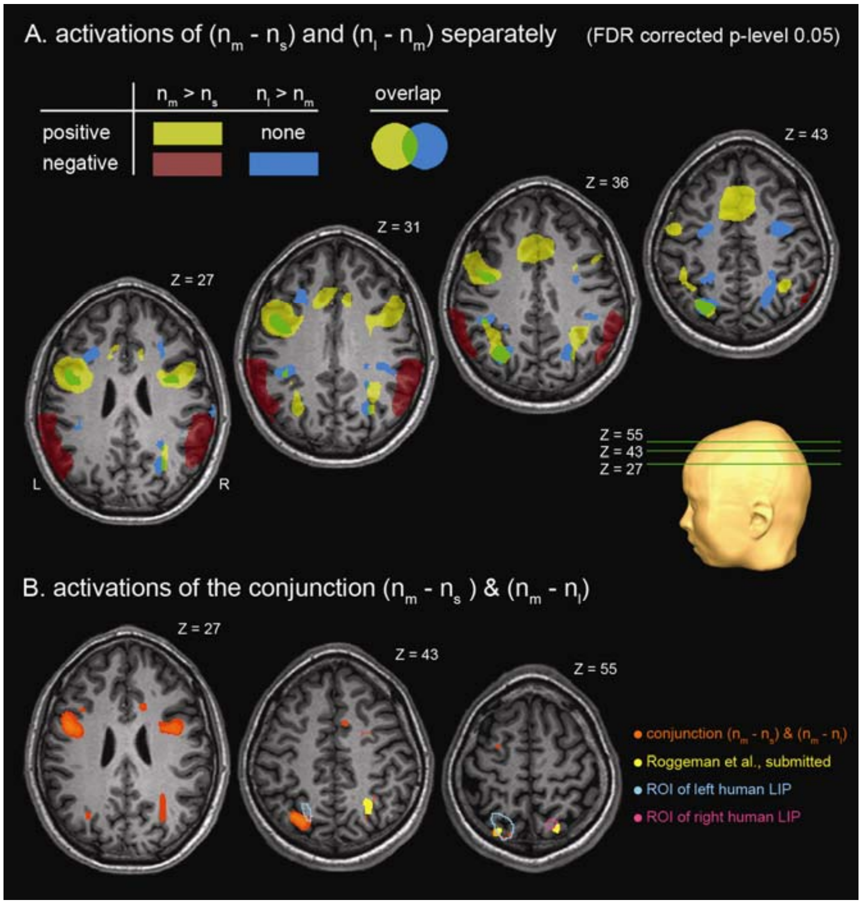


Figure 2. A. Results of the random effects analysis of the two contrasts of interest separately, thresholded at an FDR corrected level of $p < 0.05$. **B.** Clusters in red: results of the random effect analysis of the conjunction ($n_m > n_s$) & ($n_m > n_l$), thresholded at $p < 0.01$ with a cluster extent threshold of 239 voxels. See Table 2 for Talairach coordinates. Activation clusters of number-sensitive coding for a small number range (Roggeman et al., submitted) are shown in yellow. At the topmost slice, the outlines of the ROIs for human LIP are also visible (see Figure 3).

ROI analysis

We performed a ROI analysis to test the activation pattern of the human LIP, which was found to be number-sensitive for smaller numerosities in the former study (Roggeman et al., submitted, see yellow activation in Figure 2B en Figure 3A). For this purpose, the contrast saccade versus fixation was computed on the images of the localizer run, thresholded at $p < 0.0005$. Within the resulting activation network, we selected in both hemispheres a region which corresponded best with the region found on the former study (Roggeman et al., submitted), and with coordinates of human LIP as reported in literature (Sereno, Pitzalis & Martinez, 2001; Simon, Mangin, Cohen, Le Bihan & Dehaene, 2002; Koyama, Hasegawa, Osada, Adachi, Nakahara & Miyashita. 2004), which was then defined as a ROI for human LIP (Figure 3A).

The left hemisphere ROI comprised 3411 voxels (resized to 1 × 1 × 1 mm voxels) and was centered at -20 -64 53; the right hemisphere ROI comprised 917 voxels and was centered at 17 -62 50. The ROIs exhibited almost no overlap with the activations in the conjunction ($n_m > n_s$) & ($n_m > n_l$), but were situated more superior and anterior, and slightly more medial. Only the left hemisphere ROI overlapped with the most posterior and anterior end of the right hemisphere activation (see Figure 3A).

Next, the random effects analysis on the average activation over all voxels in these ROIs was computed for each contrast separately. This analysis was significant in the left hemisphere for both contrasts [$n_m > n_s$: $t(14) = 2.11$, $p = 0.035$; $n_m > n_l$: $t(14) = 3.07$, $p = 0.0021$], rendering it significant for the conjunction based on the minimum t-statistic. In the right hemisphere, this was significant for the second contrast only [$n_m > n_s$: $t(14) = -0.50$, $p = 0.62$; $n_m > n_l$: $t(14) = 2.09$, $p = 0.037$]. Note that the first contrast ($n_m > n_s$) was in the reversed direction in this hemisphere, though this was not significant.

Event-related averaging curves were calculated for the three categories n_s, n_m and n_l (Figure 3B, C). The differences between these curves were very small, as could be deduced from the random effects analyses in the ROIs. The ROIs were therefore explored further by calculating the event related averaging curves for each of the numerosities separately (Figure 3E, F). These curves showed that the activation increases in both hemispheres from numerosity 4 to numerosity 8, but then dropped again and remained constant from numerosity 16 onwards. This is

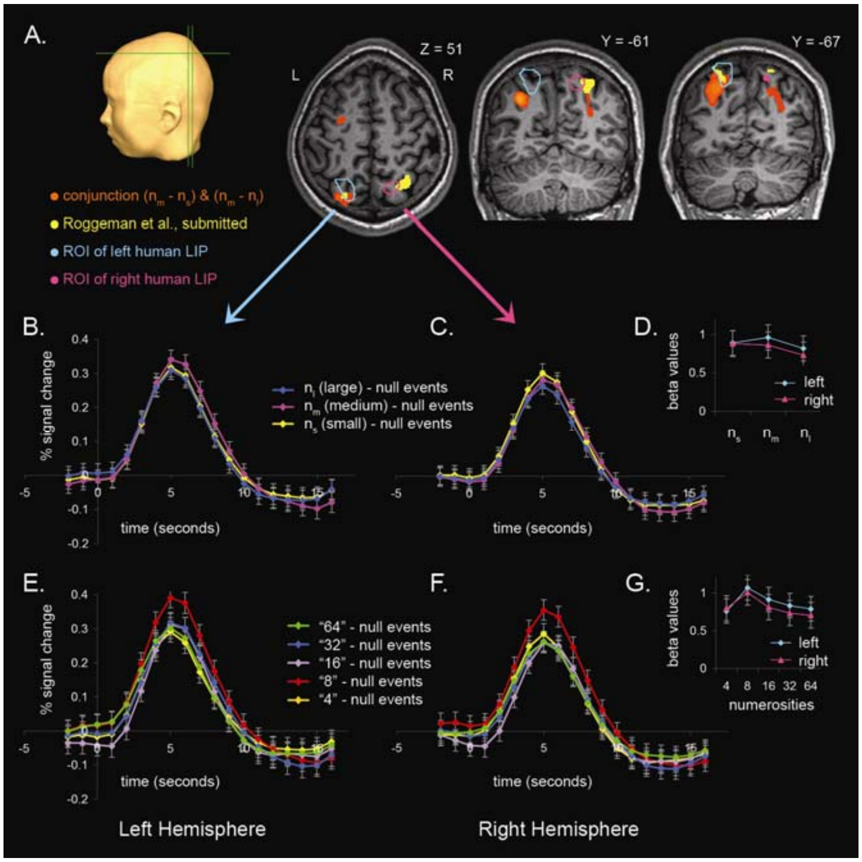


Figure 3. Number-related activation in the ROIs of human LIP as defined by the localizer task. **A.** Results of the random effect analysis of the conjunction ($n_m > n_s$) & ($n_m > n_l$), thresholded at $p < 0.01$ with a cluster extent threshold of 239 voxels, are shown in red. Activation clusters of number-sensitive coding for a small number range (Roggeman et al., submitted) are shown in yellow. Outlines for the ROIs of human LIP are shown in cyan (left) and magenta (right). **B&C.** Mean time courses, after subtraction of the time course of the null events (see Methods), of the three stimulus categories, in the left and right hemisphere ROIs of human LIP (cf. Figure 3A). Stimulus categories n_s, n_m, and n_l corresponded respectively to small, medium and large numerosities, where category n_s could be numerosity 1, 2 or 3, n_m could be numerosity 2, 3, or 4, and n_l could be numerosity 3, 4 or 5 (cf. Figure 1B). **E&F**. Mean time courses, after subtraction of the time course of the null events (see Methods), of the 5 numerosities, in the left and right hemisphere ROIs of human LIP (cf. Figure 3A). **D&G.** Beta values for the categories and numerosities in the left and right hemisphere ROIs of human LIP.

shown more clearly in Figure 3G in which we plotted the beta-values from an analysis in which we specified events in terms of numerosities, rather than categories. From this graph it is clear that the activations increase in both hemispheres from numerosity 4 to numerosity 8 only, and then decrease again, although the pattern is more obvious in the left hemisphere.

5.4 Discussion

In this study, we tried to find evidence for number-sensitive preprocessing steps for larger numbers, as earlier found for numerosities 1 to 5 (Roggeman et al., submitted).

Number-sensitive activity was found only in the lingual gyrus. This replicates the findings of the earlier study with smaller numbers. In this study, the activation found in this area was attributed to the increasing complexity of the stimuli with increasing numerosity. Indeed, even when all non-numerical parameters are controlled, the visual complexity of the stimulus pattern is still increasing with an increasing number of dots.

We could not find evidence for number-sensitive preprocessing in the superior parietal lobe or in the posterior intraparietal sulcus. The ROI analysis of human LIP also did not reveal number-sensitive activation in these regions. This is surprising as evidence for number-sensitive coding has been found in this region for larger numerosities in the macaque monkey. Roitman et al. (2007) conducted a single cell study, using numerosities varying from 2 to 32. These authors reported cells in monkey LIP whose firing rate varied monotonously with increasing numerosity, in an increasing or decreasing manner, for the whole range of numerosities used.

A number of explanations can be provided for these findings. It could be that the method used is not sensitive enough to detect number-sensitive coding for higher numerosities. Nevertheless, the finding that the activity decreased significantly from medium to large numerosities argues against this, since an insensitivity of the method should lead to no difference in the activation between the three stimulus categories.

This leads us to the conclusion that there is no number-sensitive activation for larger numerosities, or at least not in the current experiment setting. A possible explanation for the lack of number-sensitive activation is that the location map, which is the first step in the non-numerical pathway, has a limited capacity. This limited capacity can be caused by lateral inhibition, which was for example proposed by Verguts and Fias (2004) as a possible and plausible method to implement normalization of the activation pattern in the object location map. Lateral inhibition was also implemented to reduce the noise in the object location map and to achieve object normalization in Dehaene and Changeux (1993). In this implementation, the neurons that are most strongly activated (i.e., whose receptive field corresponds to the location of one of the presented objects) will inhibit neurons that are less active (i.e., whose receptive fields show less overlap with the object locations). A consequence is that total activation in the object location map is limited, and a behavioural capacity limit emerges as a result. When the number of objects strongly exceeds the map's capacity limit, the activation in the map even decreases to a level below the maximum. This behaviour was indeed verified (not reported here) using the model of Usher and Cohen (1999), and nicely fits the pattern of data which we found. The capacity limit of the map would then be between numerosity 8 and 16, based on our data, and when more objects are presented, the total activation in the map actually decreases, because the activated nodes inhibit each other.

If this account is true, the data of Roitman et al. (2007) remain to be explained. These authors did find summation coding neurons for larger numerosities. With respect to this argument, it is important to stress that the task requirements in both studies differed considerably. In particular, whereas the monkeys of Roitman et al. (2007) were not required to pay attention to the numerical stimuli, which were only given as a cue but were not behaviourally relevant in the task, our subjects were required to extract the numerosity of the displays. This could be the reason why the neurons in the object location map were less active, thus greatly diminishing the competition (by lateral inhibition) between neurons, in which case the decrease of activation for numbers larger than the capacity limit may not occur. It might even be possible that subjects have control over the level of excitation or inhibition occurring in the object location map, dependent on different tasks. Such a notion was also introduced by Usher and Cohen (1999). Evidence for this kind of control is for example found in the fact that the level of top-down attention (high or low load) is able to attenuate the level of surround inhibition in neurons in the visual cortex and beyond (Reynolds, Chelazzi & Desimone, 1999; Rees, Frith & Lavie, 1997; Kastner, De Weerd, Desimone & Ungerleider, 1998). Very recently, a method of controlling lateral inhibition by neurons upstream was also described in stimulus-sensitive areas, and was suggested to be a principal method also in higher cortical areas (Arevian, Kapoor & Urban, 2008). If the lateral inhibition in the number-sensitive coding system could similarly be attenuated in different task settings, then it could be assumed that, when no task is required, lateral inhibition would be less strictly implemented, and the activation in the number-sensitive system could be regarded as more spontaneous. This spontaneous activation could then be propelled to the place coding system, for which evidence was found by Piazza et al. (2004), also in a passive viewing task. Even though it would be far more imprecise compared to the place coding activation generated by small numbers, due to the noisier representation in the preceding number-sensitive coding system, it would still show adaptation for numerically close versus far numbers. Contrary in our study, the number-sensitive system must be actively engaged, since the extraction of the numerosity was the task at hand. Therefore reduction of noise must be implemented through lateral inhibition, leading to a capacity limit in the system.

This leads of course to another problem. If the number-sensitive system reaches a capacity limit, how were subjects still able to extract the numerosities for the larger dot patterns? It should be noted that subjects made only around 7% of errors in the whole experiment, and that errors were equally distributed over all numerosities. This is only possible if we assume that subjects relied on other, non-numerical cues, or a combination thereof, to extract the numerosity of larger dot patterns; an account for which evidence is actually readily available (Roggeman et al., PhD chapter 3; Allik & Tuulmets, 1991; Durgin, 1995). These non-numerical cues, or the interpreted result thereof, should then also be able to activate the subsequent place coding mechanism, since it was recently shown to exist for larger numerosities by Nieder and Merten (2007). These authors found place coding neurons for numerosities up to 32, in the prefrontal cortex of macaque monkeys, trained in a match to numerosity task. Based on computational modelling studies (Dehaene & Changeux, 1993; Verguts & Fias, 2004) these place coding neurons should be preceded by number-sensitive coding neurons. But if our account is true that the activation of the number-sensitive coding system collapses for larger numerosities if numerosity is important for the task (which it was in the task of Nieder & Merten, 2007), then there must be another pathway leading up to place coding neurons. This pathway could be rooted in the use of non-numerical cues to extract an estimate of numerosity.

5.5 Conclusion

We conducted an event-related fMRI experiment with dot patterns of numerosities 4 to 64 in order to find evidence for a number-sensitive coding system, as was done previously for smaller numbers (1 to 5). We found that the number-sensitive coding system reaches a capacity limit for higher numerosities. We suggest that this capacity limit originates in the object location map, and could be caused by the use of lateral inhibition between the nodes of the object location map. We further suggest that this mechanism is dependent on the particular task set, and that the capacity limit is not present (or less stringent) when numerosity is not behaviourally relevant, either because the object location map is less strongly activated or because the implementation of lateral inhibition is controlled by top-down processes. Finally, we suggest that a different mechanism based on the use of non-numerical parameters, is employed when subjects have to extract actively the numerical value for large numerosities.

Chapter 6:

General Discussion

Chantal Roggeman[1]

"The Answer to the Great Question..."
"Yes ...!"
"Of Life, the Universe and Everything ..."
"Yes ...!"
"Is ..." said the computer, and paused.
"Yes ...!"
"Is ..."
"Yes ...!!!...?"
"Forty-two," said the computer, with infinite majesty and calm.
"..."
"I think the problem is that you've never actually known what the question is."

Douglas Adams– The hitch-hikers guide to the galaxy, p152

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[1] I would like to thank Wim Fias and Tom Verguts for helpful remarks on previous versions of this chapter.

6.1 Two methods and two number ranges: an overview

The idea of summation coding was first introduced by Meck and Church (1983) as an accumulator model, in order to explain data of animal research. It was then further developed as a preverbal counting model, which was proposed as the core of human numerical representation (Gallistel & Gelman, 1992, 2000). In this view, it was considered as an alternative for other existing models based on a place coding scheme (Dehaene, 1992; Verguts, Fias & Stevens, 2005). However, no unequivocal evidence has been found to support the summation coding idea, whereas the place coding idea was supported by neural evidence found by Nieder and colleagues (Nieder, Freedman & Miller, 2002; Nieder & Miller, 2003, 2004) and Piazza and colleagues (Piazza, Izard, Pinel, LeBihan & Dehaene, 2004). Subsequently, computational modelling studies have pointed to summation coding as a necessary preprocessing step in the numerical pathway (Verguts & Fias, 2004; Dehaene & Changeux, 1993) to obtain a place coding system, rather than as an alternative. The present work sought to find support for this hypothesis.

In the first chapter, we searched behavioural support for a summation coding system in humans. Using a classic priming paradigm, we evaluated the effect of a briefly presented prime (Arabic digit or dot pattern) on the naming of a subsequently presented target number (Arabic digit or dot pattern). We used numbers in the range 1 to 5 for two reasons. First, because we wanted our subjects to be able to reliably name the dot patterns, which is only possible in the subitizing range. Seconds, because the computational modelling studies which pointed to summation coding as a necessary preprocessing step in the numerical pathway were chiefly concerned with this number range.

When primes were Arabic digits, the results showed a well-known distance-dependent priming effect, providing evidence for an underlying place coding representation (Reynvoet, Brysbaert & Fias, 2002; Reynvoet & Brysbaert, 2004, 1999). This was a replication of earlier studies using Arabic digits in the priming paradigm. In contrast, when primes were dot patterns instead of numerical symbols, we found a step-like priming effect (Roggeman, Verguts & Fias, 2007). More precisely, it was found that naming the target value was faster whenever the value of the prime was larger than or equal to the value of the target. This priming effect points to an underlying summation coding representation. In particular, if all neuronal activation patterns of all smaller numbers are included in the activation pattern of a larger number, the neural code of the target will be sufficiently pre-activated when the prime is larger than the target, which allows fast naming of the target. On the other hand, when the prime is smaller than the target, not all the neurons making up the target activation pattern will be pre-activated and additional neurons will have to be activated to name the target, resulting in increasing response time. The experiments in chapter 1 therefore brought convincingly behavioural evidence for the existence of a summation coding system in humans, for the range 1 to 5.

The study presented in the second chapter was aimed at detecting and locating brain regions which show a summation coding activation pattern in the same small number range. A summation code (or more generally, a number-sensitive code) predicts monotonously varying activation with increasing number. We therefore presented dot displays containing 1 to 5 dots, and used event-related fMRI to measure the neural activity for each numerosity. In this way, we localized the areas with monotonously varying activation for numerosities 1 to 5, and we were able to demonstrate number-sensitive preprocessing steps in the numerical pathway (Roggeman, Verguts & Fias, submitted). More specifically, our results showed that number-sensitive preprocessing occurs in relatively posterior parts of the intraparietal sulcus, comprising the human homologue of monkey LIP in the medial wall of the intraparietal sulcus. This posterior intraparietal sulcus location of number-sensitive preprocessing was complementary to the more anterior parts of the intraparietal sulcus observed in experiments that specifically investigated a place coding system (Piazza et al., 2004). The finding of a posterior number-sensitive region, together with a more anterior number-selective region within the intraparietal sulcus is consistent with the hypothesis that number-sensitive processing is an intermediate processing step for non-symbolic number processing between early visual sensory analysis and a more abstract number-selective coding system in the dorsal stream (Dehaene & Changeux, 1993; Verguts & Fias, 2004). Taken together, these experiments convincingly demonstrated the existence of a number-sensitive preprocessing step in the human non-symbolic numerical pathway.

In the next two chapters, we tested the hypothesis of summation coding for a larger number range, using the same techniques as in the first two chapters. Although the computational modelling studies, which predicted the existence of summation coding as the preprocessing step to obtain the place coding system, were limited to small numbers (Dehaene & Changeux, 1993; Verguts & Fias, 2004), there was no a priori reason why this processing system would fail with a larger number range, since human beings are able to estimate the number of large dot patterns. Moreover, a recent study demonstrated summation coding in the lateral intraparietal sulcus of the monkey (Roitman, Brannon & Platt, 2007). We therefore speculated that summation coding may also be plausible in humans when processing larger numbers.

It has long been recognized that there is a performance change when people are asked to estimate numerosities smaller or larger than 4 (Kaufmann, Lord, Reese & Volkman, 1949; Mandler & Shebo, 1982; Trick & Pylyshyn, 1993, 1994). Whereas people are usually perfect for numbers up to 4, performance drops when the to-be-estimated patterns contain more than 4 items. Whether it is the same process which reaches ceiling performance for smaller numbers (Gallistel & Gelman, 2000; Balakrishnan & Ashby, 1991, 1992), or whether there are different processes involved (Dehaene & Cohen, 1994), is a matter of debate. Taking this into account, we used numbers in the range 2 to 64, with a twofold ratio between adjacent numbers, in order to allow accurate estimation of the dot patterns (Van Oeffelen & Vos, 1982). Moreover, in all studies reported, subjects were trained before participation (Izard & Dehaene, 2008), until their performance level reached a predetermined level and were thus able to reliably name the dot patterns, as was the case for the smaller number range.

Despite this, we could not find any evidence for a summation coding system for larger numerosities. Whereas the lack of results in the third chapter could be due to an insensitivity of the method, this was not a plausible explanation in the fourth chapter, as the activity actually dropped beyond numerosity 8. As pointed out in the discussion of chapter 4, this leads to the conclusion that dot patterns in the small and large number range are processed differently.

6.2 Is there a different mechanism for enumeration of small and large numerosities?

Several findings point toward different enumeration mechanisms for small and large numbers. These will be explained in the next paragraphs. First, I will explain in more detail why the data presented in this thesis favour this conclusion. Subsequently, I will describe neural data from the literature, and test the results from these studies also in my own dataset. Finally, I will describe behavioural evidence in the literature which supports a distinction between small and large non-symbolic number processing.

6.2.1 Insensitive or inexistent?

The mechanism which was hypothesized as the core mechanism for the enumeration of non-symbolic numerosities was based on the model of Verguts and Fias (2004). This model proposed two number-sensitive preprocessing stages, an object location map and a subsequent summation coding system, which lead to a representation of the numerosity. Whereas this mechanism was confirmed for the enumeration of small numerosities, we failed to confirm it for the enumeration of larger numerosities.

We failed to find support for a summation coding system in a behavioural priming study (chapter 3). Two possible explanations were stated for this failure. A first explanation was that the method used was technically not sensitive enough. This could be caused by noise in the system: each item is represented in the object location map with a certain level of noise, and the noise in the map thus accumulates with an increasing number of dots. For larger numbers of dots, the accumulated noise would then be too high to allow detection of the summation code representation with the priming technique. The second possibility is that indeed there is no summation coding for larger numbers, and that a different system is used for the estimation of larger numerosities. The reason stated was that the increasing number of dots and the related accumulation of noise in the object location map for larger numerosities would yield a capacity limit, and therefore the summation system would be unsuitable for larger numerosities.

In chapter 4, the existence of number-sensitive preprocessing steps was investigated for larger numerosities using fMRI. Again, we failed to find evidence for the system. Importantly, the pattern of results in this study argued against an interpretation in terms of insensitivity, since we found a significant decrease for the activation from medium to large numerosities. This pattern was interpreted in terms of a breakdown of the object location map, for which evidence was found in a model of Usher and Cohen (1999). In light of this model, we assumed that there exists lateral inhibition between the nodes of the object location map. This was a plausible assumption, as the implementation of lateral inhibition was in fact mentioned in the models of Dehaene and Changeux (1993) and Verguts and Fias (2004, though it was not explicitly modeled here). This lateral inhibition between the nodes would increase with the number of active nodes. As a consequence, the total activation in the object location map is limited, and a behavioural capacity limit emerges as a result. When the number of objects strongly exceeds the map's capacity limit, the activation in the map even decreases to a level below the maximum level. Importantly, the pattern of the fMRI activation was not reflected in the behavioural results. Although the activation in the number-sensitive areas decreased from medium to large numerosities, subjects could still reliably name the larger numerosities, and did not name them as smaller numerosities. This clearly suggests that a different mechanism is at work in the estimation of larger numerosities.

6.2.2 Neural differences between processing small & large numerosities

We found only one study in the literature which made a direct comparison between the processing of small and large numerosities (Ansari, Lyons, van Eimeren & Xu, 2007). These authors conducted an fMRI experiment in which they asked subjects to indicate the larger of two numerosities. Crucially, in different blocks, they presented either dot patterns in the subitizing range (1 to 4), or dot patterns outside the subitizing range (10 to 40). The contrast between small and large non-symbolic number revealed a cluster of activation for small compared with large numbers comparisons in the right temporo-parietal junction (TPJ).

In an attempt to replicate these results and to disentangle this differential processing of small and large non-symbolic number further, we made a direct comparison between the results of chapter 2 (small numerosities) and 4 (large numerosities). Nine subjects participated in both fMRI studies, of which seven were included in an analysis over both studies. In this analysis, functional data were subjected to a GLM analysis in which all predictors of both studies were included separately. A whole brain random effects analysis was conducted for the contrast small > large, which is $[n_s + n_m + n_l]_{\text{small numerosities}} - [n_s + n_m + n_l]_{\text{large numerosities}}$, at a level of $p < 0.001$, corrected with a cluster extend threshold which was estimated at 123 voxels and which leads to a cluster-level corrected p-level of 0.05 (Forman, Cohen, Fitzgerald, Eddy, Mintun & Noll, 1995). In addition to a small right superior frontal cluster (not shown), this contrast yielded a very significant cluster at the temporo-parietal junction (TPJ) [52 -40 28, 1027 voxels, $t(6) = -18.85$, $p = 0.000001$], thus replicating Ansari et al. (2007). This cluster is illustrated in Figure 1, where we also plotted the beta values for all predictors in this activation cluster.

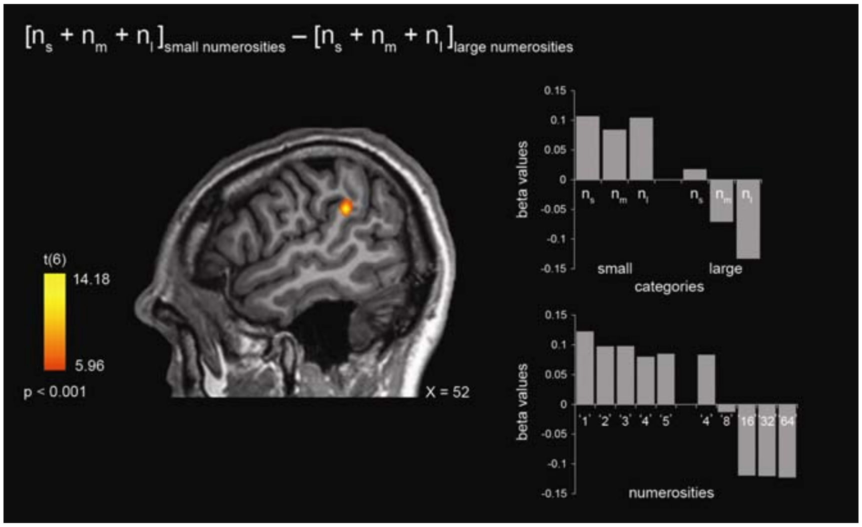


Figure 1. Activation for the contrast small > large ($[n_s + n_m + n_l]_{\text{small numerosities}} - [n_s + n_m + n_l]_{\text{large numerosities}}$): TPJ at 52 -40 28. Beta values for the categories and numerosities in this region.

Ansari et al. (2007) interpreted the activation in the right TPJ region in terms of different attentional networks in the brain. In order to interpret our results in this light, I will first describe a model of visual attention, and then turn to the interpretation of our results in terms of this model.

An influential model on the neural basis of visual attention is the model of Corbetta and Shulman (2002). These authors proposed that there are two networks for visual attention: a dorsal frontoparietal network to direct and maintain goal-directed attention or top-down attention, and a ventral frontoparietal network which is involved with stimulus-driven or bottom-up attention. The top-down attention network is situated in bilateral areas in the dorsal parietal cortex along the intraparietal sulcus (the human homologue of monkey area LIP; human LIP) and the frontal cortex at or near the putative human homologue of the frontal eye fields (FEF). This network is involved in controlling the current locus of attention. Moreover, the network maintains the attention to a stimulus in visual working memory even when the stimulus itself has disappeared. The decision which stimulus is attended to, is not taken by the attention network itself, but is modulated by both top-down contextual information and the sensory distinctiveness of the stimuli themselves (bottom-up). Top-down signals that reflect our expectations and the current task-set might influence the sensory salience of stimuli in the visual system. Sensory stimuli or unexpected events of potentially high behavioural significance also draw attention. The sum of the bottom-up and top-down signals for different stimulus features is then combined in a 'saliency map' which determines which objects are selected for spatial attention. This saliency map is then presented and maintained in the dorsal frontoparietal network, and attention is subsequently directed to the stimuli in this map.

The ventral frontoparietal network on the other hand is a purely stimulus-driven attention network. This network is situated in the more ventral occipital network that comprises the temporoparietal junction (TPJ, which include areas that are centred on the right supramarginal and superior temporal gyrus) and the ventral frontal cortex. The network is strongly lateralized to the right hemisphere. The network triggers attention to unexpected stimuli of potentially high behavioural significance. When such a stimulus is detected, the network interrupts ongoing cognitive activity and reorients the current locus of attention to the new stimulus. As such, the ventral network serves as an alerting mechanism for the dorsal system that detects potentially relevant or unexpected stimuli in the environment outside the focus of attention, or as a circuit breaker of ongoing cognitive activity when such a stimulus is detected. The network is thus strongly activated by target detection and when targets occur at an unexpected location. Once a relevant stimulus is detected, its precise localization however depends on the dorsal IPS–FEF system, since the ventral frontoparietal network does not maintain attention itself, but merely signals its presence to the dorsal frontoparietal network. Hence, the ventral frontoparietal network is merely a subsystem of the total attention system, concerned with the signalling of new stimuli only, while the representation of the stimulus in the saliency map is a concern of the dorsal frontoparietal network.

Our finding that the processing of small and large numerosities engaged the right TPJ differently reveals that spatial attention is differently engaged in both number ranges (see Figure 2). In particular, the involvement of TPJ in small numerosity processing, suggests a strong link between stimulus-driven attention and small number processing, while the suppression of this region in large numerosity processing (see Figure 1) suggests a more top-down driven attention in the case of larger numerosities. Our findings suggest that during small number processing, attention is focused on information directly extracted from the stimuli themselves (Ansari et al., 2007). The use of the stimulus-driven attention system is possible, because in our stimuli, all dots in the pattern were behaviourally relevant, that is, there were no distracters. Furthermore, they were also unexpected, as subjects did not know beforehand where or how many dots there would be. Therefore, each individual dot was in itself a salient stimulus and bottom-up attention was drawn to all dots as individual stimuli. The TPJ then signals the presence of all dots individually to the saliency map in LIP in the dorsal network, which is called in to determine the location of the stimuli (see Figure 2). Since all dots were equally salient and important, as in our stimuli, the saliency map actually is the same as an object location map. The object location map then serves as the input for the summation coding pathway (Verguts & Fias, 2004) and the number of items is determined. The reason why we did not find TPJ activation in our first study is because the TPJ shows no number-sensitive activation. The activation is the same, whatever the number of dots to be attended to, given that the number is in the subitizing range (see Figure 1). Hence, the activation was cancelled out in the contrasts. From this perspective, the reason why Ansari et al. (2007) did not find the human LIP activation is because they did not search for number-sensitive activation, but rather compared all small numerosities against all larger numerosities.

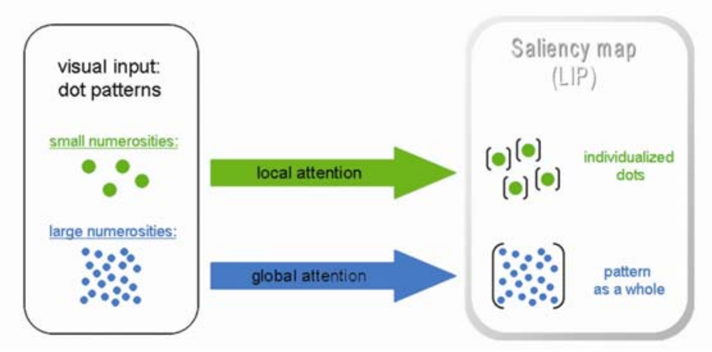


Figure 2. Differential engagement of attention for small and large dot patterns. **Small numerosities (green pathway):** each dot is individually salient. The attention is directed locally to each individual dot, or each individual dot will grab the attention. Hence, the attention is stimulus driven and TPJ is involved. **Large numerosities (blue pathway):** Attention is directed globally to the entire display. The pattern is represented as a whole in the saliency map and global parameters are available (Treisman, 2006).

In the case of large numerosities, stimulus driven attention and attention to individual stimuli is no longer an optimal strategy, because the saliency map is subject to a capacity limit (chapter 4). Hence, the stimulus-driven attention network involving TPJ is suppressed and instead top-down attention is directed away from individual stimuli and towards the entire array (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006). This is in very good agreement with an attention model of Treisman (2006). She postulates that there are 2 modes of attention. Attention can be narrowly focused on a single object, or distributed over the scene as a whole (see Figure 2). In the second mode, individual features of single objects are not available, because not attended to, but instead a different set of properties, including the global shape, global boundaries, and global relations between elements, become available (Treisman, 2006). In a series of experiments, she convincingly showed that this distributed attention mode offers some statistical properties of sets of similar objects (e.g. the mean, the range and the variance of sizes, colours, orientations of objects, including the frequencies of different element types). Furthermore, this extraction of general statistical parameters seemed to be automatic, provided that attention was globally deployed. Against this background, our pattern of data becomes plausible. In the study with large numerosities, subjects knew that most of the stimuli were outside the subitizing range. Therefore, they engaged their attention, under the influence of top-down signals dictated by the task of estimation, to the entire display, instead of to individual dots (Figure 2, blue pathway) (Ipata et al., 2006). The model of Treisman (2006) then states that statistical properties would be automatically made available. These statistical properties must include various non-numerical parameters. The attention is thus directed at extracting (a combination of) general, non-numerical cues from the entire array, and subjects arrive at an estimate of the numerosity by combining these cues.

6.2.3 Behavioural differences in processing small & large numerosities

Finally, the notion of different mechanisms for small and large numerosities is also sustained by findings in behavioural literature. A first line of evidence is the fact that preverbal infants discriminate differently between small and large number ranges (Spelke, 2000; Feigenson, Carey & Hauser, 2002; Feigenson, Dehaene & Spelke, 2004; Xu, 2003). These authors conducted a large number of studies from which it was concluded that infants are able to detect differences between large numerosities, provided that the ratio between the two numerosities is large enough. On the other hand, infants seem to be oblivious to differences in set sizes for numerosities below 4, even when the ratio between numerosities was the same as in the large numbers. More precisely, infants fail to extract numerical information when the number of dots is smaller then 4. Feigenson et al. (2002, 2004), Xu (2003) and Spelke (2000) explained this by stating that infants use different systems to assess dot patterns of small and large value. They proposed that, for small numerosities, children rely on an object file representation which is characterized by a set size limit, and which is not suitable for numerical representation. More precisely, small numbers of dots would induce infants to see the items as individual objects, but not as a set with a specific cardinal value. Large numerosities would be viewed as a whole, as a set, and thereby activate an analogue number representation. Infants are then able to discriminate between these sets on the basis of their numerosity. Infants thus make use of a qualitatively different system for small and large numerosities. Evidence for a similar distinction in human adults is not yet reported.

A second line of evidence for differences between large and small numerosities is the generally acknowledged subitizing phenomenon. This idea builds on the fact that, when adult humans enumerate dot patterns of different numerosities, there is a sharp performance difference for numerosities below and above 4 (Kaufmann et al., 1949; Mandler & Shebo, 1982; Trick & Pylyshyn, 1993, 1994). Whereas small numbers are 'subitized', large numerosities are counted or, in case insufficient time is available for the counting procedure, estimated.

6.2.4 Conclusion

Given the evidence, I propose that there are indeed different mechanisms for the processing of small and large numbers. I will describe a possible pathway for both mechanisms in the following section.

6.3 A system for small number detection

When the number of objects to be enumerated is small, say in the range 1 to 5, the model of Verguts and Fias (2004) could be validated (chapter 1 & 2). The subitizing theory of Trick and Pylyshyn (1993, 1994) is also applicable in the same number range, and so is the object-file idea of Feigenson et al. (2004, 2002), Xu (2003) and Spelke (2000). In this paragraph, I will try to show that all these theories in fact come down to the same mechanism, although different subsystems are emphasized.

6.3.1 Individuating the objects: object location map or saliency map

The model of Verguts and Fias (2004) takes an object location map as input. In this map, the to-be-enumerated items are already individuated, and are represented in the map independent of their size, form, or physical appearance; just as being 'one' countable object (see Xu & Chun, 2006; Luck & Vogel, 1997 for the existence of a similar map in a working memory task-set). The model does not state how this individuation is achieved. Such a mechanism was implemented in the model of Dehaene and Changeux (1993). In their model, this mechanism was based on cells (presumably in the primary visual cortex) responding optimally for dots which fall within its receptive field and whose size approximately matches its filter width. As such, only one cell was activated for each dot with a particular location and size, thus constituting an object location map.

Another possibility is to implement the object location map is a saliency map. Such a map was for example modelled by Itti and Koch (2000, but see also an implementation of their model in a neural network with biologically realistic dynamics by de Brecht & Saiki, 2006). The model provides a framework for the bottom-up, fast, primitive mechanism that biases the observer towards selecting stimuli based on their saliency. Briefly, the model starts from topographic feature maps, which are built in the primary visual cortex. In each of these feature maps, a representation is constructed by centre-surround computations, which are implemented as interactions within each individual feature map rather than between maps. Next, all feature maps are combined into a map which represents a unique measure of salience.

The biological reality of such saliency maps has been shown by a number of studies. Single cell recordings in macaque monkeys have indicated the existence of a number of distinct maps of the visual environment that appear to encode the saliency and/or the behavioural significance of targets. Most important for our discussion is the finding of a saliency map in area LIP (Gottlieb, Kusunoki & Goldberg, 1998; Colby & Goldberg, 1999). These authors pointed out that neurons in LIP are not merely activated by planning of saccades, but were only activated by salient and behaviourally relevant stimuli.

The construction of the saliency map can be modulated by top-down influences, goals and beliefs in certain situations. This was already mentioned by Itti and Koch (2000), who state that, although their model concerns only stimulus driven saliency, top-down attention might also interact with the saliency map. For example, top-down influence can at each moment dictate what exactly is salient (Saalmann, Pigarev & Vidyasagar, 2007). Objects in the visual scene can be salient for two reasons. Firstly, the object can be salient because it stands out from the background. In that case, it will draw stimulus driven attention. In terms of attention networks, this means that the temporo-parietal junction will be involved (Corbetta & Shulman, 2002). The TPJ, as mentioned earlier, is not involved in attention itself, but merely acts as a circuit breaker for ongoing attention. Thus, when the salient object is presented in the visual field, the TPJ will interrupt the current ongoing attention, and signal the new salient stimulus to the dorsal parietal attention network. The stimulus will then be included in the saliency map of the visual scene (Corbetta & Shulman, 2002). Secondly, an object can be salient because it matches the current criteria of the current task setting. Objects which fulfil the current task criteria will also be represented in the saliency map, because of their behavioural relevance (Gottlieb et al., 1998). This saliency map is represented in LIP, which is a part of the dorsal parietal attention network.

Attention can be defined as the spatial and, more importantly, serial analysis of objects in the scene. The actual construction of the saliency map from the visual scene however, occurs in parallel for all objects. This means that the construction of the map itself is a pre-attentive process. At first sight, this seems contradictory: the building of the saliency map is a pre-attentive process, but the map itself is a part of the attention network. This makes sense however when one considers the map as the representation of objects to which the focus of attention will be consequently directed. In other words, the map is first pre-attentively built, and only then the objects in it are attended to, because they are in the map.

It is also important to repeat in this discussion that, in the model of Verguts and Fias (2004), the object location map in fact was a saliency map. This is simply because no other objects were presented in the input, and all presented objects were salient to the same extent. The object location map is in this case the same as a saliency map. In this view, a saliency map as input is merely a more general case of an object location map, but also a more realistic one.

A saliency map is also more adequate to express the ideas of Trick and Pylyshyn (1993, 1994), than a simple object location map. In this theory, the first stage in the subitizing process is the assignment of FINSTs (Fingers of Instantiation) or reference tokens to the to-be-counted objects. These tokens provide a way of saying 'that one' without explicitly stating properties or the position of the object. The tokens are built in the visual system to select objects in the visual field for the attentional focus. The number of tokens is therefore limited: it would be pointless to select every object in the visual field. Only the objects which are thus selected will be attended to. Hence, the assignment of tokens to objects in the field is actually the same as building the saliency map: only the objects represented in the map reach conscious attention. The limited number of tokens then is the origin of the subitizing limit in Trick and Pylyshyn's (1993, 1994) theory.

Trick and Pylyshyn (1993, 1994) also state very clearly that this first stage of the subitizing process is parallel. This means that the assignment of the tokens to the object, which is the building of the saliency map, happens in parallel for all objects. In Trick and Pylyshyn's (1993, 1994) theory, this explains why there is almost no increase in reaction time when subjects enumerate 1 to 4 items (ref).

6.3.2 Enumeration of the objects: matching number names or summation code

Once the saliency map is obtained, the objects in it must be enumerated. The theory of Trick and Pylyshyn (1993, 1994) is rather vague on the implementation of this second stage. They merely stated that it is a stage of number recognition, or choice of numeric response, and that it happens attentively. Klahr (1973) states that this number recognition must involve matching each individual item with a number name, in the order of the number names, hence explaining the shallow, but significant, subitizing slope. The reason why the slope is much shallower than the counting slope is because, in the subitizing range, the whole series of needed number names can be loaded in working memory at once, whereas in counting, slots which were filled with earlier number names have to be emptied and refilled with higher number names, because of the limited capacity of the working memory.

The model of Verguts and Fias (2004) however, does implement this second stage in the subitizing process. In their model, it was shown that summation coding develops naturally in an intermediate level and yields a total activation proportional to the total number of objects in the object location or saliency map (see Figure 3, pathway in black). The activation in this summation coding level is then propagated to the number field, which links to a lexicon where the

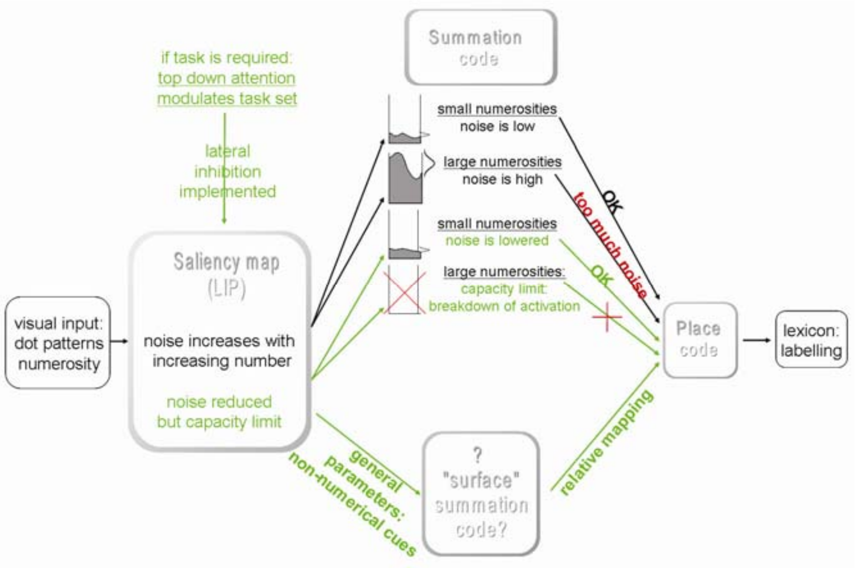


Figure 3. Different mechanisms for the enumeration of small and large numerosities. **Black pathways:** spontaneous activation, when no accurate output is requested. For both small and large numerosities, this yields a summation code. **For small numerosities**, there is not much noise in the code, and the system produces a reliable output. **For large numerosities**, there is too much noise in the system, and the place code does not yield a reliable response. **Green pathways:** In case a response is requested from the system, lateral inhibition is implemented on top-down command (upper green pathways). In the small number range, this leads to a reduction of noise. For larger numbers however, this leads to a capacity limit, and a breakdown of activation in the summation code. For larger numbers then, an alternative pathway (lower green pathway), through the use of non-numerical cues, is invoked. This pathway can also lead to a place coding activation, but the exact estimation of number from the non-numerical parameters needs an external calibration.

numerical label is assigned. The subitizing slope in this model could arise from the fact that the neurons in the summation coding field are activated with increasing thresholds. It is possible that the neurons which code for larger numerosities, the neurons with the highest thresholds, also take more time to activate and to reach their thresholds. This might explain the slight increase of time for subitizing 1 to 4 dots.

In this system, summation coding must belong to the pre-attentive stage. In the pre-attentive stage, items are treated in parallel, which seems necessary for a summation coding system. This means that the summation coding must develop before the attention is directed at the individual items in the saliency map. Still, it does not automatically generate a number output: the number '3' does not automatically pop in mind whenever you see 3 items. However, it can very easily be called if one wants to know how many items there are, suggesting that the information is readily available. This suggests that, once the summation coding system has been developed based on the input saliency map, and the saliency map is automatically activated when viewing a visual scene, the summation coding, and maybe even the place coding, will also be automatically activated. In my view, it is only the very last stage, the connection from the place coding to the lexicon where the numerical label is assigned, which is consciously controlled.

6.3.3 Enumeration does not happen in the object file account

Finally, there is the idea of the object files (Kahneman, Treisman & Gibbs, 1992), which lies at the basis of small number enumeration according to Spelke (2000), Feigenson et al. (2002, 2004) and Xu (2003). The object file theory states that the visual field is parsed into perceptual objects and a relatively undifferentiated perceptual background. The result of the perceptual processing of a visual scene is a set of object files, each containing information about a particular object in the scene. Each object file is addressed by its location, not by any feature or identifying label. The file collects the retinal image, the sensory information that has so far been received about the object at that location. It is also assumed that the number of object files is limited, hence, when one more object comes into attention, another one must be forgotten (the file cleared for the new one). The difference with the pre-attentive tokens of Trick and Pylyshyn

(1993, 1994) is that their tokens is only one feature of the object file, it can be thought of as the initial spatiotemporal label that is entered in the object file and that is used to address it. But the object files contain considerably more information than the object just being 'one'. The object location map (or the saliency map) is also only a part of the object file system: it is the particular information about the location of the objects in the visual field.

According to Spelke (2000), Feigenson et al. (2002, 2004) and Xu (2003), this mechanism is the basis of the small number enumeration used by preverbal infants. These authors proposed that infants use different systems to assess dot patterns of small and large value. In their view, large numbers of dots would be viewed as a whole, as a set, and thereby activate a kind of analogue number representation. Infants are then able to discriminate between these sets on the basis of their numerosity. Small numbers of dots on the other hand would induce infants to see the items as individual objects that can be tracked over time, but not as a set with a specific cardinal value that can be instantiated by different objects at different times. Infants will therefore attend every dot in the display separately, and open an object file for each and every dot. Infants indeed do already have the capacity to use the object file system by 10 months of age (Xu & Carey, 1996). This is the same difference between processing small and large numerosities as we proposed, based on the difference between local and global attention (Figure 2). For infants however, when the dots are individually attended to, the identity of each object is an outstanding property, but the cardinality of the set is much less outstanding, and is indeed missed by human infants and untrained monkeys (Xu, 2003; Lipton & Spelke, 2004; Xu, Spelke & Goddard, 2005).

In the model of Verguts and Fias (2004), this is illustrated by the fact that the summation coding only develops through training (in their case implemented by backpropagation). This means that the system must receive reliable feedback in order to be able to train its summation coding layer appropriately. In other words, infants must have a basic understanding of number, since otherwise the feedback simply makes no sense, before summation coding can develop. Infants must first painstakingly learn to count and learn the meaning of the number words; they must grasp the meaning of cardinality of the set, before they can usefully integrate the information from the summation coding system. This predicts that subitizing in infants will appear in development after counting.

6.4 A system for large number detection

In case a larger number of dots is presented to the visual field, it is impossible to turn the focus of attention to all dots individually. Since all dots in our displays were equal in physical appearance, the salience of all dots is the same, and no particular dot will draw stimulus-driven attention to it. Hence, the ventral attention network involving TPJ is suppressed. Instead, top-down attention will be directed towards the entire pattern as a whole (Figure 2). As such, the pattern will be represented in the saliency map. Once the pattern is in the saliency map, summation coding follows automatically (Figure 3). Then why is it impossible to read out this summation code and subitize every number of dots?

In chapter 3 and 4, we proposed the following: in the object location map, nodes are activated with a certain level of noise. Therefore, when more nodes are activated, which is the case for larger numerosities, the total noise in the system will increase. This means that the system becomes imprecise for larger numerosities, but will still present summation code activation, as in the data of Roitman et al. (2007). The system will thus generate a general idea about number, but in very vague terms, more like a sense of numerousness or a gist of the scene. However, the activation would be too noisy for reliable readout in larger number ranges (see Figure 3, black pathways).

When a correct output is required from the system, as is the case when subjects are engaged in an active numerosity task, it is therefore necessary to reduce the noise in the system. A straightforward way to implement reduction of noise in a system is through lateral inhibition of the nodes. In such an implementation, the nodes that are most strongly activated will inhibit nodes that are less active. This implies that the object location map is differently engaged dependent on the task. Very recently, a method of controlling lateral inhibition by neurons upstream was described in stimulus-sensitive areas, and was suggested to be a principal method also in higher cortical areas (Arevian, Kapoor & Urban, 2008), proving the plausibility of such a control system. If the lateral inhibition in the object location map could similarly be attenuated in different task settings, then it could be assumed that, when no accurate output is required, no lateral inhibition is implemented, and summation coding will be noisy (Figure 3, black pathways). When accurate output is required however, lateral inhibition will be implemented to reduce the noise, and a correct output will be generated (Figure 3, upper green pathways).

The system must however pay a price for this accuracy. The consequence of the implementation of lateral inhibition between the nodes of the object location map, is that the total activation in the map is limited. As a result, a behavioural capacity limit emerges. When the number of objects strongly exceeds the map's capacity limit, the activation in the map even decreases to a level below the maximum level. This behaviour was indeed verified using the model of Usher and Cohen (1999), and nicely fits the pattern of data which we found in chapter 4. This implies that, when the system is actively engaged to decide the numerosity of a set, the lateral inhibition which is implemented for accuracy, gives rise to a capacity limit which renders the system unsuitable for larger numerosities.

If this is the case, then how do subjects estimate larger numbers of dots? We assume that subjects rely on other, non-numerical cues, or a combination thereof, to extract the numerosity of larger dot patterns (Figure 3, lower green pathways); an account for which evidence is actually readily available (chapter 3; Allik & Tuulmets, 1991; Durgin, 1995). These non-numerical cues are presumably a property of the display as a whole. This makes sense, since for large numbers, attention would be directed to the pattern as a whole. This is in line with the findings of Treisman (2006), who stated that, when attention is distributed over the scene as a whole, individual features of single objects are not available, but instead statistical properties of sets of similar objects become available (Treisman, 2006). These statistical properties then could be the basis of large number estimation.

It should be noted that it is impossible to control all non-numerical cues simultaneously. This is because some of the cues are linearly related to each other. For example, the individual size of a dot and the total surface of all dots in the dot pattern, are clearly related to each other through the numerosity presented. One can only control one of these cues. Subjects could also make use of a combination of cues. In our studies for example, individual dot size and total surface where mutually controlled, and similarly for interdot distance and total area spanned. However, no control was exerted between these cues. For example, when the interdot distance is the same, but the dots are larger, the distance between the border of two adjacent dots will be smaller.

Which cues do subjects use in large number estimation? First, it has been shown repeatedly that dots which are close together are judged to be less numerous, whereas dots which are widely spaced are judged to be more numerous (Allik & Tuulmets, 1991; Vos, van Oeffelen, Tibosch & Allik, 1988; Hollingsworth, Simmons, Coates & Cross, 1991; Ginsburg, 1978). Hence, interdot distance must be a cue. Second, estimation depends on the total area spanned (Sophian & Chu, in press; Vos et al., 1988): a larger total area is judged as more numerous. Third, people judge a relative combination of the cues, rather than an absolute, since Allik, Tuulmets & Vos (1991) found that scaling of displays did not interact with numerosity processing, as long as all dimensions of the display are scaled with the same factor. All these cues could be estimated from a general attention to the display, as proposed by Treisman (2006).

How are these estimated cues then transformed into an estimate of numerosity? It is possible that some type of summation coding also works for each of these cues, or for the combination. This would then be a summation coding not for 'cardinality', but for example for 'surface'. Summation coding for non-numerical cues has already been described (e.g. Romo, Brody, Hernandez & Lemus, 1999; Romo & Salines, 2003). In any case, the estimate must also be able to activate the subsequent place coding system. This is evidenced by Nieder and Merten (2007), who recently found place coding neurons for numerosities up to 32, in the prefrontal cortex of macaque monkeys, trained in a match to numerosity task. If our account is true that the summation coding system collapses because of the implementation of lateral inhibition (because numerosity was important in the task for the monkeys), then the place coding neurons must be activated through another pathway. Nevertheless, this mapping on the place coding system is only relative. This is evidenced by research conducted by Izard and Dehaene (2008). These authors found that subjects made, as usual, severe underestimations when judging the numerosity of large dot patterns. However, the comparison, hence the relative judgment, was quite accurate. In order to be able to reliably judge the number of large dot patterns, subjects needed a 'calibration', a single absolute mapping from a dot pattern to a number. This shows that, even though estimation of non-numerical cues can be mapped to the place coding system, the mapping is not calibrated by default.

6.5 Is there a difference after all?

Finally, I want to revisit the answer to the first question. During the course of this work, we came to the conclusion that there is a different system for the estimation of small and large numerosities. In this discussion, I have elaborated on the pathways for both mechanisms (Figure 2 and 3).

The estimation of small numbers of dots starts from the signalling for each individual dot, which is subsequently represented in a saliency map. The saliency map is the input for a summation coding system, which yields an activation proportionally to the number. This activation can be passed on to the place coding system, which can link to a lexicon where a label, a number name, is attached.

In the case of large numerosities, the dots are not individually attended to. Rather, the pattern is represented as a whole in the saliency map. In case no exact output is required, the same pathway as the one for small numbers is followed, and the summation coding system yields an activation proportionally to the number. However, even if it is possible to propagate this activation to the place coding system, it is impossible to attach a label to the numerosity, because the activation is too noisy. In case exact output is required, lateral inhibition is invoked in the object location map, leading to a behavioural capacity limit in the system. The summation coding system is then rendered unsuitable, and other pathways, through the use of non-numerical cues, are invoked. These non-numerical cues are also derived from the object location map, using globally divided attention. The estimate of these non-numerical cues can also be passed on to the place coding system, although calibration is needed for accurate estimates.

Taken together, both mechanisms start with the saliency or object location map, and both mechanisms end up at the place coding system. In this sense, one could argue that it is one system after all, which is merely differently used in the small and large number range.

6.6 The road goes ever on.

As always in research, we started out to answer one question, and we ended up with several other questions. In this section, I would like to point out some of the questions which arose during the course of this work, and suggest some further research which might provide answers to them.

6.6.1 Small versus large

In this thesis, we argued that there was a difference in the processing of small and large numbers. We also attempted to directly compare the processing of small and large numbers, in order to gain a clearer understanding of the different mechanisms. This comparison was however severely limited within the scope of this thesis.

A first line of further research therefore must be to investigate this possible difference between the small and large number range. To this end, small and large numerosities should be presented in a within-subjects design, in a single experiment. The same method as used in chapters 2 and 4 could be used. It is crucial to include both numbers in the subitizing range and numbers outside the subitizing range. By testing for number-sensitive coding (increasing activation for larger numerosities) across both number ranges in the same study, a difference in the processing of small and large numbers can be exclusively determined. In case a capacity limit is indeed encountered for larger numerosities, the limit of the system can be defined more precisely.

6.6.2 Object location versus summation

A second question arose in the course of chapter 2. In this chapter, we found evidence for a number-sensitive system for the small number range. However, our method did not allow us to make a distinction between the object location map and the summation coding system in the model of Verguts and Fias (2004).

A tempting idea to tackle this question is the use of an adaptation design fMRI experiment (Grill-Spector & Malach, 2001; Krekelberg, Boynton & van Wezel, 2006; Sawamura, Orban & Vogels, 2006). In an adaptation design, the neuronal response is first adapted to a stimulus. This implies that the neuronal response will decrease when the same stimulus is repeatedly presented (Sawamura et al., 2006). This phenomenon is called adaptation. By subsequently changing one aspect of the stimulus, thus creating a deviant stimulus, one can assess if the neuronal population is sensitive to this aspect or not: if the neuronal response remains adapted, it means that the neuronal population detects no difference between the deviant and the adaptation stimuli, and hence is not sensitive to the changed aspect. On the other hand, if the neuronal response returns to its initial level, it means that the deviant stimulus is detected as something new, and hence the neuronal population is sensitive to the changed aspect (see also Piazza et al., 2004).

The principles of the summation coding system predict that, when the neuronal response is adapted to a specific numerosity, the response will remain adapted for all smaller numerosities. This is because the activation pattern for all smaller numerosities is always included in the activation pattern of a larger numerosity. On the contrary, larger numerosities will activate additional summation neurons, and hence the neuronal response will increase. The object location map on the other hand, will only be adapted when items are repeatedly presented at the same location. A distinction between the two stages can thus be made by presenting the same number of dots repeatedly at the same location in one condition (adaptation of object location map and summation system), and by presenting the same number of dots at changing positions in another condition (adaptation of summation coding only). Areas showing a decrease in activation in the first condition but not in the second must constitute the object location map.

Additionally, by presenting deviant stimuli with different numerosities, a distinction can be made between number-sensitive and number-selective areas. Indeed, number-selective areas will also show adaptation when repeatedly presented with the same numerosity. However, whereas a summation coding area will only show increased activation for larger numbers of dots, a place coding area will show increased activation for both smaller and larger deviants. The additional advantage is that both systems can be assessed and compared in the same study, thus providing an additional test of the theory which states that summation coding constitutes a preprocessing step to place coding.

6.6.3 Active versus passive

The third study I propose for further research is a test of the suggestion which was made in the discussion of chapter 4. In this chapter, we could not find evidence for number-sensitive coding using larger numbers. This was in contrast with the data of Roitman et al. (2007), who did find summation coding using single cell recording in macaque monkeys. We suggested that the difference in these findings could be explained by the differential task requirements in both studies. In particular, whereas the monkeys of Roitman et al. (2007) were not required to pay attention to the numerical stimuli, which were only given as a cue but were not behaviourally relevant in the task, our subjects were required to extract the numerosity of the displays. We suggested that, in the case numerosity is relevant and an exact output is required, lateral inhibition is invoked in the system in order to reduce noise. This in turn leads to a capacity limit in the system, rendering it unsuitable for the exact estimation of larger numerosities, hence our failure to find number-sensitive coding for larger numbers. This lateral inhibition would not be implemented when the presented numerosities are not behaviourally relevant, hence the finding of summation coding for large numbers in the Roitman et al. (2007) study.

This clearly leads to the prediction that number-sensitive coding should be found when no task is implemented. In order to test this, I propose a study in which subjects will be presented with larger numerosities. In a first condition, subjects will have to process these numerosities, while in a second condition, they will only passively view the stimuli. If our theory is correct, a capacity limit should again be found in the first condition, whereas no such limit should emerge in the second condition.

Nederlandstalige samenvatting:

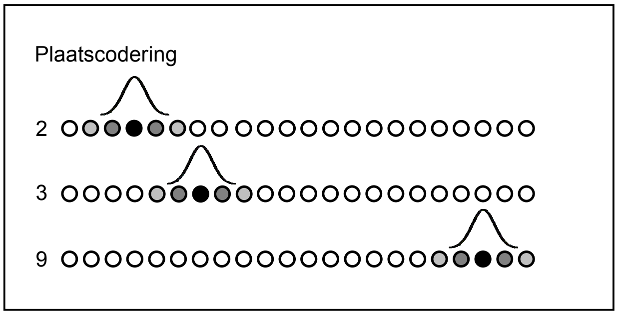
Verwerking van kwantitatieve informatie, onderzocht met fMRI

Getallen spelen een grote rol in vele aspecten van ons dagelijkse leven. Dit is onder andere omdat getallen in verschillende betekenissen kunnen worden gebruikt (Jacob & Nieder, in press). Getallen kunnen bijvoorbeeld een aantal weergeven (vijf bussen), een rangorde (de vijfde bus), of een identiteit (bus n° 5). Deze laatste betekenis steunt op het feit dat getallen eenduidig gedefinieerd zijn. In deze thesis concentreer ik me op het onderzoek van getallen in de eerste betekenis, als aanduiding van een hoeveelheid.

Getallen kunnen ook in verschillende vormen worden weergegeven; als een Arabisch cijfer (“5”), als een geschreven woord (“vijf”), als een klank (het gesproken woord “vijf”), als een woord in een andere taal (“five” of “cinq”), of letterlijk als een aantal objecten (zoals stippen “ :∴ ”), die dan tegelijk of na elkaar kunnen worden aangeboden. In deze thesis werd vooral gebruik gemaakt van getallen aangeboden onder de vorm van een aantal stippen. Dit wordt ook een numerositeit genoemd.

Het feit dat wij al deze notaties en aanbiedingsvormen van getallen door elkaar kunnen gebruiken en begrijpen, duidt erop dat mensen in staat zijn een abstractie te maken van het begrip “5”, onafhankelijk van de notatie. Dit betekent dat er ergens in de hersenen neuronen moeten zijn die geactiveerd worden voor de abstracte betekenis van het getal. Een belangrijke vraag is op welke manier deze neuronen activeren voor een specifiek getal, en dus op welke manier getallen in onze hersenen worden gecodeerd of gerepresenteerd.

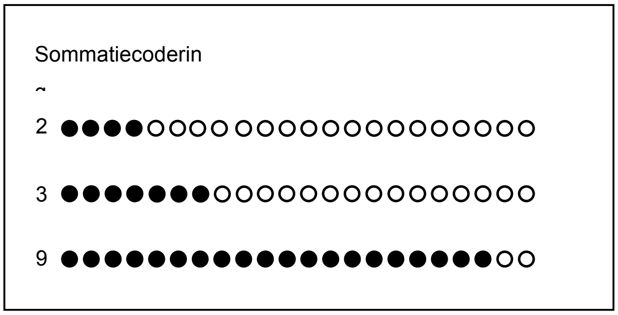
Een invloedrijk model van getalrepresentaties is het model van Dehaene (1992). Dehaene stelt voor dat neuronen specifiek reageren voor een bepaald getal. Dit betekent dat wanneer een getal “5” wordt aangeboden, een specifiek “5” neuron zal worden geactiveerd. Het is echter een gekend fenomeen dat, wanneer mensen moeten bepalen welke van 2 getallen de grootste is, zij trager zijn voor getallen die numeriek dichter bij elkaar liggen. Het is moeilijker 2 en 3 te onderscheiden dan 2 en 8. Dit noemt men het afstandseffect. Om het afstandseffect te verklaren, wordt verondersteld dat getalneuronen ook reageren op numeriek dichtbijgelegen getallen. Wanneer het getal “5” wordt aangeboden, zullen de neuronen voor “4” en “6” dus ook een beetje activeren. Om dit te illustreren, worden de getalneuronen worden meestal voorgesteld op een lijn, wat de mentale getallijn wordt genoemd (zie Figuur 1). Het activatiepatroon voorgesteld door Dehaene (1992) noemt men een plaatscodering: wanneer men de getalneuronen naast elkaar voorstelt op een mentale “getallijn”, activeert het getal een specifieke plaats op deze getallijn. Getallen die dichter bij elkaar liggen activeren gedeeltelijk overlappende plaatsen, en zijn daarom moeilijker onderscheidbaar dan getallen die verder uit elkaar liggen (zie Figuur 1). Er zijn reeds vele aanwijzingen gevonden voor plaatscodering in de hersenen. Neuronen die specifiek reageren volgens dit principe, werden gevonden in de frontale en intraparietale cortex van de makaak aap (Nieder, Freedman & Miller, 2002;



Figuur 1. Illustratie van het plaatscoderingsprincipe op de mentale getallijn. Numeriek dichtbijgelegen getallen hebben overlappende activatiepatronen (vb 2 en 3) en zijn moeilijker te onderscheiden dan numeriek verder uit elkaar gelegen getallen (vb 2 en 9). Dit verklaart het afstandseffect (naar Verguts, Fias & Stevens, 2005).

Nieder & Miller, 2003, 2004). Gedragsexperimenten die wijzen op een plaatscodering van getallen bij mensen werden uitgevoerd door Reynvoet & Brysbaert (1999, 2004) en Reynvoet, Brysbaert & Fias (2002); Piazza, Izard, Pinel, LeBihan & Dehaene (2004), Piazza, Pinel & Dehaene (2007) en Cantlon, Brannon, Carter & Pelphrey (2006) toonden tenslotte met behulp van fMRI aan dat ook menselijke hersenactivatie compatibel is met een implementatie van het plaatscoderingsprincipe.

Men weet echter nog niet hoe een getal, aangeboden in de vorm van een aantal stippen in het visuele gezichtsveld, in de hersenen wordt omgezet naar een plaatscodering. Deze omzetting werd onderzocht in een computationeel neuraal netwerk door Verguts en Fias (2004). Het bleek dat voor deze omzetting een tussenstap nodig is, waarbij neuronen monotoon reageren op het aantal stippen. Dit betekent dat de neuronen sterker geactiveerd worden naarmate er meer stippen worden aangeboden, of dat er meer neuronen actief worden naarmate er meer stippen worden aangeboden. Dit soort codering noemt men sommatiecodering, omdat de totale activatie van de neuronen de activatie van elke individuele stip sommeert. Karakteristiek aan de sommatiecodering is dat het activatiepatroon voor een kleiner getal is ingesloten in het activatiepatroon voor een groter getal (zie Figuur 2).



Figuur 2. Illustratie van het sommatiecoderingsprincipe op de mentale getallijn. Het activatiepatroon voor een getal bevat de activatiepatronen voor alle kleinere getallen (naar Verguts, Fias & Stevens, 2005).

Dit soort codering werd recent aangetoond in de laterale intraparietale cortex (LIP) van de aap. Er werden neuronen gevonden die inderdaad monotoon reageerden op het aantal aangeboden stippen (Roitman, Brannon & Platt, 2007). Er is echter tot nog toe geen evidentie gevonden voor het bestaan van sommatiecodering bij de mens. Dit was het doel van deze thesis.

In het eerste hoofdstuk trachtten we het bestaan van sommatiecodering aan te tonen op gedragsniveau. Hiervoor gebruikten we een klassiek priming paradigma (Reynvoet et al., 2002), waarbij een kort aangeboden getal (de prime) direct wordt gevold door een tweede getal (de target). De proefpersonen moeten enkel reageren op de target, door dit luidop te benoemen. Er wordt dan onderzocht welke invloed de prime heeft op de verwerking van de target. Getallen werden aangeboden onder de vorm van numerositeiten (aantal stippen). We gebruikten enkel numerositeiten van 1 tot 5, omdat proefpersonen enkel voor dit kleine aantal een snel en accuraat antwoord kunnen geven betreffende het aantal. (Dit steunt op het 'subitizing' fenomeen: het fenomeen waarbij mensen een klein aantal objecten onmiddellijk en betrouwbaar kunnen enumereren, zonder eigenlijk te tellen; men "ziet" het gewoon. Dit lukt echter maar tot 4 a 5 objecten, Kaufmann, Lord, Reese & Volkman, 1949; Mandler & Shebo 1982, Trick & Pylyshyn, 1993, 1994) De resultaten toonden aan dat proefpersonen de target sneller kunnen benoemen wanneer deze voorafgegaan wordt door een prime die groter of gelijk is aan de numerieke waarde van de target. Dit effect wijst op een onderliggende sommatiecodering representatie: Omdat in dit soort codering het neurale activatiepatroon van alle kleinere getallen ingesloten zitten in het activatiepatroon van een groter getal, zal de neurale code van een kleinere target reeds gedeeltelijk geactiveerd zijn door de voorafgaande grotere prime, zodat de target sneller benoemd kan worden. Omgekeerd, wanneer de prime kleiner is, is nog niet het volledige activatiepatroon van de target geactiveerd, zodat het langer duurt om de target te benoemen.

In het tweede hoofdstuk gingen we op zoek naar hersengebieden die een activatiepatroon in overeenstemming met sommatie codering vertonen. Een sommatiecodering voorspelt dat de activatie stijgt met een stijgend aantal stippen. We boden daarom numerositeiten aan van 1 tot 5 stippen, en registreerden de hersenactiviteit tijdens de aanbieding van de verschillende aantallen. We zochten dan naar gebieden die meer activeren tijdens de aanbieding van grotere aantallen.

Dit activatiepatroon werd gevonden in het posterieure deel van de intraparietale sulcus, onder meer in het gebied dat bij mensen overeenkomt met het LIP gebied van de makaak aap.

In de volgende twee hoofdstukken herhaalden we dezelfde experimenten met grotere aantallen (4, 8, 16, 32 en 64). We kozen voor aantallen die ver uit elkaar lagen, zodat proefpersonen de numerositeiten gemakkelijk zouden herkennen. Proefpersonen werden bovendien voorafgaand aan de experimenten getraind totdat ze een voldoende hoge score behaalden op het benoemen van de numerositeiten. Ondanks dit, konden we geen aanwijzingen vinden voor het bestaan van een sommatiecodering systeem voor grotere aantallen. Het gedragsexperiment steunend op het priming paradigma in het derde hoofdstuk leverde geen resultaat op. Proefpersonen waren echter ook erg traag in het benoemen van de aantallen en maakten veel fouten. Dit wijst erop dat de priming methode misschien niet gevoelig genoeg is om een sommatiecodering te toetsen met grotere aantallen. In het vierde hoofdstuk echter vonden we tegengestelde resultaten. In het hersengebied dat sommatieactivatie vertoonde in de studie met kleine aantallen (hoofdstuk 2), vonden we nu een stijgende activatie van 4 tot 8, waarna de activiteit terug daalde voor grotere aantallen. Dit wijst erop dat er inderdaad geen sommatiecodering is voor grotere aantallen.

Hieruit werd besloten dat kleine en grote niet-symbolische aantallen op verschillende manieren worden verwerkt. Kleine getallen lijken verwerkt te worden via een sommatiecodering tussenstap, die de informatie omzet in numerieke informatie in het plaatscodering systeem. Voor grote getallen faalt dit systeem. We stellen voor dat de numerositeit van grote aantallen geschat wordt op basis van niet-numerieke informatie, zoals de dichtheid en de verhouding van de totale oppervlakte met de oppervlakte van de individuele stippen (Allik & Tuulmets, 1991; Durgin, 1995).

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