DOTTORATO DI RICERCA
TOSCANO IN NEUROSCIENZE
CICLO XXX

COORDINATORE Prof. Renato Corradetti

The number sense in the human brain

Settore Scientifico Disciplinare M-PSI/02

Dottorando
Dott. (*Togoli Irene)*

(*firma)*

Tutori
Prof. (*Burr C. David)*
Prof. (Roberto Arrighi)

(firma)

Coordinatore
Prof. (*Renato Corradetti)*

(firma)

Anni 2014/2017

"Can you do Addition?" the White Queen asked. "What's one and one and one and one and one and one and one and one and one and one?"

"I don't know," said Alice. "I lost count.”

"She can't do Addition," the Red Queen interrupted.

Lewis Carroll, *Through the Looking-Glass, and what Alice found there*, 1875

Acknowledgments

As always happens, ideas do not arise in isolation, so if the readers will appreciate the studies in this thesis, all the credits go to the fantastic collaboration I have established with my supervisors. They generously introduced me to the fascinating “world” of cognitive neuroscience and provided me with all needed information to run well-controlled psychophysical experiments. For both reasons my deep thanks go to David Burr and Roberto Arrighi.

Thanks also to Olivier Collignon and his amazing team in the University of Louvain-la-Neuve for all the time they spent with me, discussing and encouraging my research

A special thank goes to two of mine co-authors Michele Fornaciai and Giovanni Anobile but in general to the entire PisaVisionLab research group.

Thanks for the perseverance and patience of all the subjects who participated in the experiments.

Finally, thanks to my family and my friends. The responsibility for the mistakes, as usual, is all mine.

Table of Contents

Summary

Humans and other species are endowed with perceptual mechanisms dedicated to estimating approximate quantity, an ability that has been defined as a *sense of number*. Converging evidence gathered from neurophysiological, behavioural and imaging studies, support the idea that this number sense has a truly abstract nature, being capable of encoding the numerosity of any set of discrete elements, displayed simultaneously or sequentially, and across different sensory modalities (Nieder et al., 2006; Piazza et al., 2006; Burr & Ross, 2008). It has been shown that numerosity, like most other primary visual attributes, is highly susceptible to adaptation: visually inspecting for a few seconds a large number of items, simultaneously presented, results in the perceived numerosity of a subsequent ensemble to be strongly underestimated, and vice-versa after adaptation to low numbers (Burr & Ross, 2008). Given that processing numerical information is also fundamental for the motor system to program sequences of self-movement, a further level of generalization of the number sense would be the possibility that a shared numerical representation exists between action and perception – that is, according to this view, the number sense would be generalized across presentation formats, sensory modalities, and perceptual and motor domains. In this work, we investigate numerosity perception within this theoretical framework. The first study was designed to investigate the perception of numerosity for stimuli presented sequentially by using an adaptation paradigm. This study tested whether, and to what extent, adaptation to a high or low number of events distorts the perceived numerosity of a subsequent sequence of visual events presented in the adapted location. In line with the typical dynamics of adaptation aftereffects, adapting to few events caused an overestimation of the perceived numerosity of the test stimuli, whilst adaptation to high-numerosity yielded a robustly underestimation.

We further showed that adaptation effects transcend the sensory modality and presentation format: adapting to sequences of tones affected the perceived numerosity of a subsequently presented series of flashes (and vice versa), and adapting to sequences of flashes affected the perceived numerosity of spatial arrays of items. Similar results were obtained with tactile stimuli. Moreover, adaptation occurred only when test and adaptor positions were presented at the same location in spatiotopic (external world) coordinates, as demonstrated by introducing a saccadic eye movement between the offset of the adapting stimuli and the onset of the test stimuli (Arrighi et al., 2014). In the second part of this work, we present a subsequent work examining the possibility that the perceptual and the motor system might share a common numerical representation by using again the psychophysical technique of adaptation. In different sessions, we asked the subjects to produce either a fast (high number) or slow (low number) tapping routine. At the end of this adaptation phase subjects had to estimate the number of pulses presented sequentially, or of a cloud of dots simultaneously presented either on the same side where the motor actions were performed or on the opposite side. We found that motor adaptation strongly affected numerosity estimation of the test stimuli only when they were presented on the congruent side, with no effect when the visual stimuli were displayed on the neutral, not adapted, location. Moreover, to verify the robustness of the spatial selectivity, we repeated the experiment with a new subject pool, changing the tapping hand and location. Again, the spatial selectivity of the adaptation resulted to be in external – not hand-based – coordinates (Anobile, Arrighi et al., 2016).

In the third part of this work we present another work where we evaluated the possibility that vision could drive the development of an external coordinate system for perceived numbers.

In this study, congenitally blind (CB) and sighted controls (SC) were asked to evaluate the numerosity of sounds after performing either slow or fast motor adaptation (tapping), with the dominant hand, either in an uncrossed or in a crossed posture. Robust adaptation effects were observed in both groups of participants: an underestimation of the numerosity presented was observed after the execution of fast movements and an overestimation of the numerosity was observed after the execution of slow movements, in the crossed as well as in the uncrossed posture. Taken together, these results expand previous findings showing that adaptation to self-produced actions distorts perceived numerosity of sounds. Moreover, we demonstrate that visual experience is not necessary for the development of an external coordinate system for the shared numerical representation across action and perception.

Finally, in the last part of this work, we examine the possibility of a common neural mechanism for different magnitude dimensions. Indeed, it has been recently proposed that space, time, and number might share a common representation in the human brain. For example, adaptation to visual motion affects both perceived position and duration of subsequent stimuli presented in the adapted location, suggesting that adaptation to visual motion distorts spatial maps as well as time processing (Johston et al. 2006, Burr et al., 2007; Fornaciai et al., 2016). In this study, we tested whether motion adaptation also affects perceived numerosity. Adaptation to fast translational motion yielded a significant reduction in the apparent numerosity of the adapted stimulus (of about 25%), while adaptation to slow translational or circular motion (both 20Hz and 5Hz) yielded a weaker but still significant compression of perceived numerosity. Taken together, our results generally support the idea of a common system for processing of space, time and number.

However, as changes in perceived numerosity co-varied with both adapting motion profiles and speed, our evidence suggest a complex and asymmetric interactions between the representations of space, time and number in the brain.

Taken together, the results obtained across these studies point to the existence of a generalized mechanism for numerical representation in the brain that is amodal, independent of the presentation format, shared between the perceptual and the motor systems, and based on external coordinate system.

CHAPTER 1 – GENERAL INTRODUCTION

This thesis summarized the results of the research I have carried out in the last three years, research that I have completely dedicated to the topic of the brain mechanisms underlying numerosity perception. Despite this is a relatively new topic in the filed of perceptual neuroscience in which the still open question are much more numerous than those we have found a response to, I got fascinated by studying numerosity form the very beginning and my enthusiasm even increased when I realized that all the pieces of such a complex puzzle might fit together into a coherent whole.

What are we referring to when we use the word "numerosity"? Numbers surrounds us: we use them to count the day in a month, pay for the food in the supermarket, and also in complex tasks such as sending an astronaut on the moon. The number of situations in which we use numbers are indeed impressively high. Moreover, numbers could have different formats, symbolic (i.e. Arabic numbers, numbers world, roman numbers and so on) or non-symbolic (the numerical magnitude of sets of items). But where do they come from? What are the neural systems allowing numerical processing?

The origin of numbers comes from the numerosity, a concept deeply rooted in the ontogenetic and phylogenetic history of the human being.

1.1.1 Behavioural experiments in animals

It is a common belief that animals are not capable of numerical judgments because humans have created the number system by using arbitrary symbols. Anyway, this idea has to be immediately rejected as we consider the high amount of research both in natural or experimental conditions providing evidence for a number sense in several animal species. For example, several non-human species show the ability to discriminate groups of elements in line with the idea that to recognize different numerosity might have crucial role in many survival situations as all of those in which a “fight-or-flight” response has to be provided.

Going down to details, there is evidence that chimpanzees show an aggressive behaviour only if the number of their group is one time and half higher than the number of the rival group, clearly demonstrating the ability to evaluate numerosity (Wilson et al., 2002).

In a seminal study by Rumbaugh and colleagues (1987), the authors asked untrained chimpanzees to choose in which tray there were more pieces of chocolate. In both experimental conditions, the first concerning numbers between 0 to 4 and the second up to 5, the chimpanzees chose the greater value of the summed wells on more than 90% of the trials. In few words, even in case of a complete lack of a specific training, monkeys turned out in being able to count the spatially separated quantity (Rumbaugh et al., 1987).

On the other hand, Brannon and Herbert (2000) presented monkeys with different dot arrays on a screen and trained the animals to arrange them in ascending order. In the first part of the experiment, the numerosity of the stimuli varied from 1 to 4 while in a different condition from 5 to 9. The monkeys were able to accomplish the task in both conditions suggesting that primates as well as humans are able of ordinality cognition (Brennon et al., 2000).

A chimpanzee numerical skill has been extensively studied. Inoue and Matsuzawa (2007) reported that young chimpanzees have an extraordinary capability for numerical recollection, even better than that of human adults tested with the same apparatus and following the same procedure.

Three young chimpanzees learned sequences of Arabic numerals from 1 to 9, using a touch-screen monitor connected to a computer. In the numerical sequence task, each trial was unique, with the nine numerals appearing in different on-screen positions.

In general, the performance of the three young chimpanzees was better than that of the human students tested. Indeed humans were much slower than chimpanzees in giving responses and they error rate was consistently higher (Inoue & Matsuzawa, 2007).

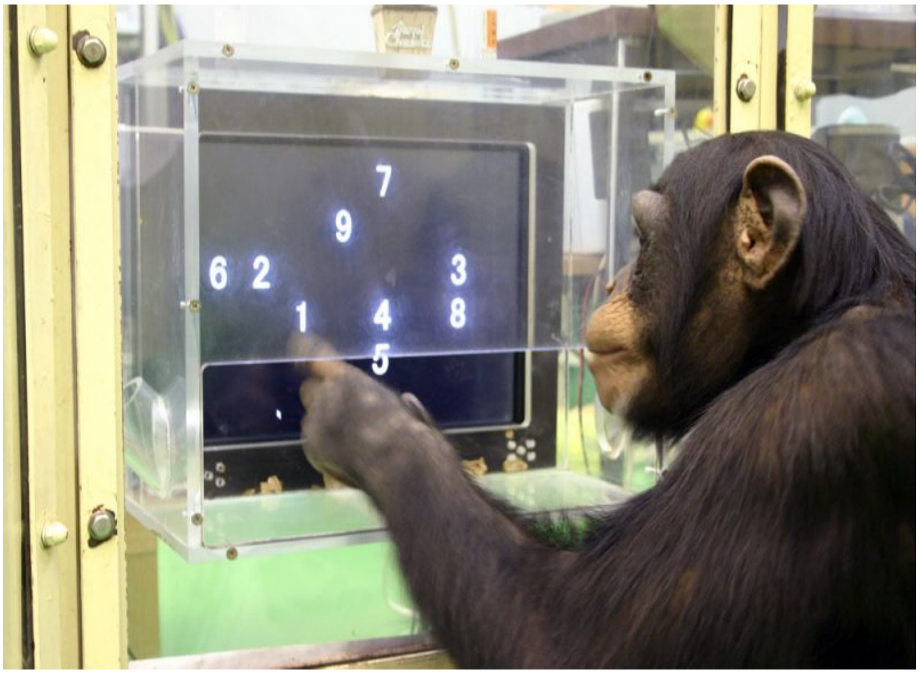


FIG. 1 ***– Inoue & Matsuzawa experiment, (2007).*** Chimpanzees at the Primate Research Institute of Kyoto University outperformed humans in competitive strategic games. Here, Aymu, a 5 1/2-year-old chimpanzee, performing a memory test on a computer screen.

Gibbon and Church (1984) have provided another line for evidence of numerical skills in mammals. They evaluated the processing of temporal information in mice using seven experiments. In the first six, a light indicated the temporal information between the beginning and the end of a trial, while, during this interval, an acoustic stimulus was presented a given number of times. The results show that rats could estimate both the global pause and every acoustic stimulus without any interference (Gibbon & Church, 1984).

Davis e Perusse (1988) have provided evidence of cross-modal (visual/auditory) numerical abilities in mice. The animals were trained to press a bar after they were presented with two visual stimuli and in a subsequent phase the experimenters tested mice capacity to generalize stimuli numerosity to another sensory modality namely audition.

In this experimental phase the bar had to be pressed after the presentation of two sounds. The results indicate that the training successfully transferred from the visual to the auditory modality to support the idea of a cross-modal numerical elaboration (Davis & Perusse, 1988).

Evidence of numerical capabilities in a different species, dolphins, have instead been provided by Kilian and collaborators (2003). Dolphins were trained to answer correctly to the numerosity of stimuli consisting of three-dimensional objects. Subsequently the dolphins successfully transferred this knowledge to two-dimensional stimuli. These findings provide substantial evidence that dolphins could make behavioural choices on the numerosity of a set independently of its perceptual attributes and that they are able to represent the ordinal relations among quantities (Kilian et al., 2003).

Another research line has been developed on birds: in the first half of the 20th century, Otto Koehler demonstrated that some species of birds are able to discriminate different numerosities (Koehler, 1937). More recently, it has been demonstrated that birds are able to repeat notes for a different number of times in different songs with this learning triggered by a prolonged exposure to a given song (Marler & Tamura, 1962).

Emmerton e Delius (1993), on the other hand, devised a laboratory study with some pigeons trained to discriminate different collections of dots. The results highlighted that the pigeons can discriminate groups of 6 vs 7 dots, proving that these animals have some rudimental numerical skills (Emmerton & Delius, 1993).

Also Scarf (2011) investigated the numerical ability in pigeons by training them to order numerical lists. Each list contained stimuli consisting of one, two, or three elements, and the animals were trained to respond to them in ascending order. The pigeons were then tested on pairs of numerosities drawn from the range of one to nine. Pigeons’ performances resulted to be above chance level, demonstrating their ability to acquire an abstract ordinal rule (Scarf et al., 2011).

***FIG. 2* – Scarf at al. experiment, (2011).** Researchers at the University of Otago in New Zealand reported in the journal Science that pigeons can compare pairs of images and order them by the lower to higher number.

A milestone amongst all studies about numerical abilities in winged animals come came from Rugani and colleagues that in 2008 were able to investigate numerical abilities in chicks.

Their results showed that young chicks spontaneously encode numerical representations of small numerosities up to three elements, whereas they use perceptual (non-numerical) cues when asked to cope with larger numerosities (Rugani et al., 2008).

Agrillo and collaborators investigated fish numerical ability using *teleosteo Gambusia holbrooki*, a class of fishes in which females have a gregarious life. They put some females in a tank, and they spontaneously choose which groups out of two they wanted to join. Twenty fishes completed the experiment showing that they could discriminate groups of 3 vs 4 (differing by just one element), and also 4 vs 8 (ratio of 1:2) (Agrillo et al., 2008).

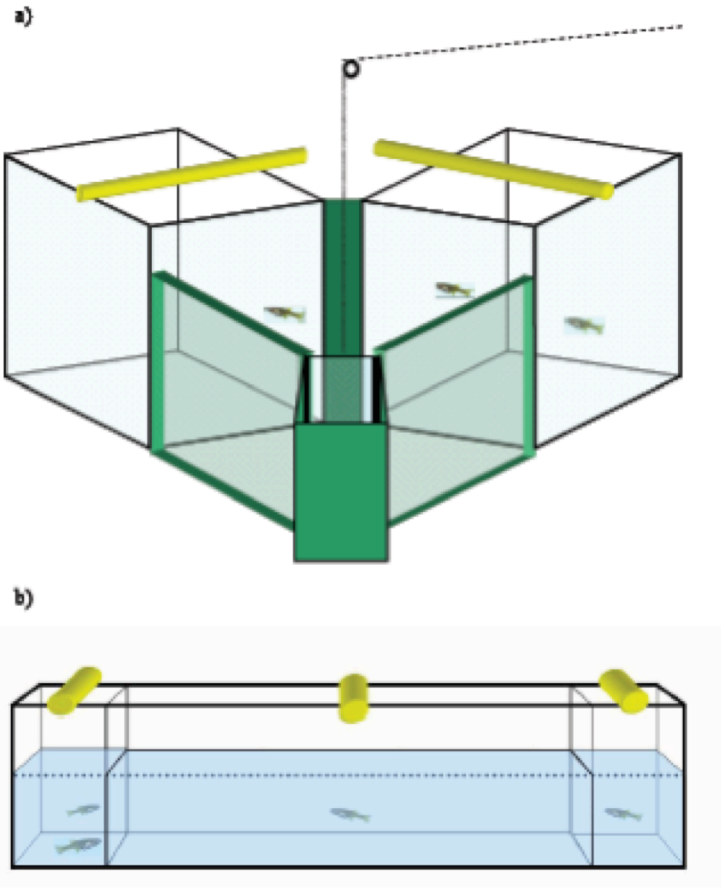


***FIG. 3* - Agrillo at al. experiment, (2008).** Schematic representation of the experimental apparatus: with subject tank and stimulus tanks. The time spent near the larger shoal was recorded as the dependent variable.

1.1.2 Behavioural experiment in children

In the last 40 years, much research has been dedicated to investigate a numerical skill on young human individuals. Gallistel and Gelman (1992) proposed a hypothesis about the existence of two representational systems involved in the numerical ability: the object-file system and the accumulator system (Gallistel & Gelman, 1992).

The object-file system is able to represent different numerosities, building a mental representation of the objects in a scene, processing them in parallel and keeping them at the same time in short-term memory. This allows the resolution of mathematical problems in an accurate way but limited to a low number of elements (up to 3 or 4). Instead, in the accumulator system, every object is a separate signal in the central nervous system.

An accumulator, at a higher level of analysis, keeps track of stimuli numerosity and then transfers this information to a long-term memory mechanism. This system is not accurate but allow us to discriminate also amongst high numbers. Much research has been dedicated to investigate the existence of these two systems, clarify the origins of the numerical knowledge and the ontogenetical development of mathematical cognition.

A classical methodology exploited with children is the habituation paradigm as it is a feasible technique to study infants that haven’t developed verbal skills yet. This technique leverages on the preference of young children to look more carefully to new objects in a scene, rather than those they have already been presented with.

In a pioneering study on 22-week-old infants, Starkey and Cooper (1980) evaluated the ability of new-borns to discriminate the number of dots in a visual set. They habituated children with two groups of dots (2 vs. 3; or 4 vs. 6), displayed simultaneously. In the test phase, the children observed for a longer period the display containing the new number of dots (different from the habituation), but only if test numerosity was low (2 vs. 3) (Starkey & Cooper, 1980).

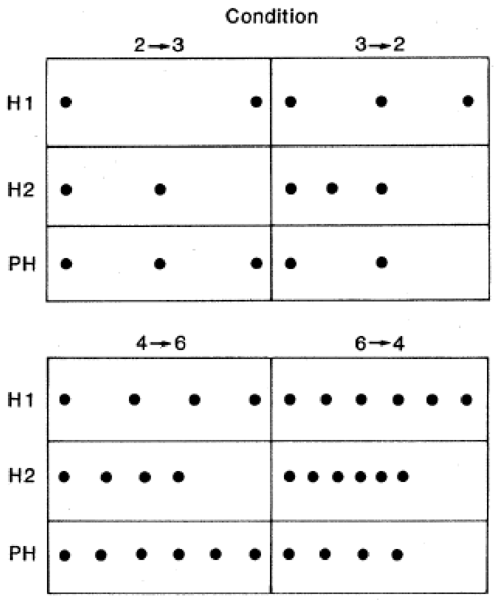


***FIG. 4* - Starkey and Cooper experiment, (1980).** Sample stimuli used in number habituation studies with infants.

Also Xu and Spelke (2000) used a habituation paradigm to evaluate numerical abilities in 6-months-old children, using a larger set of items. In the first part of the experiment, they habituated children with sets of either 8 or 16 dots by varying the size and the spatial arrangement of the stimuli to disentangle numerosity from other characteristics it usually co-vary with. At the end of the habituation phase, infants were presented with a test stimulus containing either

8 or 16 dots, and the experimenters evaluated which stimulus the newborns looked at for a longer period of time. The results showed that babies paid more attention to the new stimulus rather than that they had been habituated to. In a second experiment, the authors used the very same paradigm but reduced the ratio (2:3) between the numbers.

After a habituation with 8 or 12 elements, the children looked similarly the two groups of stimuli. The authors concluded that 6-month-old children are actually able to distinguish between the numerosity of two sets of elements but just in case of fairly large ratio of numerosity difference (Xu & Spelke, 2000).

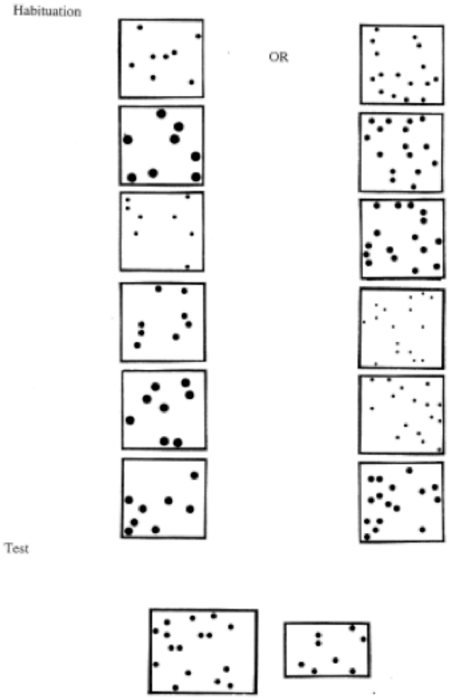


FIG. 5* - Xu and Spelke experiment, (2000).** Habituation and test displays from Xu & Spelke’s Experiment 1.***

Xu (2003) also evaluated the ability to discriminate numerosity in 6-months-old infants comparing the performance for high (4 vs. 8) or low (2 vs. 4) numbers with the same ratio (1:2). The results showed that children were able to discriminate 4 from 8 but failed to discriminate 2 from 4, providing evidence that in childhood do exist at least two different systems for the representation of high and low numbers (Xu, 2003). With the same paradigm, Cordes e Brannon (2008) tested numerosity perception in 6-months-old toddler by using a relatively high range of numbers (7 vs. 21).

The majority of the children preferred the new stimuli than the familiar (Cordes & Brannon, 2008).

Moreover, Feigenson demonstrate that 7-months-old children were able to estimate the numerosity of the stimuli also if they were displayed in different colours, geometrical patterns, or textures (Feigenson, 2004).

More directly, Wynn (1992) investigated the ability of children to make calculations.

The children were placed in front of a theatre with a mobile screen; and while the infants looked at the scene, the researchers placed in the theatre’s stage a puppet. Subsequently they put a screen to hide the puppet and they placed a second puppet on the scene. The question was: are be the babies able to carry out the addition 1+1 and figure out that beyond the screen there were two puppets instead of just one? The results indicate that children actually looked for a longer time to the incongruent scene (just one item) relative to the correct one (two items) to indicate that 5-months-old infants are able to perform mathematical additions with small numbers (Wynn, 1992).

More recently, McCrink e Wynn (2004) used the same paradigm to extend the previous results with a more numerous sets of items (i.e. 5+5 or 10-5). In this study they tested 9-months-old children; and again the children fixated for a longer time to the "new" scenario, suggesting that they are able to perform simple mathematical operations (McCrink & Wynn, 2004). To understand what is the mental representation of numbers for young children, Berteletti and Lucangeli (2010) performed a study on 3.5 and 6.5 years old children. In the first experiment, they used numbers between 1-10 or 1-100 and children were required to perform a number-to-position task (line of 25 cm in A4 paper). In the second experiment, a numerical range of 1-20 or 1-10 was used to also evaluate the representation of lower numbers. In the first experiment, the children arranged numbers in a logarithmic fashion when they used the range between 1-100, but only the younger children showed this logarithmic representation with the lower range while the 5 and 6 years old children showed a linear mapping. Similar results were found in the second experiment, concerning a numerical range between 1-20. Again, younger children showed a logarithmic representation of numbers whilst 5-6 years old children map numbers linearly. These results demonstrated that the linear representation of number developed before than the beginning of formal education, and that the use of a logarithmic mapping takes place even for relatively low numbers (Berteletti et al., 2010). Across all aforesaid studies we found much evidence supporting the idea that numerical abilities are innate and precede the formal education.

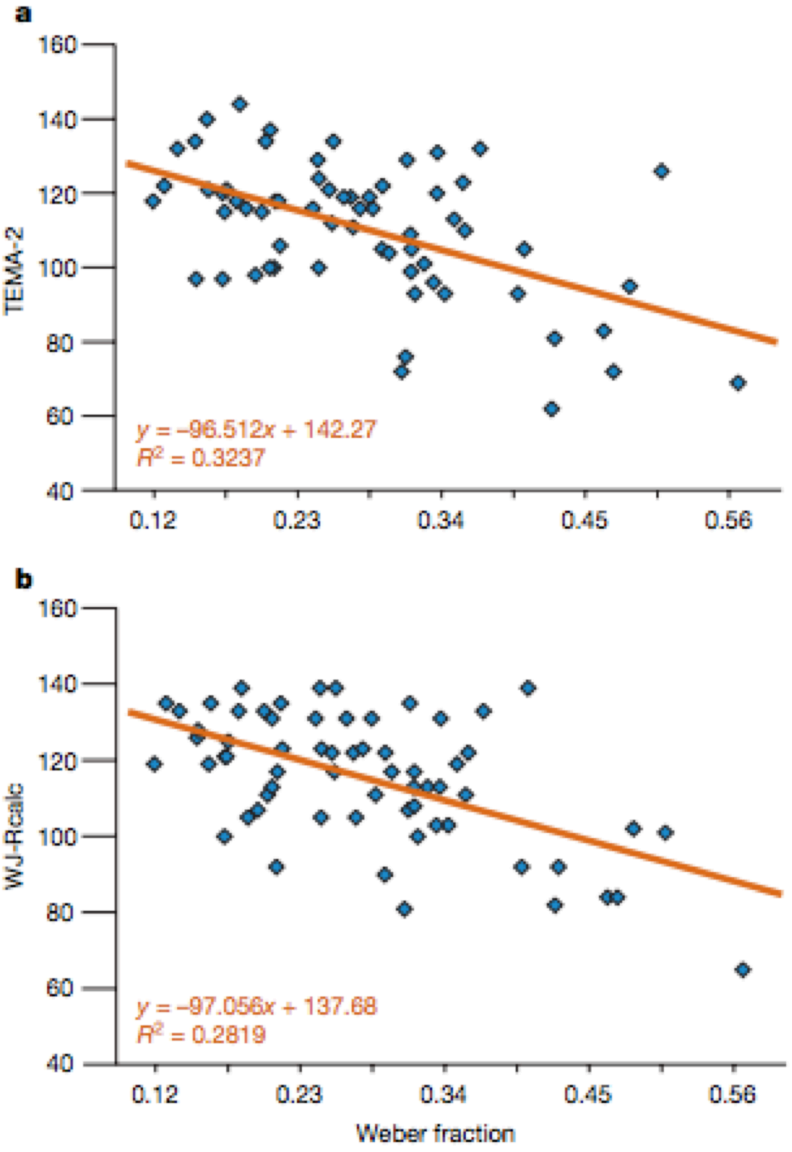
But could the accuracy of prescolar numerical ability correlates with their mathematical ability later in time?

To answer this question, Halberda and collaborators (2008), devised a longitudinal study on 64 children from 5 to 11 years old, and evaluated once every year the mathematical ability with the "early mathematical ability test second edition" (TEMA-2) and with the subtest "Numerical Reasoning" by Woodcock-Johnson (WJ-Rcalc).

Moreover they completed the RAN-colour, to evaluate the reaction time and the WASI-full for the IQ. In the test phase, subjects were represented with a set of dots presented for 200 milliseconds with stimuli representing several numerosities in two possible colours: blue or yellow. The task for the children was to simply indicate which patch contained more dots.

Despite the Authors found a high variability between the participants, mathematical skills were found to positively correlate with estimation abilities. Interestingly, the correlation was highly specific, as numerosity acuity did not correlate with none of the others cognitive test. In few words, participants with low accuracy in the numerosity perceptual task were those showing poorer mathematical skills, and vice versa (Halberda et al., 2008).

.



<u>FIG. 6</u> – Halberda et al. experiment, (2008). Linear regression of the standard score for each subject on the TEMA-2 test (a) or on the WJ-Rcalc test (b) of symbolic maths achievement and the acuity of the ANS (w). For TEMA-2 and WJ-Rcalc, higher numbers indicate better performance, whereas for the Weber fraction, lower numbers indicate better performance.

Recently, Anobile and colleagues (2016) measured discrimination thresholds of school-age (6-12 years-old) children in 3 tasks: numerosity patterns (24 dots), textured patterns (250 dots) and motion direction discrimination.

In all tasks the thresholds improved with age, but at different rates, implying the action of different mechanisms.

In particular, in the younger children, the thresholds were lower for sparse than textured patterns, suggesting earlier maturation of numerosity mechanisms. Even more importantly, numerosity thresholds for sparse stimuli correlated strongly with math skills, but neither motion-direction discrimination or discrimination of texture patterns were found to significantly correlate with math abilities (Anobile et al., 2016).

Finally, Frank and Barner (2011) investigated the not-linguistic processing of number information employing Indian children that used the mental abacus (MA) to perform rapid and accurate calculation (mentally manipulating an image of an abacus). In experiment 1, children (6-16 years-old) performed addition using the MA. The results show that increasing the number of the digits, the performance decreased: percentage of correct responses was around 67% for addition of numbers with 3 digits but it dropped down to just 23% for additions of 4 digits. In experiment 2, the Authors investigated the effect of motor and verbal interference on the calculation: the subjects made a finger tapping or they listened and repeated a story during the calculation task. The results showed that many participants were still able to perform the mathematical operations. In the experiment 3, they presented an abacus image to expert or not-experts subjects. The results suggest that untrained control participants perform in ways that are remarkably similar to MA users, giving evidence that MA expertise does not fundamentally alter the method of representation of the abacus image.

Instead, based on these results, they conclude that MA representations are optimally designed to exploit pre-existing visual representations (Frank & Barner, 2011).

1.1.3 Behavioural experiment in indigenous populations

To understand whether numerical skills are innate and independent from language, from a different point of view compared to the already discussed research on preverbal children and animals, another line of studies tested indigenous populations.

Some indigenous populations have a particularly poor vocabulary for the numerical terms, which makes them particularly interestingly for experiments in this field. A pioneering study by Pica and collaborators (2004) evaluated the numerical cognition of the Munduruku, an Amazonian population that doesn’t have words to define numbers above 5. In the first task they required subjects to indicate which set of items was larger (from 1 to 15). Aborigines carried out this task without difficulty.

Subsequently, they evaluated whether the Munduruku were capable of performing approximate operations with high numbers, using a language-independent addition task. Participants were presented with two large clouds of dots and required to estimate the approximate sum by pointing to one out of three quantities represented in different arrangements. The Munduruku performance was again remarkable (80.7% of correct answers). Finally, the Authors investigated their ability to perform subtraction. In this case the results showed that performance decreased as numbers increased with a consistent amount of mistakes when the starting number was greater than 4.

In conclusion, this population is able to compare and add approximate numbers up to 5 but struggles with exact arithmetic calculations that exceed this limit. The results support a double dissociation between a non-verbal system that uses the approximate numbers system and the numerical calculation system based on language (Pica et al., 2004).

In the same year, Gordon (2004) studied the Pirahã, another Amazon population whose counting system includes only numbers 1 and 2 whilst larger quantities are simply called "many." Even in this study, the population performed correctly in numerical estimation, but the lack of the numerical words influenced the arithmetic calculations with numbers greater than 3 (Gordon, 2004).

Izard and collaborators (2011) assessed whether in the absence of formal mathematical education it is possible to spatially map the Euclidean geometry. Izard investigated in a group of Munduruku (with a group of American and French subjects as controls) the intuitive ability to understand concepts like points, lines and surfaces. Munduruku's responses (both adults and children) were similar to those of American and French subjects revealing an intuitive understanding of Euclidean geometrical properties, even in the absence of mathematical training (Izard et al., 2011).

Finally, Butterworth (2008) compared two indigenous Australian populations speaking Warlpiri or Anindilyakwa with British subjects (control group). Warlpiri is a language that contains only generic terms such as: “single”, “double”, and “more than double”. The Anindiyakwa language has numerical categorization like “single”, “double”, “triple” and “multiple”.

Participants (young children) performed several enumeration tasks to the aim of evaluating their numerical memory, exact non-verbal addition, cross-modal matching between sounds, numerical symbols as well as the capacity to perform division.

The results indicated that the capacity to memorize numbers, to perform cross-modal matching or addition were similar to controls. This study showed that language is not a prerequisite for numerical manipulation: indigenous children have a similar performance compared to British children (Butterworth et al., 2008).

Recently, Butterworth (2011) replicates this study by investigating the estimation capacities of the indigenous population, by testing 4 and 7 years old children. In the first experiment some tokens were displayed on the ground in a given configuration and the children were asked to reproduce it. Children reproduced the arrangement without any difficulties.

In a second task, the items were covered before the test phase started, so that children were obliged to reproduce the arrangement of the tokens without any visual feedback. They were able to reproduce the configuration up to 9 tokens. Also in this experiment the results showed that the absence of a specific numerical language does not hamper the magnitude estimation skills (Butterworth et al., 2011).

1.2.1 NUMERICAL PROCESSING AND THE BRAIN

Studies about patients with brain damage highlighted the involvement of the parietal cortex in numerical processing. One of the first examples is a study by Elizabeth Warrington (1982), in which it was analysed the case of patient DRC. This patient showed a selective impairment in arithmetic calculations (dyscalculia) as a consequence of an intracerebral hematoma to the left parietal lobe. From the evaluation emerged that the meaning of individual numbers and the concept of quantity remained intact, but the patient carried out with extremely difficulty and inaccuracy operations with numbers such as additions, subtractions and multiplications (Warrington, 1982).

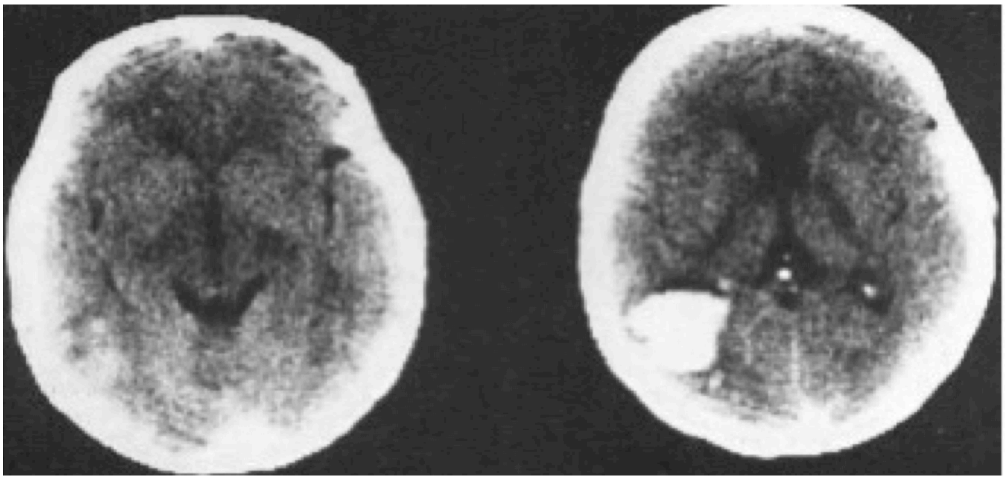


FIG. 7 ***– Warrington experiment (1982).*** The DRC's brain damage, in the left parietal lobe.

In the last few years the imaging technique such as the positron emission tomography (PET) and the functional magnetic resonance imaging (fMRI) has provided us with the possibility of unveiling which brain structures underling number calculations: to this regard, converging evidence highlighted the role of the parietal lobes combined with the precentral and prefrontal cortex. For example, Zago and Pesenti (2000) used PET to dissociate the verbal and visuospatial components involved in the computing process. Six subjects were scanned during an easy arithmetic task (one-digit multiplications) and a complex arithmetic task (two-digit multiplications).

The easy arithmetic task activated the left parietal lobe, the left frontal insula and right cerebellar cortex. The complex computation involved two distinct functional networks: the left fronto-parietal network and bilaterally the inferior temporal gyrus, both of them related to the visuo-spatial tasks (Zago et al., 2000).

Burbaud and colleagues (1999), on the other hand, investigated with an fMRI study the pattern of activation associated with mental subtraction. Eleven subjects carried out two tasks. The first one required calculation, where the numbers 13 or 17 were presented and the subject subtracted it from 500. Another task consisted in thinking a three-digits number greater than 500. During calculation, activation was observed in the left and anterior area of the prefrontal cortex, in the Broca’s area and bilaterally in the inferior parietal cortex. In the second task (without calculations) activation was mainly observed in the Broca’s area and in the prefrontal and premotor cortex (Burbaud et al., 1999).

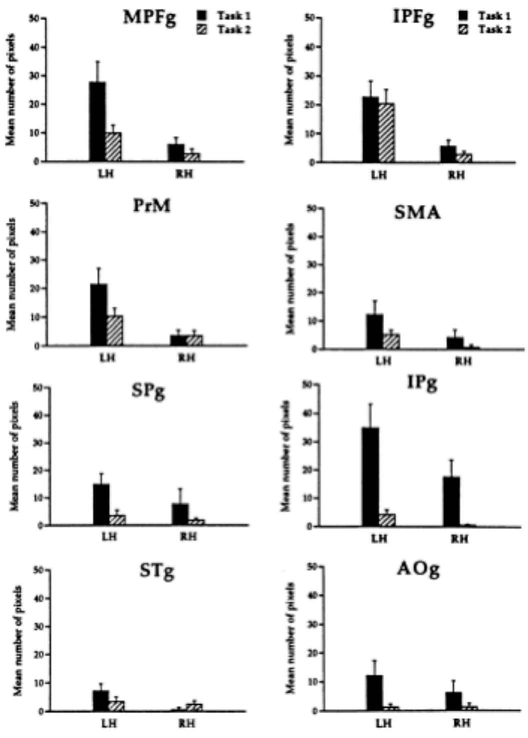


***FIG. 8* – Burbaud et al. experiment, (1999).** The area activated during the two tasks.

Recent behavioural studies showed that arithmetic requires complex processes, and many of them are not exclusive to numerical processing. For example, most language studies suggest that verbal processes play a role in calculations, but not in numerosity approximation. This topic has been investigated by, Spelke and Tsivkin (2001). Three experiments investigated the role of a specific language in human representations of number. Russian and English bilingual college students were taught new numerical operations (Experiment 1), new arithmetic equations (Experiments 1 and 2), or new geographical or historical facts involving numerical or non-numerical information (Experiment 3).

After learning a set of items in each of their two languages, subjects were tested for knowledge of those items, and new items, in both languages. In all the studies, subjects retrieved information about exact numbers more effectively in the language of training, and they solved trained problems more effectively than untrained problems. In contrast, subjects retrieved information about approximate numbers and non-numerical facts with equal efficiency in their two languages, and their training on approximate number facts generalized to new facts of the same type. These findings suggest that a specific, natural language contributes to the representation of large, exact numbers but not to the approximate number representations that humans share with other mammals (Spelke & Tsivkin, 2001).

Other studies observed that spatial tasks interfere with subtractions but not with multiplications, while linguistic tasks interfere with multiplications but not with subtractions. Lee and Kang (2002) used a dual-task paradigm to investigate the influence of phonological and visual-spatial features in arithmetic calculations. Retrieving phonological material significantly delayed multiplication performance but not subtraction, while recalling an image delayed subtraction tasks, but not multiplication. Clearly, these results are not compatible with the arithmetic idea of a unique representation of numbers and support to idea of a triple code (Lee & Kang, 2002; Dehaene et al., 2003). The triple code model of numerical processing assumes that, depending on the task, three distinct representational systems are recruited: a nonverbal representation system in which number is represented as a quantity; a verbal system where numbers are represented lexically,

phonologically and syntactically just like the other words; and a visual-spatial system in which an attention-dependent analysis would be carried out to process numbers. The model suggests that the three circuits coexist in the parietal lobe and capture many of the differences found in the performance for several numerical tasks. The model also proposes which brain areas might underpin the different processes: the intraparietal area (bilaterally) would represent the core of the non-verbal quantity system, activity in the left angular gyrus would represent number verbal processing and the superior parietal area would be associated to the visuo-spatial system.
Some detailed neuroanatomical studies have actually provided evidence supporting this model (Dehaene et al., 2003).

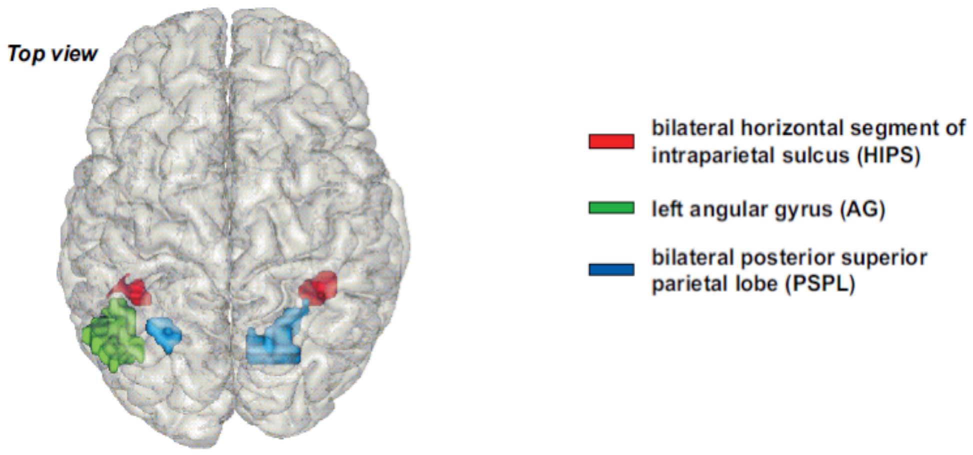


FIG. 9 ***Dehaene et al. model, (2003). –*** Key brain regions proposed to be involved in number processing: Top view perspective.

1.2.2 Quantity processing in the bilateral intraparietal sulcus

Neuroimaging studies concerning numerical processing found that the core site of activation for this ability is the horizontal segment of the intraparietal sulcus (hIPS) of both hemispheres. This region is particularly active in tasks requiring access to semantic representation of quantities as well as when subjects perform arithmetic operations. For example, in the Burbaud experiment, hIPS was found to be more active when subjects performed calculation compared to just reading numbers. Also Pesenti (2000), in a study using PET, localized the brain regions involved in numerical processing: Arabic number processing, number comparison and additions. Arabic number processing yielded a large bilateral activation of the occipito-parietal areas and a specific activation of the right anterior insula. The comparison and addition tasks revealed the involvement of the fronto-parietal network, and especially the left intraparietal sulcus, the superior parietal lobule and the precentral gyrus. Also the comparison task activated the superior right parietal lobule, while addition also activated the frontal orbital areas and the frontal insula of the right hemisphere (Pesenti et al., 2000).

Mennon and collaborators (2000), using fRMI, explored the brain areas involving in computation. The tasks (additions and subtractions) had different levels of difficulty. The authors found that hIPS activation in the right hemisphere increased if subjects calculated 2 operations instead of one (Menon et al., 2000).

Dehaene (1999) used both the fRMI and the event-related potentials (ERPs) while subjects performed exact or approximate additions.

The results showed activation in hIPS for arithmetic estimation and also tasks involving calculations (Dehaene et al., 1999).

In another fMRI study, several phonological and visuo-spatial tasks were investigated. This paradigm revealed a systematic activation of the anterior-to-posterior axis associated with all visuo-motor tasks. The computational tasks yielded two distinct activations: a bilateral activation including the anterior-mesial gyrus of hIPS and another one shared with the phonological tasks, in the left hemisphere, including the mesial hIPS and the angular gyrus (Simon et al., 2002).

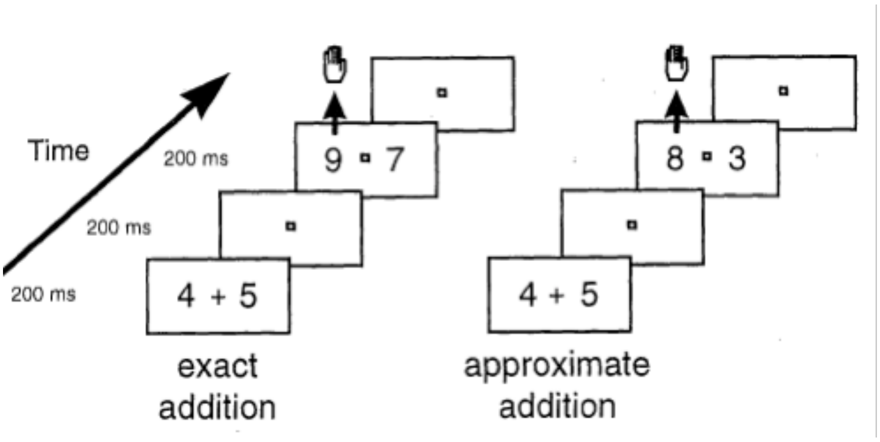


***FIG. 10* – Simon et al. experiment, (2002).** Examples of stimulus displays used in the tasks during fMRI.

HIPS was found to be also active when comparing different quantities: for instance when comparing two numbers instead of just reading them, as in Chochon's (1999) experiment. In this study, the authors used fMRI while the subjects performed several tasks: reading digits, comparing quantities, multiplication, subtraction, and reading letters.

The results showed that the prefrontal and anterior cingulate in the intraparietal circuit were activated during the numerical tasks.

The lateralization of these circuits is modulated by task requirements: during comparison, the intraparietal activation was higher in the right hemisphere, while during multiplication was higher in the left hemisphere and bilaterally during the subtraction (Chochon et al., 1999).

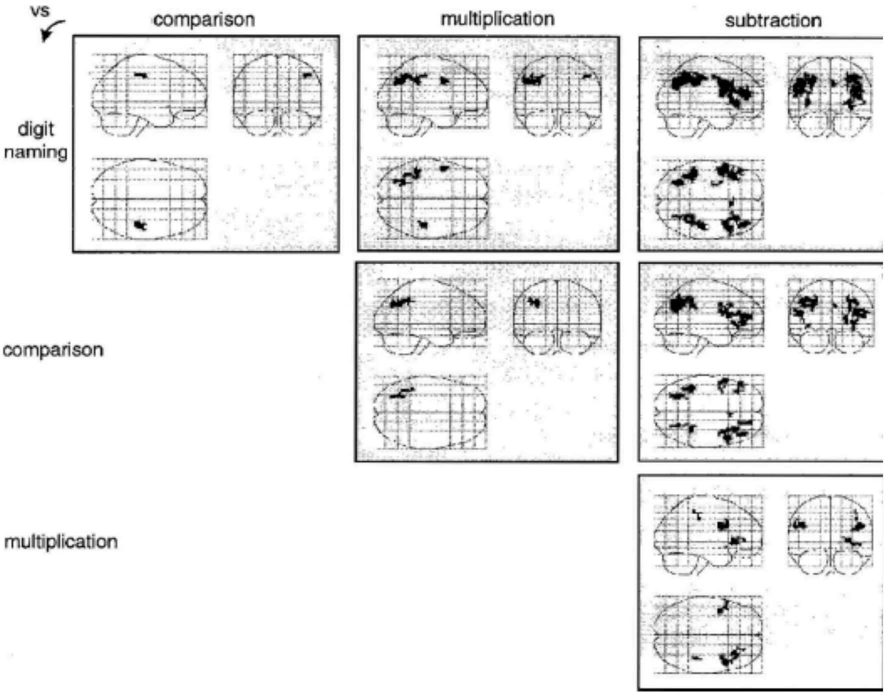


FIG. 11 ***- Chochon et al. experiment, (1999).*** Comparisons across the four numerical tasks. The glass-brain views showed the active areas for contrasts comparing any two numerical tasks ($p < 0.001$, corrected $p < 0.05$). Contrasts were masked by the corresponding contrast of the top task relative to the letter-naming control ($p < 0.001$) to focus only on activations and cancel out deactivations relative to control. Six contrasts showed significant effects, whereas the six contrasts in the opposite direction showed no significant difference.

Although in many studies the activation for numerical tasks is greater in the right hemisphere (emphasizing a possible asymmetry), reports for bilateral activations in numerical tasks are quite common.

A study by Cohen and collaborators (1996) concerning a split-brain patient strongly supported this the hypothesis of a representation of numbers in the brain in both hemispheres.

The authors tested a subject with selective lesions to half of the posterior corpus callosum. This case provided an opportunity to study the hemispherical distribution of numerical abilities in the brain and their interconnected pathways of communication. An equal-different judgment task with numbers and set of dots showed that the precise format of the digits cannot be transferred between the hemispheres, but some information about the approximate magnitudes can be transmitted. This patient was able to both recognize and compare Arabic digits displayed to the left visual field, while the arithmetic skills were severely damaged. The subject's performance was essentially normal for both, arithmetic as well as digits comparison tasks when the stimuli were displayed in the right visual field. These results support the hypothesis that both the hemispheres are both involved in identifying Arabic digits as well as in matching the corresponding magnitudes. On the contrary the verbal abilities required to name the digits and make calculations just involved the left hemisphere (Cohen & Dehaene, 1996).

More, several studies found greater hIPS activation when numerical information is compared to non-numerical information (Pesenti, 2000).

In a PET experiment, words that indicated numbers or animals were compared. The results showed that while the digits activated the right and left intraparietal sulcus, animal's names activated the inferior left temporal gyrus. The results strongly support the hypothesis that different brain regions play a role in the storage of different conceptual knowledge (Thioux et al., 2005).

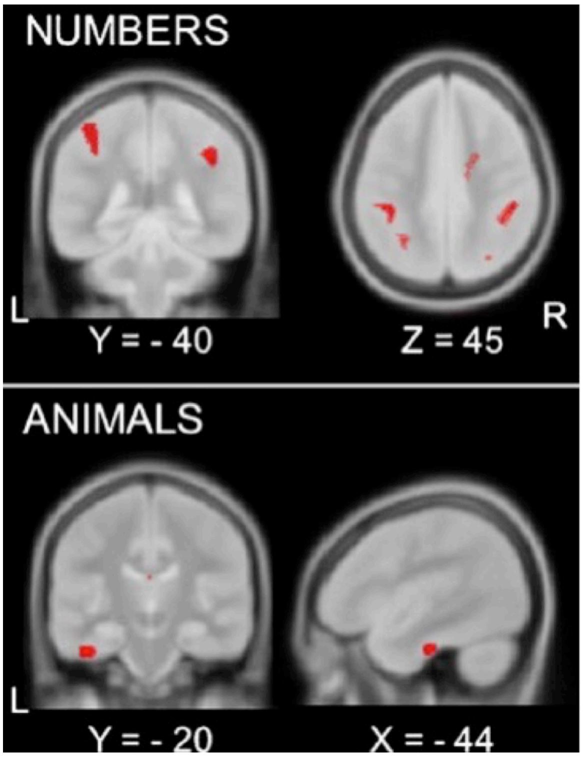


***FIG. 12* – Thioux et al. experiment, (2005).** Results of the two conjunction analyses showing task-independent activation in the left and right intraparietal sulci for numbers and in the left inferior temporal lobe for animals. The statistical parametric maps for these analyses are superimposed on the axial, coronal, and sagittal sections of an averaged normalized brain magnetic resonance imaging scan from the six subjects.

Some studies show that the activation of the hIPS is modulated by parameters such as the absolute magnitude of the numbers, and the activity of this area is higher or longer than baseline activity during mathematical operations. Kiefer and Dehaene (1997) used the ERPs technique while subjects performed multiplications and stimuli were represented via the visual or auditory modality. For both sensory modalities, it was found a huge bilateral activation of the inferior parietal area. Moreover, the results suggested that simple multiplication might involve a short-term activation of the left inferior parietal cortex, while more complex problems might require a longer processing that involve also the right homologous area (Kiefer & Dehaene, 1997).

On the other hand, the hIPS involvement seems independent from the specific format in which the numerical stimuli are presented (Arabic numerals, verbal labels or non-symbolic stimuli) a results that has been replicated in many different experiments (Piazza et al., 2002; Kiefer et al., 1997; Le Clec'H et al., 2000).

The hIPS processing of quantitative information seems to occur even when the subjects are not aware about the numeric symbols presented. In 2001, Naccache and Dehaene used the priming technique to investigate the coding of numerical quantities in the human brain. They recorded ERPs while subjects performed a task with conscious or subliminal numerical stimuli. The results indicated that hIPS encoded number in both, conscious and unconscious conditions (Naccache, 2001).

In conclusion, much evidence support the idea that hIPS encode abstract magnitude representations concerning the numerical magnitude of the stimuli, rather than the numeric symbols themselves.

Neuropsychological studies also confirm the existence of distinct semantic systems for numerical quantities and their relation to the intraparietal sulcus. There are few single-case studies that indicate that numbers are processed in different areas compared to other semantic words categories. On the one hand, patients with dementia could have widely impaired semantic processing but unaltered computation. These patients had damages in the left fronto-temporal cortex, but with an intact intraparietal sulcus (Butterworth et al., 2001). On the other hand, Cipollotti reported a case with a left parietal lesion with a complete deficit in numerical processing tasks, except for numbers from 1 to 4. This subject, conversely, retained the linguistic and semantics functions (Cipolotti et al., 1995).

In case of extremely severe brain damage even the ability to perform simple calculations (like 2 + 2) can be seriously compromised. Experimental data suggest that such a deficit is likely to be due to difficulties at the processing level, in which abstract information analysis is performed. Indeed these patients are still able to understand and produce numbers in different formats whilst, on the contrary, they showed severe difficulties in processing numerical stimuli across several format and sensory modalities. These kinds of problems did not arise from impairment at the level of the concept of numbers but at the level of the arithmetic procedures.

It is eventually worth to be noted that in most cases, these patients show deficits that transcend calculation itself and generalize to other number related task such as the bisection or comparison task.

For example, Dehaene (1997) analysed two patients: one with left subcortical lesion and the other with right inferior parietal lesion. Both of them suffered a pure anarithmetic condition: they could read Arabic numbers and write them, but they have severe problems in calculation. Extended analyses, however, showed distinct deficits. The subcortical case suffered from a selective deficit in the knowledge of verbal memories that included multiplication tables (but was not specific to these tasks) while semantic knowledge about quantities was intact. In contrast, the inferior parietal case suffered a category-specific damage on the numerical knowledge, particularly severe for subtraction, but the knowledge of arithmetic facts was preserved (Dehaene & Cohen, 1997). In many patients, damage in arithmetic tasks often coincides with other deficits, forming a cluster defined as Gerstmann's syndrome, which includes agraphia, fingers agnosia and left-right disorientation.

As Meyer (1999) observes in H.P. patient, the Gerstmann’s acalculia have lesion typically centred deep in the left intraparietal sulcus, (Mayer et al., 1999).

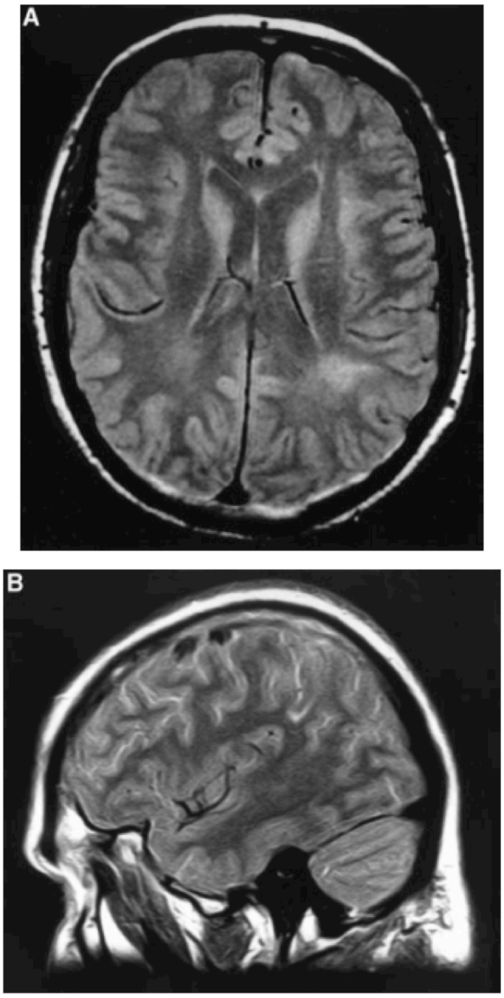


FIG. 13 – Mayer et al. experiment, (1999). MRI axial (A) and sagittal (B) sections of H.P.’s brain showing the left subangular ischaemia.

1.2.3 Verbal numeric manipulation in the left angular gyrus

Many neuroimaging studies found activation in the left angular gyrus (AG) for numerical processing tasks.

This region has a left lateralization and it is localized at the level of the inferior and posterior HIPS.

The literature about which types of tasks activate this area, suggest this area to have specific functional properties relative to the intraparietal sulcus. The left AG is likely not to be involved in the processing of non-verbal quantities, but it is strongly activated when the task involves linguistic features. Indeed the triple code model suggests that this region is part of the linguistic system and contributes to numerical processing.

Actually some operations (for example, multiplication) require a strong verbal numerical encoding, moreover the left AG is not only involved in calculations, but also in different types of speech-mediated processing like the short-term reading (Price, 1998). The experiment of Simon and co-workers (2002) noted that the angular gyrus was the only parietal site where there was an overlapping between phonemic computation and detection, which indicates that the left AG is not specific to calculation but combines arithmetic and linguistics processes (Simon et al., 2002). Several studies find an AG modulation in relation with the verbal requests of the task. For example, in the experiment of Dehaene et al. (1999) the AG was more active for exact calculations than for the approximation.

This is in line with behavioural data that indicates that exact arithmetic is stored in a language-specific format, while the approximate notions are language-independent (Xu & Spelke, 2000).

Furthermore this area shows a greater activation for operations that require the use of verbal memory (such as multiplications) rather than operations that are not stored and require some quantity manipulation. For example, Gruber and coll. (2001) performed an fMRI study and observed that the left AG activation increase during multiplications and divisions, but not in linguistic control tasks that activated the superior parietal lobule (Gruber et al., 2001).

In addition we could mention the Fulbright (2000) fRMI study, in which subjects carried out comparison and multiplication tasks. The left AG is more active during the multiplication than during the comparison (Fulbright et al., 2000).

Finally, Chochon (1999) showed that AG was more active if multiplications are made instead than subtraction or comparison tasks (Chochon et al., 1999).

Further investigations showed that this area was more active for simple problems than for complex one.

In particular Stanescu-Cosson (2000) fMRI and ERPs study, investigated some exact and approximate computing task, with high or low set of numbers. During the approximate calculation, the activated areas were the intraparietal area, the precentral area, the lateral region and the superior prefrontal region, while during the exact calculation the most active areas were the left inferior prefrontal cortex and bilaterally the angular gyrus.

As the size of the number increased, there was an increase in intraparietal regions involved and in the superior front gyrus. During the arithmetic operations with low numbers there was a greater activation of the left angular gyrus.

Probably the simple calculations (one-digit multiplications) are stored in verbal memory, while more complex calculations were more often solved using various semantic processing strategies (Stanescu-Cosson et al., 2000).

In conclusion, the contribution of the left angular gyrus in numerical processing could be related to tasks involving the linguistic bases of arithmetic. His contribution is likely to be essential to retrieve facts stored in verbal memory, but not for other numerical tasks (such as subtractions, numeric comparisons or complex calculations) that require a quantitative representation of numbers and that are most related to intraparietal sulcus.

Neuropsychological studies about acalculia reveal different functional properties of the intraparietal sulcus and of the angular gyrus, and some dissociation between various arithmetic operations.

Some patients had more difficulty to resolve multiplications than subtractions (Lee, 2000; Dehaene & Cohen, 1997), others in the reverse condition with the subtractions and not with multiplications (Dehaene & Cohen, 1997). These facts suggest that there might be dissociation between different kind of arithmetic facts and in the way in which we learn it. The multiplication involves the linguistic memory; so it requires the integrity of the linguistic numerical areas. Instead the subtractions, which are carried out through non-verbal internal numerical manipulations, would involve intraparietal areas.

Perhaps the best evidence for the dissociation between verbal or non-verbal processing in the hIPS and in the left AG come from two studies about a temporary calculation damage obtain with the brain electrical stimulation.

Firstly, the patient A.A. is stimulated in the left parietal region and in the superior temporal and frontal regions. The stimulation disturbed the calculation performance when released in the left inferior parietal region near to the angular gyrus.

In addition, the subjects performed worse in oral presentation (27%) than with a keypad (64% correct), a phenomenon that suggested a verbal coding interference (Whalen et al., 1997).

The second case used thirty patients with parieto-occipital glioma in the left hemisphere. With an intraoperative electrical functional mapping they found a double dissociation between subtraction and multiplication. The angular gyrus stimulation disturbed the performance in multiplication, but not subtraction, while intra-parietal gyrus stimulation disturbed the subtraction, but not the multiplication (Duffau et al., 2002).

The addition is a complex case because it can be solved in two ways: with memory of the basic addition operations (mostly under 10) or, similarly to subtraction, by manipulating the numerical quantities; thus, the performance is difficult to predict (Dehaene & Cohen 1997; Lee, 2000).

In conclusion, considering the neuropsychological dissociation between the different arithmetic operations we can conclude that there are two separate circuits for the numerical manipulation: one based on verbal numerical processing and one language independent.

1.2.4 Attentional process in the superior parietal system

A third active region in several tasks involving numerosity manipulation is the posterior superior parietal lobe (PSPL). This region is behind the HIPS and it is located in a mesial and superior position compare to the AG in the parietal lobe. It has been found to be active during numbers comparison (Pesenti, 2000), subtractions (Lee, 2000), number approximation (Dehaene et al., 1999) or counting (Piazza et al., 2002). It also increases its activity when subjects complete two operations instead of one (Menon et al., 2000), but its activation is clearly not specific for numbers as it has been found to play a key role in a variety of visual-spatial tasks, including hand-object grasping, attention orientation, mental rotation and spatial memory (Simon et al., 2002).

Wojciulik and Kanwisher (1999) used fMRI to determine whether different types of tasks, that required visual attention, were based on the same neural substrates. PSPL was found to be active in all tasks but as only one involved numerical manipulation, these results suggest the existence of a neural substrate common to the various functions that require visual attention (Wojciulik & Kanwisher, 1999). The Triple Code Theory suggests that this area is active when we use the attentional selection on other mental dimensions such as time or number. We also know that the representation of numerical quantities is related to a spatial representation of the numbers (mental number line), so it is conceivable that the same process of attention that is used to select the location of objects in space is the same employed when we locate a specific quantities on the mental number line.

Such attention could be particularly important in tasks requiring the selection of different quantities (Pesenti et al., 2000) or approximation (Dehaene et al., 1999). An interesting study in the neuropsychological field comes from Gobel and collaborators (2001) who test the effect of magnetic stimulation while subjects perform a comparison task with numbers between 31 and 99. In this experiment, the authors localized the right dorsal posterior parietal site like the locus where the stimulation significantly interference with performance (Gobel et al., 2001).

However, direct evidence suggesting a contribution of spatial attention in some numerical tasks was provided by Zorzi and colleagues (2002). It is well known that neglect patients perform the bisection tasks with many difficulties. When they are asked to split a line in the middle, these patients indicate a location shift on the right side, consistently with their inability to correctly represent the left side of the space.

Zorzi tested their performance in a numerical task where patients had to find the middle point of a numeric range. Patients systematically selected the wronged number selecting a higher digit than the correct one. In other words a deficit to spatial attention also affect the distribution of number along the mental number line to indicate a close link between spatial and number representation. It is worth to be noted that Zorzi's patients did not have any acaculic syndrome or other deficits in numerical tasks (Zorzi et al., 2002).

1.3.1 NUMEROSITY AND SPACE PERCEPTION

Cattell in 1886 showed the existence of a defined limit in the number of objects that are countable at a single glance. When someone sees a number of dots for a short time he is able to make a very accurate (errorless) estimation. Beyond this limit the subject could estimate the number, but with a large amount of errors (Cattell, 1886).

At the beginning of '900 century, Bourdon (1908) developed a new experimental method to reveal the basic laws of visual counting. From these experiments we did learn that when observers are presented with dots in the numerosity range between 1 and 4, the time needed to recognize them is rather identical. However, for numerosities that exceed this range both, the RTs as well as error rate consistently increase with the number of objects.

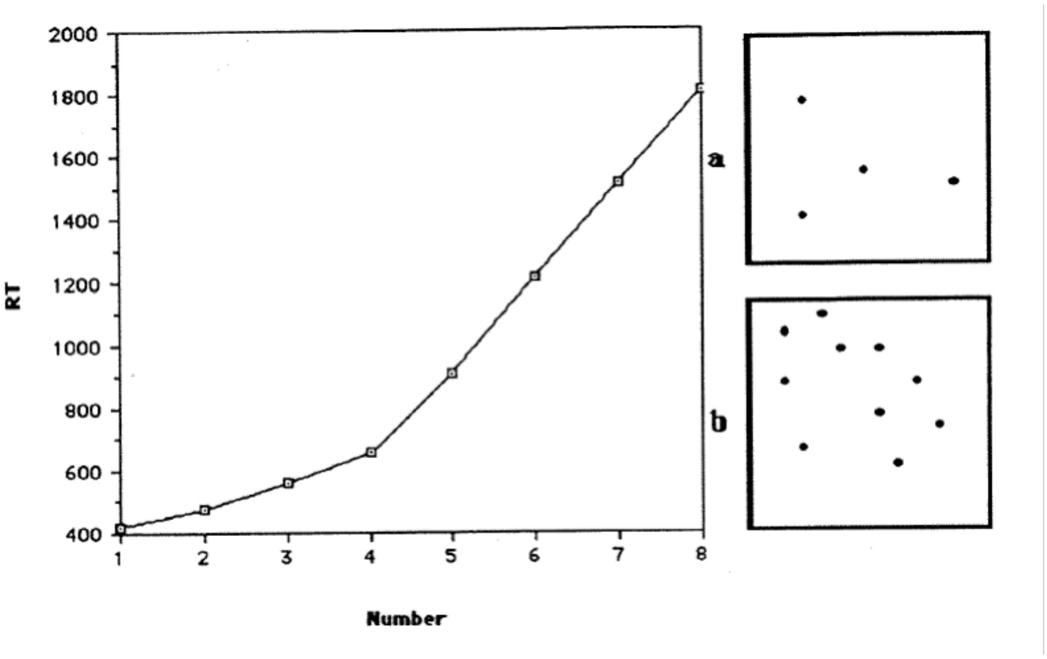


***FIG. 14* – Trick et al. experiment, (1994).** Enumerating a collection of items is fast when there are one, two or three items, but starts slowing down drastically beyond four. Errors begin to accumulate at the same point.

We now know from many experimental evidence that it takes less than half second to detect between 1 and 3 objects, about 600 milliseconds for 4 objects whilst, beyond this limit, the response time and the amount of errors increased considerably (Bourdon, 1908).

More in detail, the increment in the response time between 4 and 6 is linear, and each additional point adds a fixed duration (200-300 milliseconds) to the total time. To accurately identify sets over four dots, it is necessary to count them one by one, whilst numerosity below are accurately recognizable at a first glance. This recognition process (in absence of counting) is called “subitizing”, from “subitus”, a term that emphasizes the sudden appearance of the phenomenon. Although the subitizing is very fast, it actually takes from 400 to 600 milliseconds, that is the same time needed for complex operations such as reading loudly or recognizing a familiar face. Moreover, RTs within the subitizing range are not constant as in fact they slightly increase from 1 to 4 items.

What is the mechanism behind the subitizing? A theory suggests that we quickly recognize sets with few objects because they are arranged in identifiable geometric shapes, such as a triangle, when it comes to three objects. In conclusion, for this theory, the discrimination of numbers beyond subitizing is possible, as their arrangement cannot be linked to any familiar geometrical forms.

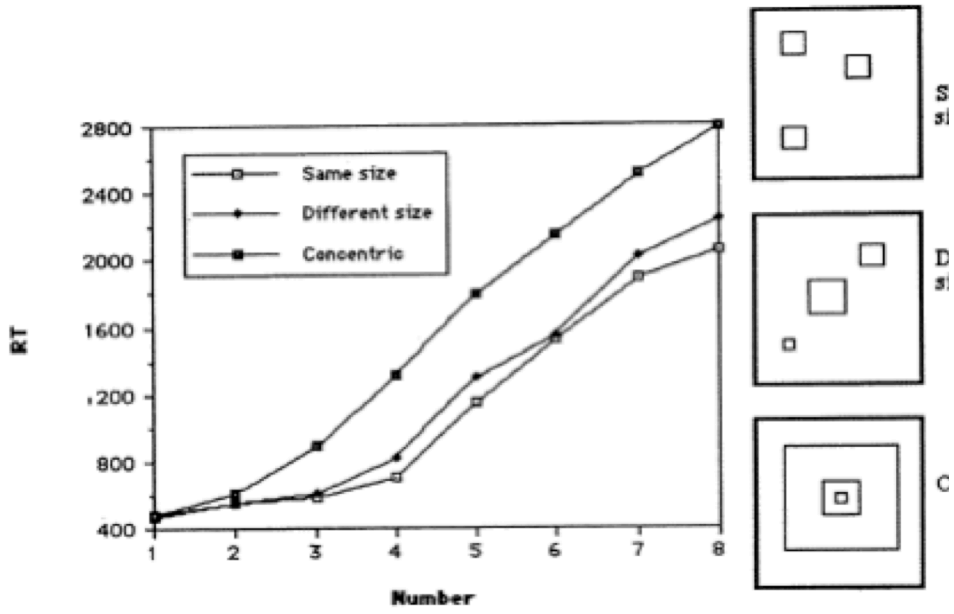


***FIG. 15* – Trick et al. experiment, (1994).** Average latencies for enumerating same size, different size, and concentric boxes. RT=reaction time.

It is quite easy to falsify this argument, as simple as to observe that we perceived the subitizing even when the objects are arranged in line or in random geometrical configurations. On the other hand Trick and Pylyshyn showed back in 1994 that it is more complex to have the subitizing effect when subsets consisting of concentric rectangles are used. The authors concluded that the subitizing requires that the objects occupy distinct positions in space (Trick & Pylyshyn, 1994). An alternative hypothesis comes from Dehaene (2010), who proposed the subitizing to be based on the ability of the visual system to locate and track objects in space. The occipital-parietal areas have neuronal populations that quickly recognize the objects location in the visual scene; this analysis is carried out independently of the size and the specific features of the stimuli.

Dehaene’s theory (2010) predicts that when we estimate objects in a setting, the occipital-parietal neurons quickly dissociate the space surrounding us in discrete objects, and then, by means of an accumulator, the approximate total amount of detected objects is calculated.
As we have previously seen, the precision of the accumulator decreases as the numbers increase, so that it becomes progressively difficult to distinguish a number “n” from its neighbours “n + 1” and “n - 1”. We can explain the effect of subitizing with this model, saying that “4” is the first number that our accumulator does not distinguish well from its neighbours “3” and “5”. Beyond this limit the accumulator continues to provide us an estimate of the number, but its precision is not enough to identify the quantity exactly: this conception is called “theory of parallel accumulation” (Hersh & Dehaene, 2010).

Gallistel and Gelman have proposed a different theory. According to that, during the subitizing subjects enumerate all the elements one by one, but with a speed such as we do not realize this process to occur. In this view, the subitizing is a wordless count, which would require to orienting the attention towards each object and would imply a serial algorithm step by step (Gelman & Gallistel, 1992).
The Gelman & Gallistel’s theory strongly contradicts Dehaene's hypothesis that we do a parallel elaboration during the subitizing, without attention, and by means of mechanisms located in the occipital-parietal cortex that extracts the objects of an image when they occupy well-defined positions.

Studies supporting Dehaene’s theory come from neuropsychological studies showing patients that, after a brain injury, become incapable of exploring the visual environment and counting single elements.

A patient, after damage to the posterior region of the brain, had vision distortions and when she described a complex image, she ignored the details and did not have an overview of the scenes. This deficit, called simultagnosia, made her unable to count, as if she always ignored a part of the dots presented.

She tried to count the stimuli, but could not direct attention to each object; during the task, she stopped with the idea of having already counted the remaining elements.

Another patient was affected by the opposite problem; he could mentally tag the objects, but counted them many times. In other words he could say that there were 15 objects whilst just 5 items were presented.

However, these patients encountered little difficulty in counting up to four objects, as with such numbers the answers were fast, safe, rather errorless. For example, the percentage of correct answers for one of these patients was 92% for three objects but it dropped down to 25% when objects numerosity was five (Dehaene & Cohen, 1994).

Recently, Burr, Turi and Anobile (2010) have carried out a study in which, by using a dual-task paradigm, it was highlighted the importance of attention in the subitizing range. It is known that in situations of high attentive loads (i.e. tasks requiring much attentive resources) as the attentional resources are limited; those assigned to perform the primary task provide an impairment in the performance in the secondary task.

Conversely, in conditions with low attentive demand, both the assignments can be carried out successfully.

If subitizing was a pre-attentive process it should not be damaged neither by tasks that require low attention, nor from those requiring a lot of attentional resources. However, the results of Burr, Anobile and Turi support the opposite idea, by showing that subitizing involve attentive resources. Even within the subitizing range, numbers up to 4, the performance in the secondary tasks worsen in the dual task condition, whilst precision (measured in terms of Weber's fractions) increased, to indicate that estimates in the subitizing range were affected by diverting some of the attentional resources to a secondary, concurrent task (Burr et al., 2010).

Despite the subitizing, every adult can estimate with a margin of uncertainty numbers higher than three and four: so we can say that beyond the boundary of subitizing dominate the approximation. Most of these approximations are veridical, although there are situations in which the estimation deviates from the exact value. For example, observers usually overestimate the number of objects arranged in a regular pattern while, on the opposite, show a tendency to underestimate irregularly distributes set. Also the context can bias numerosity estimates. For example, a bias to overestimate or underestimate a fifty dots array is found whether ten or hundred stimuli surround the target. The fact that the estimates are veridical in most cases is surprising considering that in everyday situations seldom if ever observers get feedbacks about the accuracy of their estimates.

When is it possible to have the chance to check out whether there are eighty, ninety or one hundred lentils in a jar?

Apart from this, it has been shown that a single exposure to the exact numerical information robustly improves the estimation ability (Krueger & Halloford, 1984). Our perception of large numbers is influenced both by a distance effect then by a magnitude effect and for these phenomena there is an incredible mathematical regularity. Suppose that a given person can discriminate, with an accuracy of 90%, a set of 13 dots from another reference set of 10 dots (hence, a numerical distance of 3). Let us now double the size of the reference set to 20 dots. What is the delta in numerosity needed get again 90% of correct discrimination?

The answer is quite simple: the numerical distance has to be doubled to become 6, and thus the test numerosity has to be equal to 26 dots. When the reference number doubles, so does the numerical distance that humans can discriminate within a fixed level of performance. This multiplication principle is also known as the “scalar law” or “Weber’s law”. It is remarkable to note that in the approximate perception of numerosity, humans are behaviour similarly to simpler animals such as rats or pigeons.

1.3.2 Symbols or quantities?

Human unlike other animals, uses arbitrary symbols such as Arabic digits, which are discrete and formally manipulate elements. It is a widely held belief that humans mentally represent the meaning of the digits with perfect precision. If so, the invention of mathematical symbols would have freed us from a vague representation of numbers. However, such intuition is wrong. Despite numerical symbols allow us to develop a rigorous algebra; they are not immune from approximation processes. The brain treats numeric symbols as a continuous quantity and the higher the digits; lower the precision of the representation. Transforming symbols into quantifiable amounts implies a cost in terms of processing time of our mental operations. The first demonstration was obtained in 1967, when Moyer and Landauer (1967) recorded precisely the time taken to decide which of the two digits was greater. Participants were represented with pairs of numbers and were asked to indicate which side was the biggest. The results showed that this elementary comparison takes nearly half second and is not immune to errors. Indeed, when two digits represented very different amounts, subjects' response was quick and errorless. On the contrary, when two digits were close to each other, the response-times increased (by about 100 ms) and 1/10 of the responses were wrong (smallest/greatest.) Additionally, by keeping the same distance between the numbers, the reaction times increased as the number increased, so it was easy discriminate 1 from 2, but it was a bit more difficult compare 2 and 3 and much more difficult choose between 8 and 9 (Moyer & Landauer, 1967).

Dehaene (1996) investigated the possibility of training students to evaluate if they could overcome the distance effect. The task was simple: on the screen appeared on of the numbers 1, 4, 6 or 9 and students pressed the right key if the number was greater than 5 or the left key if it was smaller. After several days of training and after 15000 trials, the participants were still slower and made more mistakes with numbers 4 and 6 (those closer to 5) than with 1 and 9 (Dehaene, 1996). A possible explanation for these results is that human brain stores the numbers in a continuous representation, and this spatial displacement (with all the relative constrains such as distance amongst numbers) is retrieved when observers are presented with numbers. For example, from a rational point of view, to decide whether 85 is higher than 74 it would be sufficient to examine the first number, because 8 is greater than 7. Counter-intuitively our magnitude system does not work this way. Indeed by measuring the time taken to compare 74 with the others numbers, it has been found a perfectly continuous curve with response times and error rate that monotonically increase with number distance.

In other words, time increases as the number to compare gets closer to the reference number, so it takes more time to decide that 85 higher than 74, rather than 89. In conclusion, all the studies dedicated to the number representation are congruent in suggesting that we represent numbers globally and then we subsequentially transform the digits into a continuous internal representation. This way when we have to compare two numbers, the comparison concerns numerical quantities but not the symbols they are represented by.

When we evaluate numbers, we do not use a linear scale, but we tend to compress the bigger numbers in a limited space; in other words, we represent the quantities according to a logarithmic gradient: the accuracy and rapidity of calculation decrease as the numbers analysed increased. To test this hypothesis, some experiments have been carried out on subjective reports. For example, choosing which number looks closer to 5 between 4 and 6, many individuals, even knowing that there is no difference, are brought to select the number 6 (Shepard et al., 1975). In another experiment the authors asked to the participants to randomly select six numbers between 1 and 50, and the participants had a systematic tendency to say the smaller numbers instead that the bigger one (Banks & Hill, 1974).

When we try to divide the continuous numerical into discrete categories, the intuition induces us to choose a compressed, logarithmic scale.

1.3.3 Spatial Numerical Association of Response Codes (SNARC)

Beyond the quantity information, the numbers are also strictly linked to a spatial dimension. Dehaene himself (1990) found evidence of such relation in a comparison experiments. The subjects classified numbers, less than or equal to 65. In this experiment the response key systematically varied: a group used the right hand to respond to the bigger number and the left for smaller numbers. The second group was required to do the opposite. The results were surprising indeed: when the number was bigger than 65 responses were faster when subjects had to press the right button instead than the left one. The opposite occurred for numbers smallest than 65.

These results suggest that humans spontaneously represent high numbers on the right side and small digits on the left (Dehaene, Dupox & Meheler, 1990).
The phenomenon of faster right-hand responses for large numbers and fast left-hand responses for small numbers has been called SNARC effect (Spatial Numerical Association of Response Codes) (Dehaene et al., 1993).
Much research has been dedicated to the SNARC effect in the last few years and many interesting properties of the SNARC effect have been reported. For example, the absolute magnitude of the numbers does not play a key role whilst it does number magnitude compared to the numerosity range taken in to consideration. For example, numbers 4 and 5 are associated to the right if the experiment use 0 to 5; instead on the left if the numerosity range 4 to 9.

Moreover it is not even important the hand used to provide the response, as when the subjects crossed their hands, it is still the right side to be associated with high numbers.

Numerical quantities are represented as a numerical line and different numbers are aligned mentally on this line where each position corresponds to a certain amount. We could explain the numerical distance effect because nearby numbers are represented by close positions into the line (so it is easier to confuse them). Also, this line is space-oriented: zero is on left, while the larger numbers extend themselves to the right, and it is the explanation of the response bias describe above. Is it arrangement innate or cultural dependent?

The performance of left-handers did not differ from those on the right-handers as all of them associate large numbers to the right. However when SNARC effect has been investigated in Iranian students (who had learned to read from right to left) no preferential association between numbers and space have been found even if results depend on the individual exposure to the Western culture. These results suggest that cultural influence is decisive: the association between mental number line and space seems to be bound to the writing direction. This relationship is internalized, from the childhood and became an integral part of the representation of numbers (Siegler & Ramani, 2008; Dehaene et al., 1993).

1.3.4 Quantity or density?

Some authors have speculated that when we extract the number of elements in a scene we could use features such as the density of the stimuli rather than the number itself. In 1991, Allik and Tuulmets presented a quantitative model of the number estimation of sets of points that is based on combined measures of spatial extension and density. In this model the authors assumed that each point perceived in the space hold a circular constant magnitude contour. In this way, the numerosity estimation depends from the total area covered by the sphere (“occupancy”). In the “occupancy model” if we kept constant the number, its estimate decreases with the total densities of the points and it is smaller for set of nearby dots. It is important to note that the occupancy is a combined measure of extension and density. More, the conditions in which Allik and Tuulmets theory can be applied are those where the stimuli are presented simultaneously.

According to authors for this type of stimulus, the occupancy can be calculated based on the spatial screening of the scene (Allik et al., 1991).

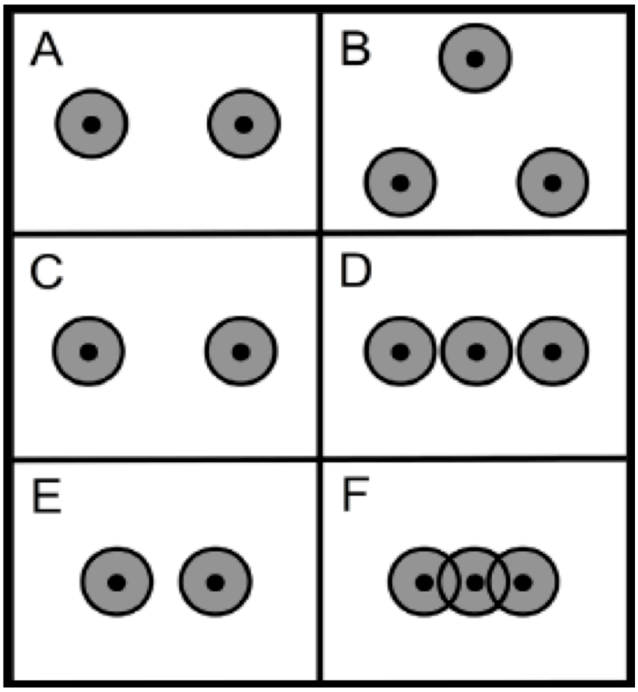


FIG. 16 – ***Kramer et al. experiment, (2011).*** Influence spheres of numerosities containing either two or three items. The black dots have a numerosity of two in Panels A, C, E, and G and a numerosity of three in Panels B, D, F, and H. In Allik & Tuulmets's occupancy model, a numerosity estimate is given by the total area (occupancy) covered by the disk-shaped influence spheres (the set-theoretical union of the gray regions, including the black dots). From Panel A to Panel B, holding density constant, numerosity and occupancy are increased by increasing the collection's spatial extent. From Panel C to Panel D, holding spatial extent constant, numerosity and occupancy are increased by increasing the collection's density. From Panel E to Panel F, holding spatial extent constant, numerosity and occupancy are increased by increasing the collection's density, but due to the resulting overlap between the influence spheres, the occupancy is smaller in Panel F than in Panel D. From Panel G to Panel H, holding the combined surface area of the dots constant, numerosity and occupancy are increased by increasing the collections density. Thus, the model's numerosity estimate is the same in Panels A, C, E, and G and in Panels B, D and H. In Panels B, D, F, and H, it is larger than in Panels A, C, E, and G, but in Panel F it is smaller than in Panels B, D, and H.

In 1995 Frank H. Durgin resumed the Allik and Tuulmets model by applying slight changes. Durgin assumed that the influence of the spheres of contour is not constant, but decreases when density increases. In line with the Allik and Tuulmets idea, quantity would be derived from the density.

To test this hypothesis, Durgin performed an experiment by leveraging on the technique of adaptation. Sixteen subjects were adapted to dense textures in a part of the visual field and were asked to compare stimuli, consisting of scatter-dot textures presented either in the adapted or unadapted locations. On one side stimuli comprised 20, 40, 80, 160 or 320 points and the density of the adapted field remained fixed while in the other field varied by 10%, 7.5% and 5%. The results showed that the adaptation produces a strong and consistent distortion in the density perceived for any set of points (from 20 to 320 points). On the contrary, for Durgin, the number by itself is not influenced (Durgin, 1995).

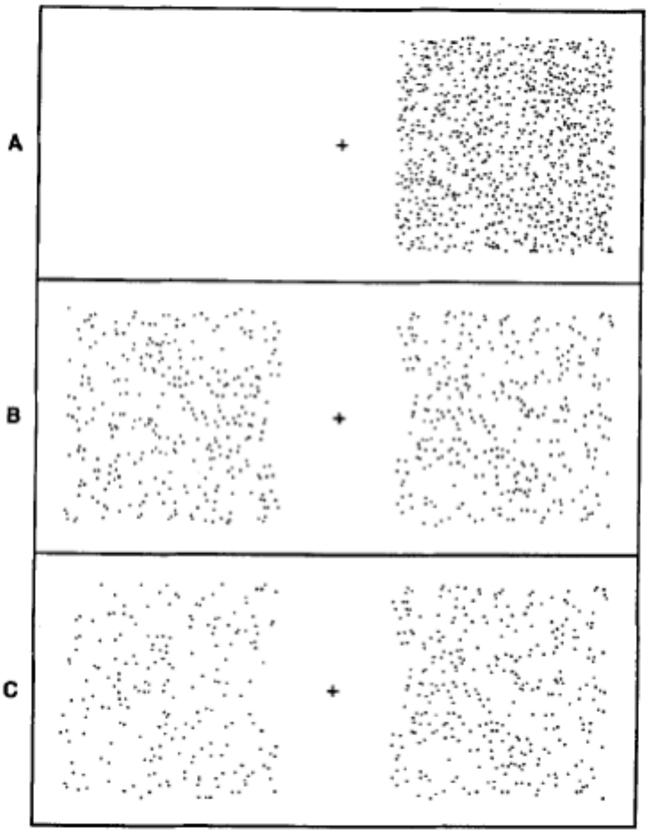


FIG. 17 ***– Durgin et al. experiment, (1995).*** Scatter-dot textures like those used for texture density adaptation. Panel A illustrates an adaptation stimulus with fixation mark. Panel B shows test fields that are objectively equal in density. Panel C represents fields that might appear subjectively equal in their numerosity after adaptation to the upper panel (the numerosity shown represent the means of the data from the current experiments: 320 dots in an adapted region were perceived equal in numerosity to 224 dots).

In 2008, Burr and Ross published an article with opposite results to Durgin. Indeed Burr and Ross demonstrated that the number is an adaptable feature such as the other visual properties of the scene (colour, size, contrast).

Four subjects discriminated the numerosity of two clouds of dots. On one side it was shown the test stimulus (variable number) and on the other side the probe (fixed number). The adaptation (cloud with 400 points) lasted 30 seconds and there was a top up of 7 secs between one trial and the other.

The results show that the adaptation strongly distorted perceived numerosity.

A second experiment employed the same procedure, but with small numbers. The results demonstrated that numerosity adaptation occurred in both directions: adapting to small numbers caused an increase in apparent number and adapting to high number decreased it. Finally, to verify that adaptation was affecting numerosity and not related factors such as density, a series of control experiments were carried out in which the size, contrast, and orientation of both test and adapter were manipulated. All the results congruently suggest that adaptation genuinely affect numerosity. The number perception is imposed immediately, automatically and without conscious control: even when we know that the numbers are the same, our brain tells us the opposite. As Burr and Ross concluded: "Just as we have the direct visual sensation of a half-dozen mature cherries, we have that of their number" (Burr & Ross, 2008).

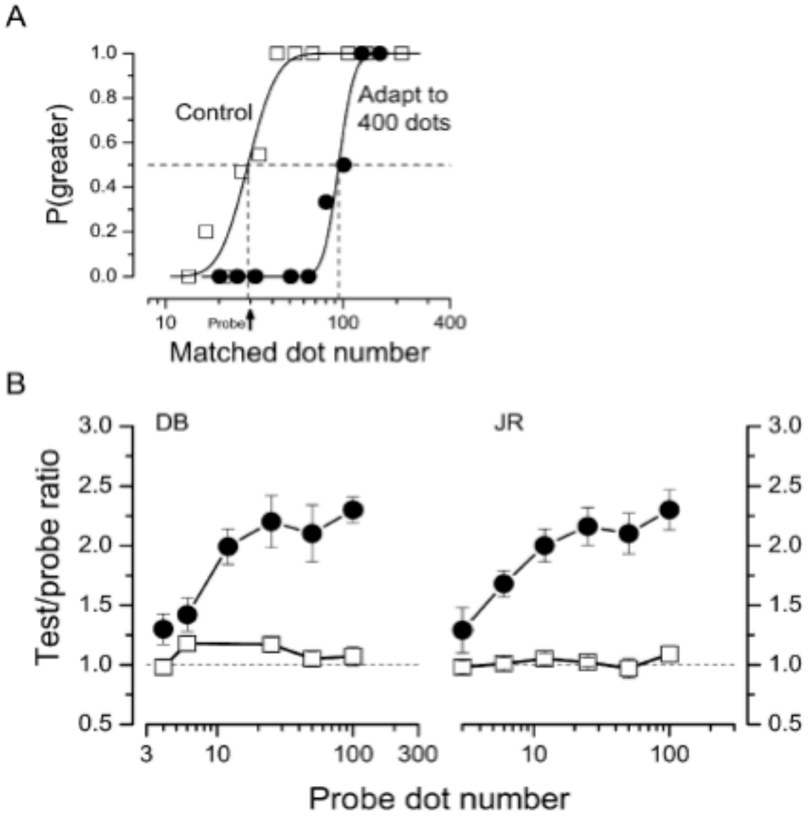


***FIG. 18* – Burr and Ross experiment, (2008).** The Effect of Adaptation on Numerosity (A) Sample psychometric functions with (filled circles) and without (open squares) adaptation, plotting the proportion of trials where the probe seemed more numerous, as a function of number of test dots. The vertical dashed lines indicate the PSE of the match, about three times higher than the probe number (indicated by the arrow) after adaptation. (B) Magnitude of adaptation (ratio of test to probe dot number at PSE) as a function of the number of dots in the probe (symbols as for Figure 1A). The error bars show ± 1 standard error of the mean (SEM), calculated by bootstrap. For a wide range of numerosities, adaptation caused a doubling of the matched number.

At odds with Durgin's hypothesis are also the results of an experiment by Kramer (2011). He proposed an innovative method to investigate the problem of density versus numerosity, keeping all the dimensions defined by a constant luminance and using second-order movement (contrast based). The author used a random number of rectangles moving with this kind of motion, and subjects estimated their numerosity.

The results show that the second-order motion estimation is possible with results very similar to those obtained with first-order motion (i.e. based on brightness) suggesting that the effect it is neither based on first-order spatial filtering, as Allik and Tuulmets suggest, nor on the perception of first order density as suggested by Durgin (Kramer et al., 2011).

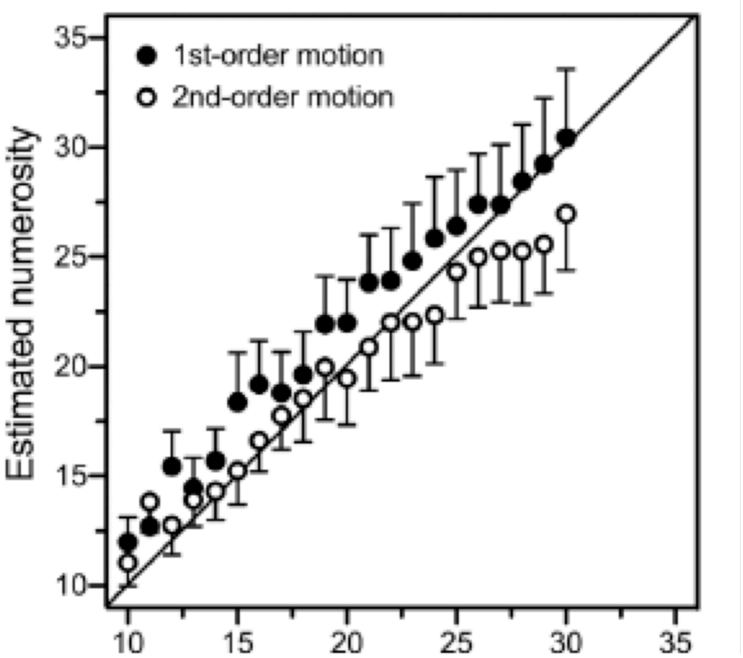


***FIG. 19* – Kramer et al. experiment, (2011).** Numerosity estimation in first-order and second-order motion. A linear-linear plot of estimated numerosity in first-order motion (filled symbols) and second-order motion (open symbols) as a function of actual numerosity.

In conclusion, to quote Brian Butterworth:

"How many spots does a hen have?"

When we look at the mantle of a spotted hen, we notice that it has many spots with a well-defined form and location, but with a quick look it is not possible to count all of them with precision, in return we can make an estimate.

How does this comparison take place?

Numerosity is a primary visual property that can be radically modified by adaptation, as the other primary visual properties of a scene.

Several studies have shown the existence of specific neurons for the number in the parietal cortex of the macaque, moreover also fMRI studies found an activation in the human intraparietal sulcus both for symbolic and non-symbolic representations of the number. These neurons are candidates for the physiological substrate of the visual sense of the number and they are adaptable. Given these assumptions, our approximate numerical estimation capabilities are no longer surprising (Butterworth, 2008).

1.4.1 –NUMEROSITY AND TIME PERCEPTION

Events are always perceived in a time line with some events ordered in sequences. Because of this we can say if an event leads or is delayed relative to another event or whether the two are synchronous. Despite this, humans do not have specific receptors to measure time. In light of this, time might not be directly evaluated at the perceptual level, to make it different from colour, luminance, shape and so forth.

Time is a complex and multi-faceted phenomenon. It is possible to evaluate how long an event lasts (duration estimate), to estimate when it occurs (time predictions) or to compare an event with another occurred before or afterwards (temporal judgment).

Both the duration estimate and the time predictions (called explicit times) require a metric representation of time, in which events can be measured on a continuous scale. Temporal judgments (called implicit times) require an ordinal time representation, in which the duration of at least two events is compared.

The tasks used to measure time are essentially of two types: perceptual discrimination, in which, for example, subjects determine whether the duration of a stimulus is greater than or equal to another or motor reproduction in which subjects reproduced time duration with a sustained, delayed or periodic motor act.

How do humans estimate time? And how and where do humans represent it in their brain?

1.4.2 Neural mechanism of time perception

A model already cited and widely used for estimates of time duration is the accumulator model (Gibbon et al., 1977; Coull et al., 2011).

In this model, a sensory signal triggers an accumulator that begins to count the impulses that are emitted by an internal pacemaker. The accumulated pulses are counted and can then be passed to the working memory for a comparison with the pulses stored in the past experience.

Although the model has been confirmed by several behavioural studies, both in humans and in animals, recently it has suffered a neurophysiological attack (none of the brain areas activity mirror the behaviour of the modules of the accumulator model) and many researchers proposed to search for a more plausible alternative. Specifically, many neuroscientists have argued that time is not represented in a centralized and supramodal timer, but rather as a property emerging from the pattern of neural discharge in some functionally specialized areas.

Some regions in the parietal lobe are involved in time analysis as well as space, both for visual and auditory stimuli. Specifically, the inferior parietal lobe plays an important role in detecting certain visual events such as the unexpected position of a stimulus, but also some kind of time analysis.

In addition, several psychophysical studies suggested that specific brain mechanisms are dedicated to detect visual time events: a link between duration and temporal frequency it is found using an adaptation paradigm.

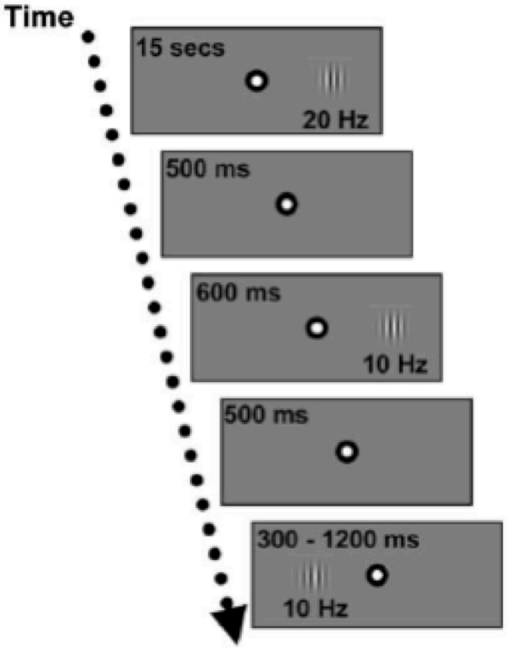


***FIG. 20* – Johnston et al. experiment, (2006).** Time course of the binary choice experiments showing an adaptation period containing an oscillating grating followed by two test intervals containing a moving grating. The subject's task was to report which test interval appeared to last longer or (in a later experiment) which had the higher temporal frequency

Alan Johnston and colleagues (2006) have demonstrated that adapting to oscillatory motion distorts apparent duration of a subsequent dynamic stimulus presented in the adapted location.
In their experiment, at the end of the adaptation phase two translating grating (test and probe) appeared sequentially to the right and to the left of a central fixation point (that is, in the adapted and neutral position respectively) with participants that had to indicate which stimulus lasted longer.
The stimulus represented on the adapted side had a fixed duration (600 ms), while the duration of the other stimulus was variable.

Both the test and probe had always a temporal frequency of 10 Hz whilst the temporal frequency of the adapter was either (20 Hz) or (5 Hz) tested in separate sessions.

The results show that adaptation to 20 Hz reduced the perceived duration of the test stimulus while adaptation to 5 Hz had relatively little effect leaving duration estimates for the test stimulus to be veridical. These results clearly imply the idea of spatially localized temporal mechanisms for visual perception (Johnston, et al., 2006).

In 2007 Burr and colleagues replicated Johnston results. However, the authors also provided evidence that the reference frame for duration perception of visual events is spatially selective in the real world, not retinotopic coordinates. Subjects were adapted to fast (20 Hz) translating gratings displayed to the left of a fixation point. After adaptation saccadic target appeared in the diametrically opposite position and subject performed a saccade on it. After 800 ms a test stimulus (again a translating grating) appeared in one of three potential positions: in the same retinotopic position (R), in the same spatiotopic position (S) or in another neutral position (C). After 500 ms, a probe (P) of variable duration appeared in a neutral location

Subjects were required to simply indicate which stimuli lasted longer.

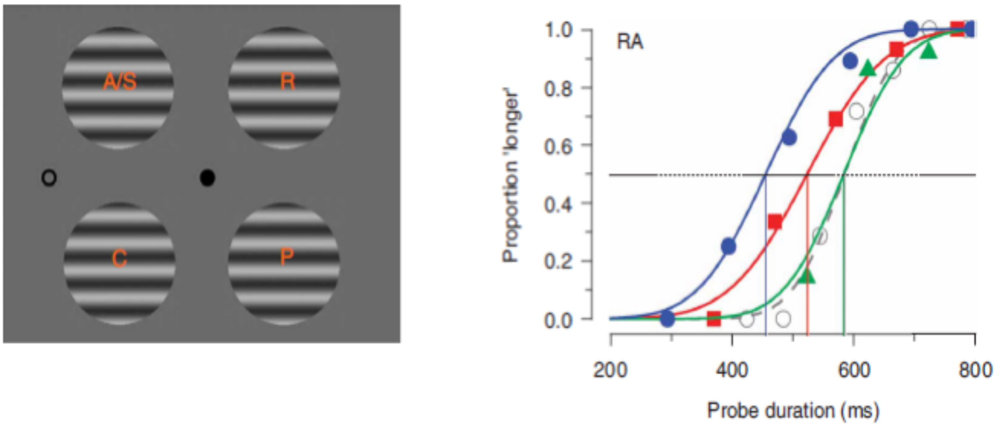


FIG. 21 **– *Burr et al. experiment, (2007).*** Illustration of stimuli and the effect of adaptation on perceived duration. On the left: Illustration of stimulus condition. On the right: example of psychometric curves for naive observer RA for the control condition (grey open circles) and for full (red squares), retinotopic (green triangles) and spatiotopic (blue filled circles) adaptation, measured with probe matched to the apparent speed of the test (Average across subjects: full 5.2 ± 0.8 Hz, retinotopic 7.1 ± 0.7 Hz, spatiotopic 9.3 ± 1.2 Hz). The vertical lines indicate the PSEs of the four different conditions.

All subjects showed a huge reduction in the perceived duration when the test stimulus matched the adapter in spatiotopic coordinates whilst the effect was almost null in the retinotopic condition. These results clearly indicate that the short-term visual events are calculated by neural mechanisms with spatially circumscribed receptors (Burr et al., 2007).

Finally, a clearly evidence of the existence of a devoted neural circuit for time visual stimuli comes from an experiment by Morrone et al (2005).

This study shows that the perceived duration (two lines presented for a short time) is distorted during saccade and the perceived order is often reversed just before the saccade. The authors suggest that this distortion of temporal perception could be related to the intraparietal neurons activity implicated in the coding of short time intervals (Morrone et al., 2005).

1.5.1 EVIDENCE FOR A COMMON SYSTEM

For features such as space and time, the hIPS selectivity declines, because for these features the intraparietal activation is not selective to distinct regions but spread all over the area.

This overlap is found not only for space and time, but also to another fundamental attribute: magnitude. For example, Pinel and colleagues (2004) investigated the neural bases of non-symbolic and symbolic numbers. They scanned with an fMRI 15 subjects while they performed comparative judgments on three dimensions: Arabic numerals, physical size, and luminance. Two large or small, dark or white numbers or letters were presented: in each trial subjects choose the largest one; moreover the reaction times were recorded. They found that all these dimensions are elaborated in the same area of the parietal cortex, specifically bilaterally in the intraparietal sulcus (Pinel et al., 2004).

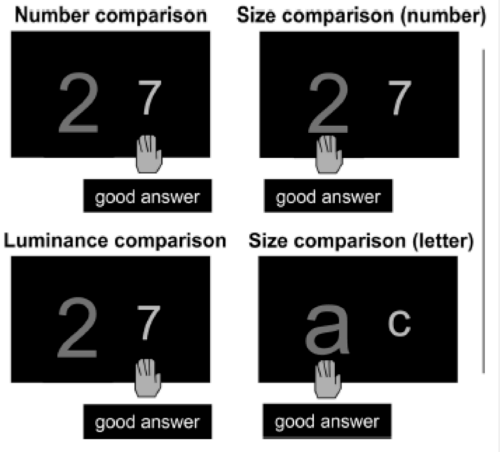


FIG. 22 ***– Pinel et al. experiment (2004).*** Examples of stimuli and correct responses for each of the four comparison tasks. Close pairs of stimuli were composed of either two small items or two large items (hence separated by a small distance). Far pairs were composed of one small and one large item (separated on average by the large distance).

The results of this study suggest that a specific area of the parietal region is active for numerical estimates; and the number is closely related to space and time.

The neurons that underpin these magnitude estimates are interconnected within the same cortex sections, and do not form distinct "modules". Far from being a problem or a surprise, these results helps to explain many observations made about the number sense. The parietal injured patients are an example of this linkage as they often they suffer of loss in the concept of number as well as of temporal judgments or sorting.

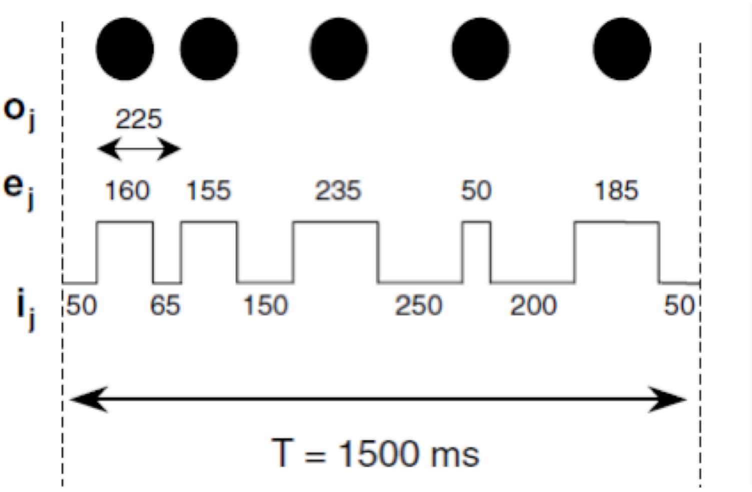
For example neglect patients with the right hemisphere damage suffered of an attentional lack towards the left side of the space, but such deficit could extend to the spatial representation of numbers (see above paragraph 1.2.4).

Indeed when asked to mark the central point of a segment, they perceive it shifted to the right but this also occur if they have to judge the position of the numbers in the number line: testing the middle point between 11-19, these patients chose a range between 17-18 and some subjects even numbers beyond the range (such as 23).

This kind of mistakes demonstrate that the mental number line is more than a metaphor and patients with damage in the spatial attention system have also a damage in the interior space system (Zorzi et al., 2002).

In the last few years, much evidence have ben gathered supporting the idea of an interaction between numbers, space, and time.

For example, large number seems to last longer on the screen than small number as shown by Valerie Dormal (2006) in an experiment where a Stroop test was used to evaluate the possible effects of facilitation and/or interference between numeric and temporal dimensions. Participants evaluated number or duration of a sequence of flashes.



<u>FIG. 23</u> – Dormal et al. experiment (2006). Temporal attributes of the stimuli shown on an example of non-periodic series with five dots and a total duration of 1500 ms (T = total signal duration; oj = event onset duration; ej = event duration; ij = interevent duration).

Thirty volunteers participated in the study, 15 in the number task and 15 in the duration comparison task. For each task, three types of stimulation were used: congruent (series with many stimuli lasted longer), incongruent (fewer series lasted longer) and neutral (fixed number). Moreover in the numerical comparison task, participants decided which series contained more points pressing one of two keys; while in the duration comparison task they evaluated which time interval was longer.

The results show faster response for congruent and neutral conditions than for incongruent in duration task on the other hand, in the numerical comparison task, there were no differences between the three conditions suggesting that duration information does not affect the number task (Dormal et al., 2006).

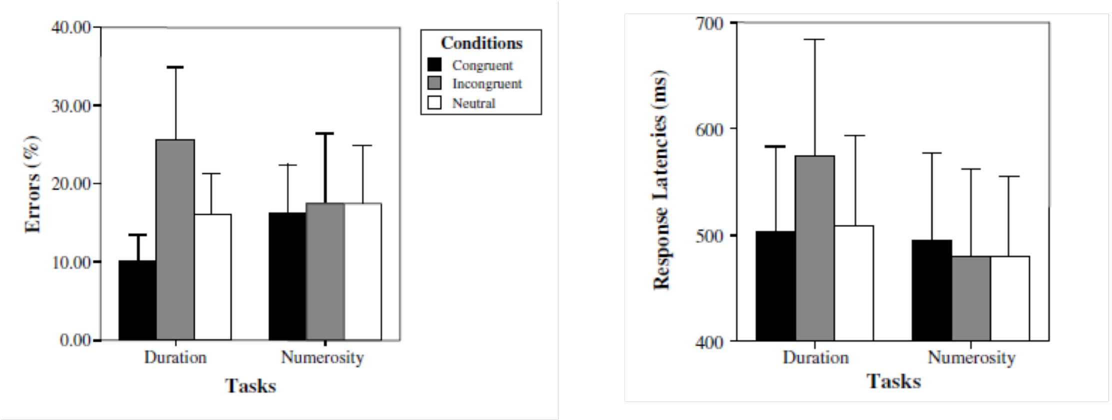


***FIG. 24* – Dormal et al. experiment (2006).** Mean percentage of errors and response latency in ms for duration and numerosity tasks as a function of condition (congruent, incongruent, or neutral). Error bars indicate the standard errors of the mean.

What is the reason for an association between time, space and number?

Brain research reveals that when we use a mental representation of numeric magnitudes, hIPS neurons are the most active, but this region is triggered also during spatial position and time exercises. Seeing a number is not only a pure abstract concept, but also an experience about concrete notions such as size, position and time.

1.5.2 A Theory of Magnitude (ATOM)

A model that has been developed to explain the link between space, time and number is Walsh's model: A Theory Of Magnitude (ATOM). The ATOM put together these three domains that show similarity (indicative of common processing mechanisms), and the roots of these connections reside in our need to have information on temporal and spatial structures of the outside world (Walsh, 2003).

According to Gelman and Gallistel, both quantities verbally numerable, such as Arabic digits, and not verbally counted, like approximate quantities (common to adult, children and animals) should be represented with the same type of mental magnitudes, because there are many concrete cases where different quantities must be combined each other for define important behavioural variables (Gallistel & Gelman, 2000).

Also Walsh takes this concept and extends it to the motor consequences of such quantity processing, and also to the transformation of it into the spatial action coordinates.

This theoretical proposal raises the question about why and how the parietal cortex, crucial for this type of tasks, should contain subregions that are important for space, numerosity, time and grasping tasks.

Cajal said, "all natural organizations, however inconstant they may seem, have a function" (Cajal, 1989).

Walsh argues that the organization of the inferior parietal cortex reflects the common need for space, time and quantity that are subsequently used in the sensory-motor transformations, which are one of the main goals of these cortical areas.

As we have already seen before, animal studies found a linkage between temporal and numerical tasks (Gibbon & Church, 1984). However, the first human studies that detected this common mechanism were about neurological patients. These studies found a clear overlap between deficits in time, space and number processing as a result of parietal lesions. On the contrary specific disorder to one of these features are extremely rare with patients with parietal lesions more likely to show combined disorders (Critchly, 1953).

As illustrated below (Fig.25), the information on these dimensions could be processed separately (a) or jointly on a common metric (b). The ATOM model supports the second kind of processing and argues that space, time and quantity are linked by a common metric already existing at birth. The inferior parietal cortex would be the common neural mechanism underlying processing of all these dimensions.

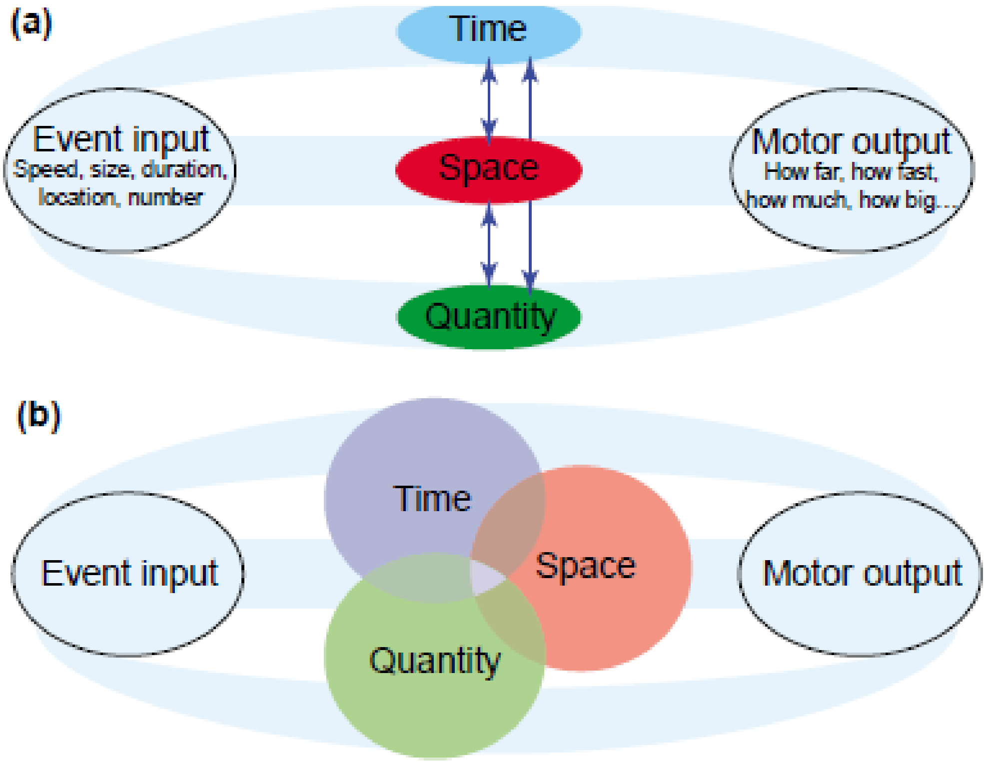


***FIG. 25* – Walsh ATOM model (2003).** Comparison of two schemas for processing time, space and quantity. The three magnitudes could be analysed separately and compared according to their own individual metrics (a), or, in a generalized magnitude system as suggested here, computed according to a common metric (b).

The connection between space and number has been analysed in many experiments.
For example Harvey and collaborator had recently demonstrated topographic maps of numerosity (Harvey, 2013; 2017), but Authors also demonstrated that the same brain regions contain maps of object size. Using ultra-high-field (7T) functional MRI and population receptive field modelling, they described tuned responses to visual object size in bilateral human posterior parietal cortex. Tuning follows linear Gaussian functions and showed surround suppression, and tuning width narrows with increasing preferred object size.

Object size-tuned responses were organized in bilateral topographic maps, with similar cortical extents responding to large and small objects.

These properties of object size tuning and map organization all differ from the numerosity representation, suggesting that object size and numerosity tuning result from distinct mechanisms.

However, their maps largely overlap and object size preferences correlate with numerosity preferences, suggesting associated representations of these two quantities.

Object size preferences in this study showed no discernable relation to visual position preferences found in visuospatial receptive fields. As such, object size maps (much like numerosity maps) do not reflect sensory organ structure but instead emerge within the brain.

Interactions between object size and numerosity maps may associate cognitive representations of these related features, potentially allowing consideration of both quantities together when making decisions (Harvey & Dumoulin, 2017).

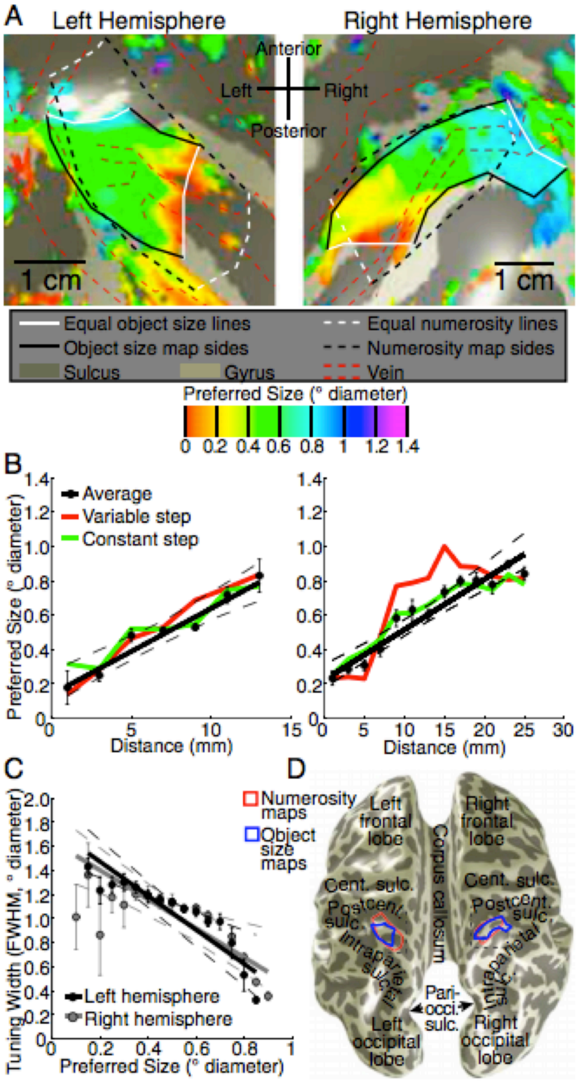


FIG. 26 – Harvey & Dumoulin experiment (2017). Topographic representation of object size. (A) Object size preferences surrounding the numerosity map (white and black dashed lines) for data averaged from both stimulus conditions. Preferred object size changes gradually between lines of equal minimal and maximal preferred object size (white lines) in both hemispheres, forming topographic maps (black and white solid lines). (B) Object size preferences progress approximately linearly along the map. Recording sites were organized by their distances from the white lines in A. The two stimulus conditions are shown as coloured lines joining condition-specific bin means. (C) Tuning width decreases as preferred object size increases. (D) Locations of object size and numerosity maps on an inflated cortical surface, relative to nearby major anatomical landmarks. Dashed boxes show the areas detailed in A. In B and C, all dots represent the mean in each bin. Error bars represent SEs. All dashed lines represent 95% confidence intervals of the fit (solid line) to the bin mean

Also the studies on time and space found a strong association between these features, proposing that spatial factors affect the perception of time. For example, De Long (1981) has developed a very interesting experiment suggesting that spatial scale is a key mediator for temporal experience and time duration. Adult subjects observed several models ranging from 1/6, 1/12 and 1/24 to the actual size. They moved a human prototypes into the model-rooms imagining them-selves to carry out appropriate activities in that space. The data presented a systematic distortion in temporal perception; indeed the duration experience is compressed on the same scale as the model, suggesting that the spatial scale affects time perception (De Long, 1981).

Instead the evidence that links time and number are mainly based on double task experiments.

Casini (1997) performed two experiments: in the first one, subjects identified the duration of two visual stimuli that changed several times their brightness during the s presentation. The second experiment used the same methodology but the stimuli had a constant brightness. The results show that brightness change increased the subjectively perceived duration (Casini & Macar, 1997). Important evidence that time and number share common resources come from three experiments carried out by Brown and colleagues (1997). The temporal task consisted in reproducing a series of stimuli presented for 2 or 5 seconds. The non-temporal tasks were: a rotator tracking (experiment 1), visual research (experiment 2) and an arithmetic task (experiment 3).

The results show that while tracking and visual tasks were not affected by the addition of the temporal task, the mental arithmetic was distorted. The mental arithmetic has been proposed to share executive functions with time estimation (Brown, 1997). Finally, Whalen's and collaborators (1999) directly investigated the relationship between time and number. In the first part, the subjects reproduced a target number (random from 7 to 25) pressing a button as fast as possible and without counting the number of pressures. The results show that subjects answered roughly correctly, and the reproduce number increased linearly respect to the target value. More, as the number increased also standard deviation increased. In the second part subjects estimated the number of points that were sequentially presented on a screen (range from 7 to 25). The results show that participants’ performance in the two experiments was remarkably similar. Indeed the number estimation was generally correct, and the average of the response and standard deviation increased as the target decreased.

Humans have a system for non-verbal number representation that is qualitatively and quantitatively similar to that of animals and pre-verbal children, as demonstrate the distance and the magnitude effects (Whalen et al., 1999).

We know that as a result of parietal injuries, a pure temporal deficit is generally less likely than a spatial or visual-motor deficiency, and as Critchley (1953) notes, spatial and temporal deficits often coincide (Critchley, 1953).

Some neuropsychological studies have provided further evidence that for common processing of spatial and temporal information.

For example, a patient with spatial neglect tested on estimation tasks, consistently overestimated the duration of the stimuli presented in the neglected space and underestimated the duration of the stimuli presented on the other side of the visual field (Basso et al., 1996). Moreover, in many studies, the parietal cortex is activated both in temporal and spatial tasks as well as in numerical processing (Rao et al., 2001; Simon et al., 2002; Piazza et al., 2002; Dehaene & Cohen, 1997; Chochon et al., 1999).

In addition several fMRI, PET and TMS studies showed that the inferior right parietal cortex is important for perception of time. In the study of Rao and collaborators (2001), fMRI was used to examine activation with various temporal perception tasks. The subjects carried out three tasks. In the time discrimination task two sounds were separated by 1200 milliseconds, after a pause another pair of sounds was presented and the subjects indicated if the second pair was longer or shorter than the first one. The second task was about sound discrimination in which two pairs of tones were presented and subjects had to say if the seconds were higher or lower than the first. Finally, a control condition was carried out with a sensory-motor task in which the subjects pressed a key after the presentation of two sounds presented with the same time interval. The experiment revealed a system associated with coding of time intervals and one related to the comparison of intervals. The activation of basal ganglia occurred early and was exclusively associated with the encoding within the time domain, while cerebellar activation was involved later, suggesting involvement in the process of the other tasks other than the time tasks.

Early cortical activation was observed in the inferior right parietal cortex and bilaterally in the premotor cortex for processing of time intervals implying these neural mechanisms play a role in the attention and in the temporal intervals maintenance. Finally late activation of the right lateral frontal cortex emerged during the comparison of time intervals (Rao et al., 2001). Spatial and temporal stimuli reliably activate the inferior right parietal cortex, while numerical tasks activate bilaterally the parietal lobes.

Piazza and collaborators carry out an fMRI study in 2006 in which subjects performed a task that involves time and numbers (estimated and calculation). The aim of the study was to investigate the bases of both the calculus and the approximation in the temporal domain of visual and auditory stimuli. Time sequences of alternating stimuli were presented (at the rate of one every three seconds). The task for the number estimation task was to decide which of the two categories (red/green visual stimuli or high/low tones) contained more items. In the calculation task subjects counted the number of transition between the two categories. Finally there was a control task in which subjects compared the first and last element of the sequence and decided whether they were equal or different. The results showed that the estimate increased the activity of the fronto-parietal network, lateralized to the right, and this activation is independent of the presentation mode (visual or acoustic). The count also enabled the left homologous areas, even in this case, regardless of the type of stimuli (images or sounds) (Piazza et al., 2006).

Finally, Belin (2002) with an fMRI examined the neuroanatomical substrates of the temporal discrimination of sounds.

The subjects listened to standard sound, and discriminated different sound durations. The results show that the time duration estimation with sound activate the right frontal parietal network as well as the right prefrontal cortex, bilaterally the basal ganglia and cerebellar hemispheres (Belin et al., 2002). Right parietal activation in numerical and temporal tasks has been obtained also with PET studies. For example, in the PET Maquet study (1996), subjects performed one of three tasks: comparing the duration of two sequentially green LEDs, intensity comparison task and a control task. Significant increase of cerebral flow was detected during the time comparison task compared to the control task, in the prefrontal cortex, in the right inferior parietal lobe, in the anterior cingulate and in the left fusiform gyrus. An increase of the brain flow during the comparison intensity task compared to the control task was observed in the right prefrontal cortex, inferior parietal lobe, right extrastriate cortex, frontal cingulate cortex and fusiform gyrus. No significant activation was observed in the temporal task compared to intensity task. The results suggest that the temporal dimension is elaborated in the same areas of other visual attributes (Maquet et al., 1996). The study of Pouthas (2000) using ERPs and Fias (2003) using PET also confirm Maquet's results, although they add a fundamental role of the right frontal area in temporal processing (Pouthas et al., 2000; Fias et al. 2003). On the other hand, Coull's study (2011) aimed to reveal the neural bases of time and space processing take advantage of both PET and fMRI. The paradigm consisted of a manipulation of attentive cues in spatial locations and time intervals.

The data show some areas of overlapping between the neural mechanisms dedicated to space and time processing. In general, while the parietal cortex is involved in temporal tasks, the left part is important for space. These areas were bilaterally activated when the two dimensions was presented simultaneously (Coull et al., 2011). Several studies used TMS and found a functional link between time, space and number in the parietal cortex. For example, Gobel and al. (2001) used TMS, while subjects compared numbers between 3 and 99. Repeating stimulation on the angular gyrus disturbed the performance, suggesting that this area mediates the spatial representation of the number (Gobel et al., 2001).

All the aforesaid results provide evidence in favour of the ATOM theory and in particular to the existence of common mechanisms to process space, time and magnitude located in the right inferior parietal cortex. These results also seem to be consistent with Dehaene's triple code theory, which suggests that the parietal cortex in both hemispheres is essential for the representation of analogue quantities. While the right parietal cortex was identified as a critical locus for temporal, spatial, and numerical estimation tasks, the left parietal cortex would be specific to computational tasks where verbal encoding is required, underlining a possible hemispheric specialization for these different numerical tasks (Dehaene, 1992; Dehaene & Cohen, 1997).

CHAPTER 2 – A GENERALIZED SENSE OF NUMBER

2.1.1 Introduction to visuo-auditory numerosity

As reported in the previous chapter, animals, including humans, can estimate the approximate quantity of arrays of objects rapidly and relatively accurately, a finding that inspired to the concept of number sense (Deahene et al., 1998; Nieder, 2005).
Converging evidence from studies of numerical competence in normal adults, patients, infants, young children, and non-human animals made many investigators to hypothesis that a domain-specific system of knowledge, present in many species, is responsible for the sense of number and forms the basis for the complex symbolic manipulation of number developed by humans (e.g. Izard et al. 2009; Viswanathan & Nieder, 2013; Dehaenen & Cohen, 1997; Gallistel & Gelman, 1992).
We have already seen before in this manuscript that several experiments investigated processing of numbers in many different formats: numerosity of spatial arrays presented (Burr & Ross, 2008; Durgin, 2008); sequentially (Piazza et al., 2006; Dormal et al., 2006) or with tasks concerning symbolic digits (Pinel, 2004).

Most of these experiments dealt with visual stimuli, even if a small subset of them exploited auditory stimuli (Piazza et al., 2006).
However, a truly abstract sense of number should be capable of encoding the numerosity of any set of discrete elements, displayed simultaneously or sequentially, in whatever sensory modality. Some evidence exists for such a generalized number sense.

In a long series of neurophysiological experiments (single cell recordings), Andreas Nieder (2012) trained monkeys to discriminate both the number of auditory sounds and visual items within the same session. While the monkeys performed this task, the activity of neurons was recorded in the lateral prefrontal cortex and ventral intraparietal sulcus, structures critically involved in numerical cognition. Groups of neurons in both areas encoded either the number of auditory pulses, visual items, or both. The finding of neurons responding to numerosity irrespective of the sensory modality supports the idea of a nonverbal, supramodal neuronal code of numerical quantity in the primate brain (Nieder, 2012).

The same group (2006) has also found that temporal and spatial enumeration processes engaged different populations of neurons in the intraparietal sulcus of behaving monkeys. Once the enumeration process was completed, however, another neuronal population represented the cardinality of a set irrespective of whether it had been cued in a spatial layout or across time. These data suggest distinct neural processing stages for different numerical formats, but also a final convergence of this segregated information to form a more abstract quantity representations (Nieder et al., 2006).

There is also evidence from functional imaging in humans for a right lateralized fronto-parietal circuit activated by both auditory and visual number sequences (Piazza, 2006), and that right IPS is involved in processing both sequential and simultaneous numerosity formats (Dormal et al., 2010).

Recently Castaldi and colleagues (2016) developed a novel rapid adaptation paradigm where adapting and test stimuli are separated by pauses sufficient to dissociate their BOLD activity. They used multivariate pattern recognition to classify brain activity evoked by non-symbolic numbers over a wide range (20-80), both before and after psychophysical adaptation to the highest numerosity. Adaptation caused underestimation of all lower numerosities, and decreased slightly the average BOLD responses in V1 and IPS. Using support vector machine, they showed that the BOLD response of IPS, but not in V1, successfully classified numerosity in both conditions: before and after adaptation. However, there was no transfer from training pre-adaptation responses to testing post-adaptation, and vice versa, indicating that adaptation changes the neuronal representation of the numerosity. Interestingly, decoding was more accurate after adaptation, and the amount of improvement correlated with the amount of perceptual underestimation of numerosity across subjects. These results suggest that numerosity adaptation acts directly on IPS, rather than indirectly via 2 other low-level stimulus parameters analysis, and that adaptation improves the capacity to discriminate numerosity (Castaldi et al., 2016).

Anyway behavioural evidence for a common number sense is somewhat limited. Barth et al. (2003) showed that there is no measureable cost in reaction times in making cross-format judgements. They used the cross-modal task to rule out participants' reliance on a single sensory cue. They reasoned that if numerosity processing is based on non-numerical cues, then cross-modal judgments would yield poorer performance in comparison to intra-modal judgments.

The results showed that adults have any drop in performance when comparing visual and auditory stimuli, which exclude their reliance on a single perceptual representation. The Authors concluded, "that these findings provide strong evidence that abstract numerosity representations must be constructed from multiple perceptual cues" (Barth et al., 2003). An opposite results have been reported by Tokita & Ishiguchi (2012). These Authors reported that precision in approximate numerosity comparisons between simultaneous, sequential and cross-format presentations is significantly different (lower Weber fractions for simultaneous presentation), suggesting multiple mechanisms for numerosity perception in different formats (Tokita & Ishiguchi, 2012). One of the more powerful psychophysical tools for investigating perception and underlying perceptual mechanisms is adaptation (Kohn, 2007; Clifford & Rhodes, 2005; Thompson & Burr, 2009). This technique has been already applied to study numerosity (Burr, 2008; 2011). So in the present study, we decided to use adaptation to test the hypothesis of a generalized sense of number. First of all we examined the adaptation with visual or auditory stimuli presented sequentially. Then we evaluated the performance in cross-modal and cross- format numerical estimation tasks; to the aim of better define the nature of the numerical processes involved in judgments of numerosity. Finally we evaluated the spatial selectivity and the reference frame of numerosity adaptation in several different conditions (Arrighi et al. 2014).

2.1.2 Material and methods

All visual stimuli were presented on a Nokia 920 C monitor (screen resolution of 800 x 600 pixels, 32 bit colour depth, refresh rate 100 Hz and mean luminance 90 cd m^{22}), subtending 36.58 x 278 at the subjects view distance of 57 cm. Stimuli were created with PSYCHOPHYSICS TOOLBOX (v.3) for MATLAB (Brainard, 1997; Pelli, 1997) on a PC computer running Windows 7.

Auditory stimuli were digitized at a rate of 65 kHz and presented through two high-quality loudspeakers (Creative SBS 250) flanking the computer screen and lying in the same plane 60 cm from the subject. Speaker separation was around 40 cm and stimuli intensity was 77 dB at the sound source.

For the sequential studies, adaptation stimuli were pseudo-random sequences of flashes or tones, displayed for 40 ms (four frames) at an average frequency of 2 or 8 items/sec. For example, a 2-item/sec adaptor within a 40 seconds adaptation period comprised 80 pulses positioned randomly throughout the interval, with the only constraint that two pulses could not fall within 40 ms of each other. Top-up periods of adaptation were presented for 6 seconds before each trial.

Test stimuli were similar, presented pseudo-randomly within a 2 seconds interval. Visual stimuli were sharp-edged white discs of 90 cd/m^{-2} and 48 diameter, displayed 12° to the left or right of fixation (usually in screen centre).

Auditory stimuli 500 Hz, ramped on and off with 5 ms raised-cosine ramps.

Most data were collected with the technique of magnitude estimation: subjects judged the number of items (visual or auditory, in space or in time) and recorded the perceived numerosity on a numeric pad.

Test numerosity ranged from 2 to 20, but we analysed only the range 5–15. This avoided the subitizing range, and also edge effects that may arise (for example from subjects knowing or guessing that the numerosity was never higher than 20). However, analysis of the entire range test gave substantially the same results.

Subjects were familiarized with the task with 20 trials, without adaptation, during which correct feedback was given, but no feedback on any other occasion. In the estimation task, the adaptor was generally displayed to the left, followed 900 ms later by a test stimulus of same size, either in the same spatial location as the adaptor or the same eccentricity on the opposite side (insets of Fig. 27b).

We also measured adaptation using a forced-choice paradigm. Here, test and probe stimuli were presented successively after adaptation, first the test to the left (same position as the adaptor), then (900 ms later) the probe to the right (same eccentricity): subjects judged whether the test or probe appeared more numerous.

The magnitude of the standard was chosen at random (between 2 and 20), and the test chosen to differ by a random amount (range ± 7), capped between 2 and 20. As before, adaptation was to the left, first for 40 s then for 6 s top-up periods.

After we verified that the adaptation effects were proportional to the magnitude of the stimulus, we plotted the psychometric function as a function of proportional difference between standard and test (difference between standard and test, normalized by the sum of the two). This procedure gave similar results for stimuli in the low (less than 10) and high (more than 10) range.

To study retinotopic/spatiotopic selectivity (Fig. 29), we used two fixation points: F1 6° left of screen centre and F2 6° to the right. The test was always displayed 6° to the left of F2, at screen centre. The adaptor was in the same screen position as the test for the spatiotopic condition, but 6° left of F1 for the retinotopic condition. For the ‘full’ adaptation condition, subjects maintained fixation at F1 and both adaptor and test were 6° to the right.

In the first cross-format experiment (Fig. 31), adapters were alternating black and white flash sequences centred 12° in left periphery and test stimuli arrays of 0.48 dots (50% white, 50% black) within a virtual annulus abutting the region of the adaptor flashes (4° and 7° inner and outer diameters).
In the other cross-format condition, subjects adapted to an array of slowly moving (0.1°/s^{1}) black and white dots (6 or 60 in separate sessions) displayed centrally within a centred 22° diameter region. Dot size was scaled to keep constant (at 10%) the amount of covered area within the adaptation area constant.
The test was a sequence of white and black abutting annuli (diameters 11° and 14°).

A total of eight subjects participated in the study, all naive of the goals of the study, except author I.T., who participated in all experiments.

Of the naive subjects, one group of five participated in the experiments shown in Fig. 27a, four of them to the rest of the estimation experiments (figures 27b,c, 29–31), as well as to the numerosity discrimination experiment (Fig. 28).

Two extra naive subjects were recruited for the cross-format experiment with sequential–simultaneous adaptation to strengthen statistical analyses, given the high variability in this condition.

All statistical values refer to Student’s t-tests.

2.1.3. Results

We first showed that the apparent numerosity of serially presented stimuli was susceptible to adaptation. Observers adapted to pseudo-random sequences of briefly flashed visual stimuli presented to the left visual field (12° eccentricity), for an initial period of 40 seconds, followed by periods of 6 seconds re-exposure before each trial. On separate sessions, the adaptors were presented on average at 2 or 8 flashes/seconds.

Subjects then judged the apparent numerosity of test flashes presented to the same spatial region, randomly distributed over a 2 seconds window.

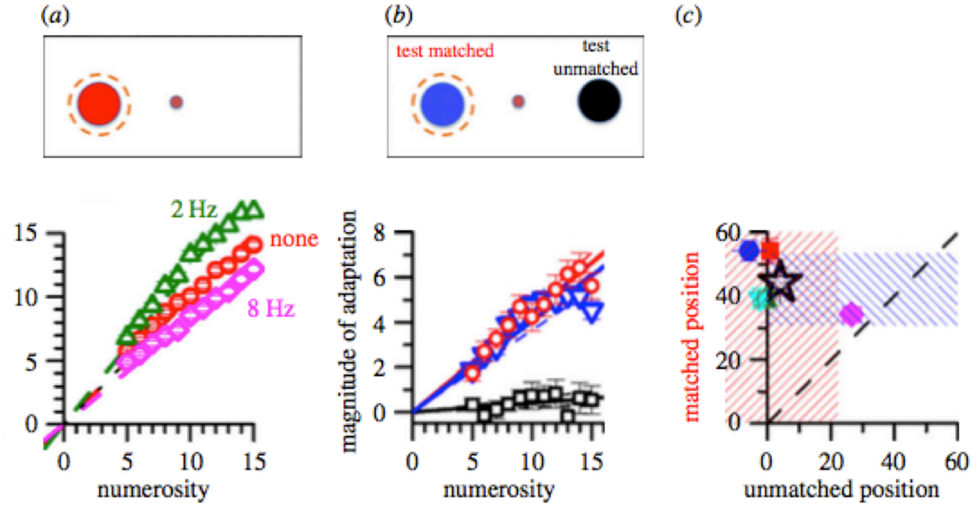


***FIG. 27* – Adaptation to sequential stimuli.** *(a) Perceived numerosity (averaged over trials and subjects) as a function of physical numerosity for the three adaptation conditions, with best-fitting linear regressions (R^2 0.98). Regression slopes: no adaptation (red symbols)=0.99; 2 flashes/s (green)=1.23; 8 flashes/s (magenta)=0.83. Only the curves for 2 and 8 flashes/s were significantly different from 1 ($p<0.001$). (b) Adaptation magnitude: perceived numerosity after adaptation to 2 Hz minus that after adaptation to 8 Hz, as a function of physical numerosity. Blue symbols are taken from the data of figure 27a. Red symbols show data when adaptor and test on the same side, black when on opposite sides, both conditions randomly intermingled. All curves are well fitted by linear regression to yield an AI, an estimate of the magnitude of adaptation. (c) AIs calculated for individual subjects for the matched condition plotted against the unmatched condition. The star shows the indexes calculated for pooled data.*

Fig. 27a plots mean estimates of numerosity (averaged over all subjects) as a function of physical number of pulses. The average estimates with no adaptation (red symbols) were quite veridical.

The data were well fitted by linear regression anchored at zero (R^2=0.99), with best-fitting slope of 0.99. Adaptation to 8 flashes/seconds systematically decreased apparent numerosity by 16% at all tested numerosities (slope of linear regression 0.83), and adaption to 2 flashes/seconds increased it by 24% (slope of regression 1.23, compared with 0.99 baseline). As the zero-anchored linear regressions all captured more than 98% of the variance in all conditions, it seems that adaptation affected all numerosities by the same proportion.

In order to obtain an index of adaptation, we subtracted the perceived numerosity after adaptation to 2 Hz from that after adaptation to 8 Hz and plotted this difference as a function of physical numerosity (blue symbols of Fig. 27b). This curve is again well fitted by linear regression (R^2=0.98) and has a slope of 0.40. We take the slope of this difference curve (multiplied by 100) as the adaptation index (AI), an estimate of the magnitude of adaptation.

If adaptation occurs at a perceptual rather than cognitive level (for example, through 'internal counting'), it should be spatially specific. To test this prediction, we adapted subjects to 2 and 8 flash/ seconds sequences positioned 12° left of fixation and tested stimuli either in the same or opposite (12° right of fixation) position, randomly interleaved within sessions.

The results are shown in the different curves (difference in perceived numerosity after adaptation to 2 or 8 Hz) of Fig 27b, separately for the matched (red symbols) and unmatched conditions (black symbols). Adaptation occurred only when test and adaptor positions were matched: the AI in that condition was 0.44 ($p_{(AI=0)}<0.0001$), comparable with the first experiment (where the test and adaptor positions always coincided), while the unmatched condition caused almost no adaptation (AI=0.04). Thus adaptation to sequential number is, like adaptation to simultaneous number, spatially specific.

Fig. 27c shows the individual data for the matched/un-matched experiment. AIs were calculated in the same way as for group data, separately for the matched position (ordinate) and unmatched position (abscissa). All except one subject showed a clear specificity for position.

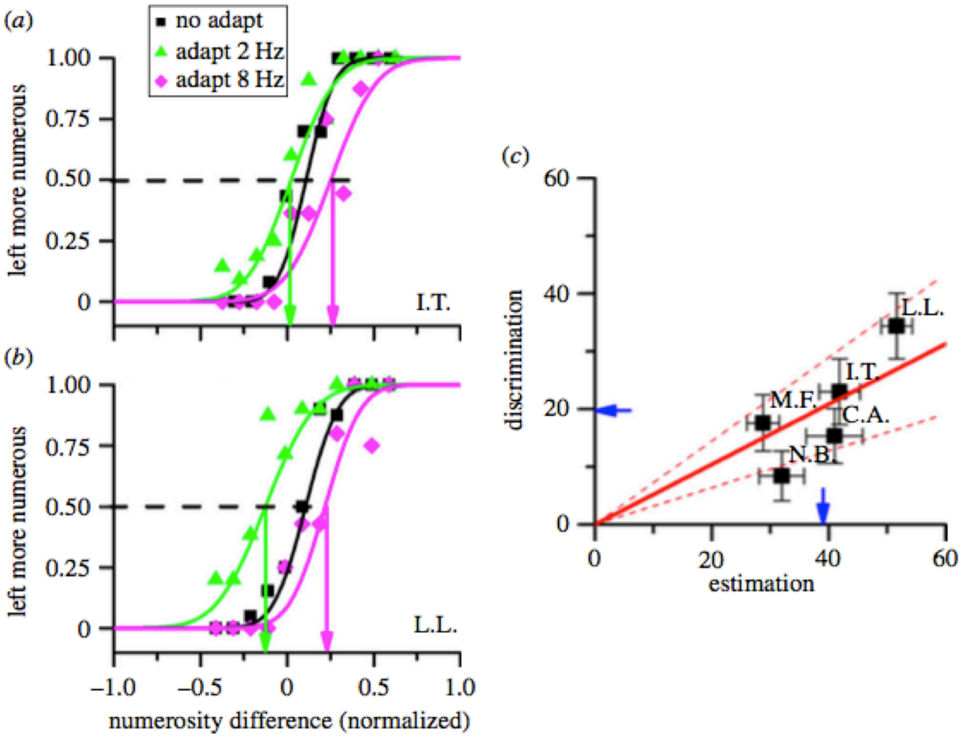


FIG. 28 – Forced-choice measurement of adaptation to sequential stimuli. *(a) Psychophysical functions for two example subjects, after adaptation to 2 Hz (green), 8 Hz (purple) or no adaptation (black). The curves plot proportion of trials when the test (falling on the adapted position) was seen as more numerous than the neutral probe, as a function of difference in normalized numerosity (normalized by the sum of test and probe numerosity). Adaptation to 2 Hz shifts the curve leftwards as subjects were biased to perceive the test stimulus as more numerous that it was, and adaptation to 8 Hz shifts the psychometric function rightwards. The point where the best-fitting curves pass 50% is considered the point of subjective equality (indicated by the coloured arrows). (b) Adaptation effect from the forced-choice comparison (difference in point of subjective equality of the 2 and 8 Hz conditions) plotted as a function of adaptation effect calculated from the naming experiment. All points are significantly different from 0, in both measures (p<0.05, bootstrap signed test). The red line shows the best-fitting zero-anchored linear regression: its slope of 0.52 suggests that the adaptation estimates from forced choice were on average one-half of those from the naming experiment. The dashed lines indicate 95% confidence interval, and the arrows near the axes the group averages.*

The spatial specificity of the adaptation allows us to employ other psychophysical techniques, such as two-alternative forced choice, similar to that used to demonstrate spatial adaptation. Subjects adapted to 2 or 8 flash/seconds sequences on the left, then two stimuli were presented sequentially, first a test to the left, then a probe to the right: subjects reported which appeared more numerous.

Average responses of 'left more numerous' were plotted as a function of the difference between test and probe (normalized to the sum of the two numerosities); to yield psychometric functions like those of Fig 28 a and b (two typical subjects).

The effect of adaptation is again clear: adapting to 2 Hz shifts the curves to the left (compared with baseline), adapting to 8 Hz to the right. The differences in the points of subjective equality (given by the 50% point of the curves) of the 2 and 8 Hz conditions again gives an index of magnitude of adaptation; in this case 23% and 34% for the two subjects. Fig. 28c plots the AIs obtained from psychometric functions against those for magnitude estimation, for each individual subject.

The data show that all subjects showed a strong and significant adaptation effect. However, the forced-choice technique tends to give a lower estimate of the adaptation effect, about half that obtained by the naming technique.

We next asked whether the spatial specificity of the adaptation was anchored in retinotopic (eye-centred) or spatiotopic (screen-centred) coordinates.

Subjects adapted to 2 or 8 flash/seconds sequences while fixating 6° left of screen centre, then saccade to 6° right of centre before the test sequence was presented. The test was always at screen centre, but in different sessions the adaptor was either in the same spatiotopic (screen) position as the test or the same retinotopic position (left of initial fixation).

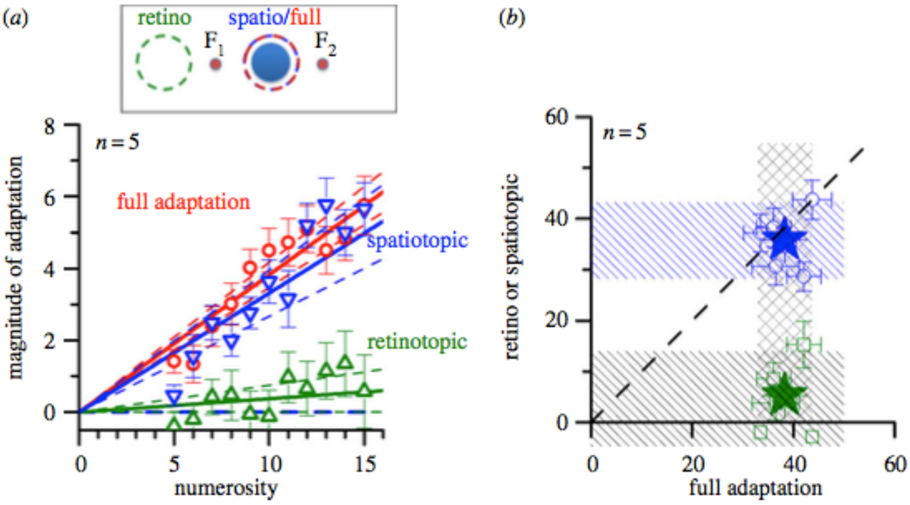
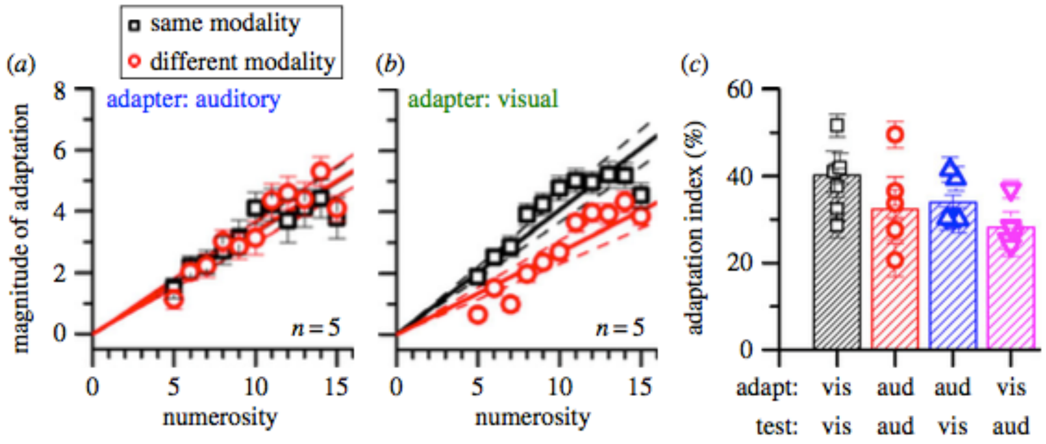


FIG. 29 ***– Spatiotopic and retinotopic adaptation.*** (a) Adaptation magnitude measured after a 12° saccade (from F1 to F2) between adaptation and test, with the adaptor in the same spatiotopic (blue symbols) or retinotopic (green symbols) position, or both (red symbols). The spatiotopic adaptation was as strong as full adaptation (no saccade), while retinotopic adaptation caused little effect. (b) Individual AIs after adaptation in the same retinotopic (green symbols) or spatiotopic (blue) positions, plotted against AIs for the 'full adaptation' condition (no saccade between adaptor and test). The dashed lines indicate 95% confidence intervals for all conditions.

Fig. 29a shows the average adaptation effect (difference between 2 and 8 Hz adaptation) as a function of numerosity. When the stimuli coincided on the screen (spatiotopic), the effect was almost as strong as the 'full adaptation' condition (when the eyes did not move): $AI_{full}=0.38$ ($p<0.001$) and $AI_{spatio}=0.35$ ($p<0.001$), not significantly different from each other ($p=0.18$). For the retinotopic condition, however, adaptation was negligible ($AI_{ret}=0.05$). Fig. 27b shows the AIs for individual subjects, plotting both the spatiotopic and retinotopic conditions against full adaptation. All five subjects showed the same effect: strong spatiotopic but little or no retinotopic adaption.



<u>FIG. 30</u> – Auditory and cross-modal adaptation. (a) Adaptation magnitude after adapting to auditory adaptors and testing with auditory stimuli (black symbols) and visual stimuli (red symbols). (b) Adaptation magnitude after adapting to visual adaptors and testing with auditory stimuli (red symbols) and visual stimuli (black symbols). (c) Bar graphs summarizing individual AIs (symbols) and pooled data (bars) for all conditions. vis, visual; aud, auditory.

One advantage of serial presentation of items is that it lends itself well to presentation in modalities other than vision, as it does not require fine spatial resolution. We therefore measured auditory adaptation to sequences of brief tones and tested numerosity estimates of both auditory and visual stimuli. The black symbols of Fig. 30a show that auditory sequences also produce strong adaptation, of the same order as the visual adaption effect (average AI=0.33). We then adapted subjects to auditory tones and tested with vision (red symbols): adaptation generalizes from audition to vision, with no significant loss in strength (AI=0.34, p=0.62). Similarly, we measured the effect of adaptation to visual sequences on the perceived numerosity of tone sequences (Fig. 30b, red symbols).

Again the adaptation effect was robust, although slightly less than the effect of vision on vision (0.28 and 0.40), possibly because audition is a more effective stimulus in time than is vision (Burr, 2009). Fig. 30c shows the adaptation effect for the four conditions, both for pooled data (bars) and for individual subjects (symbols). A crucial test for a generalized number sense is whether adaptation is possible across formats. Subjects adapted to sequences of peripherally displayed flashes (eccentricity 12°) and reported perceived numerosity of spatial arrays of dots of variable numerosity presented around the adaptation location. This arrangement of stimuli was devised to optimize adaptation aftereffects, as they seemed to be strongest in the periphery.

Adaptation to sequential stimuli strongly affected numerosity estimates of simultaneous sequences (Fig. 31a, green data points and lines), with average AIs of 0.31 (p<0.001), almost as much as for the sequential – sequential adaptation. The inverse condition was to adapt subjects to the numerosity of arrays of dots presented centrally, and test in the periphery, again on the assumption that this should elicit strongest effects. However, adaptation to simultaneous stimuli had little effect on sequential estimates. The blue symbols in Fig. 31a show the results for central simultaneous adaptors and peripheral sequential tests. Here, the average adaption index was almost three times smaller (AI=0.10): still statistically greater than zero (p=0.001), but much smaller than the symmetrical condition of sequential adaptation and simultaneous test.

We tried other versions of the adaptation test paradigm (including the same set-up as for the sequential – simultaneous adaptation), but none led to significant effects. At this stage, we cannot know whether this difference reflects a real asymmetry, or that we failed to find optimal conditions for this condition. Fig. 31b shows the adaptation effect for both cross-format conditions, with bars indicating pooled data while symbols show individual data for all subjects.

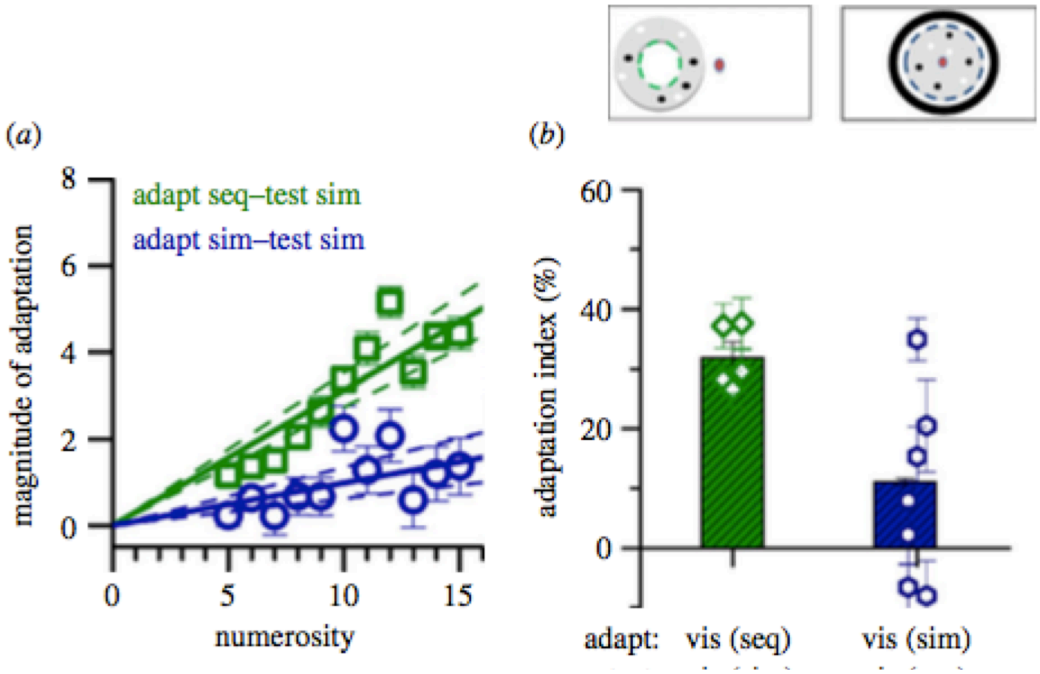


FIG.31 ***– Cross-format adaptation.*** (a) Adaptation magnitude after adapting with peripherally displayed sequential flashes and testing with peripherally displayed spatial arrays of dots (green symbols), or adapting to centrally displayed dot arrays and testing with peripheral flashes (blue symbols). The effect of sequential (seq) on simultaneous (sim) is clear (AI 1/4 0.31), but the inverse was not (AI 1/4 0.10), although both are highly statistically significant ($p< 0.001$). (b) Individual AIs (symbols) and pooled data (bars). vis, visual.

2.1.4. Discussion

The results provide strong support for the existence of perceptual mechanisms that encode numerical quantity from different senses, across space and time. Like most perceptual mechanisms, these are highly susceptible to adaptation. That the adaptation occurs across sensory modalities and across presentation formats shows that these separate ways of representing numeric information are highly interconnected, probably all feeding into one common representation of number (Arrighi et al, 2014).

That cross-modal and cross-format adaptation effects were almost as large as within-modal and within-format adaptation suggests that it is the abstract quantity system that adapts, rather than the separate systems that feed it (Arrighi et al, 2014).

It is interesting that the effect of a temporal sequence of items is spatially selective. This is reminiscent of the effect of adaptation on perceived duration: adapting a specific part of the visual field to fast motion decreases perceived duration of grating patches presented to that specific region (Johnston et al., 2006). Furthermore, adaptation of duration was selective in spatiotopic coordinates, with very little retinotopic adaptation (after compensating for effects on perceived velocity) (Burr, 2007; 2011). Similarly, we found that adaptation to sequential number was selective in spatiotopic rather than retinotopic coordinates. This is consistent with the adaptation occurring at moderately high levels of analysis, probably also related to attentional processes (Crespi et al., 2011).

Although adaptation to visual stimuli was highly spatially selective, we found clear cross-modal adaptation with spatially non-localized sounds, generated from a speaker not superimposed on the visual stimuli. Presumably, the auditory stimuli were poorly localizable in space (pure tones generated from a single speaker), and not perceived as conflictive. Under these conditions, visual stimuli dominate auditory stimuli in spatial localization, the well-known ventriloquist effect (Warren, 1981; Alais & Burr, 2004). Conceivably, if the sounds were localized more precisely in space, it would be possible to demonstrate spatially selective adaptation.

It will also be interesting to study cross-modal numerosity adaptation with tactile stimuli, which are localized spatially better than sounds.

It may be argued that sequential stimuli are not encoded as numerosity per se, but as ‘temporal rate’, and then multiplied by an estimate of duration.
This in itself would be interesting, but unlikely for several reasons.
The adaptation we report does not act at low levels of neural analysis (such as primary visual or auditory cortex, selective to temporal frequency), as it occurs cross-modally, to the same extent as within modalities.
Also the fact that the selectivity is spatiotopic, rather than retinotopic, points to high-level rather than primary sensory cortex (Crespi et al., 2011; Turi et al., 2012; D’Avossa et al., 2007).
But perhaps the strongest evidence against a temporal frequency account is that we find strong cross-format adaptation (from sequential to simultaneous), suggesting that adaptation acts on the abstract representation of numerosity, rather than indirectly via temporal rate encoding.

Of course, it remains possible that the mechanisms that encode sequential number are also involved with estimation of temporal rate, but this would not change any of the arguments advanced here.
Similar arguments have been raised about adaptation to simultaneous representations of numerosity, suggesting that it is texture density, not number, that is being adapted, and that number is perceived only indirectly, via texture mechanisms measuring density (Dakin, 2011; Durgin, 2008; Morgan et al., 2014).

Again, this does not seem likely, as much evidence suggests that number is sensed independently of density (Ross, 2010) and that the mechanisms that subserve relatively low (uncrowned) densities are distinct from those detecting higher, 'crowded' densities (Anobile et al., 2014). However, it is difficult to disprove completely the texture-density account with these types of studies. In his critique of the idea that adaptation acts on numerosity, Durgin (Durgin, 2008) suggested that 'cross-modal studies seem a more promising avenue for distinguishing after-effects of perceived number from retinotopic aftereffects in the early visual analysis of texture density. We agree completely and believe that our evidence shows unequivocally that adaption can act the abstract representation of numerosity, rather than indirectly via texture or other mechanisms.

Finally, recent findings suggest that over- and under-estimation of numerosity, in the absence of adaptation and during sequential presentation, can be achieved in the direction of those being reported here as after-effects (Lambrechts et al, 2013; Martin et al, 2017*).* In light of this it might be interesting to evaluate whether similar results are achievable by using a sequential task even in the absence of any adaptation. The idea would be to address the issue whether in these conditions; results actually reflect middle-level adaptation phenomena, as argued, or on the opposite a decisional criteria shift occurring at the level of the magnitude system. I feel like suggesting that this later hypothesis does not seem very likely. Our data suggest that in the baseline condition (without adaptation), the results for numerosity estimation were quite veridical being minimally affect by the sequential presentation.

Despite this, we still think that it would be of interest to run experiments specifically addressing whether the temporal dimension in the adaptation task is actually mediating the adaptation process (aka the rate of presentation of stimuli or tapping or the speed) as opposed to numerosity per se.

To conclude, our results fit well with the neurophysiological evidence for distinct neural representation in the intraparietal cortex, offering the interesting possibility to test this experiment with an fMRI study, for representing abstract numerical representations across modalities and formats (Nieder, 2012; Nieder et al., 2006), and also in line with psychophysical studies showing that cross-format numerosity judgements have no reaction-time or accuracy cost (Barth et al., 2003). Similar results have been reported with monkeys (Jordan et al., 2008). Taken together, all these studies argue for a generalized sense of number, quite distinct from other visual attributes, such as texture density.

2.2.1 Introduction to tactile numerosity

As we have seen in the previous paragraph we have collected evidence that adaptation affects temporal numerosity. Adapting to several seconds to a low rate (2 flashes/sec) led to perceive the sequence presented later as more numerous, while adapting to a fast sequence (8 flashes/sec) led to perceive the test as less numerous.

These studies strongly suggest that number could be regarded as a primal visual property, just like colour or shape that are similarly susceptible to adaptation, and argue in favour of a *number sense* – i.e. the ability of intuitively perceive numerosity. This number sense would process non-symbolic numerosities, regardless of the format of presentation (simultaneous vs. sequential) or the sensory modality (visual or acoustic) (Arrighi et al., 2014).

Studies on numerosity perception usually deal either with visual or auditory stimuli. However, in the last few years some researches have started to investigate numerosity in the tactile domain.

For example Gallace (2006) studied tactile numerosity in the subitizing and in counting domain.

They studied tactile numerosity judgments for combinations of 1-7 vibrotactile stimuli presented simultaneously over the body surface.

In experiment 1, the stimuli were presented once, while in experiment 2 conditions of single presentation and repeated presentation of the stimulus were compared.

The results indicate a lack of discontinuity in the slope of both the RT and error data and this in turn suggest that subitization does not occur for tactile stimuli.

By systematically varying the intensity of the vibrotactile stimuli in experiment 3, they were able to demonstrate that participants were not simply using the `global intensity' of the whole tactile display to make their numerosity tactile judgments. On the contrary participants leveraged on information concerning the number of tactors activated (Gallace et al., 2006).

In a following study (2008) the same group investigated the numerosity under condition of a bimodal stimulus presentation (visuo-tactile). In Experiment 1, they investigated numerosity judgments using both unimodal and bimodal displays consisting of one to six vibrotactile stimuli (presented over the body surface) and one to six visual stimuli (seen on the body via mirror reflection). Participants had to count the number of stimuli regardless of their modality of presentation. Bimodal numerosity judgments were significantly less accurate than predicted on the basis of an independent modality-specific resources account. These results suggested that numerosity judgments might rely on a unitary amodal system. The results of a second experiment demonstrated that costs in divided attention could not account for the poor performance in the bimodal conditions of Experiment 1. Thus, if numerosity judgments show a limitation in the amount of information that people can be aware of at any given time, this limit is multisensory in nature and not unisensory (Gallace et al., 2008).

Most of the temporal numerosity studies in which participants try to count the number of stimuli presented sequentially in a particular part of the body, have been usually performed stimulating the fingertips.

For example Lechelt (1975) presented trains of 2 to 9 signals (flashes, clicks, taps) at a rate ranging from 3 per sec. to 8 per sec. The subjects were specifically instructed to report the number of signals they were able to count. Significant modality differences were obtained. Auditory estimates were almost perfectly accurate under all conditions. Numerosity judgements of visual stimuli were found to be consistently less accurate with a consistent bias towards an underestimation. The error rate increased consistently as the rate increased from 3 per sec. to 6 per sec. but decreased for high rates such as 7 per sec. and 8 per sec. Tactile reports also underestimated the actual number of signals, the underestimation increasing linearly as a function of rate. The results showed that numerical estimates for sequentially-presented tactile stimuli were linearly related to the number of stimuli presented, and that the slope of the data fitting function was influenced by the rate of stimulus presentation. Interestingly, this result appears very similar to that obtained under conditions of visual presentation, suggesting that awareness of successive tactile events might be constrained by a temporal window of approximately 100 ms, just as in vision (Lechelt, 1975). Finally Krause and colleagues demonstrated the existence of a cross-modal semantic distance effect between symbolic and tactile numerosities. Participants received tactile stimulations on one or multiple fingers while reading Arabic digits and indicated verbally whether the amount of stimulated fingers was different from the simultaneously presented digit or not.

The larger the semantic distance was between the two numerosities, the faster and more accurate participants made their judgments.

This cross-modal numerosity distance effect suggests a direct connection between tactile sensations and the concept of numerical magnitude.

A second experiment replicated the interaction between symbolic and tactile numerosities and showed that this effect is not modulated by the participants' finger counting habits.

Taken together, this data provide novel evidence for a shared metric for symbolic and tactile numerosities as an instance of an embodied representation of numbers (Krause et al., 2013).

Here we want to extend these previous results about the relatively less-known field of tactile numerosity. First we investigated whether perceived numerosity in the tactile modality is affected by adaptation similarly to what we have reported in vision and audition. In addition we also investigated the cross-modal interactions between tactile, visual and auditory stimuli (Togoli et al., In preparation).

If the results reported in the auditory and visual modalities by Arrighi, Togoli and Burr holds true also in the tactile domain, they would provide a clear and innovative evidence of an a-modal process that process numerosity information for touch, sight and hearing.

2.2.2 Methods

14 right-handed subjects (all naive to the experimental aims of this study, less then one of the authors, IT, mean age, 27) with normal or corrected-to-normal vision participated.

Stimuli were generated using the Matlab (version R2010a) programming environment, with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). They were presented at 57 cm of distance from the subjects on a 17'' touch screen monitor (resolution 1280*1024 pixels; refresh rate 60 Hz; LG-FLATRON L1732P), on a computer running Windows 7. The auditory (digitized at a rate of 65 kHz) and tactile stimuli (tactile vibrations carrier modulated at 50 Hz) were presented through a Clark Synthesis Tactile Sound Transducer (TST429 platinum) behind the computer screen and lying in the left side 60 cm from the subject.

In separate conditions, adapting stimuli were pseudo-random sequences of flashes; tones or vibrations displayed for 40 ms (four frames) at an average frequency of 2 or 8 items/sec. Top-up periods of adaptation were presented for 6 seconds before each trial. Test stimuli were sequence of flashes, tones or vibrations (in separate session), presented pseudo-randomly within a 2 seconds interval.

Visual stimuli were sharp edged white discs of 5 cm of diameter, displayed at 8 cm from the left or right of fixation (in screen centre).

Auditory stimuli 500 Hz ramped on and off with 5 ms raised-cosine ramps, instead the tactile stimuli were 50 Hz. For all condition 30 trials was done, each for 3 times.

Data were collected with the technique of magnitude estimation: subjects judged the number of items (visual, auditory or tactile) and recorded the perceived numerosity on a numeric keypad. Test numerosity ranged from 2 to 20, but we analysed only the range 5 –15.

Subjects were familiarized with the task with 20 trials, without adaptation. The adaptor was generally displayed to the right, followed 900 ms later by a test stimulus in the same spatial location (hemifield) as the adaptor. Only in the visual condition test stimulus was presented randomly in both spatial location (same side of adaptor or at the same eccentricity on the opposite side). There are 30 trials for 5 times.

Fifteen conditions were run in the entire experiment with random combination of the different sensory modality in separate session (baseline or adaptation: visual, acoustic or tactile; test: visual, acoustic or tactile; 2 or 8 Hz).

2.2.3 Results

To test our hypothesis we used an adaptation paradigm with high (8 items/sec) and low (2 items/sec) numerosity, presented like tactile, acoustic or visual stimuli. We hypothesize that the pattern of results will follow that observed in the previous study that implied only the auditory and visual modalities (Arrighi et al., 2014). Namely we expected that adapting to low numerosity should trigger an overestimation of the test stimuli, conversely adapting to high numerosity should result in an underestimation of the test stimuli.

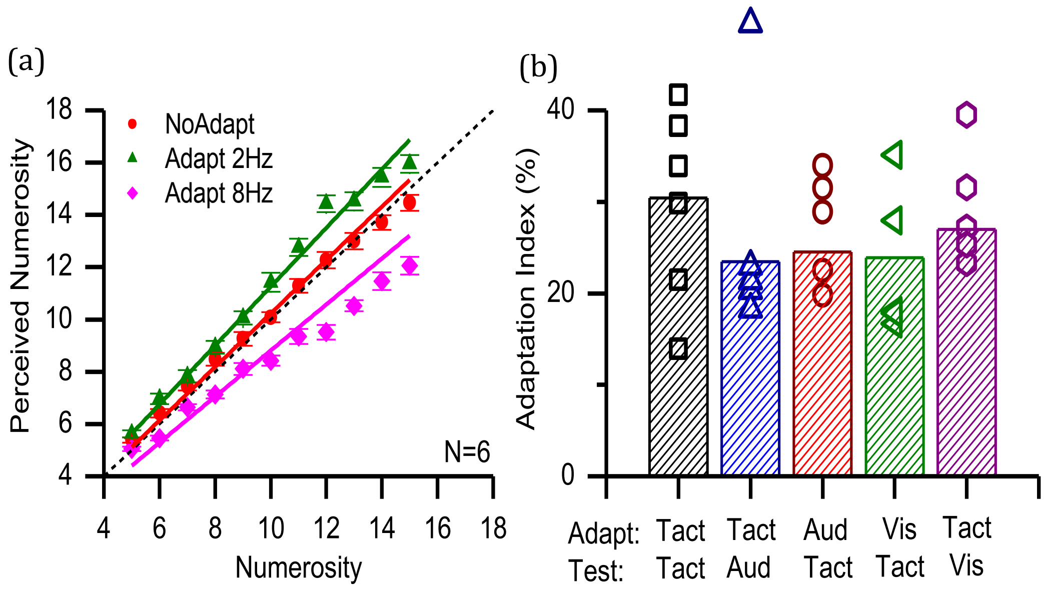


***FIG.32* – Adaptation to tactile numerosity.** *(a) Perceived numerosity in the pure tactile condition (averaged over trials and subjects) as a function of physical numerosity for the three adaptation conditions, with best-fitting linear regressions (R^2 0.99). Regression slopes: no adaptation (red symbols)=1.01; 2 flashes/s (green)=1.12; 8 flashes/s (magenta)=0.83. Only the curves for 2 and 8 flashes/s were significantly different from 1 (p<0.001). (b)* Bar graphs summarizing individual AIs (symbols) and pooled data (bars) for all conditions. Tact./Tact; Tact/Aud; Aud/Tact; Vis/Tact; Tact/Vis.

We measured numerosity by asking to the subjects to estimate the number of perceived stimuli (range evaluate from 2 to 20). Fig. 32A shows the mean estimates of numerosity (averaged over all subjects) as a function of physical number of pulses, in the pure tactile condition (adaptor and test tactile).

With no adaptation (red symbols), data were well fitted by linear regression anchored at zero (slope of linear regression 1.007), with best-fitting slope of 0.99. Adaptation to 8-flashes/sec systematically decreased apparent numerosity by 17% at all tested numerosities (slope of linear regression 0.83), and adaption to 2-flashes/ sec increased it by 12% (slope of regression 1.12). Both the data set had a good fit of linear regression (0.99 both).

Also in the other condition, in which we evaluated the cross modal sensory modality, we found a well fitted linear regression either with the visual adaptation and tactile test (NoAdapt=0.93, 2HzAdapt=1.03, 8HzAdapt=0.81), then in the opposite condition (NoAdapt=0.93, 2Hz=1.11, 8Hz=0.86); and also with the acoustic adaptation and tactile test (NoAdapt=0.95 2HZ=1.1, 8Hz=0.85), and with reverse one (NoAdapt=0.95, 2Hz=1.08, 8HZ=0.85); with a fit of linear regression equal to 0.99 in each condition.

In order to obtain the measure of adaptation, we calculate the magnitude of adaptation defined as the average of each perceived numerosity after adaptation to low number (2 items/sec) divided by that for high number (8 items/sec). Moreover we take the slope of this difference curve (multiplied by 100) as the adaptation index (AI), an estimate of the magnitude of adaptation for all conditions (Fig 32B).

In Fig. 32B we observe data in pure tactile and in all possible combinations of cross-modal conditions. The results clearly indicate that adaptation's effect are ubiquitous in all conditions despite the sensory modality combination of adapting and test stimuli.

To measure if these adaptation effects are perceptual feature in nature and not arising from a cognitive bias, we tested the effect to be spatially selective. Subjects were adapted to vibration of 2 and 8 Hz on the right hand (positioned on the right hand side) and tested visual stimuli either in the same side or opposite (left of fixation) position, randomly.

Fig. 33a show results for the matched (black symbols) and unmatched conditions (red symbols). Slope of unmatched condition was: NoAdapt=0.94, 2Hz=0.93, 8Hz=0.94; R^2=0.99.

Adaptation occurred only when test and adaptor positions were matched: the AI in that condition was 25%, while the unmatched condition yielded almost no effect. Thus adaptation to tactile numerosity affect visual stimuli similarly to visual or auditory adaptation to suggest that all these effects occurs at the perceptual level.

Fig. 33b shows the individual data for the matched/unmatched experiment. AIs were calculated in the same way as for group data, separately for the matched position (ordinate) and unmatched position (abscissa). All subject showed a clear specificity for position.

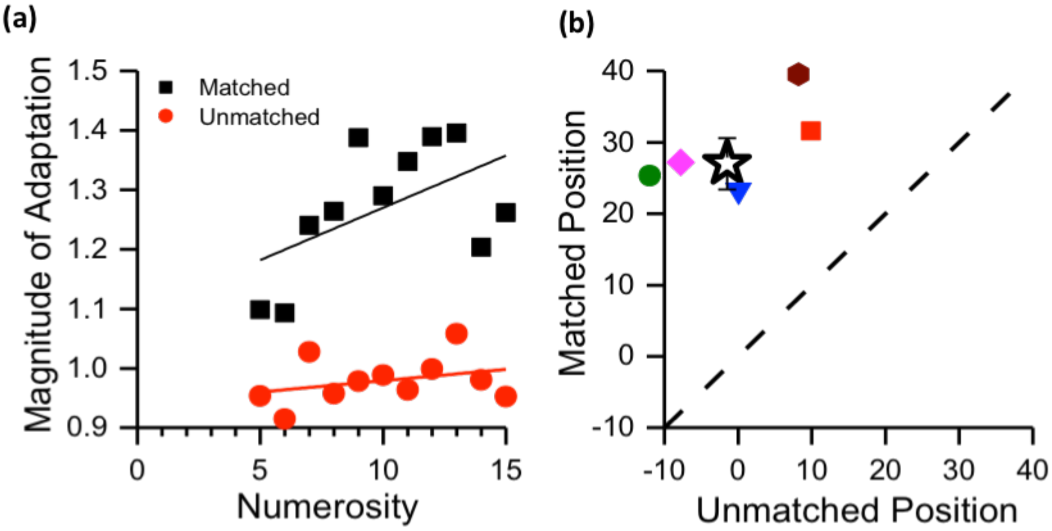


***FIG.33* – Spatial selectivity in cross modal condition** *(a) Adaptation magnitude: perceived numerosity after adaptation to 2 Hz minus that after adaptation to 8 Hz, as a function of physical numerosity. Black symbols show data when adaptor and test on the same side (Matched), red when on opposite sides (Unmatched), both conditions randomly intermingled. The adaptation was with the tactile device wile the test was visual. All curves are well fitted by linear regression to yield an AI, an estimate of the magnitude of adaptation. (b) AIs calculated for individual subjects for the matched condition plotted against the unmatched condition. The star shows the indexes calculated for pooled data.*

2.2.4 Discussion

In this study we investigated the role of adaptation on numerosity estimation in the pure tactile modality as well as in many cross modal conditions. Participants were presented stimuli from 2 to 20 items and had to estimate the number of stimuli shown. To investigate the effects of numerosity estimation, we divided the experiment in three conditions: no adaptation, 2 Hz and 8 Hz adaptations. In separate sessions we also evaluated the adaptation using different sensory modality (Togoli et al., In preparation).

Given the previous results obtained we expected that even with tactile stimuli and with cross-modal conditions the effects of adaptation persisted as it should be expected in terms of a truly generalized sense of number. Indeed the results were in line with expectations; first we see that the tactile modality is susceptible of adaptation with distortions of perceived numerosity to be around 30%.

Furthermore by using cross-modal conditions (tactile, acoustic and visual) we found similar results, with a percentile of comparable effect (acoustic adaptation and tactile test had an effect of 25%, tactile adaptation and acoustic test 23%, visual adaptation and tactile test 22%, lastly, tactile adaptation and visual test 25%). Finally we collected evidence for adaptation effect to be pure perceptual as it is spatially specific as adaptation effect on perceived duration (Burr & Ross, 2008). Adapting a specific part of the visual field to high numerosity (8Hz) decreases perceived numerosity, conversely adapting to low number (2Hz) increases perceived numerosity but the effects occurred only when the stimuli were presented to the adapted location whilst they were null for the neutral location.

The results showed that participants’ estimates were influenced by adaptation and the direction of the bias was comparable to those obtained in a recent numerosity study (Arrighi et al., 2014).

Important is that cross-modal adaptation of numerosity in the tactile modality has not been studied before, and here there is some evidence of a common process of numerical stimuli in other perceptual modalities.
Our results indicate robust and consistent interactions between the senses and the transfer of adaptation across the senses suggests that the mechanisms for numerosity perception cannot be solely unimodal. Indeed our results imply either a supramodal mechanism or strong linkages between modality-specific mechanisms for perception of numerosity.

Moreover our evidence shows that adaption affect the abstract representation of numerosity directly and not via a texture like mechanism. In line with this, adaptation effect was found even for stimuli sequentially presented and in other domains (auditory and tactile) than vision.
Our results fit well with the neurophysiological evidence for a neural representation in the intraparietal cortex about abstract numerosity across modalities and formats. They are also in line with psychophysical studies showing that cross-format numerosity judgments have no reaction time or accuracy cost.
Similar results have been reported with monkeys (Jordan et al., 2008).

Taken together, all these studies argue for a generalized sense of number: they point to a common neural patterns underlying individual quantities across modalities and underline the presence of stable and modality-general neural representations of perceptually depicted quantities.

Moreover the results provide strong support for the existence of perceptual mechanisms that encode numerical quantity from different senses, across space and time. Like most perceptual mechanisms, these are highly susceptible to adaptation.

Our current results suggesting that numerosity itself can be detected, adapting the abstract quantity system, and also open up new frontiers about numerosity in other modalities except vision and reinforces the value of the previous research on the spatial and temporal numerosity.

CHAPTER 3 – A SHARED NUMERICAL REPRESENTATION FOR ACTION AND PERCEPTION

3.1.1 Introduction

The previous results strongly suggest that the number sense is a high-generalized system, capable of combining numerical information from different senses, and across different presentation formats.

This is not the only study supporting this kind of analysis, indeed it is demonstrated that the parietal lobes in humans and macaques contain neurons that respond to changes in stimulus numerosity. However, basic non-numerical visual features can affect neural responses as several dimensions such as density or area can co-vary with numerosity. Therefore, it has been debated whether numerosity or related non-numerical features underlie neural and behavioural responses to what has been reported to be "numerosity".

To test the hypothesis that no numerical visual features underlie neural numerosity responses in a human parietal numerosity map, Harvey (2017) analysed responses to a group of numerosity stimulus configurations that have the same numerosity progression but vary considerably in their non-numerical visual features. Using ultra-high-field (7T) fMRI, the Authors measured responses to these stimulus configurations in an area of posterior parietal cortex whose responses believed to reflect numerosity-selective activity. They described an fMRI analysis method to distinguish between alternative models of neural response functions, following the population receptive field (pRF) approach.

For each stimulus configuration, they first quantified the relationships between numerosity and several non-numerical visual features that have been proposed to be previously mistaken for a numerical code. After having determined how well the responses to these non-numerical visual features fits the observed fMRI responses, predictions obtained with non numerical features were matched with those triggered by stimuli numerosity. The results demonstrated that a numerosity response model predicts observed responses more accurately than models based on simple non-numerical visual features. As such, neural responses in cognitive processing need not reflect simpler properties of early sensory inputs (Harvey et al., 2017).

Moreover previous studies found that the association cortex processes numerosity, and that sensory cortices contain topographic maps reflecting the structure of sensory organs.

Harvey, (2013) using high-field functional magnetic resonance imaging (at a field strength of 7 tesla), described neural populations tuned to small numerosities in the human parietal cortex. They are organized topographically, forming a numerosity map that is robust to changes in low-level stimulus features.

The cortical surface area devoted to specific numerosities decreases with increasing numerosity, and the tuning width increases with preferred numerosity. These organizational properties extend topographic principles to the representation of higher-order abstract features in the association cortex (Harvey et al., 2013).

Other than sensory also the motor cortices contain multiple topographic maps with the structure of sensory organs. Following this analogy, Harvey, (2017) recently hypothesised that there may be multiple numerosity maps. Numerosity perception is implicated in many cognitive functions including foraging, multiple object tracking, dividing attention, decision making and mathematics. So they used ultra-high-field (7T) fMRI and neural model-based analyses to reveal numerosity-selective neural populations organized into six widely separated topographic maps in each hemisphere. The properties of these maps are very similar to the sensory map hierarchies. These maps are found in areas implicated in object recognition, motion perception, attention control, decision-making and mathematics. Multiple numerosity maps may allow interactions with these many cognitive systems, suggesting a broad role for quantity processing in supporting many perceptual and cognitive functions (Harvey et al., 2017).

Other than in a perceptual task, numerical information is also relevant for the production of specific action sequences such as dance routines down to simpler repetitive behavioural tasks. Up to now there are few studies dedicated to investigate these numerosity mechanisms in the motor domain and even less on the interaction between numerosity processing in action and perception. The anterior part of the parietal association area in the cerebral cortex of primates has been implicated in the integration of somatosensory signals, which generate neural images of body parts and apposed objects and provide signals for sensorial guidance of movements.

Sawamura (2002) showed that this area is also active in primates performing numerically based behavioural tasks. They required monkeys to select and perform movement A five times then switch to movement B for five additional repetitions and get back to movement A in a cyclical paradigm. They found that cellular activity in the superior parietal lobule reflected the number of self-movement executed. For most units, the number-selective activity was also specific for the type of movement. This kind of numerical representation of self-action was less common amongst the units of the inferior parietal lobule, and even more rare in the primary somatosensory cortex. According to the Authors, such activity in the superior parietal lobule is useful for processing numerical information, which is necessary to provide a foundation for the forthcoming motor selection (Sawamura et al., 2002).

Moreover Sawamura in 2010 transiently and selectively inactivated area 5 to test its functional contributions to numerosity-based action selection. Two monkeys were trained to either push or turn a handle in response to a visual trigger signal by mirroring the same experimental procedures as the previous experiment. When muscimol was applied to a portion of area 5 in which the activity in the numerosity-selective cells was previously recorded, it was induced a robust increase in the number of errors for movement switching.

This transient neural inactivation also caused omission errors that were not observed before the drug injection. A control task showed that the errors were not caused by motor deficits or impaired ability to select between two possible actions.

On the contrary the results indicated that area 5 is crucial for selecting actions on the basis of numerical information about a series of actions performed by the tested individual (Sawamura et al., 2010).

Other studies have shown that counting successive sensory stimuli activates the left ventral premotor cortex. For example Kansaku (2007) tackle this issue by using functional magnetic resonance imaging and found that the upper part of the left ventral premotor cortex was preferentially activated during counting of successive sensory stimuli presented 10–22 times, while the area was not activated during small number counting up to 4. Then they used trans-cranial magnetic stimulation to assess the causal role of this area and found that stimulation of this area preferentially disrupted subjects’ enumeration of large numbers. Stimulation to the area affected neither subjects’ number word perception nor their ability to perform a non-numerical sequential letter task. The results suggest that the area is directly involved in large number counting of sequential stimuli, at least for the kind of tasks taken into consideration in the study (Kansaku et al., 2007).

Finally the human cerebellum shows strong activation also for simple numerical calculations. Arsalidou performed quantitative meta-analyses of several fMRI studies and identified some brain regions that all studies found involved in number and calculation tasks. These tasks elicited activity in a set of common regions such as the inferior parietal lobule; however, the regions in which a difference in activation was most robust were areas of the prefrontal cortices involved in specific arithmetic operations (Arsalidou & Taylor, 2011).

Recently the same group performed a meta-analysis (2017) amongst studies on children and found brain areas that fit a set of selection criteria with activity related to tasks that involved processing symbolic and non-symbolic numbers with and without formal mathematical operations, task that the Authors tagged as number tasks and calculation tasks respectively. Results (on children of 14 years old or younger) show activity in parietal (e.g., inferior parietal lobule and precuneus) and frontal (e.g., superior and medial frontal gyri) cortices, core areas related to mental-arithmetic, as well as brain regions such as the insula and claustrum, which usually are not related to such domains (Arsalindou et al., 2017).

The existence of anatomical and functional connections between number and action-generation raise the possibility that number-for-action could be encoded within a truly abstract numerosity mechanism.

To test this idea, here we measured cross-adaptation between motor repetitions and perception of numerosity.

The results show that adapting to self-generated action does affect the representations of numerosity of external events, both sequential (series of flashes) and simultaneous (dots ensembles), and that the adaptation is spatially selective in external, not hand-centred coordinates (Anobile, Arrighi, et al. 2016).

3.1.2 Materials and methods

A total of 15 adults (13 naive to the purpose of the study, 2 author; mean age 27, all right-handed with normal or corrected-to-normal vision) participated in the numerosity estimation experiments.

Six of them were tested in the sequential condition (test stimuli: sequences of flashes) and 7 of them in the 'simultaneous condition' in which test stimuli consisted of array of dots simultaneously presented.

Three of these (2 author and 1 naive subject) also participated, together with 3 additional naive subjects (mean age of group: 28), in the second experiment investigating the reference frame of the motor adaptation after-effect. Eventually, six subjects (mean age of group: 28) were tested in the experiment concerning forced-choice discrimination of numerosity. All participants gave written informed consent. Experimental procedures were approved by the local ethics committee (Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Firenze FI) and are in line with the declaration of Helsinki.

Stimuli were created and presented with Psychophysics toolbox for Matlab and displayed on a 60 Hz - 17”, touch screen monitor (LG-FLATRON L1732P) placed at a subjects view distance of 57 cm. To eliminate auditory feedback, participants wore soundproof headphones. In some conditions, hand movements were monitored by an infrared motion sensor device (Leap motion controller - https://www.leapmotion.com/) running at 60 Hz.

During the design of the experiments we computed an appropriate sample size to confidently report an effect of motion adaptation on perceived numerosity. Sample size was measured by means of a one-sample t-test assuming a value of 0 (no effect) as a Null Mean and retrieving a value for alternative mean and standard deviation from a previous study of our group (see Figures 30 and 31 in previous chapter (Arrighi et al., 2014). The analysis revealed that with a sample size of 4, a power of 0.95 was achieved with an alpha level of 0.01.

For this reason in all or experiments, we always tested a number of participants greater than 4 (see below for details).

We did not set any inclusion criteria for subject selection or their data: all data, for all experimental conditions, were analysed and reported. In all conditions where subjects estimated numerosity we tested statistical significance with a 2 x 9 repeated measures ANOVA with test numerosity (9 levels for numerosity, range 6–14) and adaptation type (low and high) as main factors.

Difference in the adaptation effects between the several adaptations conditions (visual, tactile, visual-tactile, and the two conditions with minimal feedback) were measured by a one-way ANOVA. In the numerosity discrimination task, difference in the adaptation effects for high and low adaptation were tested for statistical significance by mean of two-tailed paired t-test. For t-test analyses we measured Cohen’s d. For repeated measures ANOVA and regression analyses, we reported both Cohen’s d and h^2. Here Cohen’s d was measured transforming h^2 into Cohen’s d (Cohen, 1988).

During the adaptation phase, participants made a series of tapping movements on the left or right side of the screen until a white central fixation point turned red (the stop signal), and 1 secs later the test stimulus was presented.
Participants usually completed their current movement within 500 ms, so there was a 500 ms pause between movement-completion and test presentation.

The program continuously monitored tapping in all conditions: if a tap occurred after the presentation of the test stimulus, the trial would be aborted: in practice this never occurred. For most experiments, subjects tapped with their dominant (right) hand on the right side of the screen. For the second study, however, we also tested tapping with the right hand on the left side, and with the left hand tapping on the left side.
Five separate adaptation conditions were tested. 1) 'Visual and tactile' (action with visual and tactile feedback): each tap on the monitor surface triggered the simultaneous appearance of a visual flash surrounding the zone where the finger touched the screen. 2) 'Only tactile': participants tapped on a mouse button located beneath the screen, without visual feedback. 3) 'Only visual': participants were presented with a sequence of visual events whose rate was taken from the previous the motor adaptation condition. 4 and 5) 'Minimal feedback': participants tapped beyond the screen without touching any surface, tapping with the hand floating between the screen and a infrared sensor device fixed on the desk.

In one condition the test stimuli consisted of sequence of flashes (sequential) in the other test stimuli were ensembles of dot (simultaneous). The simultaneous condition was also used in the series of experiments shown in Fig. 35 in which we tested the reference frame of the motor adaptation effect. In one condition we replicated the previous paradigm (with fresh subjects) by asking subjects to tap with the dominant (right) hand on the right side of the screen. In another condition subjects tapped with the non-dominant (left) hand on the left side. In the third condition participants crossed their dominant (right) hand to tap on the left side of the screen. Two adaptation levels were tested separately for each condition. In one we asked subjects to make as many taps as possible within the adaptation period (high adaption), in the other to tap at a far slower rate (low adaptation): see Fig. 34 for distributions of tapping rates. In all experiments, the adaptation phase lasted 6 secs, and taps were always made with the right hand, on the right side of the monitor (hand placed 7 deg to the right of the central fixation point). After adaptation, the test phase started. In all conditions except ‘simultaneous’, test stimuli were a series of white disks (7 deg diameter), each presented for 40 ms within an interval of 2 secs. To minimize temporal regularity, each disk was temporally jittered with the rule that two consecutive stimuli could not be displayed with an inter stimuli interval less then 40 ms (max ISI of 290 ms, in case of the lowest numerosity N=6). In the simultaneous condition, test stimuli were circular clouds of dots (ensembles of half-white half-black dots, 0.3 deg diameter, presented for 250 ms within a circular region of 7 deg of diameter) centred at 7 deg eccentricity.

In the two minimal feedback conditions (Sequential and Simultaneous), test stimuli were presented both in the adapted position and the opposite side (centred 7 deg to the left of the central fixation point), randomly selected trial-by-trial.

In all conditions, after presentation of the test stimuli a virtual numerical keypad was displayed for subjects to record their response by mouse-click. Nine test numerosities were used, 6–14 inclusive.

Each participant performed about 260 trials (4/5 separate sessions), roughly equally divided between ‘low’ and ‘high’ adaptation and test numerosity levels (randomly selected trial-by-trial) leading to a total amount of trials of approximately 7500. The order of conditions was randomized between subjects.

Before starting testing, participants were familiarized with stimuli performing a block of 20 trials with sequential stimuli and 20 trials with dots stimuli. During the familiarization phase, we provided feedback of the exact number of items/events displayed. No motor (adaptation) training occurred during the training phase, and no feedback was provided during test phase.

We defined an adaptation index (AI) as the average percentage change in perceived numerosity after high and low adaptation, averaged across all numerosity.

In the two-alternative forced-choice experiment subjects were simultaneously presented with two clouds of dots (like those described above) to the right and the left of the central fixation point, both centred at 7 deg.

On each trial, the numerosity of the patch on the right hand side was chosen at random between 5 and 20 dots; that on the left differed by a random value within the range ± 5 dots (capped between 5–20).

Subjects were required to choose the more numerous. As there was variability in the numerosity of on both sides, subjects were not tempted to make a stereotypical response.

In separate sessions numerosity discrimination was preceded by fast tapping, slow tapping or no-motor action (baseline). The effect of motor adaptation was measured as the difference in points of subjective equality (expressed as percentage) between high and low adaptation. For all experiments, tapping was always with the right hand.

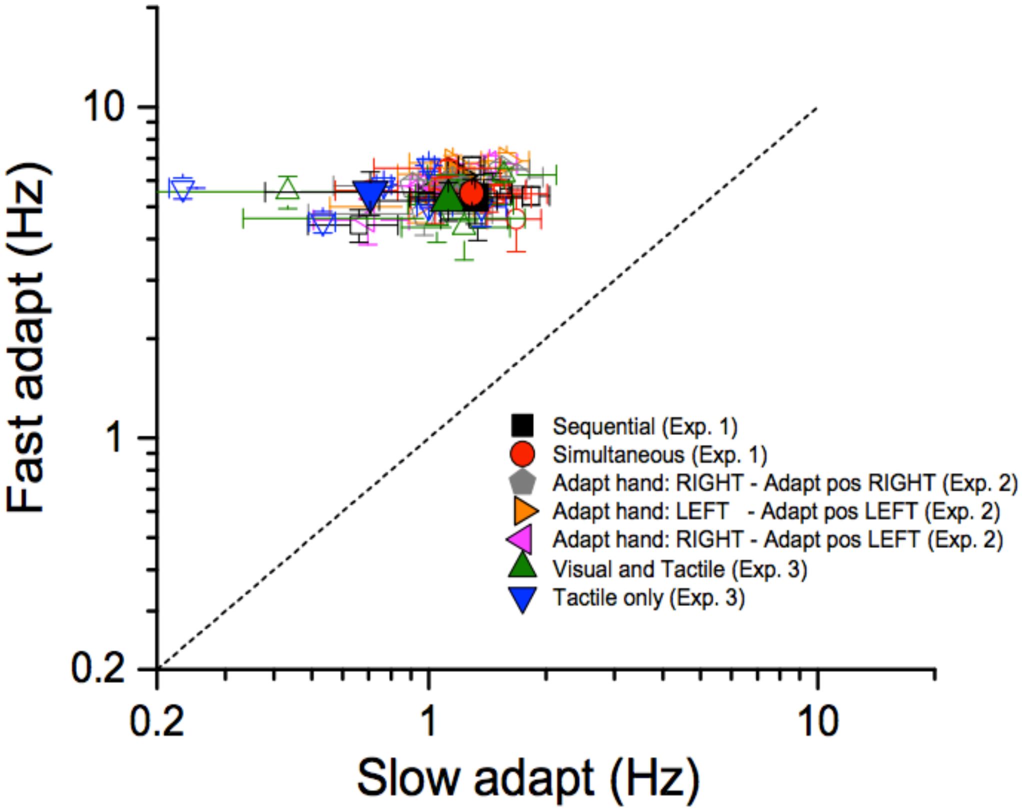


***Figure 34.* Tapping rates for high and low adaptation.** *Tapping rates (open symbols for single subject data; filled symbols for averages) for two different adaptation conditions: fast adaptation (ordinate) and slow adaptation (abscissa) for seven different experimental conditions. Black and red refers the two conditions in which subjects tapped in mid-air and then estimated numerosity of either sequential or simultaneous visual stimuli respectively. Grey, orange and violet refer to the three different versions of the simultaneous conditions devised to investigate the reference frame of adaptation: grey - subjects tapping with the right hand on the right side, orange - left hand on the left side and purple -right-hand on the left side. The adapting conditions in which subjects tapped on a surface (receiving tactile feedback) are indicated by green and blue symbols: green refers to the 'visual and tactile' condition in which participants tapped on touch-screen surface and were provided with visual feedback of their moving hand (visible) as well as by flashes on the monitor signalling the contact between the finger and the touch screen. Data in blue refer to the 'tactile only' condition in which subjects tapped on the mouse button placed beyond the screen (moving hand not visible).*

Fig. 34 plots the tapping rate for the fast against the slow adaptation conditions, expressed as actions per second (Hz). Different colours and symbols refer to different experimental conditions. On average (across trials and conditions), when asked to tap quickly, participants tapped at a frequency of 5–6 Hz (for a total number of 30–36 tapping repetitions) with almost no difference between the adapting conditions: mean 5.33 ± 0.9; 5.48 ± 0.5; 5.2 ± 0.7; 5.54 ± 0.8; 6.19 ± 0.37; 5.69 ± 0.38; 5.67 ± 0.31 for the 'sequential', 'simultaneous', 'visual and tactile', 'tactile only', 'adapt with the right hand in the right space', 'adapt with the left hand in the left space' and 'adapt with the right hand in the left space' respectively. Also tapping frequencies for the condition in which subjects tapped slowly were similar across adapting conditions with all values ranging between 0.7 and 1.3 Hz (mean 1.31 ± 0.4; 1.29 ± 0.3; 1.12 ± 0.4; 0.7 ± 0.3; 1.18 ± 0.12; 1.07 ± 0.13; 1.18 ± 0.17 for the 'sequential', 'simultaneous', 'visual and tactile', 'tactile only', 'adapt with the right hand in the right space', 'adapt with the left hand in the left space' and 'adapt with the right hand in the left space' respectively). These data clearly indicate that regardless the tapping routine to be performed on a rigid surface or in mid-air, the tapping temporal dynamics were always very similar.

We also tested whether there was a correlation between faster tapping rate and adaptation effects. There was a slight, but non-significant tendency for faster tapping rates to be associated with lower adaptation. But as the correlation was not significant, we assume that variable tapping rates was not a cause for concern for the results of these experiments.

3.1.3 Results

Each trial began with a motor adaptation phase in which participants performed tapping movements for six seconds, under two different conditions (tested on separate sessions): ‘high adaptation’, where participants were asked to tap as quickly as possible (average 5–6 taps/seconds); and ‘low adaptation’ where they tapped more slowly (average 1.12 taps/seconds).

After the adaptation phase, the test stimulus – either a sequence of flashes or a cloud of dots (tested on separate sessions) – was randomly displayed either to the same side of the screen where the hand had been tapping, or to the symmetrically opposite side. Participants estimated the numerosity of the test stimulus, which varied randomly from trial to trial within the range 6–14.

To minimize sensory feedback, participants were placed in a dark room and wore soundproof headphones, and tapped in mid-air behind the computer screen without touching any surface.

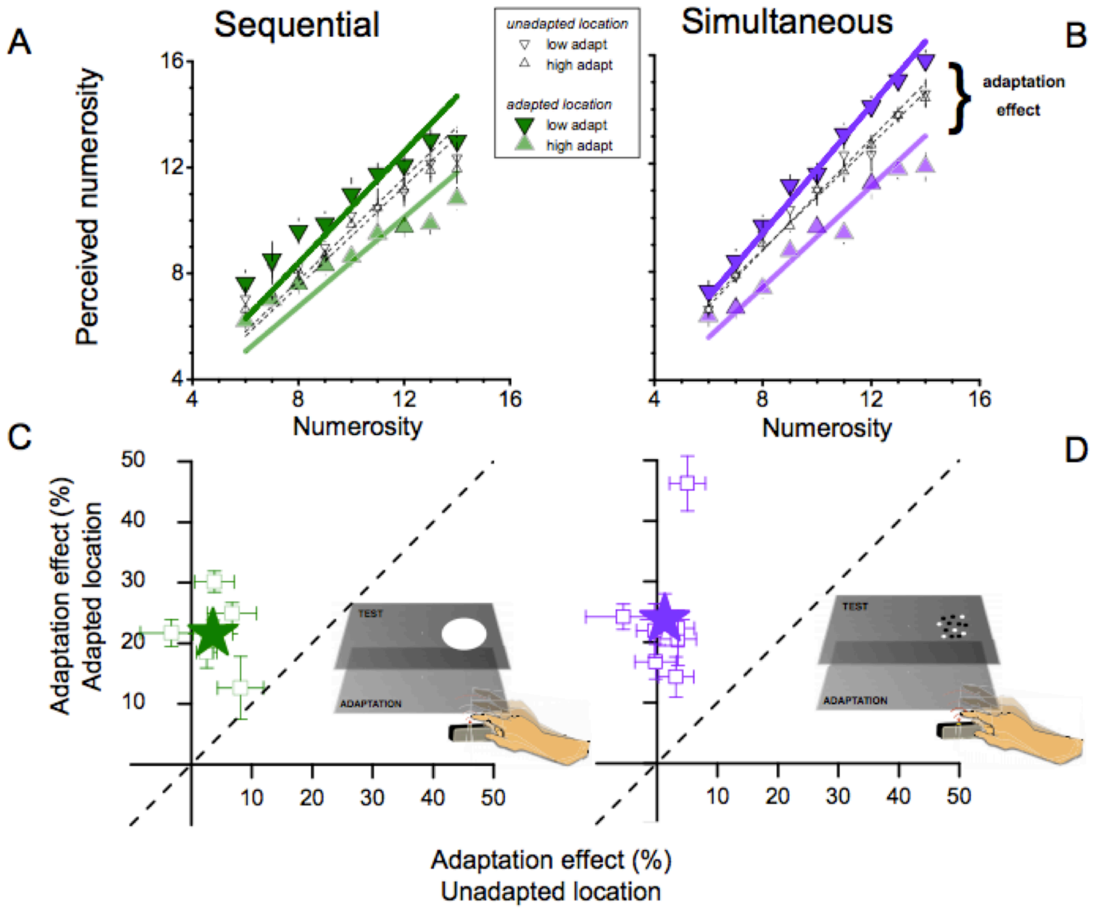


FIG.35 – Effects of motor adaptation on perceived numerosity*. (A and B) Average perceived numerosity as a function of physical numerosity for slow tapping (downward triangles) and fast tapping (upward triangles), for sequential (left) and simultaneous (right) formats. Filled symbols indicate the conditions in which stimuli were spatially congruent with the tapping region, small open symbols to estimates obtained for the unadapted location (left-hand side). (C and D). Adaptation magnitudes for individual subjects when test and tapping were spatially congruent, plotted against the spatially incongruent condition. Stars reports averages, squares single subject data. Error bars refer to ± 1 SEM.*

The results are shown in Fig. 35. Panels A & B show numerosity estimates averaged over all subjects as a function of the physical numerosities displayed. When the test stimulus was displayed on the right side of the screen (where the adaptation had occurred), rapid tapping caused a consistent underestimation of the numerosity of the test, while slow tapping caused an overestimation.

The adaptation effects were similarly strong for when the test was a sequence of flashes (Fig. 35A) as when it was an array of dots presented simultaneously (Fig. 35B).

Interestingly, the effect occurred only when the stimuli were presented on the same side as the tapping hand (the right side): when presented on the other (left) side, adaptation produced no consistent effect (Fig. 35A and B open symbols).

We defined adaptation magnitude as the percentage difference in perceived numerosity after adaptation to fast or slow tapping, averaged over all numerosities.

For sequential and simultaneous presentations, the adaptation magnitude averaged across subjects (filled symbols in Fig. 35C and D) was around 20 and 25% respectively for stimuli presented to the adapted location, a very strong effect.
For stimuli presented to the unadapted location, the average effect was only 4 & 2%. We also calculated adaptation magnitude for individual subjects. Fig. 35C and D plot adaptation magnitudes for the congruent condition (where the visual stimuli were presented to the right side), against the incongruent condition (stimuli to the left side).

All subjects showed a significant effect in the congruent condition (error bars 1 sem), but very little effect in the incongruent condition.

ANOVA showed that the congruent conditions were highly significant ($F_{(1,32)} = 70.219$, $p = 0.001$, $h^2 = 0.29$, Cohen's d = 1.278 and $F_{(1,48)} = 47.176$, $p = 0.0004$, $h^2 = 0.217$, Cohen's d = 1.062 for sequential and simultaneous condition respectively), while the non-congruent conditions were weak and insignificant (=4% effect, $F_{(1,32)} = 1.403$, $p = 0.302$, $h^2 = 0.007$, Cohen's d = 0.167 and =2% effect, $F_{(1,48)} = 0.919$, $p = 0.375$, $h^2 = 0.008$, Cohen's d = 0.179).
That the adaptation is spatially specific suggests it is of a perceptual rather than cognitive nature, and unlikely to result from a response bias or any other generalized artefact.

This first experiment revealed two clear results: that motor adaptation affects visual estimates of numerosity, for both sequential and simultaneous displays; and that the adaptation is spatially specific. The spatial specificity suggests that the effect is not a high-level, cognitive phenomenon (such as 'internal counting'), but perceptual in nature, mediated by neural mechanisms with circumscribed receptive fields. To verify the robustness of the spatial selectivity, and to understand it better, we repeated the experiment with a new subject pool, changing the tapping hand and location. In this experiment we tested only the simultaneous presentation, as this is the most revealing result.

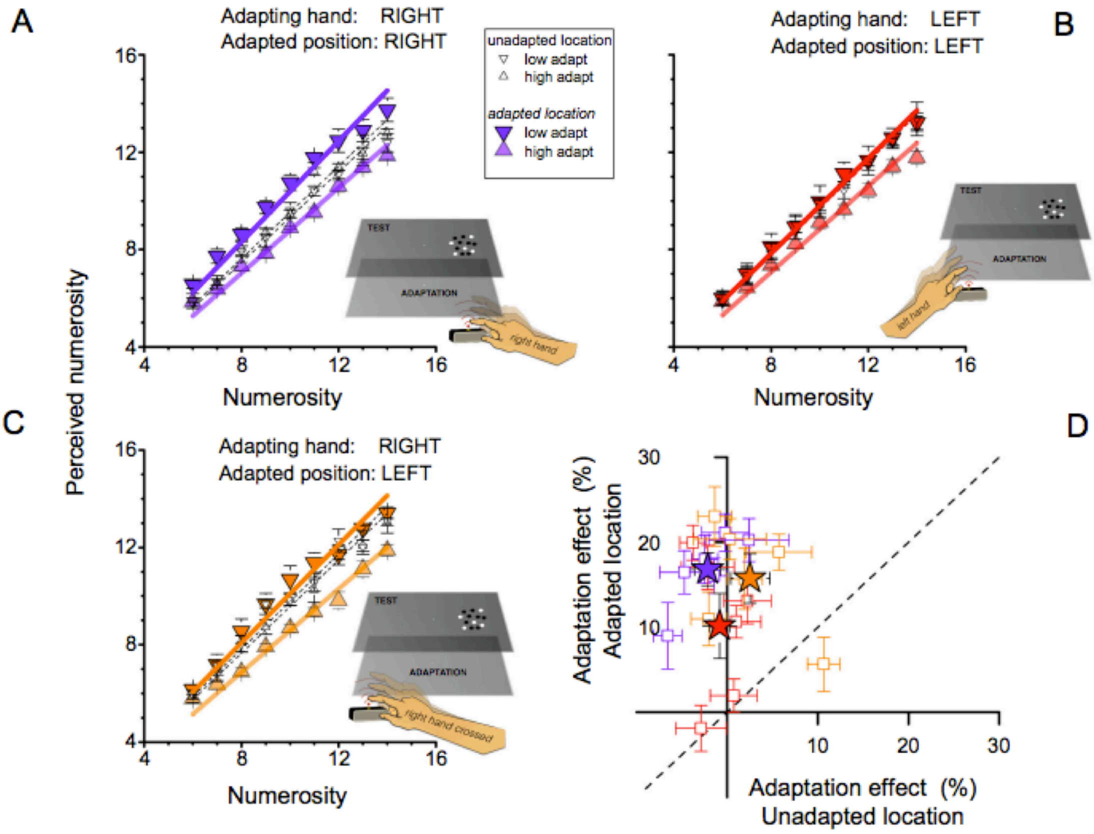


***FIG.36* – Reference frame of motor adaptation.** *(A) Average perceived numerosity as a function of physical numerosity for the slow-and fast-tapping conditions (downward and upward triangles respectively), for right-hand tapping. Filled symbols refer to trials when the stimuli were presented in the spatial region where the subjects had tapped (right side) small open symbols to trials when the stimuli were presented on the other side. This data replicates Figure 35B with a fresh subject pool. (B) Same as A, except subjects tapped with their left hands. Filled symbols refer to testing in the same spatial region where the subjects had tapped (left side), small open symbols to the right side. Other conventions like A. (C) Same as A, except the right hand tapped on the left side of the screen. Filled symbols refer to testing on the same spatial region where the subjects had tapped (left side), small open symbols to the right side. (D) Adaptation magnitudes for individual subjects when test and tapping were spatially congruent, plotted against the spatially incongruent condition. Color-coding as for A, B and C (purple: right hand, right side; red: left hand, left side; orange: right hand, left side). Stars reports averages, squares single subject data. Error bars refer to ± 1 SEM.*

The violet symbols of Fig. 36A replicate the results of the previous experiment, tapping with the right (dominant) hand and testing on both right and left sides (randomly interleaved): the adaptation effect was again strong for stimuli presented on the same side (filled symbols), and non-existent for stimuli on the other side (open symbols) ($F_{(1,40)}$ = 70.207, p = 0.000397, h^2 = 0.116, Cohen's d = 0.724; $F_{(1,40)}$ = 2.036, p=0.213, h^2 = 0.0019, Cohen's d = 0.0873; for adapted and unadapted location respectively).

The red symbols of Fig. 36B show the results for tapping on the left with the left (non-dominant) hand: again the effects occurred only for visual stimuli presented on the congruent side (left), although they were somewhat weaker ($F_{(1,40)}$ = 9.305, p = 0.028, h^2 = 0.05, Cohen's d = 0.4588; $F_{(1,40)}$ = 0.265, p = 0.629, h^2 = 0.001, Cohen's d = 0.0633; for adapted and unadapted location respectively). Fig. 36C shows results for tapping with the dominant (right) hand on the left side of the screen. Here, adaptation was found only for stimuli presented to the left side of the screen, suggesting that it is spatially selective in external rather than hand-centred coordinates ($F_{(1,40)}$ = 36.840, p = 0.002, h^2 = 0.104, Cohen's d = 0.6814; $F_{(1,40)}$ = 1.380, p = 0.293, h^2 = 0.0023, Cohen's d = 0.096; for adapted and unadapted location respectively). Fig. 36D shows the results for all six subjects. There is some variability between subjects, particular in the crossed condition, where one subject showed adaptation to stimuli on the right after tapping on the left with the right hand, but by and large the individual data reinforce the group data.

In the previous experiment, subjects tapped in mid air to minimize sensory feedback. In the next series of experiments we manipulated the amount of sensory feedback in the adaptation phase to examine interactions between sensory and motor signals. In the first condition (tactile only), subjects tapped a mouse behind the monitor, allowing for tactile feedback (Fig. 37A). The adaptation effect in this condition was strong, around 20% ($F_{(1,40)} = 743.738$, $p = 0.0001$, $h^2 = 0.203$, Cohen's $d = 1.009$). In the next condition (visual and tactile), the monitor accompanied each mouse-tap with a flash, to give visual as well as tactile feedback. Despite the extra feedback, adaptation remained around 20%, ($F_{(1,40)} = 36.746$, $p = 0.002$, $h^2 = 0.184$, Cohen's $d = 0.949$) as shown in panel B of Fig. 37. The last adaptation condition (visual only) comprised a sequence of visual flashes whose rates were determined by the adapting motor routine of the previous conditions (visual and tactile). Again, the adaptation effect was found to be strong ($F_{(1,40)} = 61.740$, $p = 0.001$, $h^2 = 0.230$, Cohen's $d = 1.093$), and similar to the other conditions, around 20% (Fig. 37C), making these three adaptation conditions equally effective as tapping in mid-air ($F_{(4,29)} = 0.475$, $p = 0.754$, $h^2 = 0.07$, Cohen's $d = 0.548$: see Fig. 36D).

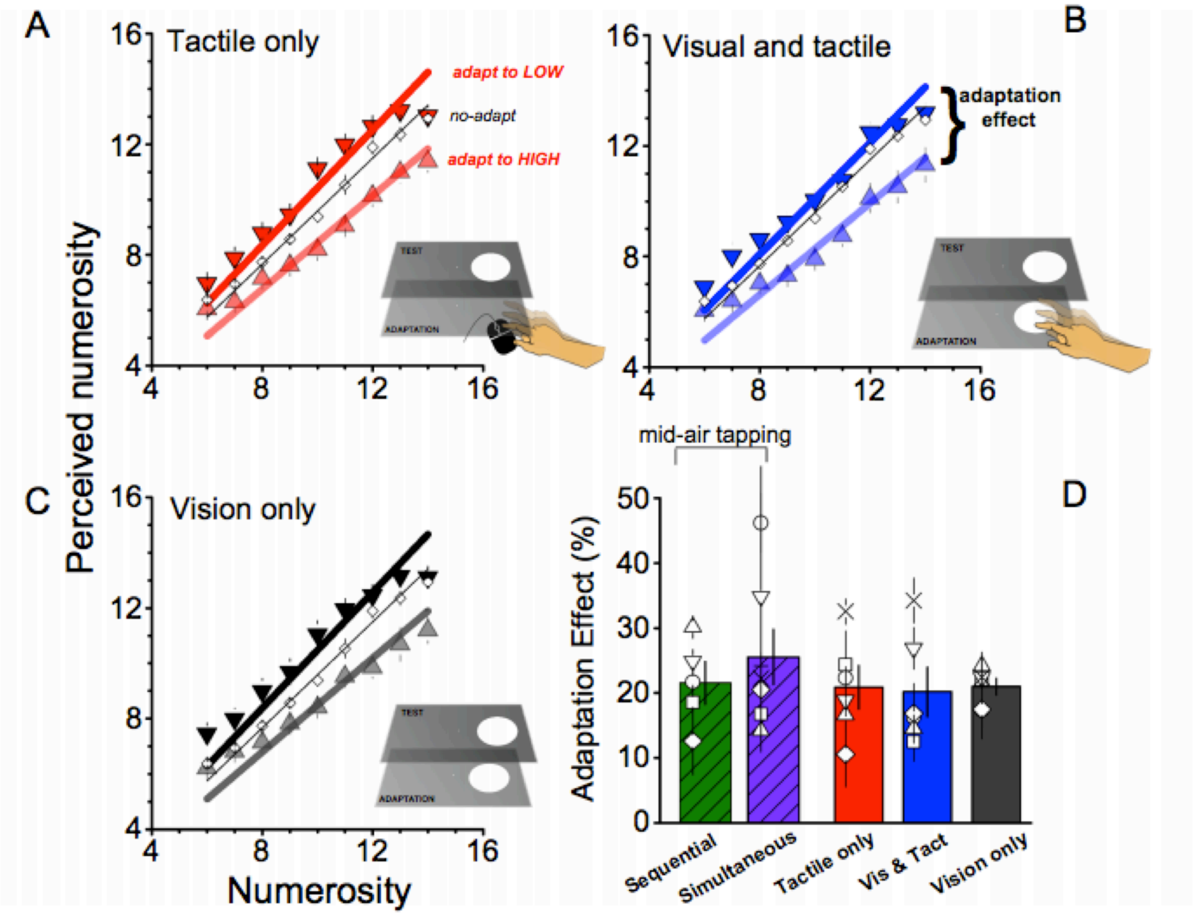


FIG.37 ***– Role of sensory feedback of motor adaptation on perceived numerosity. (****A), (B), (C) Average responses as a function of physical numerosity for slow adaptation (downward triangles), fast adaptation (upward triangles) and no adaptation (diamonds), for the three different conditions. (D) Bar graphs report the average adaptation effect for all adapting conditions (tactile only - red; visual and tactile - blue, visual only – black and the 2 conditions of Exp 1: sequential-green and simultaneous-violet). Open symbols show single subject data. Error bars report ± 1 SEM. All the conditions provided significant effects (all p-values < 0.05). The magnitude of the effect does not differ between conditions (p > 0.05)*

We also verified the results with a two-alternative forced-choice technique. Subjects adapted to high or low tapping rates, as in the first experiment (no tactile or visual feedback), then two clouds of dots were simultaneously presented to the right (adapted) and left (unadapted) positions. The numerosity of each stimulus varied from trial to trial over the range 5–20, and subjects indicated which stimulus appeared more numerous.

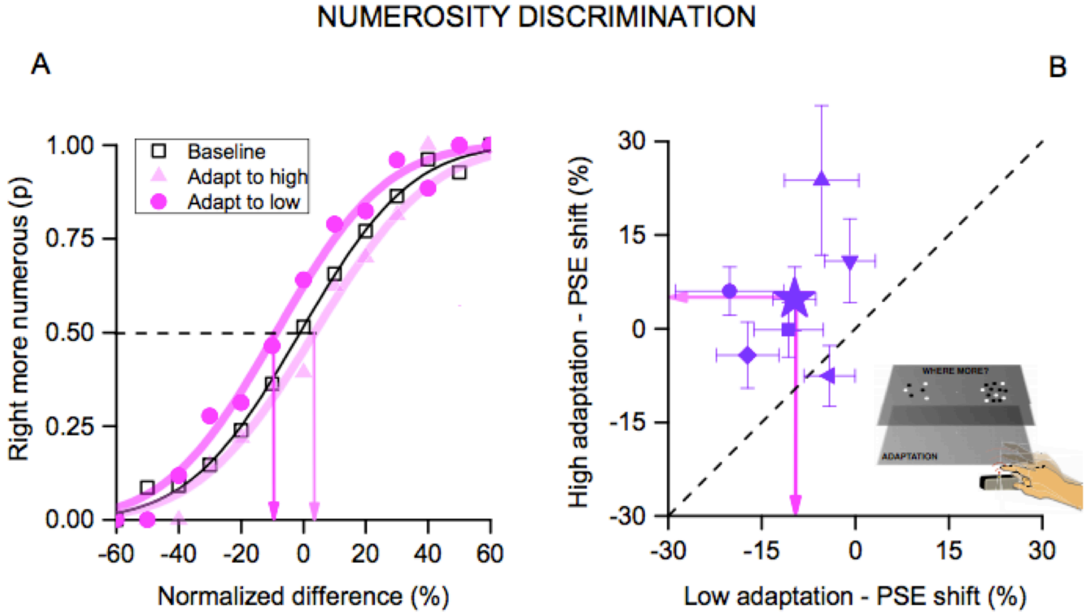


***FIG.38* – Forced-choice measurement of motor adaptation.** *(A) Psychophysical functions for pooled data (6 subjects) after adaptation to fast (light violet circles), slow (dark violet triangles) or no (black squares) tapping. The curves indicate the proportion of trials when the test was seen as more numerous than the unadapted stimulus, as a function of the numerosity difference. Adaptation to slow tapping shifted the curve leftwards, showing that subjects were biased to perceive the stimulus as more numerous that it was; and adaptation to fast tapping shifted it rightwards. The point where the best-fitting curves pass 50% is considered the point of subjective equality (PSE, indicated by the coloured arrows). (B) PSEs for individual subjects after adaptation to fast tapping (ordinate) against those after adaptation to low motor repetitions (abscissa). The filled star shows results for data averaged across subjects. Error bars report ± 1 SEM*

Fig. 38A plots average responses as a function of the difference between the right and the left stimulus (normalized to the average of the two numerosities), to yield psychometric functions. The effect of adaptation was again clear: adapting to low tapping rates shifts the curve to the left, consistent with an overestimation of the perceived numerosity ($t_{(5)}$ = 3.285, p = 0.021, Cohen's d = 1.101) and high tapping rates caused the opposite effect, even if weaker ($t_{(5)}$ = 1.237, p = 0.27, Cohen's d = 0.558).

The differences in the points of subjective equality (PSEs, given by the 50% point of the curves) of the two adapting conditions again gives an index of magnitude of adaptation, around 15%. Fig. 38B shows the PSEs for adaptation to the two conditions. Despite some variability amongst subjects the effects are quite robust and statistical significant as shown by a two-tailed paired t-test: $t_{(5)} = 3.56$, $p = 0.029$, Cohen's $d = 1.612$. This experiment confirms the main results with a different technique, and also confirms the spatial selectivity of the adaptation: if adaptation was not spatially selective, it would work equally on the presentations to the left and right sides, annulling the effect.

3.1.4 Discussion

This study shows that estimates of numerosity, both sequential and simultaneous, are strongly biased after adapting to repetitive finger tapping: rapid tapping decreases apparent numerosity, slow tapping increases it. The effect is spatially selective, primarily in external rather than hand-centred coordinates (Anobile, Arrighi, et al. 2016).

There has been a long-standing debate as to whether adaptation effects operate on numerosity per se, or via texture-density mechanisms (Burr & Ross, 2008; Anobile et al., 2014, 2015, 2016; Bell et al., 2015; Dakin et al., 2011; Durgin, 1995, 2008; Morgan et al., 2014; Ross & Burr, 2012; Ross, 2010; Tibber et al., 2012, 2013).

A similar argument could be made here: that the adaptation was to temporal frequency, rather than to numerosity.

As with spatial adaptation, there are many reasons to suggest that this is unlikely.

However, the cross-format adaptation (adapt to tapping sequence and test on dot array) clearly rules out this possibility: the spatial arrays are not temporally modulated. It is numerosity that is being adapted, not temporal frequency.

The current results reinforce the many previous studies (Izard et al., 2009; Nieder, 2012; Nieder et al., 2006; Barth et al., 2003; Brannon, 2003; Barth et al., 2005; Jordan & Brannon, 2006; Arrighi et al., 2014; Jordan et al., 2005) discussed in the introduction that point to the existence of a generalized sense of number. Most of these studies relied principally on cross-modal comparisons of number, which could occur at any processing stage, up to and including decision mechanisms. The spatial selectivity shown in our study suggests that the interaction is perceptual rather than cognitive: adapting on the left side did not affect stimuli on the right, and vice versa. Importantly, the specificity was in external coordinates, as adapting the left field with the right hand caused adaptation for visual stimuli presented to the left, not the right visual field. This complements nicely the result of our previous study (Arrighi et al., 2014), where we showed that adaptation to visual sequences affects number perception of both sequential and simultaneous presentations, in a spatially selective manner.

Interspersing an eye-movement between adaptation and test showed that the adaptation was spatially specific in external rather than eye-centred coordinates: as the current study shows the selectivity is external, not hand-centred. It would be interesting to look at the spatial tuning of the adaptation on a finer grain, to define the size of the adaptation field.

The present study shows that the adaptation is at least broadly tuned, confined to a particular hemifield. It would be very informative to determine whether there was also selectivity within each hemifield, and on how fine a grain.

Some may find the spatial selectivity of the adaptation difficult to reconcile with the concept of a generalized, abstract sense of number. However, cross-modal effects can also show spatial selectivity. For example, cross-modal integration of visual and auditory (or tactile) information occurs only if the stimuli are spatially coincident (within certain bounds) (Slutsky & Recanzone, 2001). Similarly event time, which certainly transcends modalities, and also seems to be coded in parietal cortex (Leon & Shadlen, 2003), is affected by motion adaptation, in a spatially selective manner (Burr et al., 2007; Fornaciai et al., 2016). Interestingly, the spatial selectivity of the adaptation is in external not eye-based coordinates as we observed for number, here and in the previous study (Arrighi et al., 2014).

We tested adaptation to action under various feedback conditions: visual and tactile, only visual, only tactile, and minimal feedback. All conditions produced similar amounts of adaptation. In the ‘minimal feedback’ conditions, where subjects tapped in mid-air, there was no tactile feedback from hitting a surface. We could not, however, remove all forms of kinaesthetic feedback, and therefore cannot be certain whether the adaptation signal was the intension to move, or the sensory proprioceptive feedback from the finger. But both are signals about action, whether they are ‘inflow’ or ‘outflow’.

It is interesting that this condition with reduced perceptual feedback produced the same amount of adaptation, as did the conditions with visual and/or tactile feedback. It is also interesting that the vision-only condition produced similar adaptation. Many studies have suggested that vision and action are linked (Arrighi et al., 2011; Goodale & Milner, 1992).

This study is a further clear example of their interconnection, in the encoding the numerosity of internally generated actions and externally generated events.

CHAPTER 4 – A SHARED NUMERICAL REPRESENTATION FOR ACTION AND PERCEPTION IN BLIND AND SIGHTED PARTICIPANT

4.1.1 Introduction

The results of the previous experiment suggest that the number sense generalizes even between action and perception, as shown by the finding that the number of repetitions of self-produced movements (adaptation with tapping movements) distorts perceived numerosity of subsequent visual stimuli (Anobile, Arrighi, et al. 2016).

However, vision does not represent the only sensory modality used to orient us in the environment and for controlling goal-directed actions. Furthermore, the results discussed in Chapter 2 demonstrate that the number sense generalizes also across different sensory modalities (auditory and tactile) (Arrighi et al., 2014). Overall, the previous results lead to a further question: do the adaptation effects involving the action system also generalize to other modalities beyond vision?

This cross-domain adaptation effects previously observed also show spatial selectivity in external, not hand-centered, coordinates, but the developmental process enabling such spatial specificity remains unknown. One possibility is that vision drives such development, as it has been demonstrated that early visual deprivation alters the development of an external coordinate system the perception of tactile stimuli (Röder et al, 2004), auditory stimuli (Röder et al, 2007), and also approximate numerosities (Crollen et al., 2013).

More specifically, Röder and colleagues (2004) demonstrated that when participants were required to determine the temporal order of two tactile stimuli, one applied to each hand, both sighted and late blind participants' performance was impaired when they were required to cross their hands, compared to an uncrossed hands posture, while performance of early blind participants remained unaffected across posture changes (Röder et al., 2004). In 2007, the same research group tested whether the default use of such external reference frame is innately determined or instead acquired during development by testing congenitally blind, late blind, and matched sighted controls. The paradigm used was similar to the previous experiment, but employing an auditory task. The congenitally blind participants showed a significantly larger crossing deficit than both the sighted and late blind adults (Röder et al., 2007).

Concerning numerosity perception, in a study by Crollen et al. (2013) early blind individuals and sighted controls were asked to perform a numerical comparison task devised to elicit the SNARC effect (see paragraph 1.3.3), either with hands arranged in a parallel position or with hands crossed over the body midline. Because the default use of an external coordinate system for perception and action depends on early visual experience, crossing hands reversed the SNARC effect measured in the early blind individuals. This study therefore provides more evidence that early visual experience drives the development of an external coordinates system for the visuo-spatial representation of numbers (Crollen et al., 2013).

More recently, Crollen, et al. (2017) examined whether vision may differentially shape the use of internal versus external spatial representations of touch and motor sequence learning. Early blind and sighted controls were asked to perform two tasks. The first task was a tactile temporal order judgment task (TOJ), in which participants had to determine which of their two hands (uncrossed or crossed over the body midline) received a tactile stimulus first.

The second task was a motor sequence-learning task, in which participants were trained to perform a sequence of five-finger movements. After the training session, participants were tested on their ability to produce, with the same hand but with the keypad turned upside down, the learned (internal condition) or the mirror sequence (external condition). The results show a significant transfer of motor sequence knowledge in both EB and SC irrespective of whether the representation of the sequence was internal or external. These results demonstrate that visual experience differently impacts the automatic weight attributed to internal versus external coordinate depending on task-specific spatial requirements (Crollen et al., 2017).

In line with this evidence, the study of visually deprived individuals represents a unique opportunity to test the intrinsic interplay between action and perceived numerosity. In this study, congenitally blind (CB) and sighted controls (SC) were required to perform an adaptation task with their dominant hand, either in an uncrossed or in a crossed posture, and perform a numerosity estimation task with auditory stimuli (Togoli et al., 2017).

4.1.2 Methods

28 participants took part in the experiment: 14 sighted and 14 congenitally blind participants. Both groups were composed of 4 females and 10 males. The age range of congenitally blind individuals was from 21 to 49 years old (Mean=36; SD=8), while for the sighted control group age ranged from 23 to 53 years old (Mean=35; SD=8). The two groups did not statistically differed in terms of age.

All the blind participants had a congenital blindness from birth and at the time of testing were totally blind or had only rudimentary sensitivity for brightness difference with no pattern vision. Three subjects had a left-handed preference (2 participants sighted and 1 blind) and three was ambidextrous (all blind). All participants had a normal or corrected-to-normal hearing.

All subjects provided an informed consent before participating to the study. None of the subjects reported neurological or psychological disorders.

Stimuli were auditory impulses created with the Psychophysics toolbox for Matlab and presented by means of two loudspeakers placed at 50 cm of distance from the subject. Auditory stimuli were pure tones (500 Hz tones; intensity = 77 dB), with 5-ms ramps at the onset and offset. Sighted participants were blindfolded when performing the task. In all conditions, an infrared motion sensor device (Leap motion controller - https://www.leapmotion.com/) running at 60 Hz was used to monitor hand movements.

The appropriate sample size necessary to confidently report an effect of motor adaptation on perceived numerosity with reasonable power was calculated based on the effect size reported in a previous study employing a similar technique (Anobile, Arrighi et al., 2016).

In all conditions where subjects estimated numerosity we tested statistical significance with a 2 X 5 repeated measures ANOVA, with test numerosity (5 levels for numerosity, range 16–20) and adaptation type (low and high) as main factors.

Difference in the adaptation effects between the several adaptation conditions (crossed and parallel; blind and sighted) was measured by a one-way ANOVA.

For repeated measures ANOVA and regression analyses, we reported both Cohen's d and h^2. Here Cohen's d was measured transforming h^2 into Cohen's d (Cohen, 1988).

The subjects sat in front of a table large about 120 cm with two loudspeakers positioned at 50 cm on the right and left side.

The experiment started with an adaptation phase. A recorded voice gave the starting cue and the subjects had to make a series of tapping movements for 6 seconds until a stop signal (record voice) asked them to quit the hand movement. After 1000 ms from the end of adaptation, the test stimulus was presented. Participants usually completed the adaptation movement within 500 ms from the stop signal, so there was on average a pause of 500 ms between movement-completion and test presentation.

During all experimental phases, a leap motion sensor monitored continuously the position of hand: in case a tap occurred after the presentation of the test stimulus, the trial would have been aborted but such event has never occurred.

For most experiments, subjects tapped with their dominant hand parallel to the side of the body. For the crossed condition, they also tapped with the dominant hand but hand was crossed relative to the body midline. In each experiment we tested two different adaptation conditions. In the fast adaptation we asked subjects to make as many taps as possible within the adaptation phase. In the slow adaptation we asked them to tap at a slower rate. The two experiments (parallel vs. crossed hand) and the two adaptation conditions were randomly presented in 8 experimental blocks [adaptation period x (4) and position x (4)].

To minimize temporal regularity and to avoid fusion of two or more stimuli due to minimal inter stimulus interval (ISI), we devised the adapting sequences according to the rule that two consecutive stimuli could not be presented with ISI shorter than 40 ms (with a maximum ISI of 290 ms, in case of the lowest numerosity N = 16). In each trial, test stimuli were randomly presented either in the adapted position or at the opposite, neutral location. After presentation of the test stimuli, the participants reported verbally the perceived numerosity of impulses in the tone series. Five test numerosities were used, ranging from 16 to 20. Each participant performed about 240 trials (6 separate sessions), roughly equally divided between ‘low’ and ‘high’ adaptation and test numerosity levels (randomly selected trial-by-trial). The order of conditions was randomized between subjects.

On average (across trials and conditions), when asked to tap quickly, participants tapped at a frequency of 4–5 Hz (for a total number of 24-25 tapping repetitions) with almost no difference between the adapting conditions: mean 24.46 ± 6.5; 25,88 ± 7.5 for the 'parallel, 24 ± 6.5; 25.25 ± 5.9 for the 'crossed condition in sighted and blind participants respectively. Also tapping frequencies for the condition in which subjects tapped slowly were similar across adapting conditions with all values ranging between 1,8 and 2 Hz (for a total number of 10-11 tapping repetitions): mean 10.82 ± 2,88; 10.75 ± 2.69 for the 'parallel, 11.44 ± 2.81; 11.18 ± 2.64 for the 'crossed condition in sighted and blind participants respectively). These data clearly indicate that regardless the tapping routine subjects were engaged with, the tapping temporal dynamics were always very similar indeed.

4.1.3 Results

The results of the experiment about the effect of self produced motor actions on numerosity estimates of auditory stimuli, are shown in Fig. 39 for both, sighted and blind subjects. Panels A, B, C & D show numerosity estimates averaged over all subjects as a function of the physical numerosities. When the test stimulus was presented on the same side where the adaptation had occurred, rapid tapping caused a consistent underestimation of the numerosity of the test, while slow tapping caused an overestimation. The magnitude of adaptation effects was rather the same for both, congenitally blind (Fig. 39B&D) and sighted controls (Fig. 39A&C). Moreover the adaptation effects were similar for the tapping hand kept parallel to the body (Fig. 39A&B) or crossed on the body midline (Fig. 39C&D).

Interestingly, the effect occurred only when the stimuli were presented on the same side as the tapping hand: when presented on the other side (neutral location), adaptation did not produce any significant effect (grey symbols).

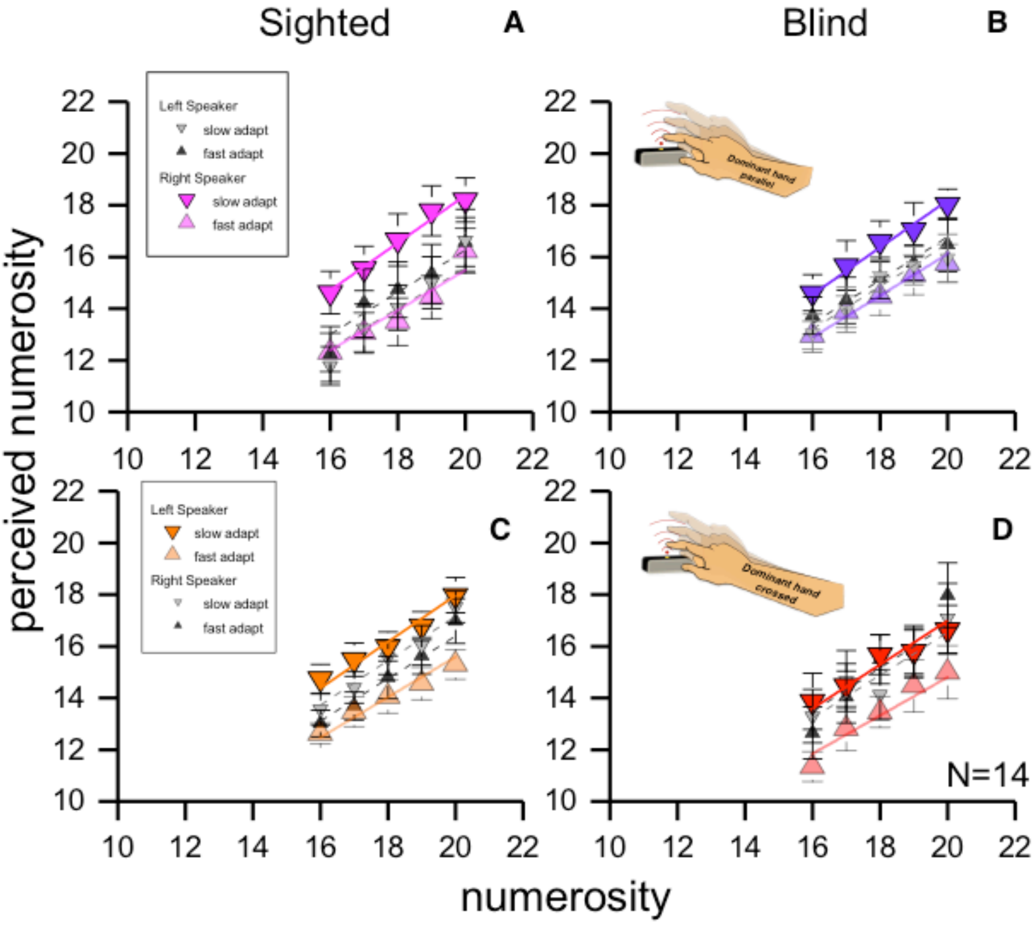


__FIG.39__ – Motor adaptation on perceived numerosity in sighted and blind subjects. *Average responses as a function of physical numerosity for slow adaptation (downward triangles), fast adaptation (upward triangles) and no adaptation (grey symbols), for the different conditions and group of subjects. A and C sighted and B and D blind participant; in the panel A and B in parallel condition and in C and D in crossed condition.*

We defined adaptation magnitude as the percentage difference in perceived numerosity after adaptation to fast or slow tapping, averaged over all numerosities. The adaptation magnitude averaged across blind subjects was around 13%, while for stimuli presented to the unadapted location, the average effect was 2%. Magnitude of adaptation for sighted controls was around 20% when sounds were presented in the adapted location, and around zero (1-2%) when presented in the unadapted position.

The pattern of result was similar for the two groups and all subjects showed a significant effect in the spatially congruent condition (error bars 1 sem), but very little effect in the incongruent condition. We also calculated adaptation magnitude for individual subjects.
Fig. 40 A and B plot adaptation magnitudes for the congruent condition (where the auditory stimuli were presented to the same side of tapping hand) against the incongruent condition (stimuli to the opposite side) both for sighted controls than for blind participants.

ANOVA showed that the congruent conditions were highly significant compared to non-congruent condition ($F_{(1,26)}$=40,667, p=0,001 and $F_{(1, 26)}$= 29,858, p=0,001, both for sighted and congenitally blind control respectively).
To summarize, we found with this experiment a pattern of results very similar to those previously reported by our group when interaction between action and perception in numerosity processing were tested just for visual numerosity and in sighted subjects (Anobile, Arrighi et al. 2016).

Here we extended these results to show that such an interaction occurs also in the auditory domain for stimuli presented sequentially (temporal numerosity). More, the results in the crossed conditions, show that adaptation was spatially selective (14% Vs. 1% for sighted control; 15% Vs. 4% for blind individuals), and that the reference frame is always anchored in external (not hand-centred) coordinates even in case of a complete lack of early visual experience (congruent conditions compared to non-congruent for sighted subjects $F_{(1,26)}=23,096$, $p=0,001$ and congenitally blind $F_{(1,26)}=8,949$, $p=0,006$).

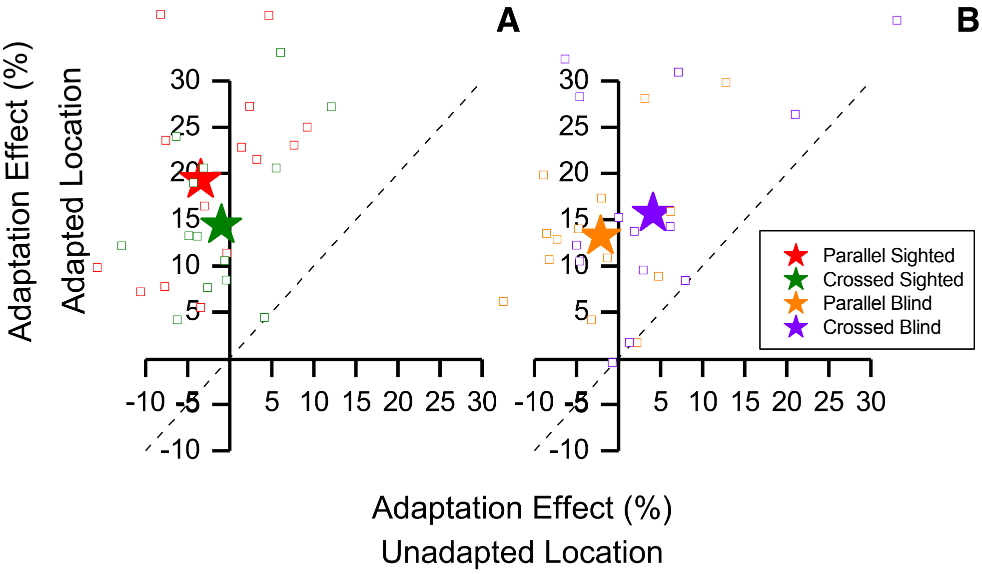


***FIG.40* – Reference frame of motor adaptation.** *Adaptation magnitudes for individual subjects when test and tapping were spatially congruent, plotted against the spatially incongruent condition. Panel A show results for sighted; panel B blind participants. Color-coding show in red dominant hand parallel for sighted; green dominant hand crossed for sighted; purple dominant hand parallel for blind; orange parallel hand crossed for blind. Stars reports averages, squares single subject data.*

4.1.4 Discussion

The main goal of the aforesaid study was to investigate whether interactions of motor and perceptual system for numerosity processing occur in external world coordinates even when visual spatial maps have not been developed. However, the study provided many other interesting results (Togoli et al., 2017)

First, we tested 14 sighted subjects and show that the numerosity estimates of sequences of sounds are strongly biased after adaptation to repetitive finger tapping: rapid tapping decreased apparent numerosity, slow tapping increased it.

Moreover this effect is spatially selective: only the stimuli presented on the same side of the tapping hand showed an adaptation effect.

The spatial selectivity shown in our study suggests that the interaction is perceptual rather than cognitive: adapting to the left side did not affect stimuli on the right, and vice-versa.

Finally, the specificity was in external rather than hand centred coordinates, indeed as adapting the left field with the right hand caused adaptation for auditory stimuli presented on the left, not the right side.

The current results reinforce many previous findings supporting the idea of a generalized sense of number. They complement nicely with the results in which we investigated numerosity adaptation across sensory modalities as we show that action and perception shared numerosity processing for both, visual and auditory stimuli (Arrighi et al., 2014).

The present results also complement well with the other study presented in this thesis in which we reported an effect of adaptation for self-produce motor pattern on perceived numerosity of external visual events. Moreover we have previously shown that the adaptation was spatially specific in external rather than hand centred coordinates and that was confirmed to be also true for congenitally blind subjects.

There are several other previous experiments that demonstrate the spatial selectivity of numerical processing as the one about tactile numerosity presented in chapter 2 of this thesis (Gallace et al., 2006; Lechelt, 1975).

In this experiment other than sighted people we tested a group of 14 congenitally blind to evaluate whether early visual experience was required in the development of an external/internal frame of reference of the auditory-action numerosity.

We found very similar adaptation effects for both, blind and sighted individuals with an overestimation after adaptation to many motor repetitions and an underestimation for few motor repetitions. All these effects were spatially selective in external world coordinates and that hold even for early blind participant, who we might have expected to show a hand centred reference frame (according to some results in the literature).

It is well known that crossing the hands can impair the execution of appropriate finger movement (Burnet et al, 1904).

Sighted people find more difficult to judge the temporal order when two tactile stimuli are presented and their hands are crossed over the midline as when they adopt a more typical uncrossed hands posture (Shore et al., 2002; Yamamoto et al., 2001).

It has been argued that because of the dominant role of vision in motor planning and execution (Pouget et al., 2002), sensory stimuli are mapped into externally defined coordinates and in crossed hand condition this mapped are in conflict and that involves both multisensory parietal and visual cortex.

Several experiments in the past few years show that performance of late blind and sighted but not of congenitally blind people was impaired by crossing the hands (Röder et al., 2004; Röder et al., 2007), both in temporal order judgments for tactile, than for auditory stimuli.

These studies suggest a critical role of childhood vision in modulating the perception of touch and sounds that arise from the emergence of specific cross-modal links during development.

Deal with numerosity; little is know about the development process through which numbers are mapped onto external physical space.

In the experiment of 2013 Crollen and colleagues perform a numerical comparison task to 5 both to early blind, late blind and sighted controls. The task was carried out either with hands parallel or hand crossed.

They found a classic SNARC effect in the uncrossed and crossed conditions in late blind and sighted control (Dehaene et al., 1993): small numbers elicited faster left-side responses, while large numbers elicited faster right-sided responses, independently of the responding hand (left or right).

Therefore this data support the idea that the crossed hands posture did not precluded the SNARC effect from occurring in sighted controls and extended this observation to the case of late blind.

Moreover these results indicate that in both groups the SNARC effect elicited in a number comparison task depends on eye-centred or world-centred coordinates rather than hand-based coordinates (Crollen et al., 2013). The results contrast with the ones of Wood (2006) showing an absence of SNARC effect in a crossed posture (Wood et al., 2006).

Completely different were the results for early blind subjects as it was reported a reversed SNARC effect. When early blind subjects performed a numerical comparison task with the hands crossed on the body midline, small numbers elicited faster left-hand responses, regardless of where in space-hands were placed. In other words early blind individuals showed a classic SNARC effect in the uncross condition but a reversed SNARC effect in crossed condition.

These results indicate the use of hand-based coordinates in early blind and are in-line with recent experiments demonstrating that early visual deprivation prevents the default-use of an external coordinate system in space perception (Collignon 2009a, 2009b; Röder 2004, 2007, 2008). The idea is that in sighted controls, crossing the hands induces a conflict between the anatomical coordinates of the responding hand and the external coordinates of the stimulus (i.e. the number) that has to be processed. In the early blind this contrast for crossing the hands would not occur because early visual deprivation prevents the automatic remapping process of number in external coordinates.

In other words, early blind would map numerical and sensory stimuli just into the body-cantered representation.

Crollen and colleagues in 2017 perform another interestingly experiment in which they investigated the role of motor production on tactile perception. Early blind and sighted controls took part in two experiments. In the first one participants were required to perform a Temporal Order Judgment task (TOJ), either with their hands in parallel or crossed over the body midline. In line with previous demonstration, crossing the hands led to a significant decrement in performance in controls (SC) but did not affect early blind (EB). In experiment 2, participants were trained to perform a sequence of five-finger movements. They were tested on their ability to produce, with the same hand but with the keypad turned upside down, the learned (internal) or the mirror (external) sequence. They observed significant transfer of motor sequence knowledge in both EB and SC irrespective of whether the representation of the sequence was internal or external. Together, these results demonstrate that visual experience differentially impacts the automatic weight attributed to internal versus external coordinates (Crollen et al., 2017).

Our research aimed to investigate the role that the visual experience plays in shaping the use of external and internal coordinate system for sensorimotor number processing. The same participants were involved in two different tasks used to disentangle the use of different coordinates in the sensory and motor fields.

Asking participants to perform a numerical estimation with the hands crossed or uncrossed over the body midline, allowed us to assess the spatial representation of auditory numerosity. Results are similar to the data of Crollen (2017).

This cross-hand effect in external frame of reference both of SC that EB is attributed to a difference in the weights that are used to integrate internal and external spatial information.

In the previous results of Crollen (2017) they found that while the weighting scheme of SC automatically favours an external coordinate system, EB preferentially rely on an internal frame of reference to perform the task.

The automatic integration of internal and external coordinates for touch localization therefore appears to be driven by developmental vision. Such integration probably helps the alignment of the spatial frames of reference that are used by the distal sense (e.g. vision and audition) and the body limbs.

For example, our ability to interact with our immediate surroundings depends on our ability to represent the location of objects with respect to our own body and especially our hands.

This process is particularly critical since the hands move constantly within the space around our body as different postures are adopted.

It has therefore been demonstrated that EB have more difficulties to optimally integrate audio-tactile information in the crossed postures due to the poorly aligned spatial coordinates of these two modalities in such conditions. However since the numerosity task is likely to be resolved using action-based coordinates, the weighting scheme used by the EB shields them from the detrimental crossing effect.

It is therefore possible that early visual deprivation alleviates the weights of external coordinates due to the reorganization or to the lack of development of brain circuits implicated in such process.

The posterior parietal cortex has been hypothesized to play a crucial role in implementing such operation in SC and this region has been repetitively shown reorganized in EB.

Motor sequence learning, on the other hand, has been shown to encompass two independent processes named “spatial” (external) and “motor” (internal). Within this view, learning a piano sonata not only requires performing specific series of finger movements (in an internal reference frame) but also requires learning the position of specific musical notes in an external reference frame.

Our statistics support the idea of a “true” absence of group differences.

The observation that both groups of participants were able to implicitly create an external spatial representation of their motor action parallels previous studies also showing an absence of difference between the sighted and blind groups to support the idea that vision is not necessary to the development of external coordinates in motor coordination. While a striatum-motor network supports the effector-dependent representation, the effector-independent motor representation has been found to recruit a hippocampus-cortical network involving prefrontal and parietal cortices. Even if visual inputs are the predominant sensory inputs of the parietal cortex, auditory and somatosensory information also access this area.

Makin, Holmes and Zohary demonstrated that the posterior intraparietal sulcus (IPS) and lateral occipital complex represent hand-centred space in a predominantly visual manner, whereas the anterior IPS was characterized by a more proprioceptive representation of the space surrounding the hand (Makin et al., 2007).

It is therefore possible that EB mainly rely on the anterior IPS to code an external representation of the space surrounding the hand. Rough the proprioceptive and auditory modalities, EB people might therefore localize objects in the external space and produce a goal-directed action toward them. Such non-visual sensory-motor loop may be sufficient to build an external sense of space, which is used to act in the external environment. In support of this hypothesis, it was demonstrated that the parietal-occipital reach-related regions retain their functional role, encoding of the spatial position of the reach target, in EB.

For summarize, our results therefore suggest task-specific differences in the way blind and sighted use specific spatial frame of references for sensory-motor processing.

In other words, our data do not support the idea that early visual experience is necessary for the development of an external coordinate system for perception and action. Our results rather suggest that it is readily accessible when participants have to perform an action in the external world.

CHAPTER 5 – MOTION INDUCE COMPRESSION ON PERCEIVED NUMBER

5.1.1 Introduction

While much evidence support the idea of a Generalized Magnitude System processing spatial, temporal and numerical information by means of a common metric, several aspects of such a mechanism are still to be understood. We will report a study aimed to further investigate some features of the hypothetical magnitude system, by addressing the issue whether motion adaptation affect similarly perception of time and numbers (Fornaciai et al., Under revision). To this aim, we studied the effect of motion adaptation on perceived numerosity, by using a paradigm similar to that used of studies about perceived time (Johnston et al., 2006; Burr et al., 2007; Fornaciai et al., 2016). Indeed, motion represents an ideal candidate to study the intertwining between different magnitudes, given that it is intrinsically defined as a combination of spatial and temporal information (i.e. modulation of spatial information over time), and that it also contains numerical information, since a moving stimulus could be defined by a certain number of changes over time. Moreover, given that motion adaptation has proven to be effective in distorting the representation of both space (e.g. positional aftereffect; Snowden, 1998; Nishida & Johnston, 1999) and time (e.g. Burr et al., 2007), it represents a good benchmark for whatever theory about a Generalized Magnitude System: if space, time and number actually share some functional mechanisms, it might be possible for motion adaptation to distort all these dimensions in a similar way.

As we had seen in the previous chapters, in our everyday lives, space, time and number processing allow us to answer some of the most basic questions necessary to understand the outside world; *where* the objects are located and their spatial relationships, *when* events occur and for *how much time*, and *how many* objects are out there.

Given the important role played by spatial, temporal and numerical information, and their intertwining in the real world, some researcher proposed the existence of a common mechanism, processing them with a similar metrics, and implemented in (at least partially) overlapping brain regions.

We had already debated such idea, in the Walsh's ATOM in which this different quantities might be processed by means of a common machinery, called Generalized Magnitude System (GMS).

This idea of a common magnitude system has been indeed supported by many experimental findings, both at the physiological and perceptual level (Burr et al., 2010) showing similar perceptual effects affecting the representation of different magnitudes, as well as mutual interactions among them (Xuan et al., 2007; 2009; Burr et al., 2011; Rammsayer & Verner, 2014; 2015; Cai & Connell, 2015).

According to this evidence, the most malleable dimension seems to be time, while time and number would not be that effective to distort space.

Such asymmetry between different dimensions led some authors to propose a different account, alternative to the ATOM theory: the more “abstract” dimensions, such as time, would be processed as metaphors of space, using the concepts of the more “concrete” spatial domain (Clark, 1973; Boroditsky, 2000; Gibbs, 2006; Casasanto & Boroditsky, 2008; Casasanto et al., 2010; Merritt et al., 2010).

However, Cai & Connell (2015) pointed out that while such asymmetry actually exist, is only depends on the resolution of the visual system for different features: while vision has a good spatial resolution, its temporal sensitivity is relatively poor, which makes temporal processing in the visual domain much more prone to distortions (Cai & Connell, 2015).

Conversely, another line of evidence seems to suggest similar perceptual distortions caused by adaptation, and particularly for motion adaptation. For example, Schwiedrzik et al. (2016), testing the influence of motion direction on numerosity representation demonstrated a clear link between the representation of space and number.

With a series of experiments, Schwiedrzik and colleagues systematically investigated the possibility to distort perceived numerosity by distorting the mental number line via adaptation to a specific direction of motion (Schwiedrzik et al., 2016).

What they found is that adapting to a given direction (i.e. left or right) shifts the perceived number of items in the adapted stimulus accordingly: rightward motion causes an underestimation, while leftward motion causes overestimation, relative to the perceived numerosity of another stimulus adapted with random motion.

These results clearly demonstrate a strong relation between motion and numerosity processing, and led the authors to conclude that the two magnitudes share some neural substrates and functional mechanisms.

Moreover, by means of control experiments it was assessed some of the properties of this motion induced numerosity adaptation, such as the effects of adapting to different numerosities (big and small numbers) and the reference frame of adaptation. According to the results, the best candidate as an underlying neural substrate for the interaction between motion and number processing is the homolog of monkey's parietal area LIP, which is a crucial area previously recognized to be involved in magnitudes processing (Walsh, 2003; Burr et al., 2011).

However, while Schwiedrzik (2016) results provide a clear demonstration of the intertwining between spatial and numerical magnitudes, the effect of motion adaptation *per se* on numerosity still remain unclear, since in their study test and probe stimuli were both adapted, and only the effect of motion direction (i.e. coherent versus random motion) was addressed (Schwiedrzik et al., 2016).

On the other hand, motion adaptation *per se,* independently of direction, but selectively for the overall motion profile, has been shown to be highly in distorting perceived time: while fast translational motion adaptation (usually 20 Hz) causes a robust compression of perceived duration (Johnston et al., 2006; Burr et al., 2007) temporal estimates after adaptation to more complex motion profiles (such radial and circular motion) remain always veridical.

Here, we investigated the relation between timing and numerical processing mechanisms exploiting visual motion adaptation.

While Schwiedrzik et al.'s (2016) focused on the spatial representation of number, moving it with directional motion, we focused instead on the similarities between adaptation effects on time and numbers. Particularly, we aimed to test for the direct effect of motion adaptation on numerosity representation, similarly to what has been done on perceived time (Johnston et al., 2006; Burr et al., 2007; Fornaciai et al., 2016).

Indeed, while at first glance numerical magnitudes and motion are two seemingly unrelated dimensions, recent investigations pointed out the involvement of motion-sensitive mechanisms in numerosity processing, which appear to play a role at the early processing stages where the items are normalized for non-numerical visual attribute (Dehaene & Changeux, 1993 and Verguts & Fias, 2004 for computational models of numerosity perception). Thus, motion processing seems to be involved in both visual time perception (Bueti et al., 2008; Fornaciai et al., 2016) and numerosity perception (Schwiedrzik et al. 2016), which could make both dimensions similarly prone to distortions due to motion adaptation.

To investigate this possibility, we first used sinusoidal oscillating grating, trying to find similar adaptation-induced distortions as previously demonstrated on perceived duration.

We also exploited a more complex motion profile (i.e. circular motion), to further investigate the difference between uni-directional and complex motion adaptation pointed out by Fornaciai et al. (2016) on perceived duration.

If time and number are actually related dimensions, sharing a common metrics, we expected to find a general effect of motion adaptation on perceived numerosity, independently from directional effects and shifts on the mental number line as showed by Schwiedrzik et al. (2016).

However, since adaptation might act at different levels along the visual stream, adapting to different motion profiles could give rise to two possible outcomes. On the one hand, if adaptation operates directly at the level of the magnitude system (i.e. IPS), numerosity should be affected by motion adaptation in a similar fashion compared to time (i.e. same motion profile specificity).

On the other hand, if adaptation operates *before* the magnitude system, somewhere in the visual stream conveying domain-specific information toward higher-level areas, so we could expect different outcomes adapting with different motion profiles, since adaptation may work differently at different levels and on different early encoding mechanisms.

Since we used adaptor stimuli (i.e. gratings) largely different from test stimuli (i.e. cloud of dots), we also devised a series of control experiments in order to exclude the possible confounding factors provided by adaptation effects on dimensions only indirectly related to numerosity, such as contrast/visibility or spatial frequency.

5.1.2 Methods

A total of 30 subjects participated in the study (13 females, age ranging from 21 to 30 years) each of them involved in either one or multiple conditions. All the participants were naive to the purpose of the study, with the exception of authors I.T. and M.F., who participated to all experimental conditions. Experimental procedures were approved by the local ethics committee (Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Firenze, FI), and were in line with the declaration of Helsinki. All participants gave written informed consent.

All visual stimuli were generated with the Psychophysics Toolbox V.3 (Kleiner et al., 2007) for MatLab (version 2010b) running on a PC computer, and presented on a Barco CRT monitor (Barco Calibrator Line), subtending 40 x 30 degrees of visual angle at the viewing distance of about 57 cm. Screen resolution was set to 800 x 600 pixels with a refresh rate of 100 Hz. In the numerosity discrimination task stimuli consisted of clouds of dots arranged within an invisible annulus (the inner and external edge located at 1° and 5° from the stimulus center, respectively) with a minimum inter-dots distance of 0.75 deg. Adapters consisted of either translating or rotating patches moving at high (20 Hz) or low (5 Hz) temporal frequency, with each combination of adapting profile and speed tested in separate sessions.

Translating adapters were luminance modulated gratings (spatial frequency = 1 cycle per degree) drifting horizontally with a direction reversal occurring every 2 seconds.

Circular motion adapters were windmill-like rotating gratings, with spatial frequency increasing from 0.5 to 1.2 cpd from the outer to the inner border respectively. Both classes of adapters were windowed within an annular mask (distance from the center to the inner and outer edge equal to 1 deg and 5.5 deg respectively), with borders blurred by a Gaussian smoothing (spatial constant equal to 0.15 deg) and were presented either with a Michelson contrast of 90% or 50% (tested in in separate sessions).
On each trial, subjects were simultaneously presented with two stimuli, a test and a reference, both presented at a horizontal eccentricity of 10° respectively to the left and to the right of a central fixation point. The subjects' task was to indicate which stimulus contained more dots by pressing the appropriate key on a keyboard (2AFC – 2-Alternatives Forced Choice). The numerosity of the reference stimulus was kept constant (15 dots) whilst the test numerosity varied from trial to trial according to an adaptive QUEST staircase (Watson & Pelli, 1983) within a range of ± 0.3 log units relative to the reference numerosity.

We measured subjects' accuracy by mean of the point of subjective equality (PSE) defined as the median of the best-fitting cumulative Gaussian function to the data representing the percentage of responses "test as more numerous" against test physical numerosity. Precision was instead measured as the just noticeable difference (JND), defined as the standard deviation of the underlying Gaussian function. On separate sessions, subjects performed numerosity discrimination after being adapted to fast (20 Hz) or slow (5 Hz) translational or circular motion.

Each trial started with the presentation of the adapter stimulus, displayed in the left portion of the screen with a horizontal eccentricity of 10 deg (same location as the following reference stimulus). The adapter was presented for 20 s on the very first trial with a top up of 8 s in all following trials. After 500 ms from the adapter offset, test and reference were presented according to the procedure described above. To assess whether and to what extent motion adaptation affects perceived numerosity, we calculated a perceived numerosity reduction index, defined as the difference between post-adaptation and baseline PSE, normalized by this latter and transformed in percentage:

Perceived numerosity reduction = -1 * ((PSE_adapt – PSE_baseline)/PSE_baseline) * 100 (1)

With PSE_baseline and PSE_adapt representing participants' accuracy in the baseline and adaptation condition respectively.

Note that as compressive effects result in negative effects when measured as the difference between baseline and post-adaptation PSEs, when calculating the perceived numerosity reduction index we reversed the sign of the effect. Fourteen participants were tested in the main experiment. A series of control experiments (just concerning adaptation to translational motion) were carried out to test whether motion adaptation aftereffects are numerosity range-dependent and whether they might be accounted for in terms of some sort of masking effect.

To these aims we tested, in separate conditions, the effect of motion adaptation on perceived numerosity on both: a higher range (around 50 dots) or on lower range (3 dots to fall within the subitizing regime). Finally, in additional conditions we reduced the adaptor contrast from 90 to 50%, in order to minimize the effect of contrast masking on perceived numerosity. Six additional participants were tested in three control experiments concerning discrimination of larger numerosities, low numerosity (within the subitizing range) and adaptation to low contrast stimuli. For each of these experimental conditions we generally collected from 3 to 5 sessions of data each of which containing 30 trials.

5.1.3 Results

Fig. 41 shows psychometric functions for two subjects obtained by plotting the proportion of trials where the test stimulus was judged as more numerous than the reference, as a function of test numerosity. The left and the right panels of the figure show the results for the condition concerning adaptation to translational and circular motion respectively. Adaptation to translational motion strongly compressed perceived numerosity as shown by the consistent leftward shift of the red curves in the left panel of Fig. 41. However, the aftereffects co-varied with the adapting speed as shown by adaptation to slow translation that compress perceived numerosity but to a much lesser extent.

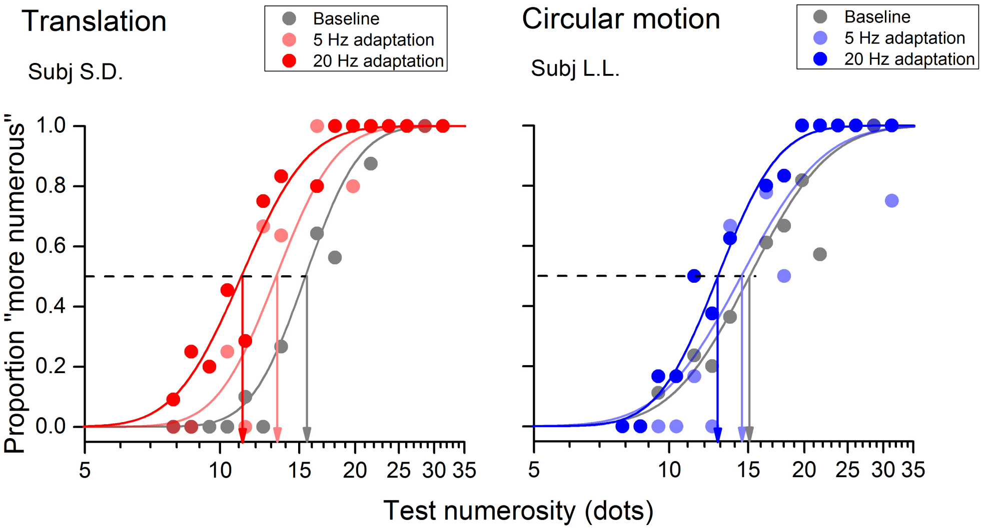


FIG. 41 – Psychometric functions for the numerosity discrimination task*. Psychometric functions showing the proportion of trials the test stimulus appeared more numerous than the reference stimulus (fixed numerosity equal to 15 dots), as a function of the numerosity of the test. The panel on the left refers to adaptation to translational motion and the panel to the right to adaptation to circular motion. Data in grey indicate the baseline condition in which the discrimination task was performed without adaptation. Data in light colour refer to condition in which the adapting speed was slow (5Hz) and full coloured lines refer to adaptation to fast motion (20 Hz). Despite the adapting motion profile being translational or circular, motion adaptation induced a compression of perceived numerosity as indicated by the leftward shift of the psychometric functions. However, adaptation to translational motion induced a much more robust compression of perceived numerosity to suggest a complex - profile dependent – interaction between motion and numerosity processing.*

Adaptation to fast circular motion also yielded a significant compression of perceived numerosity even if numerosity distortions were weaker that that triggered by fast translational motion. On the contrary, slow circular motion slightly affected perceived numerosity as shown by the light blue curve in the right panel of Fig. 41 almost overlapped with the curve for the baseline condition (gray). To better quantify adaptation effects, we measured the amount of compression in perceived numerosity induced by motion adaptation as a normalized difference between baseline and post-adaptation PSEs (see Methods).

Fig. 42 shows the amount of compression averaged across all subjects for adaptation to both fast and slow translational and circular motion.

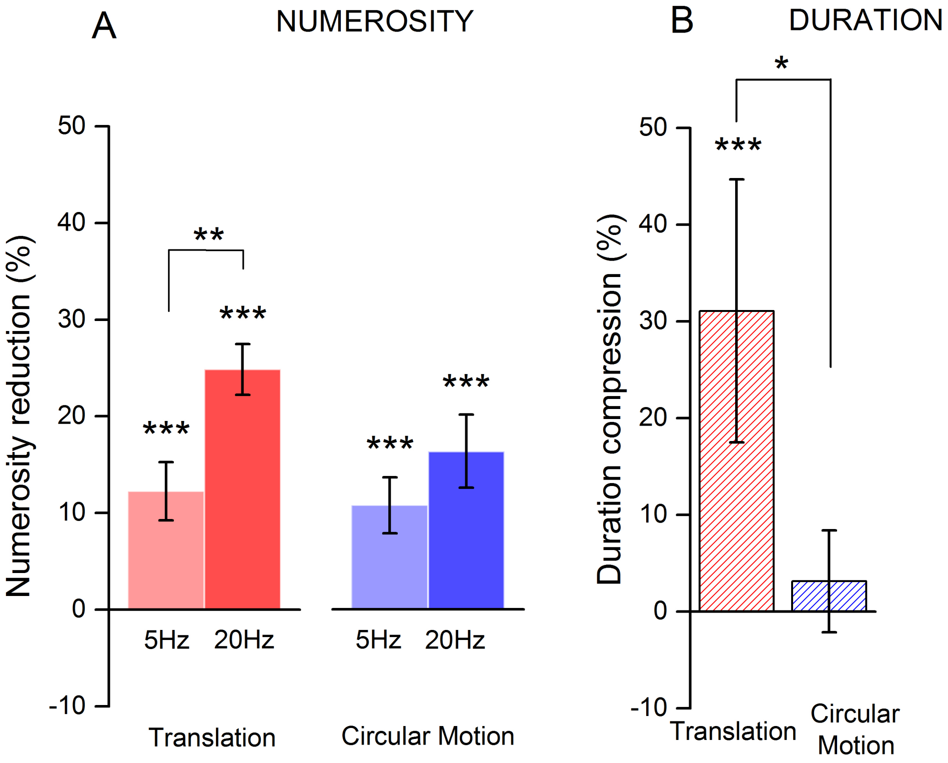


FIG. 42. Average numerosity compression for adaptation to translational or circular motion. *Panel A: Reduction in perceived numerosity induced by adaptation to translational (in red) or circular motion (in blue). In all conditions, numerosity reduction was calculated as the difference between post-adaptation and baseline PSEs, normalized by the baseline. Adaptation to fast translational motion strongly compressed perceived numerosity by on average 20-25%. Fast rotational motion yielded a robust compression (around 15-17%) but it was significantly smaller than that induced by rapid translation. Perceived numerosity was also distorted by adaptation to slow rotation and translation, with the two motion profiles providing similar compression of perceived numerosity: around 10% Panel B: Reduction of stimuli perceived duration induced by adaptation to fast translational -red hatched bar- or rotational -blue hatched bar- motion (data from Fornaciai et al., 2016). Whilst adaptation to translation robustly affect perceived duration and numerosity (in both cases providing a compression of about 20-30%), after adaptation to slow translational motion, estimates of perceived numerosity are slightly distorted but those about stimuli duration remain veridical. Asterisks above each bar refer to tests comparing pre- and post-adaptation PSEs. Asterisks between bars refer to tests comparing the magnitude of the adaptation across different conditions. Error bars represents S.E.M. * p < 0.05, ** p < 0.01, *** p < 0.001.*

Fast translational motion compressed perceived numerosity by about 25% whilst slow translation provided around one half of such an effect (compression around 12%). Adaptation to circular motion also affected perceived numerosity but to a lesser extent. A sustained exposure to a fast circular motion, reduced perceived numerosity of about 17% whilst slow circular motion (5 Hz) provided compression similar to that achieved for slow translational motion (around 12%). A series of paired-sample t-test showed that post-adaptation PSEs were significantly lower compared to baseline measures, in all the adaptation conditions taken into account: translation 5 Hz ($t_{(13)} = 3.97$, $p < 0.001$), translation 20 Hz ($t_{(13)} = 8.92$, $p < 0.001$), rotation 5 Hz ($t_{(13)} = 3.92$, $p < 0.001$); rotation 20 Hz ($t_{(13)} = 4.23$, $p < 0.001$). Furthermore, the magnitude of the effects across different conditions (perceived numerosity change index; see Methods), was compared using a two-way ANOVA using as main factors "speed" and "motion profile". The results showed a significant main effect of speed ($F_{(1,55)} = 9.25$, $p = 0.004$) whilst neither the effect of motion profile ($F_{(1,55)} = 2.77$, $p = 0.102$) nor the interaction amongst the two ($F_{(2,55)} = 1.38$, $p = 0.245$) was found to be significant. However, a post-hoc multiple comparison test (Holm-Sidak multiple comparison) showed that while adaptation to translational motion at different speeds provides significantly different effects (i.e. larger effect with 20 Hz adaptation; $t_{(13)} = 3.04$, $p = 0.004$), such a difference was found not to be significant for circular motion ($t_{(13)} = 1.32$, $p = 0.193$).

The magnitude of the changes in perceived numerosity induced by motion adaptation varied consistently according to the to the adapting motion profile and was also dependent by the adapting speed. However, adaptation aftereffects varied widely even across participants. Might this variability be related to inter-individual difference in sensitivity to numerosity? In a recent study, Van der Burg and colleagues (2013) reported that the size of audiovisual recalibration, induced by exposure to audio-visual pairs, strongly correlated with the width of the simultaneity window: the more tolerant the simultaneity judgments, the stronger the recalibration effect (Van der Burg et al., 2013). To investigate the relationship between sensitivity in numerosity discrimination and adaptation magnitude, we compared the precision of baseline numerical judgments (JNDs) with the magnitude of the adaptation effect. The results are shown in Fig. 43A-B for both adapting profiles and speeds.

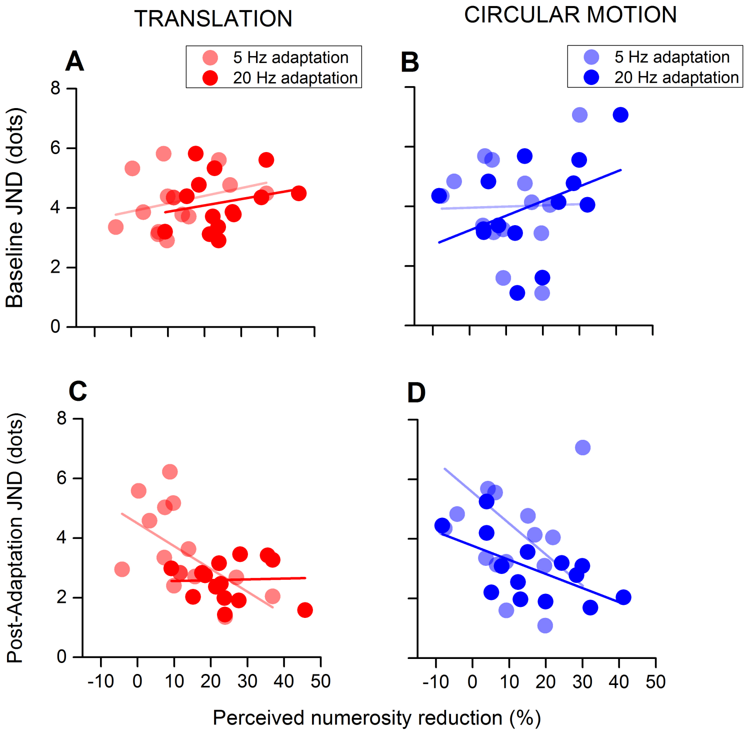


FIG. 43. The relation between baseline and post-adaptation JNDs and adaptation effects. *(A-B) Pre-adaptation (baseline) sensitivity for numerosity discrimination (JND) plotted as a function of post adaptation numerosity reduction for (A) translational and (B) circular motion. None of the correlations concerning baseline JND turned out being statistically significant, suggesting independency between precision in numerosity discrimination and susceptibility to motion adaptation. (C-D) Correlations between post-adaptation JND and adaptation magnitude for translational and circular motion (C and D respectively). In most cases post-adaptation JNDs negatively correlated to the magnitude of the adaptation to indicate a concurred reduction of PSEs and JNDs to reflect an increase in precision for lower perceived magnitude in line with Weber's law.*

For adaptation to translational motion (both 20 and 5 Hz) and slow circular motion, correlations were found to be small and far from being statistically significant (translation 5Hz: r = 0.30, p = 0.27; translation 20Hz: r = 0.22, p = 0.42; circular motion 5Hz: r = 0.02, p = 0.92). A more consistent correlation emerged for adaptation to fast circular motion (r = 0.42) but even in this case statistical significance was not reached (p = 0.13). We also analyzed correlations between the reduction in perceived numerosity and post-adaptation JNDs (Fig. 43C-D).

Post-adaptation JNDs significantly decreased as reduction of perceived numerosity increased for circular motion (both, 5 and 20 Hz) as well as slow translation. In all three conditions, the bigger the numerosity underestimation, the higher the precision (Pearson correlations, translation 5Hz: $r = -0.56$, $p = 0.029$; circular motion 5Hz: $r = -0.63$, $p < 0.015$; circular motion 20Hz: $r = -0.60$, $p = 0.02$). The results of a significant negative correlation between post-adaptation JNDs and adaptation magnitude indicate that Weber-Fechner's law is obeyed: the precision of perceptual estimates is proportional to the magnitude of the sensory input. This in turns makes the effects of motion adaptation on perceived numerosity likely to be perceptual in nature and not due to non-perceptual factors such as changes in decision criteria. However, there is an exception. Post adaptation JNDs did not correlate with adaptation magnitude for fast translational motion (Pearson correlations, translation 20Hz: $r = -0.07$, $p = 0.82$). A possible explanation for this lack of correlation might be a lack of variability in the data. Indeed, JNDs after adaptation to fast translation – that is the most efficient condition to trigger compression of perceived numerosity, were found to be all very small regardless the magnitude of adaptation (see Fig. 43 C). This might suggest the existence of a maximum level of precision that cannot be exceeded with this edge effect, preventing correlations to occur.

A possible concern about these results is that motion adaptation might affect perceived numerosity indirectly, for example via a non-specific masking mechanism. This idea generates several hypotheses that we tested with a series of control experiments.

We first addressed the issue of whether adaptation is specific for a given numerosity range.

Recent results suggest that numerosity perception is mediated by different mechanisms: an errorless mechanism for numerosity within the subitizing range (1-5), a mechanism obeying Weber's law for higher numerosities in which the number of items can only be approximately estimated, and a texture-density mechanism following a square root law operating when items are too dense to be individually segregated (Anobile et al., 2014; Anobile et al., 2015). Here we investigated the effects of adaptation to translational motion on numerosity perception for reference numerosity about three times higher than that exploited in Experiment 1 (from n = 15 to n = 50) but still falling in the estimation range as well as for numerosity falling within the subitizing range (n = 3). Predictions are clear: while the effect on the higher numerosity range should be comparable to those observed in Experiment 1, estimates in the subitizing range should not be affected by adaptation and remain veridical. Indeed, previous studies showed that subitizing mechanisms are virtually immune to adaptation, unless attentional resources are diverted as for example by presenting a concurrent additional task (Burr et al., 2010; Anobile et al., 2012). Panels A and B of Fig. 44, show adaptation effect for reference numerosities of 3 and 50 dots respectively. Motion adaptation strongly affected discrimination for numerosity around 50 dots, with the reduction in perceived numerosity being rather similar to that achieved for a reference numerosity of 15 dots (see Fig. 42). Namely, adaptation to translational motion yielded a reduction of about 25% for translation at 20 Hz and of about 14% for slow (5Hz) translation.

Both effects resulted to be statistically significant as shown by one-way R.M. ANOVA with Holm-Sidak multiple comparison procedure versus control: baseline vs. 20Hz adaptation, $t_{(5)} = 5.867$, $p < 0.001$ and baseline vs. 5Hz adaptation, $t_{(5)} = 3.432$, $p = 0.006$), to indicate that both adaptation conditions yielded a significant shift of the PSEs compared to baseline. On the contrary, motion adaptation did not provide any significant change in perceived numerosity when the numerosity range was kept in the subitizing range ($F_{(2,4)} = 2.330$, $p = 0.159$) as shown by panel A of Fig. 44.

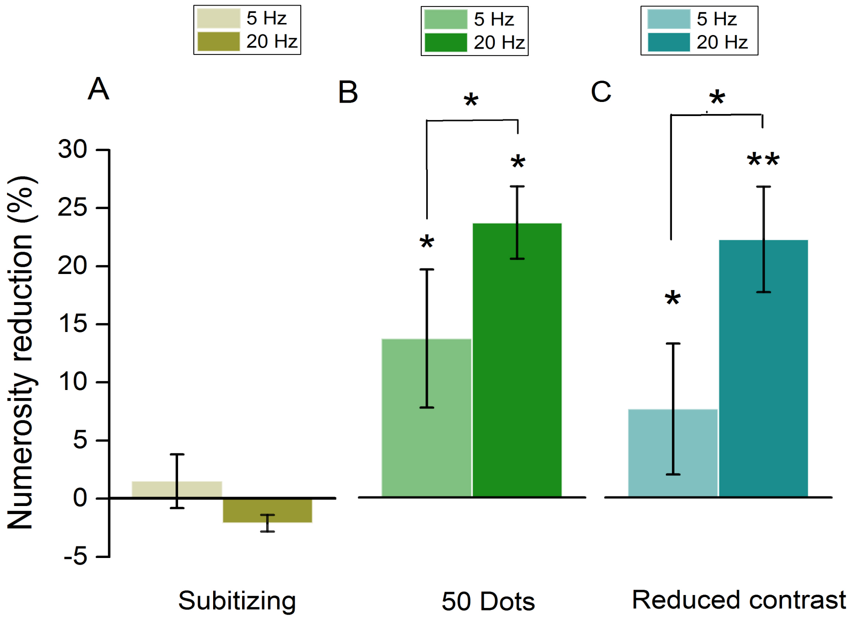


FIG.44 – Adaptation to different numerosity regimes and to low contrast adapters. *Panels A, B: Perceived numerosity reduction induced by motion adaptation in the subitizing range (reference numerosity = 3 dots; panel A) or the estimation range (numerosity 3 times higher than in Exp 1; panel B). Motion adaptation did not affect perceived numerosity in the subitizing range. On the contrary, perceived numerosity in the estimation range was found to be consistent despite reference numerosity being 15 (as in Exp 1) or 50 dots. (C) Motion adaptation-induced numerosity reduction effects after adaptation to translational motion, in the condition where the adaptor contrast was reduced to 50%. Error bars represent S.E.M. * p < 0.05, ** p < 0.01.*

Finally, we tested whether adaptation compress perceived numerosity via a spurious effect, that is, by reducing the visibility of the adapted stimuli. Despite this hypothesis had already been partially falsified by the results on the subitizing range, we devised a new version of Experiment 1 to investigate the effect of adaptation to fast translational motion, with adapters of a reduced contrast: from 90% to 50%. The idea is to leverage on the finding that when adapters are lower in contrast than test stimuli, perceived contrast (and thus visibility) of the latter remains unaffected (Georgeson, 1985). Panel C of Fig. 44 shows the results for adaptation to low contrast adapters. In general, the pattern of results for low and high contrast adapters is quite similar. Even with adapters with a Michelson contrast of 50%, fast translational motion (20 Hz) distorted perceived numerosity by about 20%, while slow translation (5 Hz) to a lesser extent, about 7-8%. A one-way R.M. ANOVA confirmed that in both conditions post-adaptation PSEs were significantly different from baseline (Holm-Sidak multiple comparison versus control [“baseline”]: baseline versus 5 Hz: $t_{(4)} = 2.526$, $p = 0.035$; baseline versus 20 Hz: $t_{(4)} = 5.057$, $p = 0.002$), and that effects provided by adaptation to fast translational motion were stronger than those achieved for slow translation: paired sample t-test on numerosity reduction values, $t_{(4)} = 2.943$, $p = 0.0211$. Taken together, these results about the magnitude of adaptation aftereffect in the subitizing range (Fig. 44, panel A) and those for low contrast adapters (Fig.44, panel C) congruently support the idea that the effects of motion adaptation on perceived numerosity are unlikely to be accounted for in terms of visibility reduction of the adapted stimuli.

5.1.4 Discussion

In the present study, we investigated the effects of visual motion adaptation on perceived numerosity (Fornaciai et al., Under revision). Our results show that a sustained exposure to either translational or circular motion compresses numerosity estimates of stimuli subsequently presented in in the adapted location. The magnitude of adaptation is temporal frequency-dependent with adaptation to fast motion (20 Hz) providing a much stronger effect than adaptation to slower motion (5 Hz). Adaptation also shows a trend to be dependent on the adapting motion profile with fast translation to be more effective than fast circular motion, even if this difference was not found to be statistically significant. We controlled for the possibility that motion adaptation affected numerosity indirectly, for example by reducing the visibility (perceived contrast) of the adapted stimuli. None of our results support this idea. First, motion adaptation selectively affects numerosity perception in the estimation range (> 5 items) but not in the subitizing regime (< 5 items). However, a low-level effect such as a reduction in perceived contrast should affect the stimulus' visibility regardless of numerosity, making possible to miss one or more items even at extremely low numerosities. Second, adaptation to low-contrast adapters provides rather identical effects than high-contrast stimuli. However, it has been reported that perceived contrast of high contrast stimuli is minimally affected by adaptation to low contrast adapters (Georgeson, 1985) to suggest that changes in perceived numerosity induced by low contrast adapters could not be accounted for in terms of reduced visibility of the adapted stimuli.

Even if the effect of motion adaptation on numerosity is genuine, might it be not perceptual in nature but related to some unspecific cognitive or decisional factor? Two lines of evidence stand against this hypothesis. First, the effect is spatially localized. We adapted a region of space on the left of a central fixation point. Then we simultaneously presented a reference and a test stimulus in the adapted and neutral location respectively. The changes in the PSEs found in the adaptation condition (relative to the baseline), suggest that adaptation selectively affect one of the two stimuli: if motion adaptation affected both, we would not have recorded any PSE shift. The second evidence supporting a perceptual nature of these adaptation aftereffects is even more substantial: in most conditions we found a consistent negative correlation between numerosity compression and post-adaptation JNDs. In other words, when the subjects perceive fewer stimuli, as shown by their PSE, performances become more precise in line with the scalar variability of Weber’s law.

At which stage of visual processing might motion and numerosity perception interact? A first hypothesis is that motion and numerosity interact at a relatively late stage, as proposed by theoretical frameworks suggesting the existence of neural machinery dedicated to magnitude processing (i.e. a theory of magnitude [ATOM], Walsh, 2003) in the parietal lobe (Bueti & Walsh, 2009; Burr et al., 2010). When the activity of these neural circuits mediating a common representation of quantity is affected, processing of multiple perceptual dimensions might be distorted.

Indeed, one of the hypotheses tested in this study is that perceived numerosity might be affected by motion adaptation similarly to perceived duration

(Johnston et al., 2006; Burr et al., 2007; Fornaciai et al., 2016). Our results show that adaptation to fast translational motion compresses perceived numerosity of about the same extent (20-25%, see Fig. 42) as it does with duration. This result is consistent with the idea of a “common magnitude system”, processing spatial, temporal and numerical information as initially proposed by Walsh (2003). These results also complement those by Schwiedrzik and colleagues (2016) that showed motion direction to strongly bias the perceived number of items (clouds of dots) as if the adapting direction would provide a shift along the mental number line and linking together the dimensions of space and number. However, the similarities between the effects of motion adaptation on perceived duration and numerosity are limited to fast translational motion and do not generalize to the other conditions took into account. For instance, it has been reported that adaptation to circular motion does not affect duration estimates, leaving them veridical (Fornaciai et al., 2016). Conversely, we found here that adaptation to circular motion robustly affects perceived numerosity (up to 16% for fast rotation). Similarly, slow translational and circular motion (5 Hz), both known to have little or no effect on perceived duration (Johnston et al., 2006; Curran and Benton, 2012; Fornaciai et al., 2016), were instead found to significantly compress perceived numerosity (by around 10%) even if to a lesser extent than fast motion. Our results suggest that motion adaptation – for both time and number – might operate somewhere at an intermediate level between the early stations of visual analysis and the higher-level parietal magnitude system itself, and not directly on the magnitude system itself.

This possibility suggested by our data could explain the difference in the pattern of effect registered on different magnitudes. Indeed, for time perception, the lack of effect for complex motion adaptation might be mediated by a different level of adaptability of the different substrates mediating the processing of simple and complex motion (i.e. MT or MST, respectively). Moreover, in the case of time perception, while it has been shown a direct involvement of area MT in duration processing (Bueti et al., 2008), other areas such as MST may play a secondary role: this could easily explain the strong difference found in Fornaciai et al.'s study. However, such distinction is not possible in the case of numerosity, and it is likely that the mechanisms purely concerned with number do not discriminate between different motion profiles – which makes both simple and complex motion similarly suitable as adaptors.

An alternative hypothesis is that such interaction occurs at an early stage. Fornaciai and colleagues (2017) have recently found signature of numerosity processing at around 100 ms after stimulus onset, with this activity likely to tap on early visual areas such as V2 or V3.

Intriguingly these two areas have been recently reported to be highly sensitive to global motion and this in turn, make V2 and/or V3 perfect candidates to underpin interactions between motion and numerosity processing (Furlan & Smith, 2016).

Finally, the idea that motion mechanisms might affect numerosity processing at early stage is in line with evidence that numerosity estimates are strongly affected by the spatiotemporal properties of visual stimuli (Fornaciai and Park, In press).

Perceived numerosity of clouds of moving dots randomly changing their locations either abruptly or smoothly, are systematically biased towards overestimation, but with smooth motion yielding a reduced effect to indicate a role of motion integration in numerosity processing. However, as our results do not allow us to disentangle the precise neural substrate of motion adaptation effects on perceived numerosity or other magnitudes, this remains an interesting open question for future studies. Overall, our results suggest a close link between motion processing and numerosity perception, in line with previous studies (Schwiedrzik et al., 2016; Fornaciai & Park, In press). The close relationship between motion and numerosity, on the one hand, supports the idea of similar, although at least partially dissociable, pathways for the processing of different magnitudes.

On the other hand, however, the difference between the effect of complex motion adaptation on perceived numerosity and perceived duration (Fornaciai et al., 2016), suggests that magnitude-specific effects of motion adaptation occur at different levels of the visual processing stream.

CHAPTER 6 - GENERAL CONCLUSION

Numerosity is a growing field of research, crossing many disciplines, including vision research, human and animal cognition, anthropology, developmental psychology, clinical and basic psychology, and computational neuroscience. However, the mechanisms of numerosity perception are still poorly understood and highly debated. One reason why this topic is particularly compelling is that numerosity is intrinsically correlated with many other physical features. The first main goal of my PhD it has been to investigate whether and to what extent the number sense is a general or a domain specific. The second main goal was to investigate whether and to what extent numerosity perception tap on perceptual mechanisms similar to those for temporal or spatial perception. Indeed, more than 15 years ago, it has been proposed that different quantities, including time, space or number, are processed by a common mechanism (Walsh, 2003; Pinel et al., 2004), henceforth called generalized magnitude system (GMS).

At the end of these three years what are the main results that have been achieved?

6.1.1 The sense of number is adaptable

A clear signature of the existence of a dedicated perceptual mechanism is its susceptibility to adaptation (Clifford & Rhodes, 2005; Thompson & Burr, 2009): several seconds of exposure to a given stimulus (say a leftward moving pattern) change the appearance of stimuli viewed in the same position, causing a negative aftereffect (in this case, illusory rightward motion of stationary stimuli). Adaptation, ubiquitous throughout sensory systems, represents a form of experience-dependent plasticity in which our current sensory experience is intimately affected by how we viewed the world only moments before (Barlow & Foldiak, 1989; Boynton, 2004; Kohn, 2007; Solomon & Kohn, 2014). It is a widely held belief that adaptation pose numerous functional advantages, including serving to auto calibrate perceptual systems to their environment by dynamically tuning its responses to match the distribution of stimuli to make maximal use out of the limited working range of the system. Burr and Ross (2008) showed that also numerosity perception is strongly susceptible to adaptation.

After a period of adaptation to dense or sparse dot clouds (say about 30 seconds), subsequently viewed dot clouds appear to differ considerably in their numerosity, showing a strong negative aftereffect. Based largely on the fact that numerosity shows adaptation, combined with other known facts such as the approximation to Weber’s law (threshold varies proportionally with number of items), the results led Burr and Ross to suggest that number was a ‟primary-visual-attribute.”

It has been suggested that the adaptation may be mediated by a homologue of neurons found in monkey lateral intraparietal cortex (LIP; Roitman, Brannon, & Platt, 2007).

As LIP cells have reasonably circumscribed receptive fields, they will respond to the numerosity within that receptive field, not across the entire visual field. Of course, this selectivity is functional: animals need an estimate of number of apples (fish, or lions) in a given part of the scene in order to take appropriate action.

A consistent part of my research, it has been dedicated to extend Burr and Ross results.

In chapters 2, 3 and 4 I show that the same effect of numerosity adaptation Burr and Ross (2008) found for visual stimuli simultaneously presented (spatial numerosity) were also achieved with sequentially presented stimuli. In all cases adaptation showed the typical rebound aftereffect: adapting to high numerosity yielded compression of apparent numerosity and adapting to low numerosity an overestimation.

6.1.2 The sense of number is cross modal

All our data support the idea that numerosity perception is intimately a cross-modal process. We have already discussed about the possible neural correlate in the ventral intraparietal sulcus (IPS) and lateral prefrontal cortex in which some neurons encode the numerosity for both auditory and visual sensory modalities (Nieder, 2012). There also exists evidence from functional imaging in humans for a right lateralized fronto-parietal circuit activated by both auditory and visual number sequences (Piazza et al., 2006).

Here we provided clear behavioural evidence for such cross modal feature in chapter 2, 3 and 4.

In the chapter 2 we used an adaptation paradigm concerning both, visual that auditory stimuli, to show that in both conditions we found a huge distortion in the perceived numerosity of the stimulus (test) subsequentially presented in the adapted location.

Same adaptation effects were found in all cross modal conditions: adapting to visual stimuli distorted perceived numerosity of sounds and vice versa. The effect was similar in all conditions with none statistical significant difference amongst them.

In the chapter 2 we also presented the results about adaptation effect on tactile numerosity within that modality or in cross modal conditions (visuo-tactile or audio-tactile). Again adaptation was found to be robust and all combination of stimuli sensory modalities provided similar effects. Of course all these results strongly suggest that the number sense is a high-generalized system, capable of combining numerical information from different senses.

Moreover the ability to generalize across different modalities of perception but also action is an important component of what we call the *number concept.* Let us suppose, that a people systematically utters the word "four" whenever he or she sees four objects, but randomly picks the words "three," "four," or "nine" when he or she hears four sounds or makes four jumps. Although performance is no doubt excellent with visual stimuli, we would be reluctant to grant the people knowledge of the concept of "4", because we consider possession of this concept to entail being able to apply it to many different multimodal situations.

It’s clear that the numerical information have an implication also in the production of specific action, both in everyday live than in specific situation, for example in performing music or dance. Again we talked about the neural circuits probably implicated in this mechanism like neurons in area 5 of the superior parietal lobule of monkey (Sawamura et al. 2002; 2010) or left ventral premotor cortex activated by counting successive sensory stimuli (Kansaku et al. 2007).

Here we provided behavioural evidence in favour of this generalized system that involved not only the perceptual but also the motor system. We presented these results in the chapter 3 and 4 in which we found an effect of adaptation for self-produce movement on visual numerosity (chapter 3) and on auditory stimuli (chapter 4, in this case both in sighted control than in congenitally blind participants). Again this is a clear proof of a human supramodel mechanism that involve not only perceptual but also extend to the motor systems.

6.1.3 The sense of number transcends stimuli presentation format

Other than cross modal, a generalized sense of number should process stimuli numerosity independently from their format being it simultaneous or sequential. People are obviously able to encode numbers in many different conditions: despite the person is watching a set of three dots or looks at a sequence of three dots, anyway he o she recognizes the concept of 3. Also in this case there is electrophysiological and imaging evidence supporting this issue: the hIPS is a “amodal” brain regions which are not attached to a specific format of presentation.

If a brain region is to encode an abstract concept, one that is not tied to specific format, it is essential that it respond to the entire relevant format of stimulation in which the concept can be communicated.

Also our study support the idea of an a-modal sense on number with behavioural evidence we reported in chapter 2, 3, 4 and 5 with the results about adaptation in the cross format conditions. In chapter 2 we demonstrated that a sequence of flashes was able to adapt a cloud of dots. We observed strong underestimation with high sequence and an overestimation with a low number.

In the chapter 3 we saw that also a sequence of action is able to adapt perceived numerosity of visual stimuli, both simultaneously and sequentially presented. More, in chapter 4 we reported the same interaction between action and perception for numerosity processing of sounds.

Adaptation effects in all these different conditions were found to be similar to suggest that all these different numerosity processes tap on a common perceptual mechanism.

Finally in the chapter 5 we presented some innovative data about a study that framed numerosity within the theoretical framework of the ATOM theory. Also the results of this study support the idea of a number sense that is quite malleable and what is more strictly related to perceptual mechanism processing other dimension such as time and space.

6.1.4 The sense of number is spatially selective and coded in real world coordinates

An issue that frequently pop put in our studies is the spatial selectivity of the number sense.

In the chapter 2, 3 and 4 we reported adaptation effects just for the stimuli presented in the adapted location with an almost complete lack of adaptation for those presented elsewhere. In the chapter 3 and 4 we found an effect of adaptation only in the location where the hand had been tapping and not in the symmetrically opposite side whatever the sensory modality of the test stimuli: visual (chapter 3) or auditory (chapter 4).

These results are a clear signature that all the adaptation effect reported in our study are perceptual in nature and not yielded by cognitive or response bias we also investigated the reference frame and found that numerosity aftereffect is exclusively coded in an external reference frame.

In the chapter 2 we found that the effect after a saccade is mapped on spatiotopic, not retinotopic, coordinates. Also in the chapter 3 and 4, we changed the position of the tapping hand and found that the effect was spatially selective in external, not hand centred coordinates. Indeed when subjects tapped with the left hand or with the right hand crossed on the middle line (thus tapping on the left side), the effect was on the left for both, visual stimuli (see chapter 3) and auditory stimuli (see chapter 4).

In our studies we addressed the nature of the remapping from action to an external reference frame.

Previous findings show that an external frame of reference is dominant in action spatial tasks, (Crollen et al., 2017).

This has led to the assumption that the remapping process occurs rather automatically, without a vision feedback: indeed this effect was found both in sighted control than for congenitally blind (chapter 4).

6.1.5 The number sense without vision

Much evidence suggests a close link between space and numbers. Indeed the main code for representing space is vision, so in the last few years many studies addressed the issue of the development of a numerical representation in lack of any visual experience. For example, several researchers have addressed this question by studying the impact of early visual deprivation on a range of numerical processes: numerical comparison, parity judgment, numerical bisection, numerical estimation, subitizing, and finger counting. Szücs and Csépe (2005) tested a group of 8 congenitally blind and 8 blindfolded sighted participants on an auditory numerical comparison task in which a given number had to be compared with a reference equal to 5. The aim of the study was to address whether the blind participants show the typical behavioural distance and SNARC effects usually observed in typical subjects for numerical comparison task. In addition, electroencephalographic (EEG) data were collected in order to investigate whether blind participants showed, alike sighted people, modulations of the amplitude of several EEG parameters as a function of numerical distance between the test and the reference number (Dehaene, 1996). The results indicated that both groups of participants presented robust distance and SNARC effects, suggesting that blind and sighted participants used a similar spatial metric to represents numbers, that is, a mental continuum oriented from left to right.

In addition, similar brain circuits appeared to be recruited in both groups, as no apparent discrepancies in the activation amplitude or areas of activation. Indeed, EEG recording showed, in both groups of participants, similar parietal and frontal ERP deflections at around 200 ms and a similar distance effect. More, the results did not even reveal any discrepancy in the ERP topographies and the ERP distance effect between to suggest that number comparison relies on similar neural circuits in blind as well as sighted participants. In conclusion, it seems that despite a complete absence of visual experience, early blind subject develop a close-to-typical number representation in terms of brain area involved and amplitude of neural responses. These pioneering findings have inspired a consistent numerous of experimental studies that subsequently have been carried out to better understanding how numbers are represented in the brain of early blind people (Szücs & Csépe, 2005).

For Castronovo and colleagues decided to replicate the previous study but took into consideration a wider numerical range. In this study, subjects were engaged in parity judgment task in which they had to compare two numbers within the range 5 -55. Again, blind and sighted participants presented exactly the same distance and SNARC effects, to suggest that they share the same semantic numerical representation even for high numerosity range (at least up to around 50).

Because blind and sighted participants displayed a similar SNARC effect, Castronovo and colleagues suggested that vision does not act as a prerequisite for the development of an internal representation of numbers mapped onto external physical space.

However, better way to investigate whether early blind subjects have a spatial representation of numbers, similar to that of sighted controls subjects, it might be to investigate whether the SNARC effect revers in blind when they provide manual responses with the arms crossed.

This is exactly what Crollen and colleagues (see chapter 4) did in their study published on Cortex (Crollen et al., 2013). They had three groups of participants, early blind, late blind and sighted controls. Participants were required to perform a numerical comparison task against number 5 in two different conditions, either with hands parallel or with hands crossed over the body midline. Moreover, in order to test for the specificity of this effect, participants were also required to carry out a parity judgment task. The results revealed that sighted controls and late blind reversed the SNARC effect (faster responses with the left hand – located on the right- for numbers higher than 5) when they provided manual responses with the arms crossed. However, the opposite was true for early blind subjects as they always responded faster to small numbers with the left hand regardless the hand position. Taken together, these results suggest that in early blind the numerical space is encoded in hand centred coordinates in line with recent experiments demonstrating that early visual deprivation prevents the default-use of an external coordinate system in space for perception and action (Crollen et al., 2013; Collignon et al., 2009a, 2009b; Röder et al., 2004, 2007, 2008).

Pasqualotto and colleagues (2014) tested congenitally and late blind together with blindfolded sighted participants in a random number generation task where in each block subjects’ heads were alternately turned left or right before uttering the number. They found that ‘random’ number generation was biased according to the head position in all group of subjects. However, whilst participants with visual experience generated smaller numbers for left turns, and larger numbers for right turns, early blind participants showed an opposite bias.

These results suggested a role for visual experience in the development of spatial and numerical representations, which is supported by cultural differences in number representation, and provide converging evidence for visually driven organization of the parietal cortex (Pasqualotto et al., 2014).

While these findings together suggest that vision drives the development of the automatic integration of internal and external coordinates (Crollen et al., 2013; Pasqualotto et al., 2013), recent results demonstrated that bimanual coordination in the congenitally blind was constrained by external-spatial factors, like in the sighted (Heed & Röder, 2014) and that external coordinates may affect tactile localization in congenitally blind in the context of an action that requires external spatial coding (Heed et al., 2015). It is therefore conceivable that congenitally blind do integrate information from internally and externally defined reference frames, but that they do so according to another weighting scheme than the sighted. Integration in the congenitally blind could be restricted to situations in which the use of the non-preferred external reference frame is required by the task. The experiments reported above suggest that movement is a good candidate to bias spatial localization towards an external coordinate system in sighted as well as in blind individuals.

As movements are commonly used to interact with objects located in the external world (e.g., typing on a computer), relying on an external representation within a motor context would indeed seem more appropriate even in early blind individuals. Interestingly, within the motor literature, a variety of different laboratory-based protocols demonstrated that motor sequence learning involves, like touch perception, the processing of internal and external spatial coordinates.

In order to examine how visual experience affects the internal/external coding of space for touch and movement, Crollen and colleagues (2017) performed an experiment with early blind (EB) and sighted controls (SC). In experiment 1, participants were required to perform a Temporal Order Judgment task (TOJ), either with their hands in parallel or crossed over the body midline. In line with previous evidence, crossing the hands provided a significant decrement in performance in SC but did not affect EB. Then in a second experiment, participants were trained to perform a sequence of five-finger movements. They were tested on their ability to produce, with the same hand but with the keypad turned upside down, the learned (internal) or the mirror (external) sequence. They observed significant transfer of motor sequence knowledge in both EB and SC irrespective of whether the representation of the sequence was internal or external. Together, these results demonstrate that visual experience impacts differentially the automatic weight attributed to internal versus external coordinates depending on task-specific spatial requirements (Crollen et al., 2017).

Given that processing numerical information is also fundamental for the motor system to program sequences of self-movement, as discussed in chapter 4, we have recently investigated a further level of generalization of the number sense by assessing the possibility that a shared numerical representation exist between action and perception, that is, across domains.

The aim of our experiment was twofold. On one side we wanted to assess to what extent motor adaptation affected numerosity perception of non-visual stimuli (acoustics). A second goal was to investigate the reference frame of adaptation (external world vs hand centered) in congenital and acquired blind subjects. The rationale of this study was to test the idea that a default use of an external coordinate system in space for number perception and action might (or not) depend on early visual experience.

A robust adaptation effect was observed in both groups of participants: an underestimation of the numerosity presented was observed after the execution of fast movements and an overestimation of the numerosity was observed after the execution of slow movements, in the crossed as well as in the uncrossed posture. Taken together, these results expanded previous findings showing that adaptation to self-produced actions distorts perceived numerosity of sounds. Moreover, we demonstrated that visual experience is not necessary for the development of an external coordinate system for the shared numerical representation of action and perception.

6.1.6 Conclusion

To conclude all or experimental work strongly support the idea of a generalized sense of number. Almost all experiments carried out during the last three years that have been reported in this thesis, stands for this idea with no exception. Clearly the number sense is independent from the sensory modality and the format of presentation and it is spatially selective in external reference frame. Despite we don’t have a external sensory system dedicated to the elaboration of number, like the retina for vision or the cochlea for audition, numbers are elaborated in our brain circuits and the probable locus of elaboration tap on neural circuits of the parietal and prefrontal cortex. The generalize sense of number is a very important feature in our life as it is likely to significantly increase the chances of survival. This might be the reason why humans share this system with many other animals and it has been evolved since a long time ago.

The sensory precision of number perception refines during development, and varies considerably between individuals (Halberda et al., 2008; Anobile et al., 2017). Importantly, strong correlations have been found between precision in numerosity judgments and formal math abilities (Halberda et al., 2008; Piazza, 2010; Anobile et al., 2017). It is likely that humans exploited this sense of number as a starting box to developed more complex and cognitive abilities such those needed for calculation or formal arithmetic (Piazza, 2010). There is evidence that training on non-symbolic approximate number tasks yields improvements in symbolic arithmetic performance in adults (Park & Brannon, 2013), school-age children (Wilson et al., 2006) and preschoolers (Park et al., 2016).

Consequently it is important to understand how we represent numbers in our brain and determine whether there is a unitary neuronal basis for all forms of numerical representation. Deficits in the sense of numbers might have serious consequences in subjects’ quality of life.

Discovering the neural basis of number is important for educational interventions, diagnosis, classification and design of rehabilitation programs for people suffering from learning disabilities such as dyscalculia, a goal that we hope to have provided a contribution to (as small as it might be) with all the researches reported in this thesis.

Reference

Agrillo, C., Dadda, M., Serena, G., & Bisazza, A. (2008). Do fish count? Spontaneous discrimination of quantity in female mosquitofish. *Animal Cognition*, *11*(3), 495–503. https://doi.org/10.1007/s10071-008-0140-9

Alais, D., & Burr, D. (2004). Ventriloquist Effect Results from Near-Optimal Bimodal Integration. *Current Biology*, *14*(3), 257–262. https://doi.org/10.1016/S0960-9822(04)00043-0

Allik, J., Tuulmets, T., & Vos, P. G. (1991). Size invariance in visual number discrimination. *Psychological Research*, *53*(4), 290–295. https://doi.org/10.1007/BF00920482

Anobile, G., Arrighi, R., Castaldi, E., Grassi, E., Pedonese, L., Moscoso M., P. A., & Burr, D. C. (2017). Spatial but Not Temporal Numerosity Thresholds Correlate With Formal Math Skills in Children. *Developmental psychology*. http:// doi.org/10.1037/dev0000448

Anobile, G., Arrighi, R., Togoli, I., & Burr, D. C. (2016). A shared numerical representation for action and perception. *eLife*, *5*(AUGUST). https://doi.org/10.7554/eLife.16161.001

Anobile, G., Castaldi, E., Turi, M., Tinelli, F., & Burr, D. C. (2016). Numerosity but not texture-density discrimination correlates with math ability in children. *Developmental Psychology*, *52*(8), 1206–1216. https://doi.org/10.1037/dev0000155

Anobile, G., Cicchini, G. M., & Burr, D. C. (2014). Separate Mechanisms for Perception of Numerosity and Density. *Psychological Science*, *25*(1), 265–270. https://doi.org/10.1177/0956797613501520

Anobile, G., Cicchini, G. M., & Burr, D. C. (2016). Number As a Primary Perceptual Attribute: A Review. *Perception*. https://doi.org/10.1177/0301006615602599

Anobile, G., Cicchini, G. M., & Burr, D. C. (2012). Linear mapping of numbers onto space requires attention. *Cognition*, *122*(3), 454–459. https://doi.org/10.1016/j.cognition.2011.11.006

Anobile, G., Turi, M., Cicchini, G. M., & Burr, D. C. (2015). Mechanisms for perception of numerosity or texture-density are governed by crowding-like effects. *Journal of Vision*, *15*(5), 4. https://doi.org/10.1167/15.5.4

Arrighi, R., Togoli, I., & Burr, D. C. (2014). A generalized sense of number. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), 20141791–20141791. https://doi.org/10.1098/rspb.2014.1791

Arrighi, R., Cartocci, G., & Burr, D. (2011). Reduced perceptual sensitivity for biological motion in paraplegia patients. *Current Biology*. https://doi.org/10.1016/j.cub.2011.09.048

Arsalidou, M., Pawliw-Levac, M., Sadeghi, M., & Pascual-Leone, J. (2017). Brain areas associated with numbers and calculations in children: Meta-analyses of fMRI studies. *Developmental Cognitive Neuroscience*. https://doi.org/10.1016/j.dcn.2017.08.002

Arsalidou, M., & Taylor, M. J. (2011). Is 2+2=4? Meta-analyses of brain areas needed for numbers and calculations. *NeuroImage*, *54*(3), 2382–2393. https://doi.org/10.1016/j.neuroimage.2010.10.009

Banks, W. P., & Hill, D. K. (1974). The apparent magnitude of number scaled by random production. *Journal of Experimental Psychology*, *102*(2), 353–376. https://doi.org/10.1037/h0035850

Barlow, H. B., & Földiák, P. (1989). *Adaptation and decorrelation in the cortex*. *The Computing Neuron*.

Barth, H., La Mont, K., Lipton, J., & Spelke, E. S. (2005). Abstract number and arithmetic in preschool children. *Proceedings of the National Academy of Sciences*, *102*(39), 14116–14121. https://doi.org/10.1073/pnas.0505512102

Barth, H., Kanwisher, N., & Spelke, E. (2003). The construction of large number representations in adults. *Cognition*, *86*(3), 201–221. https://doi.org/10.1016/S0010-0277(02)00178-6

Basso, G., Nichelli, P., Frassinetti, F., & di Pellegrino, G. (1996). Time perception in a neglected space. *NeuroReport*, *7*(13), 2111–2114. https://doi.org/10.1097/00001756-199609020-00009

Belin, P., McAdams, S., Thivard, L., Smith, B., Savel, S., Zilbovicius, M., … Samson, Y. (2002). The neuroanatomical substrate of sound duration discrimination. *Neuropsychologia*, *40*(12), 1956–1964. https://doi.org/10.1016/S0028-3932(02)00062-3

Bell, J., Manson, A., Edwards, M., & Meso, A. I. (2015). Numerosity and density judgments: Biases for area but not for volume. *Journal of Vision*, *15*(2), 1–14. https://doi.org/10.1167/15.2.18.doi

Berteletti, I., Lucangeli, D., Piazza, M., Dehaene, S., & Zorzi, M. (2010). Numerical estimation in preschoolers. *Developmental Psychology*, *46*(2), 545–551. https://doi.org/10.1037/a0017887

Boroditsky, L. (2000). Metaphoric structuring: Understanding time through spatial metaphors. *Cognition*, *75*(1), 1–28. https://doi.org/10.1016/S0010-0277(99)00073-6

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

Boynton, G. M. (2004). Adaptation and attentional selection. *Nature Neuroscience*, *7*(1), 8–10. https://doi.org/10.1038/nn0104-8

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Brannon, E. M. (2003). Number knows no bounds. *Trends in Cognitive Sciences*. https://doi.org/10.1016/S1364-6613(03)00137-2

Brannon, E. M., & Terrace, H. S. (2000). Representation of the numerosities 1-9 by rhesus macaques (Macaca mulatta). *Journal of Experimental Psychology: Animal Behavior Processes*, *26*(1), 31–49. https://doi.org/10.1037/0097-7403.26.1.31

Brown, S. W. (1997). Attentional resources in timing: Interference effects in concurrent temporal and nontemporal working memory tasks. *Perception & Psychophysics*, *59*(7), 1118–1140. https://doi.org/10.3758/BF03205526

Bueti, D., & Walsh, V. (2009). The parietal cortex and the representation of time, space, number and other magnitudes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1525), 1831–1840. https://doi.org/10.1098/rstb.2009.0028

Bueti, D., Bahrami, B., & Walsh, V. (2008). Sensory and Association Cortex in Time Perception. *Journal of Cognitive Neuroscience*, *20*(6), 1054–1062. https://doi.org/10.1162/jocn.2008.20060

Burbaud, P., Camus, O., Guehl, D., Bioulac, B., Caillé, J. M., & Allard, M. (1999). A functional magnetic resonance imaging study of mental subtraction in human subjects. *Neuroscience Letters*, *273*(3), 195–9.

Burnett, C. T. (1904). Studies in the influence of abnormal position upon the motor impulse. *Psychological Review*, *11*(6), 370–394. https://doi.org/10.1037/h0074642

Burr, D. C., Ross, J., Binda, P., & Morrone, M. C. (2011). Saccades Compress Space, Time, and Number. In *Space, Time and Number in the Brain* (pp. 175–186). https://doi.org/10.1016/B978-0-12-385948-8.00012-8

Burr, D. C., Turi, M., & Anobile, G. (2010). Subitizing but not estimation of numerosity requires attentional resources. *Journal of Vision*, *10*(2010), 1–10. https://doi.org/10.1167/10.6.20

Burr, D., Banks, M. S., & Morrone, M. C. (2009). Auditory dominance over vision in the perception of interval duration. *Experimental Brain Research*, *198*(1), 49–57. https://doi.org/10.1007/s00221-009-1933-z

Burr, D., & Ross, J. (2008). A Visual Sense of Number. *Current Biology*, *18*(6), 425–428. https://doi.org/10.1016/j.cub.2008.02.052

Burr, D., Tozzi, A., & Morrone, M. C. (2007). Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nature Neuroscience*. https://doi.org/10.1038/nn1874

Butterworth, B., Cappelletti, M., & Kopelman, M. (2001). Category specificity in reading and writing: the case of number words. *Nature Neuroscience*, *4*(8), 784–6. https://doi.org/10.1038/90484

Butterworth, B., Reeve, R., & Reynolds, F. (2011). Using Mental Representations of Space When Words Are Unavailable: Studies of Enumeration and Arithmetic in Indigenous Australia. *Journal of Cross-Cultural Psychology*, *42*(4), 630–638. https://doi.org/10.1177/0022022111406020

Butterworth, B., Reeve, R., Reynolds, F., & Lloyd, D. (2008). Numerical thought with and without words: Evidence from indigenous Australian children. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(35), 13179–13184. https://doi.org/10.1073/pnas.0806045105

Cai, Z. G., & Connell, L. (2015). Space-time interdependence: Evidence against asymmetric mapping between time and space. *Cognition*, *136*, 268–281. https://doi.org/10.1016/j.cognition.2014.11.039

Casasanto, D., & Boroditsky, L. (2008). Time in the mind: Using space to think about time. *Cognition*, *106*(2), 579–593. https://doi.org/10.1016/j.cognition.2007.03.004

Casasanto, D., Fotakopoulou, O., & Boroditsky, L. (2010). Space and time in the child's mind: Evidence for a cross-dimensional asymmetry. *Cognitive Science*, *34*(3), 387–405. https://doi.org/10.1111/j.1551-6709.2010.01094.x

Casini, L., & Macar, F. (1997). Effects of attention manipulation on judgments of duration and of intensity in the visual modality. *Memory & Cognition*, *25*(6), 812–818. https://doi.org/10.3758/BF03211325

Castaldi, E., Aagten-Murphy, D., Tosetti, M., Burr, D., & Morrone, M. C. (2016). Effects of adaptation on numerosity decoding in the human brain. *NeuroImage*, *143*, 364–377. https://doi.org/10.1016/j.neuroimage.2016.09.020

Castronovo, J., & Seron, X. (2007). Semantic numerical representation in blind subjects: The role of vision in the spatial format of the mental number line. *The Quarterly journal of experimental psychology*, *60*(1), 101-119. https://doi.org/10.1080/17470210600598635

Cattell, J. M. (1886). The time taken up by cerebral operations. *Mind*. https://doi.org/10.1093/mind/os-XI.42.220

Chochon, F., Cohen, L., van de Moortele, P. F., & Dehaene, S. (1999). Differential contributions of the left and right inferior parietal lobules to number processing. *Journal of Cognitive Neuroscience*, *11*(6), 617–30. https://doi.org/10.1162/089892999563689

Cipolotti, L., Warrington, E. K., & Butterworth, B. (1995). Selective Impairment in Manipulating Arabic Numerals. *Cortex*, *31*(1), 73–86. https://doi.org/10.1016/S0010-9452(13)80106-2

Clark, H. H. (1973). Space, time, semantics and the child. *Cognitive Development and the Acquisition of Language*, 27–63. https://doi.org/10.1080/10643389.2012.728825

Clifford, C. W. G., & Rhodes, G. (2005). *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision*. *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision*. https://doi.org/10.1093/acprof:oso/9780198529699.001.0001

Cohen Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., Van De Ven, V., … Linden, D. E. J. (2005). Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, *43*(9), 1238–1248. https://doi.org/10.1016/j.neuropsychologia.2004.12.017

Cohen, J. (1988). Statistical power analysis for the behavioral sciences. *Statistical Power Analysis for the Behavioral Sciences*. https://doi.org/10.1234/12345678

Cohen, L., & Dehaene, S. (1996). Cerebral networks for number processing: Evidence from a case of posterior callosal lesion. *Neurocase*, *2*(November), 155–174. https://doi.org/10.1080/13554799608402394

Collignon, O., Davare, M., Olivier, E., & De Volder, A. G. (2009). Reorganisation of the right occipito-parietal stream for auditory spatial processing in early blind humans. a transcranial magnetic stimulation study. In *Brain Topography* (Vol. 21, pp. 232–240). https://doi.org/10.1007/s10548-009-0075-8

Collignon, O., Charbonneau, G., Lassonde, M., & Lepore, F. (2009). Early visual deprivation alters multisensory processing in peripersonal space. *Neuropsychologia*, *47*(14), 3236–3243. https://doi.org/10.1016/j.neuropsychologia.2009.07.025

Cordes, S., & Brannon, E. M. (2008). The difficulties of representing continuous extent in infancy: Using number is just easier. *Child Development*, *79*(2), 476–489. https://doi.org/10.1111/j.1467-8624.2007.01137.x

Coull, J. T., Cheng, R.-K., & Meck, W. H. (2011). Neuroanatomical and Neurochemical Substrates of Timing. *Neuropsychopharmacology*, *36*(1), 3–25. https://doi.org/10.1038/npp.2010.113

Crespi, S., Biagi, L., d'Avossa, G., Burr, D. C., Tosetti, M., & Morrone, M. C. (2011). Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. *PLoS ONE*, *6*(7). https://doi.org/10.1371/journal.pone.0021661

CRITCHLEEY, M. (1953). Parietal lobes. *Giornale Di Psichiatria E Di Neuropatologia*, *81*(4), 872–873. https://doi.org/10.1136/bmj.2.4851.1416

Crollen, V., Dormal, G., Seron, X., Lepore, F., & Collignon, O. (2013). Embodied numbers: The role of vision in the development of number-space interactions. *Cortex*, *49*(1), 276–283. https://doi.org/10.1016/j.cortex.2011.11.006

Crollen, V., Albouy, G., Lepore, F., & Collignon, O. (2017). How visual experience impacts the internal and external spatial mapping of sensorimotor functions. *Scientific Reports*, *7*. https:// 10.1038/s41598-017-01158-9

d'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D. C., & Morrone, M. C. (2007). Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nat Neurosci*, *10*(2), 249–255. https://doi.org/10.1038/nn1824

Dakin, S. C., Tibber, M. S., Greenwood, J. A., Kingdom, F. A. A., & Morgan, M. J. (2011). A common visual metric for approximate number and density. *Proceedings of the National Academy of Sciences*, *108*(49), 19552–19557. https://doi.org/10.1073/pnas.1113195108

Davis, H., & Pérusse, R. (1988). Numerical competence in animals: Definitional issues, current evidence, and a new research agenda. *Behavioral and Brain Sciences*, *11*(4), 561. https://doi.org/10.1017/S0140525X00053437

Dehaene, S., & Cohen, L. (1994). Dissociable mechanisms of subitizing and counting: neuropsychological evidence from simultanagnosic patients. *Journal of Experimental Psychology. Human Perception and Performance*, *20*(5), 958–975. https://doi.org/10.1037/0096-1523.20.5.958

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition*, *44*(1–2), 1–42. https://doi.org/10.1016/0010-0277(92)90049-N

Dehaene, S. (1996). The Organization of Brain Activations in Number Comparison: Event-Related Potentials and the Additive-Factors Method. *Journal of Cognitive Neuroscience*, *8*(1), 47–68. https://doi.org/10.1162/jocn.1996.8.1.47

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General*, *122*(3), 371–396. https://doi.org/10.1037/0096-3445.122.3.371

Dehaene, S., & Changeux, J. P. (1993). Development of elementary numerical abilities: a neuronal model. *Journal of Cognitive Neuroscience*, *5*(4), 390–407. https://doi.org/10.1162/jocn.1993.5.4.390

Dehaene, S., & Cohen, L. (1997). Cerebral Pathways for Calculation: Double Dissociation between Rote Verbal and Quantitative Knowledge of Arithmetic. *Cortex*, *33*(2), 219–250. https://doi.org/http://dx.doi.org/10.1016/S0010-9452(08)70002-9

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences*. https://doi.org/10.1016/S0166-2236(98)01263-6

Dehaene, S., Dupoux, E., & Mehler, J. (1990). Is numerical comparison digital? Analogical and symbolic effects in two-digit number comparison. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(3), 626–641. https://doi.org/10.1037/0096-1523.16.3.626

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*. https://doi.org/10.1080/02643290244000239

Dormal, V., Andres, M., Dormal, G., & Pesenti, M. (2010). Mode-dependent and mode-independent representations of numerosity in the right intraparietal sulcus. *NeuroImage*, *52*(4), 1677–1686. https://doi.org/10.1016/j.neuroimage.2010.04.254

Dormal, V., Seron, X., & Pesenti, M. (2006). Numerosity-duration interference:A Stroop experiment. *Acta Psychologica*, *121*, 109–124. https://doi.org/10.1016/j.actpsy.2005.06.003

Duffau, H., Capelle, L., Sichez, N., Denvil, D., Lopes, M., Sichez, J.-P., … Fohanno, D. (2002). Intraoperative mapping of the subcortical language pathways using direct stimulations. An anatomo-functional study. *Brain*, *125*(Pt 1), 199–214. https://doi.org/10.1093/brain/awf016

Duffy, C. J., & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. *Journal of Neurophysiology*, *65*(6), 1346–1359.

Durgin, F. H. (1995). Texture density adaptation and the perceived numerosity and distribution of texture. *Journal of Experimental Psychology: Human Perception and Performance*. https://doi.org/10.1037/0096-1523.21.1.149

Durgin, F. H. (2008). Texture density adaptation and visual number revisited. *Current Biology*. https://doi.org/10.1016/j.cub.2008.07.053

Emmerton, J., & Delius, J. D. (1993). 21 Beyond Sensation: Visual Cognition in Pigeons. Vision, brain, and behavior in birds, 377

Feigenson, L. (2005). A double-dissociation in infants' representations of object arrays. *Cognition*, *95*(3). https://doi.org/10.1016/j.cognition.2004.07.006

Fornaciai, M., Arrighi, R., & Burr, D. C. (2016). Adaptation-Induced Compression of Event Time Occurs Only for Translational Motion. *Scientific Reports*, *6*(1), 23341. https://doi.org/10.1038/srep23341

Fornaciai, M., & Park, J. (in press). Spatiotemporal feature integration shapes approximate numerical processing. *Journal of Vision*, *17*(13), 1–15.

Fornaciai, M., Togoli, I., & Arrighi, R. (Under Revision). Motion-induced compression of perceived numerosity. *Scientific Reports.*

Frank, M. C., & Barner, D. (2012). Representing exact number visually using mental abacus. *Journal of Experimental Psychology: General*, *141*(1), 134–149. https://doi.org/10.1037/a0024427

Fulbright, R. K., Molfese, D. L., Stevens, a a, Skudlarski, P., Lacadie, C. M., & Gore, J. C. (2000). Cerebral activation during multiplication: a functional MR imaging study of number processing. *AJNR. American Journal of Neuroradiology*, *21*(6), 1048–54.

Furlan, M., & Smith, A. T. (2016). Global Motion Processing in Human Visual Cortical Areas V2 and V3. *Journal of Neuroscience*, *36*(27), 7314–7324. https://doi.org/10.1523/JNEUROSCI.0025-16.2016

Gallace, A., & Spence, C. (2008). The cognitive and neural correlates of "tactile consciousness": A multisensory perspective. *Consciousness and Cognition*. https://doi.org/10.1016/j.concog.2007.01.005

Gallace, A., Tan, H. Z., & Spence, C. (2006). Numerosity judgments for tactile stimuli distributed over the body surface. *Perception*, *35*(2), 247–266. https://doi.org/10.1068/p5380

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition*, *44*(1–2), 43–74. https://doi.org/10.1016/0010-0277(92)90050-R

Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences*. https://doi.org/10.1016/S1364-6613(99)01424-2

Georgeson, M. A. (1985). The effect of spatial adaptation on perceived contrast. *Spatial Vision*, *1*(2), 103–12. https://doi.org/10.1163/156856885X00125

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, *84*(3), 279–325. https://doi.org/10.1037/0033-295X.84.3.279

Gibbon, J., & Church, R. M. (1984). Simultaneous Temporal Processing. *Journal of Experimental Psychology: Animal Behavior Processes*, *10*(1), 1–29. https://doi.org/10.1037/0097-7403.10.1.1

Gibbs, R. W. (2006). Metaphor interpretation as embodied simulation. *Mind and Language*. https://doi.org/10.1111/j.1468-0017.2006.00285.x

Göbel, S., Walsh, V., & Rushworth, M. F. S. (2001). The Mental Number Line and the Human Angular Gyrus. *NeuroImage*, *14*(6), 1278–1289. https://doi.org/10.1006/nimg.2001.0927

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*. https://doi.org/10.1016/0166-2236(92)90344-8

Gordon, P. (2004). Numerical Cognition Without Words: Evidence from Amazonia. *Science*, *306*(5695), 496–499. https://doi.org/10.1126/science.1094492

Gruber, O. (2001). Dissociating Neural Correlates of Cognitive Components in Mental Calculation. *Cerebral Cortex*, *11*(4), 350–359. https://doi.org/10.1093/cercor/11.4.350

Halberda, J., Mazzocco, M. M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, *455*(7213), 665–668. https://doi.org/10.1038/nature07246

Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic Representation of Numerosity in the Human Parietal Cortex. *Science*, *341*(6150), 1123–1126. https://doi.org/10.1126/science.1239052

Harvey, B. M., & Dumoulin, S. O. (2017). Can responses to basic non-numerical visual features explain neural numerosity responses? *NeuroImage*, *149*, 200–209. https://doi.org/10.1016/j.neuroimage.2017.02.012

Harvey, B. M., & Dumoulin, S. O. (2017). A network of topographic numerosity maps in human association cortex. *Nature Human Behaviour*, *1*(2), 36. https://doi.org/10.1038/s41562-016-0036

Harvey, B. M., Fracasso, A., Petridou, N., & Dumoulin, S. O. (2015). Topographic representations of object size and relationships with numerosity reveal generalized quantity processing in human parietal cortex. *Proceedings of the National Academy of Sciences*, *112*(44), 13525–13530. https://doi.org/10.1073/pnas.1515414112

Heed, T., & Röder, B. (2014). Motor coordination uses external spatial coordinates independent of developmental vision. *Cognition*, *132*(1), 1-15. https://doi.org/10.1016/j.cognition.2014.03.005

Heed, T., Möller, J., & Röder, B. (2015). Movement induces the use of external spatial coordinates for tactile localization in congenitally blind humans. *Multisensory research*, *28*(1-2), 173-194. doi:10.1163/22134808-00002485

Hersh, R., & Dehaene, S. (1998). The Number Sense: How the Mind Creates Mathematics. *The American Mathematical Monthly*, *105*(10), 975. https://doi.org/10.2307/2589308

Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*. https://doi.org/10.1016/j.cub.2007.10.027

Izard, V., Pica, P., Spelke, E. S., & Dehaene, S. (2011). Flexible intuitions of Euclidean geometry in an Amazonian indigene group. *Proceedings of the National Academy of Sciences*, *108*(24), 9782–9787. https://doi.org/10.1073/pnas.1016686108

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences*, *106*(25), 10382–10385. https://doi.org/10.1073/pnas.0812142106

Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology*, *16*(5), 472–479. https://doi.org/10.1016/j.cub.2006.01.032

Jordan, K. E., & Brannon, E. M. (2006). The multisensory representation of number in infancy. *Proceedings of the National Academy of Sciences*, *103*(9), 3486–3489. https://doi.org/10.1073/pnas.0508107103

Jordan, K. E., Brannon, E. M., Logothetis, N. K., & Ghazanfar, A. A. (2005). Monkeys match the number of voices they hear to the number of faces they see. *Current Biology*, *15*(11), 1034–1038. https://doi.org/10.1016/j.cub.2005.04.056

Jordan, K. E., MacLean, E. L., & Brannon, E. M. (2008). Monkeys match and tally quantities across senses. *Cognition*, *108*(3), 617–625. https://doi.org/10.1016/j.cognition.2008.05.006

Kiefer, M., & Dehaene, S. (1997). The Time Course of Parietal Activation in Single-digit Multiplication: Evidence from Event-related Potentials. *Mathematical Cognition*. https://doi.org/10.1080/135467997387461

Kilian, A., Yaman, S., von Fersen, L., & Güntürkün, O. (2003). A bottlenose dolphin discriminates visual stimuli differing in numerosity. *Learning & Behavior*, *31*(2), 133–142. https://doi.org/10.3758/BF03195976

Kleiner, M., Brainard, D. H., Pelli, D. G., Broussard, C., Wolf, T., & Niehorster, D. (2007). What's new in Psychtoolbox-3? *Perception*, *36*, S14. https://doi.org/10.1068/v070821

Koehler, O. (1950). The ability of birds to count. Bulletin of Animal Behaviour, 9, 41-45.

Kohn, A. (2007). Visual Adaptation: Physiology, Mechanisms, and Functional Benefits. *Journal of Neurophysiology*, *97*(5), 3155–3164. https://doi.org/10.1152/jn.00086.2007

Kramer, P., Di Bono, M. G., & Zorzi, M. (2011). Numerosity estimation in visual stimuli in the absence of luminance-based cues. *PLoS ONE*, *6*(2). https://doi.org/10.1371/journal.pone.0017378

Krause, F., Bekkering, H., & Lindemann, O. (2013). A feeling for numbers: Shared metric for symbolic and tactile numerosities. *Frontiers in Psychology*, *4*(JAN). https://doi.org/10.3389/fpsyg.2013.00007

Krueger, L. E., & Hallford, E. W. (1984). Why 2 + 2 = 5 looks so wrong: on the odd-even rule in sum verification. *Memory & Cognition*, *12*(2), 171–180. https://doi.org/10.3758/BF03198431

Lambrechts, A., Walsh, V., & van Wassenhove, V. (2013). Evidence accumulation in the magnitude system. *PloS one*, *8*(12), e82122. doi:10.1371/ journal.pone.0082122

Le Clec'H, G., Dehaene, S., Cohen, L., Mehler, J., Dupoux, E., Poline, J. B., … Le Bihan, D. (2000). Distinct Cortical Areas for Names of Numbers and Body Parts Independent of Language and Input Modality. *NeuroImage*, *12*(4), 381–391. https://doi.org/10.1006/nimg.2000.0627

LECHELT, E. C. (1975). TEMPORAL NUMEROSITY DISCRIMINATION: INTERMODAL COMPARISONS REVISITED. *British Journal of Psychology*, *66*(1), 101–108. https://doi.org/10.1111/j.2044-8295.1975.tb01444.x

Lee, K. M. (2000). Cortical areas differentially involved in multiplication and subtraction: A functional magnetic resonance imaging study and correlation with a case of selective acalculia. *Annals of Neurology*, *48*(4), 657–661. https://doi.org/10.1002/1531-8249(200010)48:4<657::AID-ANA13>3.0.CO;2-K

Lee, K. M., & Kang, S. Y. (2002). Arithmetic operation and working memory: Differential suppression in dual tasks. *Cognition*, *83*(3). https://doi.org/10.1016/S0010-0277(02)00010-0

Leon, M. I., & Shadlen, M. N. (2003). Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron*, *38*, 317–27. https://doi.org/S0896627303001855 [pii]

Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is That Near My Hand? Multisensory Representation of Peripersonal Space in Human Intraparietal Sulcus. *Journal of Neuroscience*, *27*(4), 731–740. https://doi.org/10.1523/JNEUROSCI.3653-06.2007

Maquet, P., Lejeune, H., Pouthas, V., Bonnet, M., Casini, L., Macar, F., … Comar, D. (1996). Brain activation induced by estimation of duration: a PET study. *NeuroImage*, *3*(2), 119–26. https://doi.org/10.1006/nimg.1996.0014

Marler, P., & Tamura, M. (1962). Song “dialects” in three populations of White-crowned Sparrows. *The Condor*, *64*(5), 368–377. https://doi.org/10.2307/1365545

Martin, B., Wiener, M., & van Wassenhove, V. (2017). A Bayesian Perspective on Accumulation in the Magnitude System. *Scientific Reports*, *7*. 10.1038/s41598-017-00680-0

Mayer, E., Martory, M. D., Pegna, A. J., Landis, T., Delavelle, J., & Annoni, J. M. (1999). A pure case of Gerstmann syndrome with a subangular lesion. *Brain*, *122*(6), 1107–1120. https://doi.org/10.1093/brain/122.6.1107

McCrink, K., & Wynn, K. (2004). Large-number addition and subtraction by 9-month-old infants. *Psychological Science*, *15*(11), 776–781. https://doi.org/10.1111/j.0956-7976.2004.00755.x

Menon, V., Rivera, S. M., White, C. D., Glover, G. H., & Reiss, A. L. (2000). Dissociating Prefrontal and Parietal Cortex Activation during Arithmetic Processing. *NeuroImage*, *12*(4), 357–365. https://doi.org/10.1006/nimg.2000.0613

Merritt, D. J., Casasanto, D., & Brannon, E. M. (2010). Do monkeys think in metaphors? Representations of space and time in monkeys and humans. *Cognition*, *117*(2), 191–202. https://doi.org/10.1016/j.cognition.2010.08.011

Morgan, M. J., Raphael, S., Tibber, M. S., & Dakin, S. C. (2014). A texture-processing model of the "visual sense of number." *Proceedings of the Royal Society B: Biological Sciences*, *281*(1790), 20141137–20141137. https://doi.org/10.1098/rspb.2014.1137

Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience*, *8*(7), 950–954. https://doi.org/10.1038/nn1488

MOYER, R. S., & LANDAUER, T. K. (1967). Time required for Judgements of Numerical Inequality. *Nature*, *215*(5109), 1519–1520. https://doi.org/10.1038/2151519a0

Naccache, L. (2001). The Priming Method: Imaging Unconscious Repetition Priming Reveals an Abstract Representation of Number in the Parietal Lobes. *Cerebral Cortex*, *11*(10), 966–974. https://doi.org/10.1093/cercor/11.10.966

Nieder, A. (2012). Supramodal numerosity selectivity of neurons in primate prefrontal and posterior parietal cortices. *Proceedings of the National Academy of Sciences*, *109*(29), 11860–11865. https://doi.org/10.1073/pnas.1204580109

Nieder, A. (2005). Counting on neurons: the neurobiology of numerical competence. *Nature Reviews Neuroscience*, *6*(3), 177–190. https://doi.org/10.1038/nrn1626

Nieder, A., Diester, I., & Tudusciuc, O. (2006). Temporal and spatial enumeration processes in the primate parietal cortex. *Neuroforum*, *12*(4), 267–269. https://doi.org/10.1126/science.1130308

Nishida, S., & Johnston, a. (1999). Influence of motion signals on the perceived position of spatial pattern. *Nature*, *397*(6720), 610–612. https://doi.org/10.1038/17600

Park, J., & Brannon, E. M. (2013). Training the approximate number system improves math proficiency. *Psychological science*, *24*(10), 2013-2019. https://doi.org/10.1177/0956797613482944

Park, J., Bermudez, V., Roberts, R. C., & Brannon, E. M. (2016). Non-symbolic approximate arithmetic training improves math performance in preschoolers. *Journal of experimental child psychology*, *152*, 278-293. https://doi.org/10.1016/j.jecp.2016.07.011

Pasqualotto, A., Taya, S., & Proulx, M. J. (2014). Sensory deprivation: visual experience alters the mental number line. *Behavioural brain research*, *261*, 110-113. https://doi.org/10.1016/j.bbr.2013.12.017

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442. https://doi.org/10.1163/156856897X00366

Pesenti, M., Thioux, M., Seron, X., & Volder, A. De. (2000). Neuroanatomical Substrates of Arabic Number Processing, Numerical Comparison, and Simple Addition: A PET Study. *Journal of Cognitive Neuroscience*, *12*(3), 461–479. https://doi.org/10.1162/089892900562273

Piazza, M., Mechelli, A., Butterworth, B., & Price, C. J. (2002). Are Subitizing and Counting Implemented as Separate or Functionally Overlapping Processes? *NeuroImage*, *15*(2), 435–446. https://doi.org/10.1006/nimg.2001.0980

Piazza, M., Mechelli, A., Price, C. J., & Butterworth, B. (2006). Exact and approximate judgements of visual and auditory numerosity: An fMRI study. *Brain Research*, *1106*(1), 177–188. https://doi.org/10.1016/j.brainres.2006.05.104

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Trends in cognitive sciences*, *14*(12), 542-551. https://doi.org/10.1016/j.tics.2010.09.008

Pica, P. (2004). Exact and Approximate Arithmetic in an Amazonian Indigene Group. *Science*, *306*(5695), 499–503. https://doi.org/10.1126/science.1102085

Pinel, P., Piazza, M., Le Bihan, D., & Dehaene, S. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron*, *41*(6), 983–993. https://doi.org/10.1016/S0896-6273(04)00107-2

Pouget, A., Deneve, S., & Duhamel, J.-R. (2002). A computational perspective on the neural basis of multisensory spatial representations. *Nature Reviews Neuroscience*, *3*(9), 741–747. https://doi.org/10.1038/nrn914

Pouthas, V., Garnero, L., Ferrandez, A. M., & Renault, B. (2000). ERPs and PET analysis of time perception: spatial and temporal brain mapping during visual discrimination tasks. *Human Brain Mapping*, *10*(2), 49–60. https://doi.org/10.1002/(SICI)1097-0193(200006)10:2<49::AID-HBM10>3.0.CO;2-8 [pii]

Price, C. J. (1998). The functional anatomy of word comprehension and production. *Trends in Cognitive Sciences*. https://doi.org/10.1016/S1364-6613(98)01201-7

Rammsayer, T. H., & Verner, M. (2014). The effect of nontemporal stimulus size on perceived duration as assessed by the method of reproduction. *Journal of Vision*, *14*(5), 1–10. https://doi.org/10.1167/14.5.17.doi

Rammsayer, T. H., & Verner, M. (2015). Larger visual stimuli are perceived to last longer from time to time: The internal clock is not affected by nontemporal visual stimulus size. *Journal of Vision*, *15*(3), 1–11. https://doi.org/10.1167/15.3.5.doi

Rao, S. M., Mayer, a R., & Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature Neuroscience*, *4*(3), 317–23. https://doi.org/10.1038/85191

Röder, B., Rösler, F., & Spence, C. (2004). Early Vision Impairs Tactile Perception in the Blind. *Current Biology*, *14*(2), 121–124. https://doi.org/10.1016/j.cub.2003.12.054

Röder, B., Kusmierek, A., Spence, C., & Schicke, T. (2007). Developmental vision determines the reference frame for the multisensory control of action. *Proceedings of the National Academy of Sciences*, *104*(11), 4753–4758. https://doi.org/10.1073/pnas.0607158104

Röder, B., Föcker, J., Hötting, K., & Spence, C. (2008). Spatial coordinate systems for tactile spatial attention depend on developmental vision: Evidence from event-related potentials in sighted and congenitally blind adult humans. *European Journal of Neuroscience*, *28*(3), 475–483. https://doi.org/10.1111/j.1460-9568.2008.06352.x

Roitman, J. D., Brannon, E. M., & Platt, M. L. (2007). Monotonic coding of numerosity in macaque lateral intraparietal area. *PLoS Biology*, *5*(8), 1672–1682. https://doi.org/10.1371/journal.pbio.0050208

Ross, J. (2010). Vision senses number directly. *Journal of Vision*, *10*(2), 1–8. https://doi.org/10.1167/10.2.10

Ross, J., & Burr, D. (2012). Number, texture and crowding. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2012.01.010

Rugani, R., Regolin, L., & Vallortigara, G. (2007). Rudimental numerical competence in 5-day-old domestic chicks (Gallus gallus): Identification of ordinal position. *Journal of Experimental Psychology: Animal Behavior Processes*, *33*(1), 21–31. https://doi.org/10.1037/0097-7403.33.1.21

Rumbaugh, D. M., Savage-Rumbaugh, S., & Hegel, M. T. (1987). Summation in the chimpanzee (Pan troglodytes). *Journal of Experimental Psychology. Animal Behavior Processes*, *13*(2), 107–115. https://doi.org/10.1037//0097-7403.13.2.107

Sawamura, H., Shima, K., & Tanji, J. (2002). Numerical representation for action in the parietal cortex of the monkey. *Nature*, *415*(6874), 918–922. https://doi.org/10.1038/415918a

Sawamura, H., Shima, K., & Tanji, J. (2010). Deficits in action selection based on numerical information after inactivation of the posterior parietal cortex in monkeys. *Journal of Neurophysiology*, *104*(2), 902–910. https://doi.org/10.1152/jn.01014.2009

Scarf, D., Hayne, H., & Colombo, M. (2011). Pigeons on par with primates in numerical competence. *Science (New York, N.Y.)*, *334*(6063), 1664. https://doi.org/10.1126/science.1213357

Schwiedrzik, C. M., Bernstein, B., & Melloni, L. (2016). Motion along the mental number line reveals shared representations for numerosity and space. *eLife*, *5*(JANUARY2016). https://doi.org/10.7554/eLife.10806.001

Shepard, R. N., Kilpatric, D. W., & Cunningham, J. P. (1975). The internal representation of numbers. *Cognitive Psychology*, *7*(1), 82–138. https://doi.org/10.1016/0010-0285(75)90006-7

Shore, D. I., Spry, E., & Spence, C. (2002). Confusing the mind by crossing the hands. In *Cognitive Brain Research* (Vol. 14, pp. 153–163). https://doi.org/10.1016/S0926-6410(02)00070-8

Siegler, R. S., & Ramani, G. B. (2008). Playing linear numerical board games promotes low-income children’s numerical development. *Developmental Science*, *11*(5), 655–661. https://doi.org/10.1111/j.1467-7687.2008.00714.x

Simon, O., Mangin, J. F., Cohen, L., Le Bihan, D., & Dehaene, S. (2002). Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron*, *33*(3), 475–487. https://doi.org/10.1016/S0896-6273(02)00575-5

Slutsky, D. A., & Recanzone, G. H. (2001). Temporal and spatial dependency of the ventriloquism effect. *Neuroreport*, *12*(1), 7–10. https://doi.org/10.1097/00001756-200101220-00009

Snowden, R. J. (1998). Shifts in perceived position following adaptation to visual motion. *Current Biology*, *8*(24), 1343–1345. https://doi.org/10.1016/S0960-9822(07)00567-2

Solomon, S. G., & Kohn, A. (2014). Moving sensory adaptation beyond suppressive effects in single neurons. *Current Biology*. https://doi.org/10.1016/j.cub.2014.09.001

Spelke, E. S., & Tsivkin, S. (2001). Language and number: A bilingual training study. *Cognition*, *78*(1), 45–88. https://doi.org/10.1016/S0010-0277(00)00108-6

Stanescu-Cosson, R., Pinel, P., van De Moortele, P. F., Le Bihan, D., Cohen, L., & Dehaene, S. (2000). Understanding dissociations in dyscalculia: a brain imaging study of the impact of number size on the cerebral networks for exact and approximate calculation. *Brain : A Journal of Neurology*, *123 (Pt 1*, 2240–2255. https://doi.org/10.1093/brain/123.11.2240

Starkey, P., & Cooper, R. (1980). Perception of numbers by human infants. *Science*, *210*(4473), 1033–1035. https://doi.org/10.1126/science.7434014

Szűcs, D., & Csépe, V. (2005). The parietal distance effect appears in both the congenitally blind and matched sighted controls in an acoustic number comparison task. *Neuroscience letters*, *384*(1), 11-16. https://doi.org/10.1016/j.neulet.2005.04.050

Thioux, M., Pesenti, M., Costes, N., De Volder, A., & Seron, X. (2005). Task-independent semantic activation for numbers and animals. *Cognitive Brain Research*, *24*(2), 284–290. https://doi.org/10.1016/j.cogbrainres.2005.02.009

Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology*. https://doi.org/10.1016/j.cub.2008.10.014

Tibber, M. S., Greenwood, J. A., & Dakin, S. C. (2012). Number and density discrimination rely on a common metric: Similar psychophysical effects of size, contrast, and divided attention. *Journal of Vision*, *12*(6), 8–8. https://doi.org/10.1167/12.6.8

Tibber, M. S., Manasseh, G. S. L., Clarke, R. C., Gagin, G., Swanbeck, S. N., Butterworth, B., … Dakin, S. C. (2013). Sensitivity to numerosity is not a unique visuospatial psychophysical predictor of mathematical ability. *Vision Research*, *89*, 1–9. https://doi.org/10.1016/j.visres.2013.06.006

Togoli, I., Arrighi, R., Anobile, G., Crollen, V., & Collignon, O. (2017). A shared numerical representation for action and perception in blind and sighted individuals. In European Conference on Visual Perception 41th edition, Berlin, Germany.

Togoli, I., Arrighi, R., & Burr, D. (In preparation). A tactile sense of number.

Tokita, M., & Ishiguchi, A. (2012). Behavioral evidence for format-dependent processes in approximate numerosity representation. *Psychonomic Bulletin & Review*, *19*(2), 285–293. https://doi.org/10.3758/s13423-011-0206-6

Trick, L. M., & Pylyshyn, Z. W. (1994). Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychological Review*, *101*(1), 80–102. https://doi.org/10.1037/0033-295X.101.1.80

Turi, M., & Burr, D. (2012). Spatiotopic perceptual maps in humans: evidence from motion adaptation. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1740), 3091–3097. https://doi.org/10.1098/rspb.2012.0637

Van der Burg, E., Alais, D., & Cass, J. (2013). Rapid Recalibration to Audiovisual Asynchrony. *Journal of Neuroscience*, *33*(37), 14633–14637. https://doi.org/10.1523/JNEUROSCI.1182-13.2013

Verguts, T., & Fias, W. (2004). Representation of Number in Animals and Humans: A Neural Model. *Journal of Cognitive Neuroscience*, *16*(9), 1493–1504. https://doi.org/10.1162/0898929042568497

Viswanathan, P., & Nieder, A. (2013). Neuronal correlates of a visual “sense of number” in primate parietal and prefrontal cortices. *Proceedings of the National Academy of Sciences*, *110*(27), 11187–11192. https://doi.org/10.1073/pnas.1308141110

Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2003.09.002

Warren, D. H., Welch, R. B., & Mccarthy, T. J. (1981). The role of visual-auditory “compellingness” in the ventriloquism effect: Implications for transitivity among the spatial senses. *Perception & Psychophysics*, *30*(6), 557–564. https://doi.org/10.3758/BF03202010

Warrington, E. K. (1982). The fractionation of arithmetical skills: A single case study. *The Quarterly Journal of Experimental Psychology Section A*, *34*(1), 31–51. https://doi.org/10.1080/14640748208400856

Watson, A. B., & Pelli, D. G. (1983). Quest: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113–120. https://doi.org/10.3758/BF03202828

Whalen, J., Gallistel, C. R., & Gelman, R. (1999). Nonverbal Counting in Humans: The Psychophysics of Number Representation. *Psychological Science*, *10*(2), 130–137. https://doi.org/10.1111/1467-9280.00120

Whalen, J., McCloskey, M., Lesser, R. P., & Gordon, B. (1997). Localizing Arithmetic Processes in the Brain: Evidence from a Transient Deficit During Cortical Stimulation. *Journal of Cognitive Neuroscience*, *9*(3), 409–417. https://doi.org/10.1162/jocn.1997.9.3.409

Wilson, M. L., Britton, N. F., & Franks, N. R. (2002). Chimpanzees and the mathematics of battle. *Proceedings. Biological Sciences / The Royal Society*, *269*(1496), 1107–12. https://doi.org/10.1098/rspb.2001.1926

Wilson, A. J., Revkin, S. K., Cohen, D., Cohen, L., & Dehaene, S. (2006). An open trial assessment of" The Number Race", an adaptive computer game for remediation of dyscalculia. *Behavioral and brain functions*, *2*(1), 20. https://doi.org/10.1186/1744-9081-2-20

Wojciulik, E., & Kanwisher, N. (1999). The generality of parietal involvement in visual attention. *Neuron*, *23*(4), 747–764. https://doi.org/10.1016/S0896-6273(01)80033-7

Wood, G., Nuerk, H. C., & Willmes, K. (2006). Crossed hands and the SNARC effect: A failure to replicate Dehaene, Bossini and Giraux (1993). *Cortex*, *42*(8), 1069–1079. https://doi.org/10.1016/S0010-9452(08)70219-3

Wynn, K. (1992). Addition and subtraction by human infants. *Nature*, *358*(6389), 749–750. https://doi.org/10.1038/358749a0

Xu, F. (2003). Numerosity discrimination in infants: Evidence for two systems of representations. *Cognition*, *89*(1). https://doi.org/10.1016/S0010-0277(03)00050-7

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition*, *74*(1). https://doi.org/10.1016/S0010-0277(99)00066-9

Xuan, B., Chen, X. C., He, S., & Zhang, D. R. (2009). Numerical magnitude modulates temporal comparison: An ERP study. *Brain Research*, *1269*, 135–142. https://doi.org/10.1016/j.brainres.2009.03.016

Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision*, *7*(10), 2. https://doi.org/10.1167/7.10.2

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience*, *4*(7), 759–765. https://doi.org/10.1038/89559

Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., & Tzourio-Mazoyer, N. (2001). Neural Correlates of Simple and Complex Mental Calculation. *NeuroImage*, *13*(2), 314–327. https://doi.org/10.1006/nimg.2000.0697

Zorzi, M., Priftis, K., & Umiltà, C. (2002). Brain damage: Neglect disrupts the mental number line. *Nature*, *417*(6885), 138–139. https://doi.org/10.1038/417138a