UNIVERSITY OF TRENTO

Doctoral School in Cognitive and Brain Sciences

The development of number processing and its relation to other parietal functions in early childhood

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2009

“Nella nostra infanzia c'è sempre un momento in cui una porta
si apre e lascia entrare l'avvenire”.
(Graham Greene)

Alla mia famiglia,

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THE PRESENT THESIS

The project has explored the developmental trajectories of several cognitive functions related to different brain regions: parietal cortex (quantity manipulation, finger gnosis, visuo-spatial memory and grasping abilities) and occipito-temporal cortex (face and object processing), in order to investigate their contributions to the acquisition of formal arithmetic in the first year of schooling. We tested preschooler, first grader and adult subjects, using correlational cross-sectional and longitudinal approaches. Results show that anatomical proximity is a strong predictor of behavioural correlations and of segregation between dorsal and ventral streams' functions. This observation is particularly prominent in children: within parietal functions, there is a progressive separation across functions during development.

During preschool age, presymbolic and symbolic number systems follow distinct developmental trajectories that converge during the first year of primary school. Indeed a possible cause of this phenomenon could be due to the refinement of the numerosity acuity during the acquisition of symbolic knowledge for numbers.

Among the tested parietal functions, we observe a strong association between the numerical and the finger domain, especially in children. In preschoolers, finger gnosis is strongly associated with non-symbolic quantity processing, while in first graders it links up to symbolic mental arithmetic. This finding may reflect a pre-existing anatomical connection between the cortical regions supporting the quantity and finger-related functions in early childhood. In contrast, first graders exhibit a finger-arithmetic association more influenced by functional factors and cultural-based strategies (e.g. finger counting).

Longitudinal data has allowed us to individuate which cognitive functions measured in kindergarteners predicts better the success in mental arithmetic in the first year of school. Results show that finger gnosis, as well as quantity and space–related abilities all concur at shaping the success in mental calculation in first graders.

These results are important because, primarily, they are the first to observe a strong relation between visuo-spatial, finger and quantity related abilities in young children, and, secondly, because the longitudinal design provides strong evidence for a causal link between these functions and the success in formal arithmetic. These results suggest that educational programs should include training in each of these cognitive domains in mathematic classes.

Finally, specific applications of these findings can be found within the domain of educational neuroscience and for the rehabilitation of children with numerical deficits (dyscalculia).

GENERAL INTRODUCTION

Chapter 1

THE PARIETAL LOBE AND ITS RELEVANCE IN NUMBER PROCESSING

Parietal cortex has a crucial role in a vast series of cognitive and sensory-motor processes among which the manipulation of numerical information (Culham & Kanwisher, 2001). In the first part of this chapter I briefly illustrate the anatomical and functional properties of parietal cortex in adults together with their development during childhood. I then focus on number processing and discuss the relevance of different sub-regions of parietal cortex for representing and manipulating numbers.

1.1 The parietal lobe

1.1.1 Anatomical aspects

The parietal lobe is delimited from the frontal lobe by the central sulcus (CeS) and from temporal and occipital cortices by superior/middle temporal gyrii, the transverse occipital sulcus (TOS) and the parieto-occipital sulcus (POS).

The somatosensory cortex, localized in the post-central gyrus (PCG), covers the cortical area between the CeS and the post-central sulcus (PCS). All the regions that are posterior to the PCG constitute the posterior parietal cortex (PPC) which is divided into inferior (IPL) and superior parietal lobules (SPL) by an antero-posterior oriented sulcus, called intraparietal sulcus (IPS). The IPL is further composed by angular gyrus (AG) and supramarginal gyrus (SMG; see Fig. 1; (Culham, Cavina-Pratesi, & Singhal, 2006)).

Despite inter-individual variability, the IPS is composed by three parts: an ascending and anterior branch from the post-central sulcus, a horizontal segment placed centrally to the IPS, and a descending branch approaching the occipital cortex (Molko, et al., 2003).

Fibres bundles of the corpus callosum put in relation the parietal lobes of the two brain hemispheres. In the adult brain the left and right parietal lobes are quite symmetric.

However, certain asymmetries have been reported in favour to grater gray matter in the left hemisphere in the AG, the posterior part of SPL and IPS (Watkins, et al., 2001).

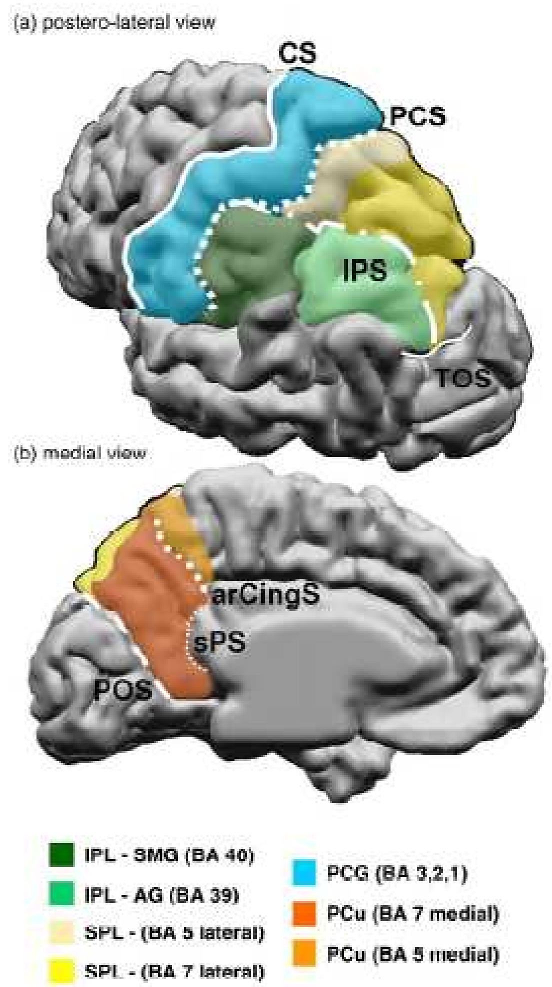


Fig. 1. The posterior parietal cortex (PPC). Anatomical illustration of the postero-lateral (a) and medial (b) views of the left hemisphere of the human brain (pial surface) of one subject. The white lines highlight the principal sulci: central sulcus (CS), postcentral sulcus (PCS), intraparietal sulcus (IPS), transverse occipital sulcus (TOS), parieto-occipital sulcus (POS), the ascending ramus of the cingulate sulcus (arCingS) and the subparietal sulcus (sPS). Different colors represent different anatomical subdivisions of the PPC: the postcentral gyrus (PCG), the superior parietal lobule (SPL), the precuneus (PCu) and the inferior parietal lobule (IPL), which is divided into the supramarginal gyrus (SMG) and angular gyrus (AG). The SPL and PCu include both Brodmann areas 5 (BA5) and 7 (BA7). Note, the PCG is part of the parietal lobe, but is not included in the PPC (reproduced from Culham et al., 2006).

1.1.1.1 Development

During development, and in particular during the first several years of life, the human brain undergoes a long and non-linear process of maturation characterized by both progressive and regressive changes. Two general laws seem to govern brain maturation. First, the maturation of somato-sensory and visual cortices constitutes the basic step for subsequent development of highly integrated associative cortices. Second, the brain maturation follows its philogenesis with a delay in the development of phylogenetically more recent regions, such as the inferior parietal or the dorsolateral prefrontal cortex (Gogtay, et al., 2004). Brain development is typically investigated by using different approaches based on physiological, cognitive, and imaging techniques.

At birth, the brain of a child is only one-quarter to one-third of the adult brain, reaching its peak at 14,5 years for males and 11,5 years for female (Giedd, et al., 1999). Driven by genetic and environmental factors, the dendritic branching of neurons and their synaptic connections increase robustly during the first years of life up to adolescence, with a time-course that varies enormously by brain region. Moreover a long processes of myelinization allows a faster conduction speed of the information shared by interconnect brain regions (Toga, Thompson, & Sowell, 2006). Subsequently to this amplification of neural connections, a curious process of dendritic pruning and synapse delectation occurs, with the aim to remove weak and overproduced connections, and to reach a high level of efficiency and specialization. Interestingly, an heterochronous synaptic pruning for different regions has been shown in both primate and human cortical development (Giedd, et al., 1999; Gogtay, et al., 2004; Huttenlocher, 1979).

Some physiological investigations showed even that different degree of myelination comparing the dorsal and the ventral streams (Goodale & Milner, 1992). The progression of myelination of dorsal regions seems to continue up to adolescence, while more ventral and deep brain structures were myelinated earlier. On average, the level of myelination differs comparing these two streams, such that dorsal cortex exhibits an inferior myelinisation level compared to the ventral cortex (P. R. Huttenlocher, 1990; Toga, et al., 2006).

Recently, studies demonstrated a more complex panorama regarding brain maturation. Indeed maturational processes occurs firstly in dorsal parietal cortices, (e.g. in primary sensorimotor areas), then spread rostrally over the frontal cortex and finally, in the lateral and caudal parts of the parietal, occipital, and the temporal cortex (Gogtay, et al., 2004).

Imaging data suggest a non-linear changes in gray matter (GM) density during childhood up to prepubertal age followed by a postpubertal loss (Giedd, et al., 1999; Jernigan & Tallal, 1990). The GM density represents an indirect measure concerning the outcome of dendritic and synaptic processes within a complex architecture of glia, vasculature, and neurons. Indeed a loss of GM density was reported over time in relation to the postmortem synaptic pruning exhibited in adolescence and adulthood (Sowell, et al., 2003; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999).

Most studies based on imaging techniques have adopted a particular method called "volumetrical parcellisation" trying to define the neurodevelopmental trajectories of each cerebral region in terms of grey and white matter growth curves (Toga, et al., 2006).

Structural imaging data demonstrated that most cerebral regions, such as parietal and frontal cortices, exhibit a cubic-like developmental trajectory with an increase in childhood, followed by a decline during adolescence and a stabilization of cortical thickness in adulthood. This developmental trend can be described on the base of regionally specific inverted U-shaped trajectories of gray matter volumes.

Within the parietal regions, the first area to reach its thickness peak is the somatosensory cortex (at about 7 years), while the posterior polymodal regions reach the peak later, at 9-10 years (Shaw, et al., 2008).

This time course was also showed in a longitudinal pediatric imaging study, in which data suggest similar developmental trajectories for both frontal and parietal cortices, in contrast with temporal and occipital maturation. Specifically, the gray matter density developmental curves reach the peak first in the frontal and parietal lobes, and then in the temporal lobe (16 years of age). After that age, gray-matter loss occurs (Giedd, et al., 1999).

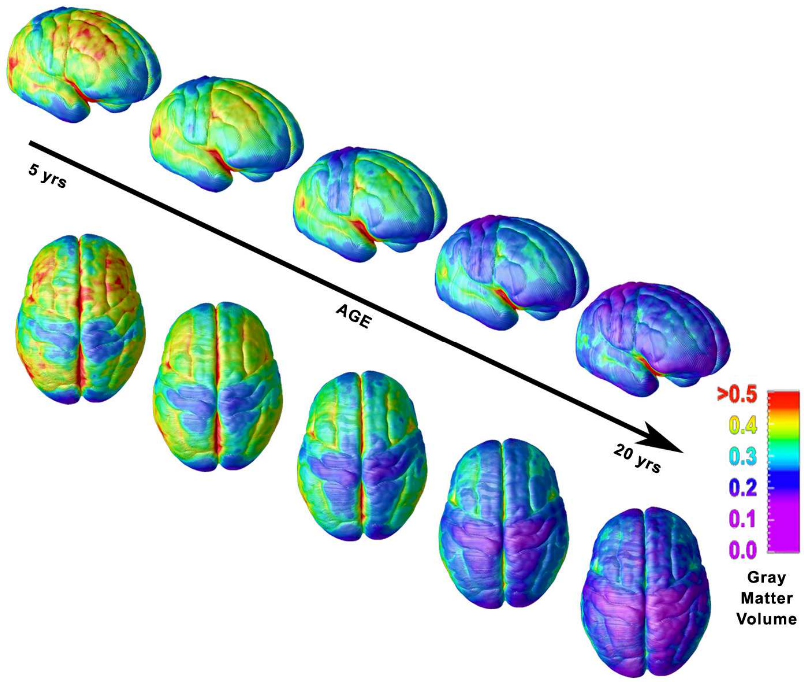


Fig. 2. Right lateral and top views of the dynamic sequence of GM maturation over the cortical surface. The side bar shows a color representation in units of GM volume (from Gogtay et al., 2004).

1.1.2 Functional aspects

Functionally, the parietal lobe represents a typical example of associate cortex recruited in processing information coming from different sensory districts and thus involved in several cognitive functions (Culham & Kanwisher, 2001). In particular, it constitutes the major component of a neural network massively involved in space and action processing called “dorsal stream”, in contrast with occipito-temporal network, the “ventral stream”, more dedicated to the analysis of perceptual features and form recognition (Goodale & Milner, 1992).

Neurophysiological recordings in monkeys have evidenced a fine parcellisation of parietal lobe into sub-regions on the basis of neurons’ response properties (Rizzolatti, Luppino, & Matelli, 1998). For example, multiple sub-regions involved in coding different body parts such as the arm, leg and face were found in the posterior parietal lobe. For example, one of the best studied representations, the arm one, is represented at least 8 times. Indeed, many functional motor representations ("motor fields") can be located in different anatomical areas coherently with some recent studies of corticospinal projections (He, Dum, & Strick, 1993, 1995). Each parietal area is connected with motor areas by a complex system of "predominant" and "additional" connections. Each segregated parieto-frontal functional circuit is involved in a specific sensory-motor transformation for action, constituting the functional unit of the cortical motor system (Rizzolatti, Fogassi, & Gallese, 1997).

Furthermore, recent evidences have redesigned the role of IPL and SPL. Indeed anatomical data have now showed that posteriorly, both lobules receive somatosensory and visual inputs. Anteriorly, however, these two lobules showed significant differences: SPL is involved in the somatosensory processing, while IPL has a role in the integration of the somatosensory and visual information (for a review see (Caminiti, Ferraina, & Johnson, 1996; Rizzolatti, et al., 1997; Wise, Boussaoud, Johnson, & Caminiti, 1997)).

Studies on monkey brain have contributed to understand in depth the parietal organization, suggesting important differences and some homologies across species, comparing the human to the macaque parietal regions (Orban, Van Essen, & Vanduffel, 2004). First, we see a specific expansion of both parietal and frontal lobes in humans, in particular in the region of IPL and IPS. Second, imaging data revealed peculiar differences in the responses to same stimuli while comparing directly human to monkey brains (Orban, et al., 2003; Van Essen, et al., 2001). For example, some main differences consist in a higher sensitivity for motion, especially for 3D motion, of intraparietal regions in humans compared to monkeys, suggesting the presence of specific areas for visuospatial processing in human intraparietal cortex (Vanduffel, et al., 2002). Despite these observations, at a physiological level, a typical posterior-to-anterior organization was observed in both monkeys and humans (Culham & Kanwisher, 2001).

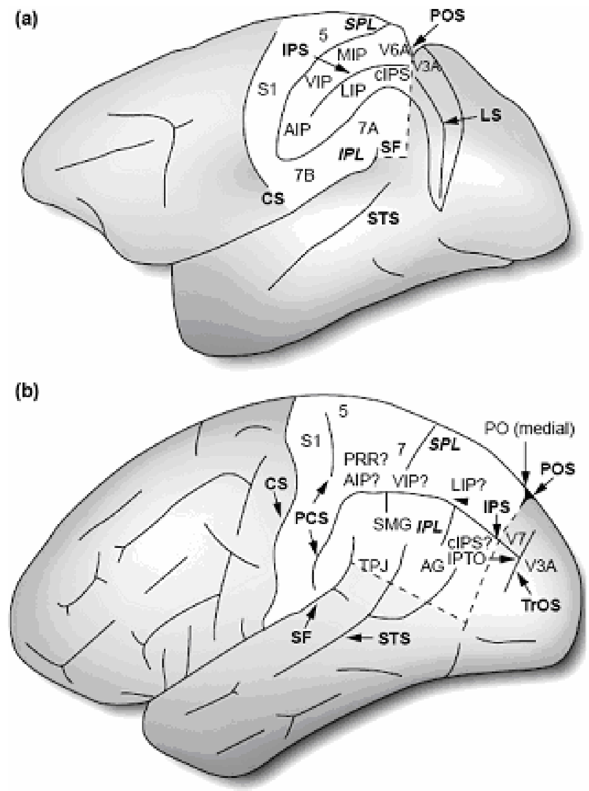


Fig. 3. Comparison of monkey and human parietal lobes. Lateral view of (a) macaque monkey brain and (b) human brain, showing parietal lobes in white (from Cuhlam & Kanwisher, 2001).

Among the potential homologues areas identified, three of them - areas LIP, VIP and AIP - are particular relevant here (fig. 3), considering their roles and locations within the intraparietal area (Grefkes, Ritzl, Zilles, & Fink, 2004).

Posterior to IPS, a human homologous of monkey area LIP was identified. This region is characterized to be sensitive to target-oriented saccades in the space with a retinotopic organization of its responses which are even effectors-independent, as seen in monkey (Ben Hamed, Duhamel, Bremmer, & Graf, 2001; Sereno, Pitzalis, & Martinez, 2001).

Converging data suggests the role of LIP in spatial updating in both humans and monkeys.

For example, in a double-saccade task using event-related fMRI, it was possible to show that when the position of the target moves, the LIP activity also shifts, to represent the new spatial location of the target coherently with the spatial rearrangement based on eye-centred framework (Medendorp, Goltz, Vilis, & Crawford, 2003).

The other tentative human homologous region is the VIP area, typically responsive to motion in a multimodal way in monkey. Considering this property, only one region in the depth of the IPS was found activated by visual, tactile and auditory motion (Bremmer, et al., 2001). However, the anatomical divergences concerning IPS between human and macaque brain needs additional studies on this line.

The neurons of AIP area are specifically recruited in hand-centred coordinates during fine grasping (Culham, et al., 2003; Shikata, et al., 2003). Some regions of IPS were considered as AIP homologues due to their dual involvement in the identification of grasped objects and in selective impairment in patients regarding grasping actions (Binkofski, et al., 1998).

Neuroimaging studies demonstrated the functional specialization of parietal regions contrasting hand versus eye movements, and grasping versus pointing (Grafton, Fagg, Woods, & Arbib, 1996; Kawashima, et al., 1996). In particular, grasping actions was contrasted to reaching and pointing movements. Imaging data show stronger activations for grasping actions on the anterior part of the IPS in contrast to reaching (Culham, et al., 2003), while pointing movements selectively recruits even the HIPS and the posterior part of the superior parietal lobule bilaterally (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Indeed, coherently with what found in monkey brain, the hypothetical presence of an AIP homologous in human brain should be located more anteriorly compared to homologues areas LIP and VIP (Hubbard, Piazza, Pinel, & Dehaene, 2005).

Recently, an extensite study on parietal functions was showed in Simon, Mangin, Cohen, Le Bihan, Dehaene (2002). The authors found a common orderly and topographically defined organization in all examined subjects for grasping, pointing, saccades, calculation, attention and phoneme detection. This observed systematic posterior-to-anterior parcellization converges with neurophysiological studies on monkey parietal lobe (Rizzolatti, et al., 1998) and with the proposed parcellization of human parietal cortex in monkey homologous subregions LIP-VIP-AIP. Moreover, in relation to the IPC, and in particular the AG, the data showing two lateral intraparietal areas associated with functions (calculation and phoneme detection) particularly developed in the human species. Those areas were surrounded by visuospatial areas plausibly homologous to the monkey areas

AIP, MIP, V6A, and LIP. This organization fits well with the cytoarchitectonic model of human parietal lobe (proposed in (Eidelberg & Galaburda, 1984)) indicating a significant expansion of human inferior parietal lobule whose activity is related to language and calculation.

1.1.2.1 Development

A restrict number of developmental studies measuring brain activity using functional imaging techniques show a complex pattern of changes in brain activation from childhood to adulthood (Gaillard, et al., 2000; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003), often accompanied by an increasing hemispheric specialization. Specifically, across ages, imaging data often show an increasing activation in task-related regions together with a decreased activation in regions less relevant to the task (Rivera, Reiss, Eckert, & Menon, 2005). Speculatively, both maturational processes and experience may contribute to the transition from a widespread activation pattern to a focal one as the result of plasticity reduction and higher efficiency (Durston & Casey, 2006; Durston, et al., 2006). On this wave, even increasing number of neural connections was reported during the development (Brown, et al., 2005).

The parallel between brain development and cognitive development is evident and supported by the fact that the improvement of cognitive capacity during childhood may coincide with a progressive specialization and reorganization of the anatomical structures (Casey, Giedd, & Thomas, 2000; Chugani, Phelps, & Mazziotta, 1987; Diamond, 1996; Flavell, Beach, & Chinsky, 1966; Huttenlocher, 1979; Keating, Keniston, Manis, & Bobbitt, 1980; Rakic, Bourgeois, & Goldman-Rakic, 1994).

Other variations in the brain activity from childhood to early adulthood (from 9 to 18 years of age) were also reported in relation to visual working memory, in that older children showed higher neural activations compared with younger counterparts in superior frontal and intraparietal cortices (Klingberg, Forssberg, & Westerberg, 2002).

Although the recent introduction of sophisticated techniques (e.g. fMRI) contributed to open a fascinating research field concerning the interplay between anatomical brain development and functional performance, further investigations are necessary about the neural bases of parietal functions in normally developing children. Indeed, despite a clearer panorama about the overall anatomical development of parietal cortex, the specific contributions of developing parietal subregions on behavioral performance lacks of relevant evidences.

1.2 Parietal circuits for number processing

1.2.1 In non human animals

The extraction of numerical information from the environment (the number of objects in a set) is thought to be a phylogenetically old ability, because it is found in animals of many different species (Boysen & Capaldi, 1993). These findings suggest a preverbal precursor system for our language-based counting and arithmetic. In particular, rhesus monkey has represented the best model for testing the non human numerical cognition and their neural correlates, due to our knowledge regarding its brain functional and anatomical organization. At a behavioral level, monkeys can distinguish sets of items on the basis on their numerical quantity and even learn the ordinal relations of the numbers from 1 to 9 (Brannon & Terrace, 1998; Brannon & Terrace, 2000). These animals are not only able to match and compare sets on the basis of their number, but also to perform simple addition or subtraction between sets of items (Hauser, Carey, & Hauser, 2000; Hauser, MacNeilage, & Ware, 1996). At a neural level, single cell recordings found relevant contributions of two highly interconnected regions (Chafee & Goldman-Rakic, 2000; Quintana & Fuster, 1999), the lateral prefrontal (LPFC) and posterior parietal cortices (PPC), in such numerical processes (Nieder, 2005; Nieder & Dehaene, 2009). In particular, in the PPC, numerosity-selective neurons were found responsible for the extraction of numerical information from a visual scene. Overall, the highest presence of numerosity-selective neurons was found in the lateral prefrontal cortex (31% of all randomly selected cells, (Nieder, Freedman, & Miller, 2002)), followed by the fundus of the intraparietal sulcus (18%, (Nieder & Miller, 2004); see Fig. 4). Other number-encoding neurons were even found in the superior parietal lobe SPL (Sawamura, Shima, & Tanji, 2002).

Specifically, the time course within this fronto-parietal network was investigated analyzing the activity modulation over time. Results showed that the PPC number-encoding neurons are activated faster, and in particular show an early onset of the selectivity for the numerical information, while the LPFC neurons show the onset of number selectivity firing much later (Nieder & Miller, 2004). These findings suggest that the first stage of extraction of numerical information is represented by parietal areas and then LPFC has the role to amplify and maintain this information. All the numerosity-selective neurons of both frontal and parietal areas constitute a sort of bank of overlapping numerosity filters.

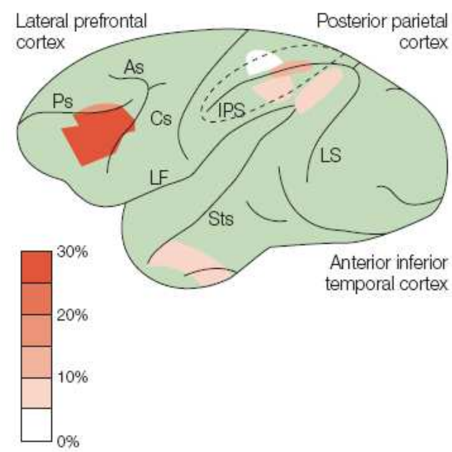


Fig. 4. Lateral view of a monkey brain that shows the recording sites in the lateral prefrontal cortex, the posterior parietal cortex and the anterior inferior termporal cortex. The proportions of numerosity-selective neurons in each area are colour coded according to the scale shown (from Nieder, 2005).

Interestingly, the neurons' sequentially-arranged, overlapping tuning curves preserved an inherent order of cardinalities. Thus, the numerosities are not isolated categories, but they are reciprocal categories which exist in relation to one another (Nieder, 2005).

1.2.2 In humans

A robust record of clinical evidences from brain-lesioned patients (Cohen, Dehaene, Chochon, Lehéricy, & Naccache, 2000; Grafman, Passafiume, Faglioni, & Boller, 1982; Takayama, Sugishita, Akiguchi, & Kimura, 1994) and imaging data using PET and fMRI

(Dehaene, et al., 1996; Fulbright, et al., 2000; Pesenti, Thioux, Seron, & De Volder, 2000; Rueckert, et al., 1996) point to a crucial role of parietal cortex in number processing. However, neural activations of PPC were found also for other cognitive functions related to language processing (Paulesu, Frith, & Frackowiak, 1993), visuo-spatial attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000) and visuo-motor control (Culham, et al., 2006). Thus, the crucial question is whether PPC contributions are specific for numerical domain, and distinct from other verbal, spatial and visuo-motor functions (Simon, et al., 2002).

Here, I describe the model proposed by Dehaene and colleagues, exploring the different parietal circuits for number processing and their specific contributions ((Dehaene, Piazza, Pinel, & Cohen, 2003); Fig. 5). Several imaging studies demonstrate a sensitivity of posterior parietal cortex for different levels of numerical elaboration, such as number comparison (Chochon, Cohen, van de Moortele, & Dehaene, 1999), approximate calculation (Venkatraman, Ansari, & Chee, 2005), simple (Simon, et al., 2002; Zago, et al., 2001) and complex exact calculation (Ischebeck, et al., 2006) and counting (Piazza, Mechelli, Butterworth, & Price, 2002). With the aim to clarify the organization of number related-processes in the parietal cortex, a meta-analysis of several different published fMRI studies was performed (Dehaene, et al., 2003), suggesting the presence of three neural regions recruited for different aspects of number processing: the bilateral horizontal segment of intraparietal sulcus (HIPS), the left AG and the bilateral posterior superior parietal lobule (PSPL).

The HIPS, alternatively defined “core quantity system”, is consistently implicated in the processing of numerical magnitude. This region is thought to underlie the semantic representation of magnitude, because it is task- and notation-independent and modulated by a numerical quantity-dependent semantic metric.

The other parietal circuits that seem to be systematically involved in number processing are involved in both numerical and non-numerical domains. The angular gyrus (AG) in the inferior parietal lobule seems to support the verbal aspects of number processing (Stanescu-Cosson, et al., 2000). Indeed, this region is active for language-related processes, such as in phoneme detection (Simon, et al., 2002). Fundamental contributions of the AG were shown for exact and automatic calculation, such as multiplications and simple additions which are performed, in adults of western societies on the basis of retrieval of memorized tables (Chochon, et al., 1999; Lee, 2000).

Finally, the PSPL supports visuo-spatial processes, attention and spatial working memory associated with the manipulation of numbers and they contribute to explain the numerous interactions between numbers and space (Hubbard, et al., 2005).

In sum, despite little information about the interplay among HIPS, AG and PSPL, all these regions differently participate to the networks devoted to number processing in humans.

Here, I describe in depth the specific role of each region within the neural circuit for number processing.

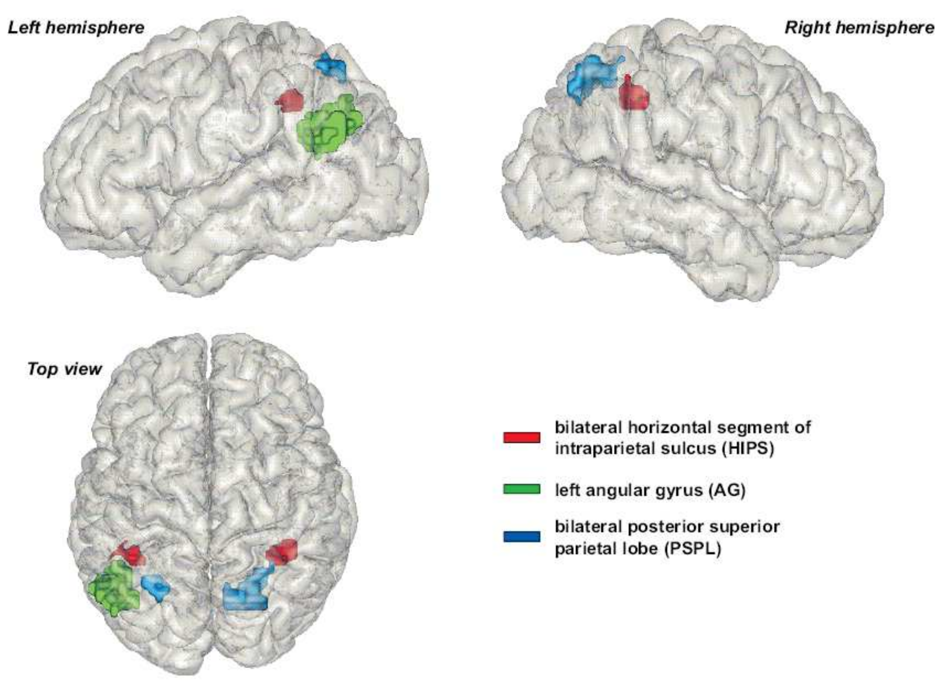


Fig. 5. Three-dimensional representation of the parietal regions of interest. For better visualisation, the clusters show all parietal voxels activated in at least 40% of studies in a given group (Dehaene et al., 2003)

The horizontal segment of the intraparietal sulcus

According with the idea of a core quantity system, the HIPS region should be recruited for all tasks requiring numerical processing. Indeed, this area is robustly activated during different tasks involving number comparison and arithmetic (Chochon, et al., 1999; Menon, Rivera, White, Eliez, et al., 2000; Stanescu-Cosson, et al., 2000).

Subtractions seem to elicit stronger HIPS activations compared with multiplications (Chochon, et al., 1999; Lee, 2000), especially for operations with large numbers (Stanescu-Cosson, et al., 2000). Indeed the results of additions and multiplications with small numbers are frequently retrieved from verbal memory without true access to magnitude information, and this fact results in a less systematic activation of the HIPS activity in these tasks with respect to complex calculation (Cohen, et al., 2000).

Less clear is the HIPS role for exact and approximate calculation: exact arithmetical operations (e.g. additions) may evoke less HIPS activation than approximate operations ((Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999) but see (Venkatraman, et al., 2005), for contrasting results). Probably, different factors might determine these non-converging results: methodological discrepancy among studies and inter-individual variability about the strategies used to perform the task, especially for the approximate operations, could contribute to make uncertain the neural dissociation between the exact and approximate calculation.

To address the true sensitivity of HIPS for numerical information, several imaging studies used more controlled tasks, such as number comparison. Interestingly, HIPS activation is inversely related to the numerical distance: close numbers (e.g. 5 - 4) elicited stronger activations than distant numbers (e.g. 5 - 9), irrespective of the numerical notations, such as dots arrays (Piazza, Giacomini, Le Bihan, & Dehaene, 2003), Arabic digits (Pinel, Dehaene, Riviere, & LeBihan, 2001) or number words (Le Clec'H, et al., 2000).

The notation-independent coding of numerical quantity in the HIPS was found even using a fMRI adaptation paradigm (Piazza, Pinel, Le Bihan, & Dehaene, 2007). Indeed the shape of neural activity showed distance-dependent modulations of both HIPS and frontal regions irrespective to the numerical notation, supporting the idea of an abstract coding of approximate number shared by dots, digits, and number words. More specifically, multi-voxel pattern analysis on imaging data found the presence of both format-specific and format-general number codes in human parietal cortex, where neural populations are more numerous, but more broadly tuned for non-symbolic than symbolic numbers (Eger, et al., 2009).

In children, age-related changes in the HIPS recruitment during the comparison of non-symbolic magnitudes were found (Ansari, Dhital, & Siong, 2006). In particular, the activation of left HIPS increases during the processing of non-symbolic magnitude with age, suggesting the presence of age-related changes in functional neuro-anatomy regarding the basic levels of numerical cognition. However, bilateral HIPS activations were showed even when no comparisons are requested such as in the case of passive exposure to numerical quantities when participants viewed sets of items with a variable number (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Thus, considering the existence of numerosity-selective neurons in the VIP and their location anterior to PSPL and posterior to area AIP (Nieder & Dehaene, 2009), the HIPS is thought to be the human homology of monkey area VIP (Hubbard, et al., 2005).

Taken together, these findings are in favor of amodal (notation independent) system of numerical representation in HIPS which is modulated by a semantic metric and which activity changes with age.

The posterior superior parietal lobe

The posterior superior parietal lobe is thought to be the human homology of monkey area LIP. Indeed this region is involved in target-oriented saccades in the space showing a retinotopic organization of its responses irrespective to the effectors, as found in monkey (Sereno, et al., 2001). A robust record of data suggested that even the PSPL is recruited when subjects performed different numerical tasks, such as number comparison (Pesenti, et al., 2000), parity judgment (Thioux, Pesenti, Costes, De Volder, & Seron, 2005), subtraction (Lee, 2000), additions (Venkatraman, et al., 2005), multiplications (Zago, et al., 2001), counting (Piazza, et al., 2002) and numerical estimation (Piazza, et al., 2004).

In number comparison tasks, PSPL (as well as IPS) is activated irrespective of the number notation, with its neural activity modulated by distance between number words (Kaufmann, et al., 2005), two-digit numbers (Pinel, et al., 2001) and dots array (Piazza, et al., 2004). Considering the important role of this area in attention orienting (Coull, Frith, Buchel, & Nobre, 2000; Coull & Nobre, 1998), the PSPL is thought to reflect the unspecific spatial processes subsidiary to the core magnitude system in the HIPS, especially in the numerical manipulation on the internal representation through attention shifts (Hubbard, et al., 2005). Indeed, the posterior superior parietal lobe (PSPL) is thought to support attentional orientation to the mental number line in tasks requiring number manipulation (Menon, Rivera, White, Glover, & Reiss, 2000; Pesenti, et al., 2000).

The angular gyrus (AG)

The activations of this brain region do not exhibit stronger influence of numerical distance (Pinel, et al., 2001). Indeed, the neural activity of AG is thought to reflect verbal or linguistic components of the manipulation of numbers. First, AG is not active during non-symbolic numerical information processing (Pesenti, et al., 2000; Piazza, Mechelli, Price, & Butterworth, 2006) (Piazza, et al., 2004). On the contrary, all study reporting activation in this region used symbolic numbers as stimuli. More precisely, AG activation is associated to arithmetic operations such as additions (Menon, Rivera, White, Glover, et al., 2000), subtractions (Burbaud, et al., 1999) and multiplications (Gruber, Indefrey, Steinmetz, & Kleinschmidt, 2001). In particular, AG is intensively recruited for the solution of exact additions, with greater activations for small problems (2+3) than large ones (7+5; (Stanescu-Cosson, et al., 2000)) showing a peculiar role for arithmetical facts retrieval. Furthermore, the activity of angular gyrus also increases after training with complex operations indicating the transition from computation to retrieval strategy in solving the trained problems(Delazer, et al., 2003).

This lobule constitutes a sort of bridge between arithmetic and language, indeed some small additions and multiplications problems are thought to be solved automatically (Ashcraft &

Battaglia, 1978) by using a sort of phonological associations accessible from the verbal representation of numbers (Dehaene, 1992).

Some evidences are in favor of this interpretation, such as a better performance for addition and multiplication problems if showed in the same language used to learn them (Spelke & Tsivkin, 2001). Second, both arithmetical facts and language processing induced activations in same (left) dominant hemisphere and, more specifically, parietal regions for phoneme detection and subtraction are partly overlapped in the AG (Dehaene, et al., 2003; Fiez & Petersen, 1998; Simon, et al., 2002).

More evidence comes from interference studies (Lee & Kang, 2002) showing that phonological rehearsal delayed significantly the performance in multiplication but not in subtraction, whereas visuo-spatial suppression interfered with subtraction but not multiplication performance. This result suggests the influence of phonological loop on the multiplication problems and of visuo-spatial sketchpad on subtraction.

Some observations arise at this point. Imaging and physiological data have contributed to clarify the neuroanatomy of parietal cortex in terms of structural organization, even showing relevant homologies between human and monkey brain. Additionally, some imaging studies tried to define parietal circuits that differently contribute to the verbal, visuo-spatial, and quantity-related aspects of number processing. Unfortunately, for my knowledge, less is known about the developmental trajectories of this parietal circuit and its progressive emergence in children. Indeed, although a clearer panorama about the functions that recruit parietal areas such as grasping, pointing, saccades, calculation and attention in adults, further studies are necessary to explore the anatomical changes in the neural correlates of these functions during the brain development.

Chapter 2

NUMBER REPRESENTATIONS

From birth, humans are sensitive to numerical information, in either the form of the approximate number of objects in large sets or in the form of the exact number of objects in small sets. Both types of numerical sensitivity, are thought to be part of the Number Sense (see below) (Dehaene, 1997; Feigenson, Dehaene, & Spelke, 2004) are language-independent and shared with other species. During enculturation, a long process of symbolization allows children to have a more precise and discrete concept of both small and large quantities. In contrast to the large approximate numerosity representation, the symbolic number representation is precise, discrete, language-specific and influenced by culture.

In this chapter, I consider the main characteristics of Number Sense and its development showing the changes in the internal Weber fraction across ages. After introducing the models regarding the approximate representation of numbers, I focused on symbolic numbers.

2.1 Presymbolic numerical representation

The presymbolic representation of number constitutes an evolutionary tool that humans share with other species, constituting a sort of sixth sense: the "Number Sense" (Dehaene, 1997). The sensitivity for numerosities is fundamental for survival and feeding, such as, for example, discerning the number of approaching predators (McComb, Packer, & Pusey, 1994). A vast class of species like non-human primates, dolphins, rats, salamanders and pigeons (Brannon & Terrace, 2000; Kilian, Yaman, von Fersen, & Gunturkun, 2003; Meck & Church, 1983; Uller, Jaeger, Guidry, & Martin, 2003; Xia, Emmerton, Siemann, & Delius, 2001) can discriminate numerosities by using an approximate and compressed representation, exhibiting the same psychophysical effects (Weber-Fechner law, see (Dehaene, 1997)) found in humans engaged in similar tasks.

Numerical relevant behaviors were consistently found also in untrained animals, in wild environments (Hauser, et al., 1996), and where number information was spontaneously extracted (Hauser, Dehaene, Dehaene-Lambertz, & Patalano, 2002; McComb, et al., 1994). Adopting the violation-of-expectation paradigm (Wynn, 1992b) frequently used with infants, untrained monkeys exhibited a natural sense for numerosities and basic arithmetical relations between numerical quantities (Hauser, et al., 1996).

Both behavioral and electrophysiological studies suggest that numerosity extraction is not dependent on the specific modality of stimuli presentation, suggesting a modality-independent representation of number.

For example, the amodal features of numerosity representation were shown in a study (Church & Meck, 1984) where cats were trained to press the left lever for two flashes or two sounds, while the right lever for four flashes or four sounds. Then, cats spontaneously started pressing the right lever even for a combination of two sounds and two flashes.

Electrophysiological studies confirm that number coding neurons exhibit amodal characteristics. In cats, for example, some neurons of the posterior associative cortex fire for a specific number as presented as visual and auditory stimulus modality (Thompson, Mayers, Robertson, & Patterson, 1970). Number neurons were also identified in the monkey's parietal cortex related to the number of motor sequences performed by the monkeys (Sawamura, et al., 2002) or visual objects memorized by the monkeys (Nieder, et al., 2002). Finally, some number neurons of the monkey IPS respond for both sequential and simultaneous presentation of numerical stimuli (Nieder, Diester, & Tuduscius, 2006).

These characteristics of approximation, compression, and invariant to modality are observed even in humans, under the conditions when counting cannot take place (for instance in childhood when children haven't received yet a formal knowledge about counting or in adulthood when the task demands fast reaction times or the stimuli are presented too quickly and/or masked). Under the non-counting conditions, the ability to compare the numbers of items in sets is noisy and approximate: subject's responses become more accurate as the ratio between numbers to be compared increase, according with Weber’s law (Gallistel & Gelman, 2000).

Moreover the subject’s performance show no cost comparing numerosities across-modalities compared to within modality (auditory and visual) or across vs. within-format (sequential or simultaneous) presentation (Barth, La Mont, Lipton, & Spelke, 2005; Cordes, Gelman, Gallistel, & Whalen, 2001; Hauser, Tsao, Garcia, & Spelke, 2003; Piazza, et al., 2004). This general ratio-dependent behavior common to all sensory modality, is taken as to indicate the presence of a universal mechanism for approximate number processing, and supports the idea of an abstract and amodal representation of numerosity.

However, the question of the scaling of the number line remains unclear. Current models propose that numbers are internally represented either on a logarithmically compressed continuum with fixed internal variability (Dehaene & Changeux, 1993) or on a linear scale with increasing standard deviation of the internal noise (Gallistel & Gelman, 2000). Both models accurately accounts for Weberian ratio-dependent performance. Indeed, in the case of numerosity discrimination, performance improves when the distance between the numerosities increases, as predicted by the Weber’s law: namely, the extent to which two stimuli can be discriminated is determined by their ratio (Piazza, et al., 2004; Pica, Lemer, Izard, & Dehaene, 2004).

In an electrophysiological and behavioral study on monkeys by using a match-to-sample task, Nieder and colleagues (Nieder & Miller, 2003) found a peculiar symmetric data distribution when data are plotted on a logarithmic scale. While this finding was used in favor of the logarithmic scaling model, it was noticed that the observed symmetry on a Log scale represents the solely expression of Weber’s law (which is predicted by both linear and logarithmic number line models; (Piazza & Izard, 2009)).

Preverbal approximate representations are also used to perform simple arithmetical operations. Indeed, some preverbal skills allow infants to judge the exactness of the solution of some basic problems like “1+1=2”, and not 3 (Wynn, 1992a).

Interesting results were obtained studying preschool children before the acquisition of a formal knowledge of number by using computer-based tasks (Barth, et al., 2006; Barth, et al., 2005). The paradigm simulates approximate calculation (e.g. additions and subtraction) with dots arrays. More precisely, a first dots array was presented and occluded by a panel, and then another array joined the first one behind the panel. After removing the panel, a third dots array differing from a small or large ratio from the correct sum was displayed. The participants had to compare it to the exact sum and decide whether is contained more or less dots. 5- and 6-years old children exhibited an above-chance ratio-dependent performance for approximate additions and subtractions with non symbolic stimuli. The contributions of perceptual factors or exact calculation strategies were excluded by successive studies (Barth, et al., 2006; Gilmore, McCarthy, & Spelke, 2007).

2.1.1 The Weber's fraction and its development

On the basis of psychophysical and behavioral data, the measurement of the limits of human senses attracted several authors, E.H. Weber introduced a law able to specify the weakest different threshold (behavioral Weber fraction) necessary to produce a noticeable variation of the sensory experience, showing that the perception of a stimulus change depends on both the magnitude of the change (Δs) and the stimulus baseline intensity (s) (Gescheider, 1997). Stimuli for which the Weber's low holds (mostly sensory, such as loudness, brightness) can be thought of being internally represented on approximate and compressed continuum (Dayan & Abbott, 2001). The same reasoning can be applied to the case of the internal representation of numbers. Indeed, one can think that numerosity (n) is represented on an internal continuum that is approximate and compressed (either logarithmically scaled or linear with increasing noise). In this way, the numerosity can be represented by a Gaussian distribution with mean Log(n), and with a constant width/standard deviation w, alternatively called the *internal Weber fraction*. This parameter represents the degree of precision of the internal representations of numerosities. Thus, $2w*100$ represents the difference (%) between two numbers that is necessary to perceive them as different with high confidence. For example, a w of 0.2 reflects an ability to discriminate two sets differing by about 40% (e.g. 10 versus 14 items). The relation between behavioral and internal Weber's fractions depends on the task, indeed a model of decision making is assumed in a given task (see (Dehaene, 2007) for a review).

Intersingly, empirical data seem to achieve remarkably with what predicted by this psychophysical model (Dehaene, 2007). Comparable magnitudes of internal Weber fraction were found on the base of subject performance in different tasks (e.g. same-different task, lager-smaller task). Indeed the value of w in adults across different cultures in a larger-smaller or same-different judgment task is around 0.15 (Piazza, et al., 2004; Pica, et al., 2004). Moreover similar estimations for w were found on the basis of data from magnitude comparison tasks (dot arrays) in French (0.12) and Amazonian adults (0.17), even if the numerical lexicon of the Amazonian indigene people was restricted to 5 (Pica, et al., 2004).

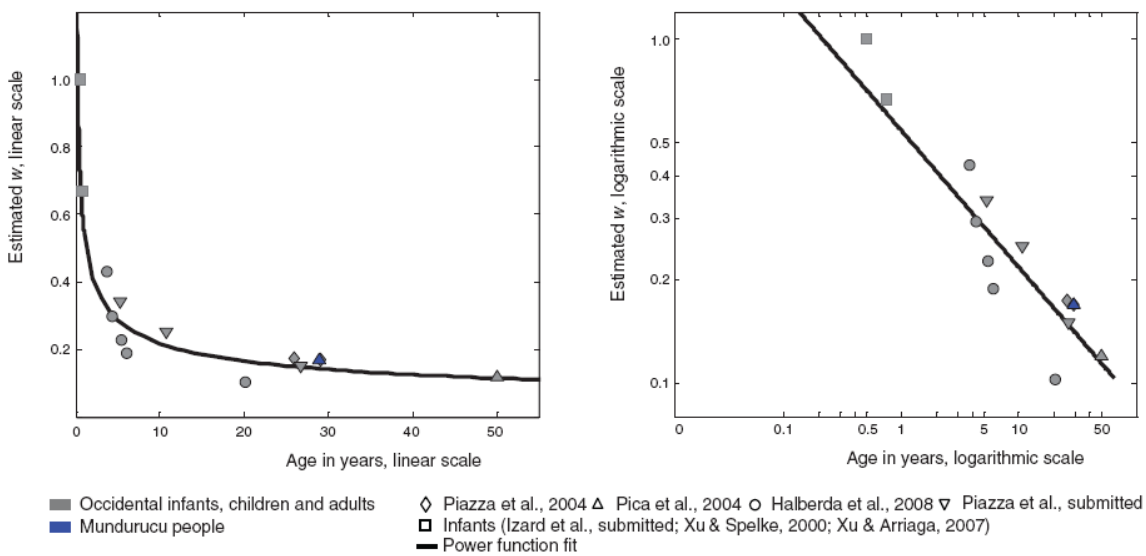


Fig. 6. Development of the precision of the approximate numerical representations. The graphs regroup the values of w estimated in different papers (from Piazza & Izard, 2009).

Ratio-dependent numerical behavior also showed the presence of an approximate numerical sensitivity in preverbal infants, albeit with drastically less precision of the internal representation of number than adults (Halberda & Feigenson, 2008; Piazza & Izard, 2009). Development changes in the Weber's fraction were documented during childhood with a dramatic refinement over the first year of life: 1.0 at 6 months, (infants discriminate numerical changes for ratios of 2:1, e.g. 4 dots vs. 8 dots (Lipton & Spelke, 2003; Xu & Spelke, 2000), 0.5 at 9 months (e.g. 8 vs. 12 dots), improving gradually until late childhood (0.40 at 5 years, 0.25 at 10 years), describing a typical power function (Halberda & Feigenson, 2008; Lipton & Spelke, 2003; Xu & Spelke, 2000).

As in adults (see above) also in children, similar values of w were obtained in both auditory and visual domains across ages (Lipton & Spelke, 2003; Wood & Spelke, 2005), suggesting that it is the internal representation of number itself, and not the visual or auditory sensitivity, that is improving.

The factors liable for the reduction of w with age are still unknown, although maturational processes and arithmetic education may play a significant role. However, the presence of similar values of w in different cultures, even when formal education for arithmetic is absent or limited, supports the maturational interpretation. In sum, this law seems pervasive in numerical cognition and stable across cultures, life span and animal species while performing different numerical tasks (Piazza & Izard, 2009).

2.1.2 Models of early numerical abilities

Several models were proposed with the aim to accounting for the natural preverbal sensitivity for approximate numerical information.

An original explanation of the ability to discriminate roughly the numerosity of sets of objects by using the metaphor of accumulator was proposed by (Meck & Church, 1983) and elaborated by Gallistel & Gelman (2000). According to this model, for each discrete numerosity, an imprecise amount of "energy" enters in the accumulator. The total amount is proportional to the counted numerosity. The quantity of energy entering in the accumulator varies trial by trial, thus the variability of accumulator state for a particular numerosity increases with the magnitude, following the classical trend described by Weber's law. In other terms, the energy can be represented as a sort of water stream with an inconstant discharge. Thus, we get different amount of water (in our hypothetical glass) keeping constant the acquisition time. This variability increases with the number of water acquisition which is proportional with the counted numerosity.

Interestingly, recent electrophysiological evidences have showed the presence in macaque monkey LIP of number neurons with an accumulator-like coding scheme (Roitman, Brannon, & Platt, 2007). Important differences regard the neural functional properties of these LIP neurons from those number neurons found in monkey area VIP and cat posterior cortex (Nieder & Miller, 2004; Sawamura, et al., 2002; Thompson, et al., 1970). First, LIP neurons exhibit numerosity sensitivity, rather than selectivity. Indeed these neurons code monotonically with the number of visual objects rather than to a given number. Second, the numerosity accumulator neurons receive the information coming from limited retinotopic receptive fields, thus they only code for a bunch of items displayed in their receptive field, and not for the overall amount of the presented items. This property derives also from the particular anatomical location of these neurons in area LIP, more dorsally and caudally with respect to VIP, that typically code for spatial information on the base of eye-centered co-ordinates (Hubbard, et al., 2005; Nieder, 2005; Piazza & Izard, 2009). Thus, LIP accumulator neurons is thought to constitute an intermediate step from the basic extraction of sensorial information to VIP number neurons following a hierarchical processing.

One of the first examples of connectionist approach to number cognition was proposed by Dehaene and Changeux (Dehaene & Changeux, 1993). This model also assumes an accumulation stage, but it also introduces a numerosity detection system. Three layers were considered within this model: an input “retina”, a map of objects location and an array of numerosity detectors. Through the retina, each stimulus is normalized and converted in a size-independent representation of the object. The same happens also for sounds by using an echoic auditory memory. The output of this location map is summed to yield an estimate of input numerosity and, then, sent to numerosity detectors tuned for a given numerical quantity. In this way, a given numerosity cluster will be active if the relative summation cluster is active, but those representations for higher numerosity are not. This model has received confirmation from electrophysiological recordings in monkey brain (Nieder &

Dehaene, 2009; Nieder & Miller, 2004). Then, the data suggest a parallel encoding of numerosity, which would be difficult to explain by the accumulator model that is, by definition, serial. More likely, the model of Dehaene and Changeux (1993) suggests an approximate detection of numerosity based on a analog magnitude process, and in parallel fashion. Again, the numerosity detectors proposed by this model become less selective with increasing center numerosities following the Weber's law.

More recently, another neural network model was suggested for the representation of number in animals and humans by Verguts and Fias (2005).

Firstly, number-selective neurons are created on the base of an initially neural network trained for given non-symbolic stimuli as input (e.g., collections of dots) under unsupervised learning. Interestingly, at the neural level the resultant network exhibits the properties of number-selective neurons previously hypothesized by Dehaene and Changeux (1993) and recently found by Nieder and colleagues (Nieder, et al., 2002; Nieder & Miller, 2003), showing the classical numerical effects such as distance and size effects. Then, the network was stimulated by the simultaneous presentation of symbolic and non-symbolic inputs. Interestingly, the previous number-selective neurons started learning the numerical magnitude of symbols. During this process, number-selective neurons do not quantitatively change their coding scheme (thus show reminiscent properties of the original network), but show a quantitative improvement in the representation efficiency of neurons after the presentation of symbolic input.

This finding represents concrete evidence regarding how symbolic cognition originates from a neural systems previously devoted to numerosity information from perceptual input, suggesting the reciprocal influence between non-symbolic and symbolic number processing (Verguts & Fias, 2005). Specifically, these data are in favor of hypothetical refinement of neuronal tuning for numerosity after the acquisition of symbolic numbers.

2.1.3 The case of small numbers

Small numbers (up to 3 objects) seem to represent a special category from early childhood. Indeed, in infants, opposite behavioral patterns were shown in case of processing small or large sets of items. While in case of large sets of items, the children responses are more selective for the numerical information rather than other non-numerical parameters (such as area, (Wood & Spelke, 2005), the inverse pattern of results was found for small numerosity whose processing is more influenced by non-numerical continuous parameters (Xu, Spelke, & Goddard, 2005) then numerical information.

Indeed most studies evidence the role of some perceptual variables, such as total surface area, brightness, density etc. All these non-numerical variables seem to co-vary with the numerosity, with the relative impossibility to determine whether infants respond to continuous spatial dimensions rather than number itself (Feigenson, Carey, & Spelke, 2002). Although some studies documented that infants respond according to the numerical magnitude versus other continuous spatial parameters (Brannon & Gautier, 2003), the performances of 6- and 8- month-old and in 10- and 12-month-old infants seem to be respectively related to the contour length (Clearfield & Mix, 1999) or surface area and volume (Feigenson, Carey, & Hauser, 2002).

In adults, numerosity identification is as fast as accurate up to sets with three or four items, while for larger sets errors rate and reaction times increase progressively of about 200-400 ms/item (Revkin, Piazza, Izard, Cohen, & Dehaene, 2008). This pattern of data reflects the presence of two separate processes in exact numeration, the subitizing for small sets and counting for larger sets. The nature of subitizing was recently explored. On one hand, subitizing may reflect the use of a common numerical estimation mechanism for both small and large numbers (Dehaene & Changeux, 1993; Gallistel & Gelman, 1991) that follows the Weber's law. According to this hypothesis, low internal variability in the representation of small numbers may describe the advantage for the identification of small numerosities. On the other hand, subitizing may be considered a dedicated mechanism for apprehending a small number of items in parallel also present in infants (Feigenson, et al., 2004).

Interestingly, Trick and Pylyshyn (1994) proposed to consider this mechanism as a parallel tagging process that operates over small sets in the early stage of visual analysis. The idea of a dedicated mechanism was support by Revkin and coll. (2008). Indeed, using a numerosity naming and dot comparison tasks respectively in adults, the subitizing range appears dissociated from the internal Weber's fraction, underling its distinction from number sense domain. Our visual system can select a fixed number of about four objects based on their spatial information or to encode their details, respectively for objects individuation and identification, also explaining the limited capacity of working memory to process and successively maintain visual information.

In summary, human beings can extract the numerical quantity of sets without verbal counting. This ability depends on the presence of an innate sensitivity for numerosity, which is approximate, analog, language-independent, ratio-limited and well described by the Weber-Fechner law. This system represents a rudimental residual of our evolution shared with other species and observed in adults, preschool children and in indigene groups with limited number lexicon. Moreover, the activity of this system starts early in the development, as confirmed in several studies in infants and newborn babies (Izard, Sann, Spelke, & Streri, 2009). In case of few items (< 4), a particular mechanism could be recruited to count rapidly discrete elements in the visual scene, the subitizing.

2.2 Symbolic numerical representation

Humans come to life equipped with an approximate system for representing large numerosity and with an exact system for tracking exact small numerosities. During development children acquire symbols for numbers which represent a precise way to represents even large numerical information. Despite diverging ideas about the role and the relations among Arabic and verbal representations, there is a general consensus about the functional dissociations among symbolic representations on the base of what found in brain-damaged patients. Indeed functional separations were found for comprehension and production mechanisms, between Arabic and verbal codes and, finally, between lexical and syntactical process for each code (McCloskey, Macaruso, & Whetstone, 1992). The anatomical segregation of Arabic and verbal codes was even supported by imaging data (Pinel, et al., 1999). In the next sections, I explore the verbal and Arabic codes, their interplay and the relation with the preverbal representations during development. Then, I focus on the contributions of language and verbal counting on the development of symbolic numbers.

2.2.1 Verbal and Arabic codes

Every model of number processing has to consider the dual nature of Arabic and verbal codes. The verbal naming of numerical quantity varies among the cultures (Hurford, 1987). Despite this diversity, some common principles concerning its linguistic organization are universally shared. One of them is the similar size of the lexicon, which divides the units, from the teens and the decade names. Then, the traces of additive or multiplicative relations expressed by the syntactic order of items (such as in twenty + five and two*hundred respectively) are on the base of a more or less transparent ten-base structure of numbers. Indeed, while Chinese numbers above 10 respect explicitly additive and multiplicative rules (i.e. eleven is spoken as “ten one”), this is not valid for some western languages such as

German, English, French, Spanish and Italian which are not regular base-10 systems. For these reasons, at the beginning Chinese and western children showed similar performances for number up to 10 (Miller, Smith, Zhu, & Zhang, 1995), but for larger numbers Chinese children from the age of 4/5 years to all elementary school ages perform better compared to western children on counting beyond 10 (Stevenson & Stigler, 1992).

Arabic digits represent the most common notation for encoding numerical quantity enabling children to read, write and understand even large numerical quantity in an exact fashion. Overall, despite a less attention on the acquisition of this notational system compared to the acquisition of verbal counting, developmental data does not show particular difficulties in learning the digits from 1 to 9 (Hughes, 1986). The only exception to this is represented by zero which determines specific difficulties in children while writing numbers (e.g. 203) containing a null position (Wellman & Miller, 1986)), responsible of a modification of the kinematics of the numerical handwriting (Lochy, Pillon, Zesiger, & Seron, 2002). Comparable results were found even with brain-damaged patients who showed impairments syntactic and lexical errors regarding the zero (Grana, Girelli, & Semenza, 2003). Probably this is due to the absence of correspondence with the verbal counting, but the real nature of this problem is still unclear. Specifically, in childhood, the main difficulties are represented by the positional nature of Arabic notation where the position occupied by the digit determines its value.

The acquisition of Arabic numbers, as well as verbal counting, can be differentiated in several phases on the base of the child's ability to identify and handle them. First, preschoolers have to distinguish Arabic digits (0-9) from non-numerical symbols (Noël, 2001). At 3 years of age, their performances are at chance. About 1 year later, children identify as numerical symbols the Arabic numbers (90%) but also letters. 5 years old children are sensitive for Arabic symbols and their related quantity information, and are even able to put in relation the Arabic numbers with the relative words (for 70% of cases).

In the late preschool age, at 5 years, children can compare the numerical information (the magnitude) contained in Arabic symbols while solving addition and subtraction problems (Gilmore, et al., 2007) however they seem to do so in a strictly approximate fashion (considering their approximate cardinality and not the exact numerical value). Cross-sectional studies exploring the ability to compare Arabic digits in preschoolers, school age children and adults, showed that numerical distance influences all groups performances with a stronger effect in younger children (Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Dehaene, Dehaene-Lambertz, & Cohen, 1998; Holloway & Ansari, 2008). Converging results were reported also by Duncan and McFarland (Duncan & McFarland, 1980).

These findings suggest similar Arabic representations in both children and adults which are influenced by our approximate system for numerosity. The decrement of the slope of numerical distance in young children might reflect their progressive refinement of magnitude mapping on symbolic numbers. Indeed a strong automatic access to Arabic number magnitude was reported at 7-8 years of age, roughly 1-2 years later the ability to compare Arabic numerals (Girelli, Lucangeli, & Butterworth, 2000; Rubinstein, Henik, Shahar-Shalev, & Berger, 2000). In other terms, the experience of children with Arabic numerals induces a more precise mapping of magnitude on these symbols, progressively amplifying their competence with larger numbers (Mussolin & Noel, 2007, 2008), and automatizing the access to semantic representations.

During the development, verbal numerals are acquired and used before Arabic numerals. Despite the fact that in western cultures number-words are use to teach the Arabic code at school, these two codes can be dissociated as suggested in neuropsychological studies by using transcoding task consisting in the transformation from a numerical format to another one (e.g. from Arabic notation to number-word, (Cipolotti & Butterworth, 1995; McCloskey, et al., 1992)).

However, some evidences from developmental studies on learning and cross-linguistic aspects support the idea of a verbal influence of Arabic code, at least in the first stages. Indeed the transparent verbal systems of Southeast Asia based on a clear ten-base organization can facilitate the acquisition of Arabic digits compared to western nontransparent systems (Miura, et al., 1994). Thus, at least initially, the acquisition of an Arabic system seems to be dependent on the transparency of preexisting verbal system for numbers. Generally, at the second grade, children can establish a direct association between the analogue quantity and the Arabic digits without verbal recoding, suggesting the dissociation of these two codes (see also (Donlan, Bishop, & Hitch, 1998)).

Several models were proposed to describe the multi-notational system for numbers on the base of the performance of brain-damaged patients (Deloche & Seron, 1987; McCloskey, Caramazza, & Basili, 1985). Among them, the model proposed by Dehaene ((Dehaene, 1992) (Dehaene & Cohen, 1995); Fig. 7), called “triple code model. The name of this model derives by the assumption that numbers can be mentally represented in a visual system, a verbal system and a quantity system recruiting three different neural circuits. The visual system is sensible for the encoding of strings of Arabic numbers and its neural equivalent is probably represented by occipito-temporal regions. The verbal system is involved in the lexical, phonological and syntactical representation of numbers. Despite a first location in the left frontal and temporal language areas, recently this system is thought to depend on the angular gyrus (Pesenti, et al., 2000; Zago, et al., 2001). The last system, also called the core semantic system for numbers, contains an abstract representation of size and distance relations among numbers (Dehaene, et al., 2003). This system emerges from the activity of intraparietal sulcus (IPS) during number comparison, approximate calculation and subtraction, and may play a crucial role in the interaction between numerical and a spatial domains.

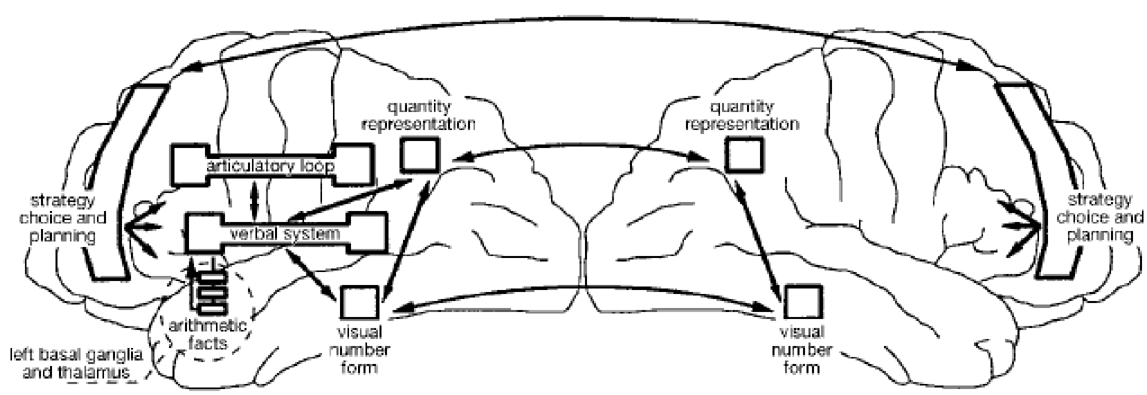


Fig. 7. Schematic anatomical and functional depiction of the triple-code model, adapted from (Dehaene & Cohen, 1995).

After acquiring a vast body of formal knowledge on the Arabic and verbal numbers, procedures (verbal and finger counting) and arithmetical principles (e.g. one-to-one correspondence), children learn to retrieve the results of simple calculation. Since 4 or 5 years of age, children can solve simple additions using a vast repertoire of strategies (Siegler & Shrager, 1984). For instance, they can start from 1 adding the two operands, helped by fingers and verbal counting, or children can consider the larger operand and then counting forward for a number of positions equal to the magnitude of the smaller operand. These two strategies are called counting all and counting on (Baroody, 1987; Fuson, 1982) or sum and min procedures, respectively (Ashcraft, 1982; Groen & Parkman, 1972). Interestingly, cross-sectional and longitudinal findings showed the progressive shift from the use of counting all to counting on during schooling (Siegler & Jenkins, 1989). Thought practice, some arithmetic facts can be stored in our long-term memory determining a direct retrieval of the results without counting or computing, and helping us in the solution of complex operation via decomposition in partial results (Ashcraft, 1982). The transition from counting-based strategies to retrieval-based ones characterizes the acquisition of all simple operations (Siegler, 1988), despite the doubtful nature of the stored representation of these problems. Arithmetical facts can be conceptualized as abstract formats (McCloskey, et al., 1985), with operation-dependent nature (e.g. a preferential verbal format for the solution of multiplications and some additions, (Dehaene & Cohen, 1995)) or individual preference (Noel & Seron, 1993).

The use of a retrieve-based strategy for arithmetic facts depends on the size of the operands (the problem-size effect, (Geary, 1996)). Indeed longer RTs and more inaccurate responses were described in relation to the operand sizes (e.g. 2+3 vs. 7+8) in the solution of all the problems involving additions (Ashcraft & Battaglia, 1978), subtractions (Geary, Frensch, & Wiley, 1993) and multiplications (Campbell, 1987).

This effect seems to reflect the associative strength of a problem with a given result compared with other possible (not correct) responses (Siegler & Shrager, 1984), well described by the peak distribution around the correct answer for simple operations, in contrast with a flat distribution of more difficult problems. Children's performances in simple problems can be influenced even by a more internal threshold, the confidence criterion, related to the child reliability about the exactness of the retrieval response (R. S. Siegler, 1988).

2.2.2 From pre-symbolic to symbolic numbers

Despite a fast and easy acquisition of the first verbal numbers, the implicit association between the verbal labels to specific quantities can elicit particular difficulties. A sort of "transition phase" was reported during which children know the number words, but they are unable to associate them to precise cardinalities. During the early development, a considerable amount of time is necessary to understand the exact quantity hidden behind number words such as "three" and "four" (Wynn, 1992b). Even the particular nontransparent and conventional structure of the first numbers especially of western languages does not help the number understanding. In this way, the name dose not contribute to inform about the relative quantity, thus "four" is bigger than "five" just because its position on the verbal sequence. The transition from a preverbal representation to a verbal code involves a long period in which it is necessary to constitute a precise and automatic access to exact cardinal quantity from simple number names. Jordan and other authors (Huttenlocher, Jordan, & Levine, 1994; Jordan, Levine, & Huttenlocher, 1995) proposed the presence of a precise computational mechanism applicable to small quantity independently of linguistic or cultural influences. This mechanism may depend on the objects file manipulation or on an abstract representation based on discrete and symbolic code.

According to Butterworth (Butterworth, 1999, 2005), the core of our arithmetical abilities consist in the innate capacity to discriminate, represent and manipulate small numerosities (subitizing). In Butterworth's proposal, three separated components are thought to play a relevant role in numerical representation and processing. This component involves: our innate ability to discriminate small numerosities (subitizing), the functional use of fingers through fine motor movements (finger movement), and the accuracy of the finger representation (finger gnosis). Within this framework, subitizing represent a fundamental component for the mapping of verbal numbers to numerosities (Benoita, Lehalle, & Jouenb, 2004).

Coherently to Butterworth’s proposal, a recent vast work on first graders (N=146) showed clear dissociations among three behavioral tasks regarding subitizing speed (on RTs), finger gnosis and finger tapping, while arithmetical abilities were predicted from subitizing skills both directly and indirectly via number knowledge (Penner-Wilger, Fast, LeFevre, Smith-Chant, & et al., 2007). Clinical studies on dyscalculic children indicate a impaired subitizing skill (Landerl, Bevan, & Butterworth, 2004) in dyscalculia.

Fewer studies have focused the attention on the relation between preverbal representations and numbers presented in the Arabic form. Behavioral data suggests that the comparison of large numbers in adults follows firstly a sequential procedure (processing the different digits one after the other), and only successively they used a holistic procedure taking account of the overall quantity (Hinrichs, Berie, & Mosell, 1982; Poltrock & Schwartz, 1984). Contrastingly, in adults, comparisons of one- or two-digit numbers suggests the idea that Arabic numbers are directly activated and processed holistically on the basis of analogue representation, rather than considering the digits and their position in the number. Coherently to this, no decade break effect was reported while comparing two-digit numbers (Brysbaert, 1995; Dehaene, Dupoux, & Mehler, 1990; Reynvoet & Brysbaert, 1999). However, numbers larger than two-digit numbers seem to be compared using an analytical procedure regarding a serial analysis of the number components. Moreover, unclear evidences concern the numerical threshold for the passage from a holistic to an analytical processing and about the between-subjects variability.

Interestingly, a distance effect was showed in a magnitude comparison task in both children and adults, suggesting an early access of analog representation of numbers. This analog representation of numerosity was firstly documented by the study of Moyer and Landauer (Moyer & Landauer, 1967) by using an Arabic numerical comparison task. These authors found an inverse correlation between RTs and error rate with the numerical difference. In other terms, small numerical distances (e.g. 3-4) elicited slower RTs and higher error rates than large distances (e.g. 3-9). This phenomenon was called “numerical distance effect” and it assumes that numbers are automatically converted into an internal-analog representation and compared each other (but see (Verguts & Fias, 2005) for a different interpretation). This effect was found also comparing number words (Foltz, Poltrock, & Potts, 1984), dots arrays (Buckley & Gillman, 1974) and, even for two-digit Arabic number comparison (Dehaene, et al., 1990) suggesting a holistic representation of numbers bigger than 9 on the number line (Brysbaert, 1995), in contrast with a compositional single-digit representation (Nuerk, Weger, & Willmes, 2001). Beyond the numerical distance, another effect may reflect the number magnitude processing. The “size effect” determines higher latencies in comparing large than small numbers (Moyer & Landauer, 1967) due to the stronger compression (Dehaene, 2003) or higher variability (Gallistel & Gelman, 1992) for larger numerosities

A ratio-dependent performance in preschool age was found by Gilmore and colleagues (Gilmore, et al., 2007) while children solve exact addition problems, underling the common influence of Weber’s law in both presymbolic and symbolic representation of numbers. Again, numerical distance at 6 to 8 years old children found in symbolic and non-symbolic numerical tasks correlates with arithmetic outcome.

Specifically, children showed that mathematical achievement correlated with symbolic distance effect with a peak at age of 6 followed by a progressive decline up to 8 years, but not to non-symbolic distance effect (Holloway & Ansari, 2008). Differences in the relation between symbols and magnitudes were accounted to explain this result, although other mechanisms can be involved, e.g. the identification of Arabic numbers or symbolic mapping onto a magnitude representation. Taken together, these findings support the idea that preverbal numerical representation constitutes a natural basis for formal arithmetic.

Interestingly, mathematical competence from kindergarten to sixth grade was compared with the ability to compare non-symbolic numerosities of 14 years old children (Halberda, Mazzocco, & Feigenson, 2008). Despite a high variability in the Weber's fraction among participants, data showed that numerosity acuity (the precision of the numerosity comparison) at age of 14 retroactively correlated with the early mathematical skills, even controlling the effect of speed of processing and IQ. Thus, the precision in non-symbolic numerical information processing was tightly related to symbolic mathematical competence from the age of 5 years (see Fig. 8). However, further studies are necessary to investigate the casual role of number sense acuity on mathematical achievement and the effect of mathematic on the refinement of magnitude representation.

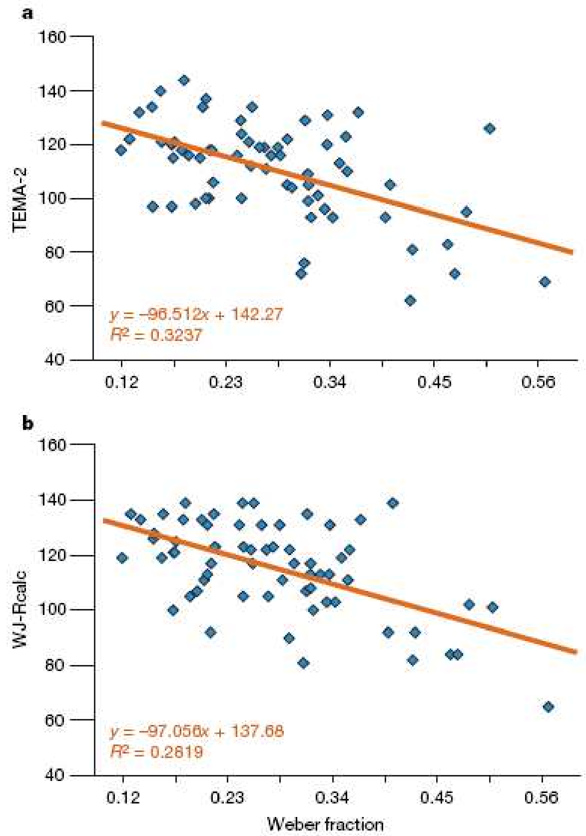


Fig. 8. Linear regression of the standard score for each subject on the TEMA-2 test (a) or on the WJ-Rcalc test (b) of symbolic maths achievement and the acuity of the ANS (w). For TEMA-2 and WJ-Rcalc, higher numbers indicate better performance, whereas for the Weber fraction, lower numbers indicate better performance (from Halberda et al., 2008).

A recent study investigates the mapping of acquired symbolic numbers on a preexisting system for approximate quantity in children. Data show that children develop the ability to map between symbolic and non-symbolic number representations from 6 to 8 years of age (Mundy & Gilmore, 2009). Then, using a Stroop-type task in school age children and adults, it was possible to note the level of automatic numerical processing (Girelli, et al., 2000). The task consists in comparing the physical size or the magnitude of two different numbers written in congruent or incongruent dimensions in respect to the numerical magnitude. In the case of physical comparison, the mismatch between physical and numerical information afflicted just older children and adults, suggesting the gradual process of automatization in Arabic number processing.

In summary, the easy structure of Arabic code, especially for small quantities, is quickly learnt and used but a long phase is necessary for accessing to the associated precise quantity in an automatic fashion.

2.2.3 The role of counting

The acquisition of counting represents the first attempt toward a precise and symbolic representation of numbers. In this way, children progressively learn a particular way to symbolize numerosity ("digitization") that allows us to better identify larger numerical quantity and constitutes the starting point for our capacity to perform complex arithmetical operations. As seen above, from about the age of 2 children start to recite the sequence of number words but do not understanding basilar principles related to counting (Wynn, 1990). Indeed, roughly 4 years are necessary to acquire all the sequence of number words and its properties, from a sterile repetition of words to a deeper knowledge of their meaning (Wynn, 1992b).

This long-lasting process was documented in English speaking children who progressively acquire the meaning of "one", after about 6 months the meaning of "two", 9 months later the meaning of "three" up to "twenty" at 6 years old. The number "four" seems to represent the turning point of this process, which, once acquired, allows children to understand the logic of number chain and the successor function (Gelman & Gallistel, 1978; Wynn, 1992b).

The refinement of verbal counting continues from age 4 to age 7 o 8 with orderly qualitative differences in the elaboration of number words sequence, extensively studied by Fuson (Fuson, 1988; Fuson, Richards, & Briards, 1982). Five different phases of elaboration were identified: a) string level, number words are undifferentiated in a forward form starting always by 1, b) unbreakable list level, number words start to be distinguishable , c) breakable chain level, the number words sequence can by recited from arbitrary points , d) numerable chain level, the words are abstracted and become units that can be matched and counted, and finally, e) bidirectional chain level, the sequence can be repeated in forward and backward direction.

The practice of verbal object counting represents a fundamental factor of the development of these phases and the acquisition of important principles (Gelman & Gallistel, 1978). Indeed counting procedure contributes to the acquisition of five different counting principles:

1. the one-to-one correspondence between objects and number words. This principle implies that every object must be counted only once.
2. the fixed order of the number words sequences while counting (stable order principle),
3. the flexible order of elements counted for the cardinality of the set (order irrelevance principle),
4. the nature-independent format of elements that can be counted (abstraction principle) and
5. the cardinality of a set represented by the last word in the count (cardinality principle).

The role of counting principles in the development of number knowledge was demonstrated in a recent study on children (Le Corre & Carey, 2007, 2008). Interestingly, this studies show that, while the numbers from “one” to “four” are mapped onto the core representation of small magnitudes before the acquisition of counting principles, verbal numbers beyond “four” are only mapped onto analog representation about six months after the acquisition of counting principles. Then, since the verbal numbers learned prior to the introduction of counting principles are within the numerical range up to 4, this is taken as evidence that the construction process involves a system dedicated to small numbers (alone or together with analog representation of small numbers), but does not involve analog magnitude representation of sets larger than 5 elements (Le Corre, Van de Walle, Brannon, & Carey, 2006).

Developmental studies showed that children are able to verbally quantify sets only for known number words (within their counting range), while other numerosities elicit scalar variability typical of the approximate number sense (Dehaene, 1997; Le Corre & Carey, 2007; Wynn, 1992b). 3-years-old preschoolers can disentangle small known number words from larger unknown ones, but it is not sure if they use a strategy based on numerical ordering or magnitude (cardinality). Indeed the first evidence for a clearer understanding of numerical cardinality beyond the counting range emerged generally from 5 years of age (Lipton & Spelke, 2006). Indeed if a large set of items beyond the counting range is presented together with its number word, children can detect the cardinality changes in case of addition or removal of items but no changes are reported in case of items rearrangement or substitutions. This means that after a long process to learn the meanings of the first three number words, 5 years old children understand the logic of number words meanings applying a specific, unique cardinal values.

Doubts on the interplay of verbal counting and preverbal approximate system in the construction of an exact number system still remain. Indeed the verbal counting may represent a first way to map well-known number words onto approximate representation despite the unclear nature of this mapping. Furthermore the approximate system for numerosity may contribute to give the basic conception of counting (e.g. in the numbers ordering) that constitutes an essential element for verbal counting (Dehaene, 1997; Wynn, 1992b). Alternatively, other authors suggest the innate nature of principles involved in learning to count verbally (Gelman & Gallistel, 1978). In contrast, Fuson (Fuson, 1988) points out the primary role of experience in the discovery of counting principles.

In summary, several studies show on innate, preverbal, non-symbolic ability to extract numerical information from the environment even in newborn infants (Izard, et al., 2009). Then other studies focused their attention on the long constitution process of a symbolic system for numbers, supported by the contribution of counting. However, some doubts remain regarding the interaction of the developmental trajectories of these two systems during the development, indeed the only common ratio-dependent behavior for symbolic and non-symbolic numerical processing across ages is not enough to clarify even and when these two systems converge during the early childhood coherently with a longitudinal prospective.

Chapter 3

CONTRIBUTIONS OF NON-NUMBER RELATED PARIETAL FUNCTIONS TO NUMBER PROCESSING

As shown in the previous chapters, number cognition emerges as a function of a complex interplay between a set of abilities mostly related to parietal cortex comprising quantity processing, visuo-spatial abilities, finger gnosis and objects estimation through action. At the behavioral level, important relations among these functions are found across ages in children, adults and patients. This chapter contributes to better describe these relations on the basis of behavioral and functional imaging findings in healthy and brain-injured adults and children. It will become clear that despite convincing evidence for significant relations among these domains, there is still a quite crucial open question on whether and to what extent these relations are based on genuine and specific functional links among these domains or whether and to what extent they reflect common maturational processes of close cortical regions.

3.1 Space

More than a century ago, several investigations by Galton (1880) on mental imagery suggested that many western educated adults mentally represent numbers in a stable and mostly 2-dimensional internal space, organized on idiosyncratic number-lines. Some individuals even report a series of visuo-spatial properties associated with numerical information, such as color, and brightness, which give rise to particular configurations occupied by the sequence of numbers ((de Hevia, Vallar, & Girelli, 2008; Galton, 1880) for a review, Fig. 9).

From Galton's initial report, the idea of a spatially oriented number line assuming the interplay between spatial and numerical processing has found systematic support in both subjects with and without synaesthesia (Piazza, Pinel, & Dehaene, 2006; Seron, Pesenti, Noël, Deloche, & Cornet, 1992).

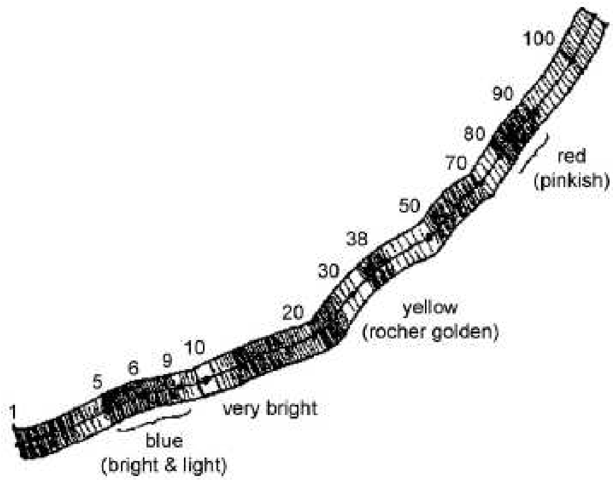


Fig. 9. A 'number form'. Illustration of the mental image evoked by a subject when thinking about numbers (from Galton, 1880).

A behavioral effect was classically used to document the effect of space in the representation of numbers: the SNARC (as in Spatial Numerical Association of Response Codes) effect (Dehaene, Bossini, & Giraux, 1993). This effect reflects an RT advantage for small numbers when subjects respond using the left response key, and an advantage for large numbers with the right response key. This effect was found in number comparison, parity judgments and ordering tasks (de Hevia, et al., 2008; Dehaene, et al., 1993; Hubbard, et al., 2005).

Interestingly, this effect is purely determined by the position of response keys and not by the hands position, indeed crossing the hands does not reverse the SNARC effect (Dehaene, et al., 1993). Curiously, the SNARC effect can be inverted by manipulating the spatial representation considered by the participant: while a standard SNARC effect emerges in case of typical number comparison, asking participants to image the numbers on a clock face determined a reverse association between magnitude and response side (Bachtold, Baumuller, & Brugger, 1998).

The SNARC effect was found not only when the response keys are disposed horizontally, but also for vertical dispositions of response keys, with small numbers associated to the bottom key and the larger ones with the top key, such as in a thermometer or in the Cartesian axes (Ito & Hatta, 2004).

This effect emerges in different tasks even when the number magnitude is irrelevant for response selection. Indeed spatial coding of numbers can interfere with non-numerical task involving spatial judgment (de Hevia, Girelli, & Vallar, 2006). The SNARC effect was found when required to discriminate the orientation of bars superimposed on an Arabic digits (Fias, 2001).

Another effect pointing towards an automatic association of number to spatial locations is observed in physical bisection tasks. When asked to indicate the midpoint of a line composed of small numbers, the subject's midpoint was placed on the left of the real midpoint and vice versa for larger numbers (Calabria & Rossetti, 2005; Fischer, 2001). Numerical magnitude can afflict even the eye movements toward left or right targets (Schwarz & Keus, 2004). Indeed small digits elicit faster target detection in the left visual filed, whereas right target are identified faster when large digits were shown (Fischer, Castel, Dodd, & Pratt, 2003).

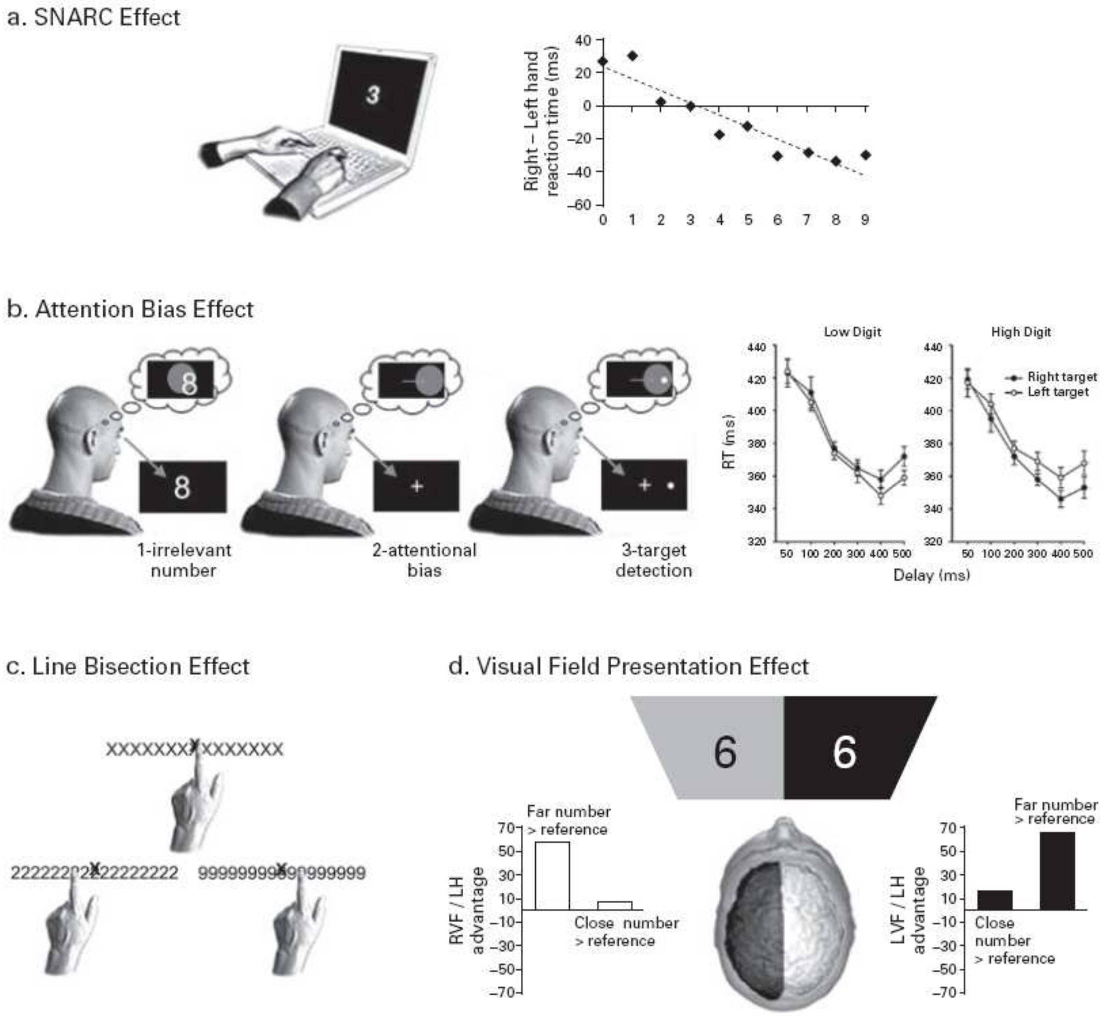


Fig. 10. Behavioural studies demonstrating numerical-spatial interactions. (a) SNARC effect. Subjects respond whether a number is even or odd. Right-minus left-hand reaction time differences are plotted, with values greater than 0 indicating a left-hand advantage. (b) Attention bias effect. Presentation of a non-informative digit at fixation leads to an automatic shift of attention to the left or right, and subsequently faster responses to visual targets. Graphs indicate reaction times to detect a visual target on the left or right side of space after presentation of a "low" or "high" digit. Open symbols indicate left-sided targets and filled symbols, right-sided targets. (c) Line bisection effect. When asked to point toward the midpoint of a line, subjects are accurate when the line is composed of x's (center indicated by bold x). However, when the line is composed of 2's or 9's, pointing deviates from the midpoint. (d) Visual field presentation effect. When a number is presented in one visual field, an interaction between numerical distance and visual field is observed. Numbers that are smaller than the standard show an advantage for LVF/RH presentation, and vice versa. Adapted from Hubbard et al., 2005.

Electrophysiological evidences demonstrate that number magnitude interferes during the response-related stages, after the closure of perceptual operations but before response selection (Keus, Jenks, & Schwarz, 2005). Additionally, EEG data showed that non-informative symbolic cues with spatial meaning, such as arrow and numbers, can elicit an automatic shift of attention (Ranzini, Dehaene, Piazza, & Hubbard, 2009) with a negative deflection (EDAN and ADAN components) on the hemisphere contralateral to the direction of attention for occipito-parietal and frontal regions, contributing to evidence that number automatically evoke association with space.

The interplay between space and number domains afflicts even actions.

A study of Song and Nakayama (Song & Nakayama, 2008) found direct relation between the numerical deviation and the deviation of hand trajectories, suggesting that numerical magnitude of the target is encoded as well as the numerical proximity or order along a hypothesized mental number line. Taken together, these results are important proofs about the existence of systematic interactions between number and space.

If we consider the SNARC effect as an index of the spatial representation of numbers, the first documented presence that spatial numerical association in the response codes was found at the age of 9 (Berch, Foley, Hill, & Ryan, 1999). Indeed cultural and education habits can influence the SNARC effect. For example, Iranian subjects exhibit a weaker SNARC effect compared to Western subjects, probably due to their right-left reading direction (Dehaene, et al., 1993). Again, Arabic speakers are faster to compare two visually presented numbers when the larger number is placed on the left side (Zebian, 2005). The spatial features of number representation were also linked to finger-counting habits: American students start to count objects by raising the fingers on the left hand while Italian adults use the right hand first. Indeed, contrary to American subjects, Italian subjects reflect a systematic association of number from1 to 5 to the right hand due to their finger-counting habits (Di Luca, Grana, Semenza, Seron, & Pesenti, 2006).

During childhood, a reduced visuo-spatial span, as measure by Corsi blocks, has sometimes observed in children with mathematical difficulties (Bull, Johnston, & Roy, 1999). Recently, it has been showed that the Corsi span represent a good predictor of the preverbal numerical performance in preschool children, but not in grade 1 children (Rasmussen & Bisanz, 2005). Moreover, Facoetti and colleagues (Facoetti, Trussardi, & Zorzi, 2007) found that that dyscalculia is associated with a defective visuo-spatial orienting in the right visual hemisphere indicated by the absence of inhibition of return effect. These authors suggest the presence of impairment in the right parietal cortex, particularly involved in the control of attention orienting. Subsequently, this deficit also influences negatively the number processing, limiting the ability to explore the representational space of the mental number line.

Another line of evidence in direct favor to the involvement of spatial codes in number processing comes from clinical studies on patients with (right) hemineglect that systematically misplace the midpoint of a numerical interval to bisect ((Zorzi, Priftis, Meneghello, Marenzi, & Umilta, 2006; Zorzi, Priftis, & Umilta, 2002); Fig. 11). The midpoint is generally shifted rightward and error rate increases with the size of the interval, as observed in the physical bisection of simple lines. This distortion seems to emerge from the impaired representational form of spatial neglect rather than an impaired access to numerical representations (Vuilleumier, Ortigue, & Brugger, 2004). When asked to process number as in a clock face, these patients exhibit greater difficulties than controls for numbers larger than 6, placed on the left side of the clock face. These results confirm the dynamic and flexible nature of the spatial representation of numbers.

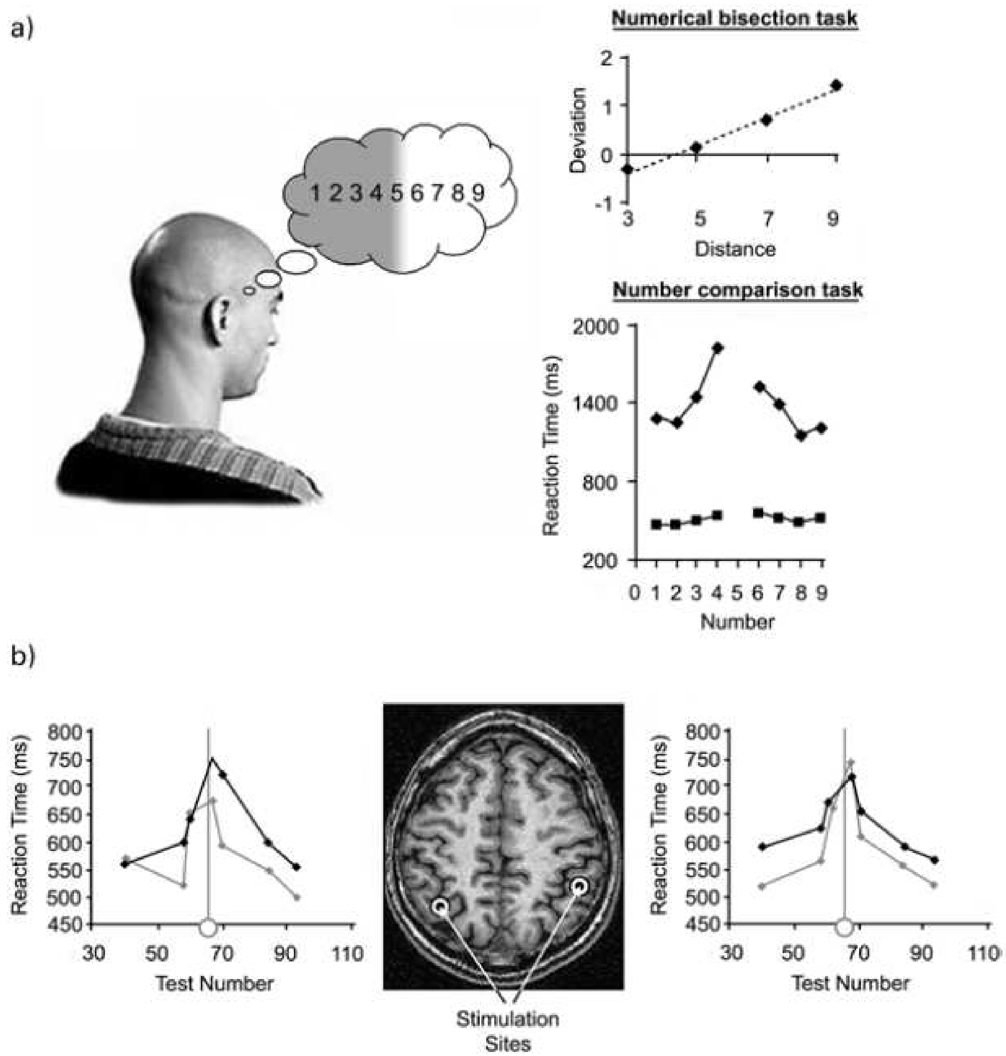


Fig. 11. Hemispheric effects in numerical-spatial interactions. (a) Neglect patients also demonstrate severe deficits in numerical distance and number bisection tasks. The upper graph shows the deviation on a number-interval bisection task, as a function of interval size, while the lower graph shows reaction times on a magnitude judgment task with 5 as the standard. (b) When rTMS is applied to the angular gyrus, responding to a number greater than the standard takes longer than in the no-stimulation condition. (Adapted from Hubbard et al., 2005).

The implications concerning a spatial representation of numbers emerge even during mental arithmetic. Indeed a so called “operational momentum” was described in several studies (McCrink & Wynn, 2009). Empirically, this effect emerges solving additions in which incorrect results is generally larger than the correct solution, and for subtractions, where the incorrect results is smaller than the correct solution. In other terms, the answers to addition problems were systematically overestimated and the answers to subtraction problems were systematically underestimated.

Recently, Knops and colleagues (Knops, Thirion, Hubbard, Michel, & Dehaene, 2009) showed that the cortical region in the posterior parietal cortex (homologous to monkey VIP) selectively implicated in eye movement execution is also involved in arithmetic calculation (both symbolic and non-symbolic). Indeed, a classifier trained to determine the direction of saccades, left or right, from the fMRI signal measured in PPC generalized to an arithmetic task. Its left versus right classification could be successfully used to sort out subtraction versus addition trials.

However, a non-spatial interpretation of the operational momentum sees it as the consequence of the compression and expansion of the internal representation of quantity while adding or subtracting on a compressed continuum. In this way, the neural circuit dedicated to additions and subtractions process “can first undo the internal compression of the operands, thus avoiding gross inaccuracy”, but “ if this internal decompression is inaccurate, a small compressive bias might persist, thus causing the observed momentum effect” (McCrink, Dehaene, & Dehaene-Lambertz, 2007). Neurally, it is known that the posterior parietal cortex (homologues to monkey LIP) contains neuronal populations that perform vector addition for saccade programming (Pouget, Deneve, & Duhamel, 2002). It is thus possible that it is the internal structure or connectivity of such region that is reflected by the results of the classifier and not the execution of spatial operations per se.

In summary, despite some less clear effects with still open interpretations, most of the studies reported show an intensive interplay between space and numbers in healthy subjects and brain-lesioned patients, with a typical association (SNARC effect) of small numbers with left response side, and large numbers with right response side. In particular, neglect patients exhibit an impaired number bisection which reflects representational difficulties not specific to numbers domain.

3.2 Fingers

Before the invention of symbols for numerosities, humans were unable to count and numbers were implicitly embodied in the intrinsic features of environment. Without number words, our ancestor started to manipulate numerosities by using bones, sticks of wooden, stones and so on. Among these methods, another way to count and to communicate quantity information was represented by body parts, such as toes, arms, elbows, shoulders, but also lips, nose and eyes. Nowadays body counting strategies persist in some tribes of New Guinea (e.g. Islander from Torres, Papuans etc.) and, despite the heterogeneity of their strategies, most cultures share the use of a fruitful body part, the fingers, as a sort of personal abacus always available (Ifrah, 1981).

Finger counting is not a recent discovery, but a conventional widespread technique used at every epoch (even by Sumerians, Babylonians, Maya and Aztec populations) that reached the maximum development in China allowing to count up to three billion with both hands by using combinations of phalanges and fingers (Ifrah, 1981).

Curiously, cross-linguistic evidences documented the thick relation of digital domain with the origins of some number words and verbal counting. For example, in English the word "five" shares a common root with "fingers" and "first"; alternatively in Slavic languages the word "pet" (five) derives from "pest" (hand). At present, despite the introduction of a formal knowledge of numbers represented by Arabic system, the use of fingers to count constitutes a fundamental pedagogic tool for mathematical teaching and learning during school years (Butterworth, 1999).

Some characteristics of fingers may elicit their use, parallel to counting words, to help the transition between approximate numerosity representation to exact and symbolic number knowledge (Fayol & Seron, 2005).

1. First, finger counting represents a preliminary step toward the acquisition of the number concept of bases (Butterworth, 1999). Although the use of a base-12 system would be more fruitful for number processing due to its combination with 2-3-4 and 6, historically finger counting has pressed on a base-10 system for pragmatic reasons.

2. Second, unlike language, fingers configurations offer iconic relationships with the objects they represent. Indeed fingers can represent the cardinality of a set, irrespective of the nature of the set items, and even in absence of reference objects.

3. Third, finger counting of objects requires a correspondence between words (which have time but not space) and objects (placed in the space but undifferentiated in time). This type of association is named one-to-one correspondence. These levels, temporal and spatial, elicited different types of errors in children from 3 to 6 years old: objects can be skipped (not counted), repetitively counted (counted twice) or just pointed with the finger (without receiving a word; (Fuson, 1988)).

4. Fourth, the stable order principle is reflected by the sequence of finger movements.

The extension of these principles also on fingers counting determines a process of familiarization with frequent fingers configurations allowing a direct access to their semantics (Wiese, 2003) and a link between each finger with a specific number. Coherently to this, 7 years old children extract numerical information faster for habitual fingers configurations of numbers from 2 to 9 compared with unfamiliar configurations, suggesting their holistic representation (Noel, 2005).

5. Finally, the practice with verbal and finger counting contributes to detecting some regularities at the basis of mathematical thinking (e.g. arithmetical properties) and to “digesting” numerical features such as ordinality and cardinality.

A longitudinal study on 5-6 years old children showed that finger abilities, finger discrimination and graphestesia were significant predictors of the subsequent arithmetical performance after one (Fayol, Barrouillet, & Marinthe, 1998) and three years (Marinthe, Fayol, & P., 2001). The specific contribution of finger gnosis is also confirmed by another study on school age children, in which the predictive power of finger gnosis is selective for number domain, in contrast with what predicted by other cognitive abilities, such as processing speed (Noel, 2005). On this wave, a recent study reinforcing the idea of a deep link between the finger and the number domain is a training study, showing that 8-weeks training in finger gnosis ameliorates the arithmetical outcome of first graders (Gracia-Bafalluy & Noel, 2008). In this study, children were separated into three groups: an "untrained group" with low finger gnosis abilities, a "trained group" with low finger gnosis abilities who received the training, and a "skilled group" composed of children with high scores in finger gnosis tests. Once training was concluded, the trained children exhibited an improvement in arithmetical competence, reaching levels of scores similar to skilled children.

Fingers seem to be recruited by children in relation to numerical processing or arithmetical problems. It is well documented that finger counting plays a crucial role in the acquisition of symbolic numbers, contributing to the transition from an approximate representation of numerosity to symbolic numbers (Fuson, 1988; Jordan, Kaplan, Ramineni, & Locuniak, 2008). This body parts represent a sort of pointer while enumerating, assist the verbal counting and allow us to communicate and compare numerosities. A recent study has tracked longitudinally the relation between the frequency of finger use and number combinations from kindergarten to second grade. The data

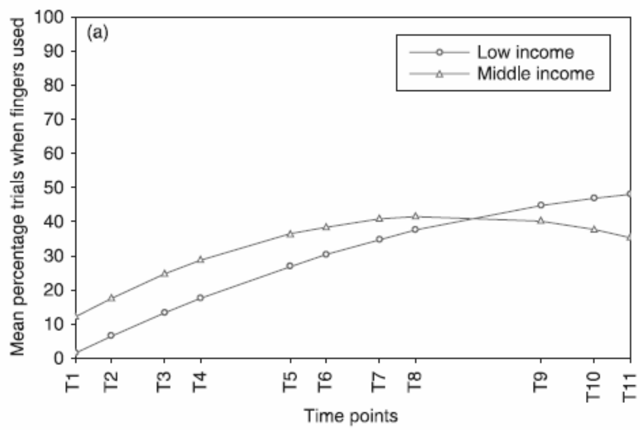


Fig. 12. Fitted growth trajectories for mean percentage of trials on which fingers were used on number combinations, by income status (from Jordan et al., 2008).

showed a quadratic trend from a significant positive correlation in kindergarten, to decreasing positive correlations in first and second grades, and to a small but significant negative correlation by the end of second grade ((Jordan, et al., 2008); Fig. 12). This indicates the relevant role on fingers use during the early steps of formal mathematical education with a natural decrement of the use of this strategy once that the arithmetical procedures are robustly consolidated.

From a functionalist point of view, the co-occurrence of deficits in calculation and fingers discrimination, as well as the interaction between finger gnosis and math in normally-developing children, arise experientially in the course of the normal development. This suggests that "the representation of numbers is not only co-located with, but also linked to, the representation of fingers" (Penner-Wilger & Anderson, 2008). Indeed, individuals who could not or did not use their fingers to represent quantities (i.e. children with Spina Bifida), have impaired finger gnosis that is co-morbid with mathematical difficulties (Banister & Tew, 1991; Barnes, Smith-Chant, & Landry, 2005). Interestingly, children with developmental coordination disorder (DCD) exhibiting a deficit in finger motor agility with a preserved finger gnosis do not show arithmetical deficits (Cermak & Larkin, 2001). This finding suggests the role of finger, in particular of digital gnosis, in the acquisition of numerical representation during the development through the creation of a hypothetical functional/developmental link between these two domains. Alternatively, however, it could also reflect that the impairment in DCD is unrelated to parietal damage.

In this way, the acquisition of fingers counting may be a process of assimilation of digital configurations, previously observed and then repeated. On the same wave, implicit representations of number-related actions may be created on the base of frequent associations between visuo-motor finger configurations and related movements (Butterworth, 1999). Moreover, other overlapping activations were found in the intraparietal sulcus bilaterally for both numerical magnitude judgments and "how many raised fingers" task on a hand picture (Thompson, Abbott, Wheaton, Syngeniotis, & Puce, 2004), suggesting that finger configurations may share common processes with symbolic numerical knowledge.

Additional indirect supports on the functional interpretation were based on recent neuroimaging data of Zago et al. (2001) who found activation of premotor area corresponding to the finger representations during single-digit multiplications, while Andres and colleagues ((Andres, Seron, & Olivier, 2005)) showed an activation of hand motor circuits during dot counting task in adults. Both these studies speculated that these findings represented an evidence of a developmental numbers-fingers trace in the brain.
Nowadays, the investigation about connections between SMG and AG with premotor areas contributes to clarify the anatomical circuits of finger movements and their relation with number domain. Anatomical proximity was found for the sites responsible for finger agnosia and acalculia in the SMG or close to the IPS (Roux, Boetto, Sacko, Chollet, & Tremoulet, 2003).

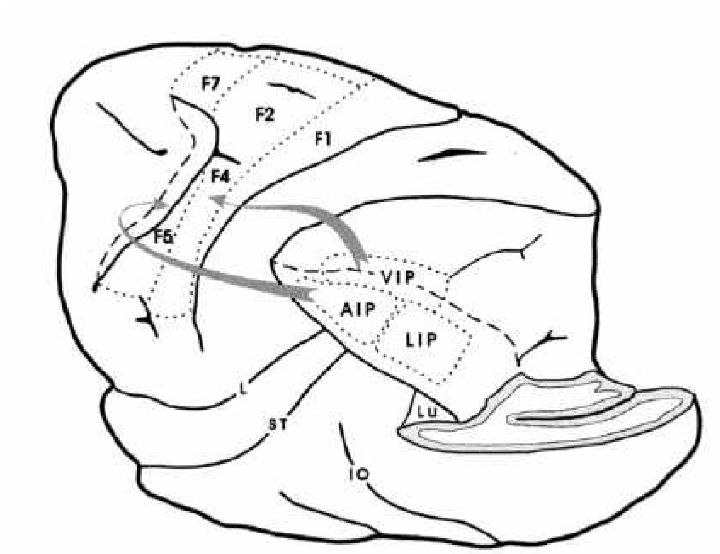


Fig. 13. Parietal projections from areas located in the lateral bank and in the fundus of the intraparietal sulcus in the macaque monkey. In order to show these areas, the intraparietal sulcus has been opened and the occipital lobe removed (from Rizzolatti et al., 1998).

Recent developed MRI techniques, such as the multiple-fiber diffusion tractography (Aron, Behrens, Smith, Frank, & Poldrack, 2007; Rusconi, Pinel, Dehaene, & Kleinschmidt, 2009), makes possible to quantify the connectivity in vivo. A parieto-premotor network (Fig. 13) was found in several studies documenting connections of premotor regions with IPS, a region sensible for number quantity, and AG, responsible of bimanual finger movements and higher-order aspects of motor control (e.g. conscious access of one's own actions; (Farrer, et al., 2008; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Pesenti, et al., 2001)). These supramarginal regions were recruited during fine control of hands and finger movements, even while gesturing (Mühlau, et al., 2005). Mirror neurons system was hypothesized to play a role for digital representation of numbers with the presence of a neural substrate for both finger movement execution and observation (Rizzolatti & Craighero, 2004).

Again, a TMS study demonstrated a concomitant disruption of performance in both numerical tasks and digital gnosis tasks after stimulation of angular gyrus, confirming the anatomo-functional contiguity of the relative regions (Rusconi, Walsh, & Butterworth, 2005). Taken together, these findings suggest that both number processing and finger knowledge seems to be grounded in neighboring, and sometimes overlapped, regions of the parietal cortex. Thus, the presence of such common maturational pathways might well predict the observed correlations, in both infants and adults.

3.3 Action: Grasping

Despite several studies that have deeply investigated the grasping abilities in both monkeys and human, just recent neuroimaging data contributed to clarify the neural circuits for grasping. Here, I describe the kinematis of grasping in humans and its neural mechanisms. Next, I summarize the current state of knowledge about the influence of numerical information on grasping actions.

The mechanic of grasping in humans is dependent on several types of object attributes. Jeannerod was the first who analyzed grasping in terms of variation of the distance between the thumb and the index finger, the so-called grip aperture. Indeed, during a reach-to-grasp action, the initial and progressive opening of the grip is followed by gradual closure in order to make contact with the objects' (Fig. 14). A fundamental process for a successful grasp implies a transformation of the intrinsic-visual features (one of the most important of which is the size) of the objects into motor actions (Jeannerod, 1984, 1997). Jeannerod identified a particular time during grasping when the thumb-index distance is the largest (maximum grip aperture, hereafter MGA) that occurs within 60-70% of reaching duration and it is significantly modulated to object size. Over and above size, other properties, such as texture, weight, fragility, size of the contact surface, also seem to influence the kinematics of grasping.

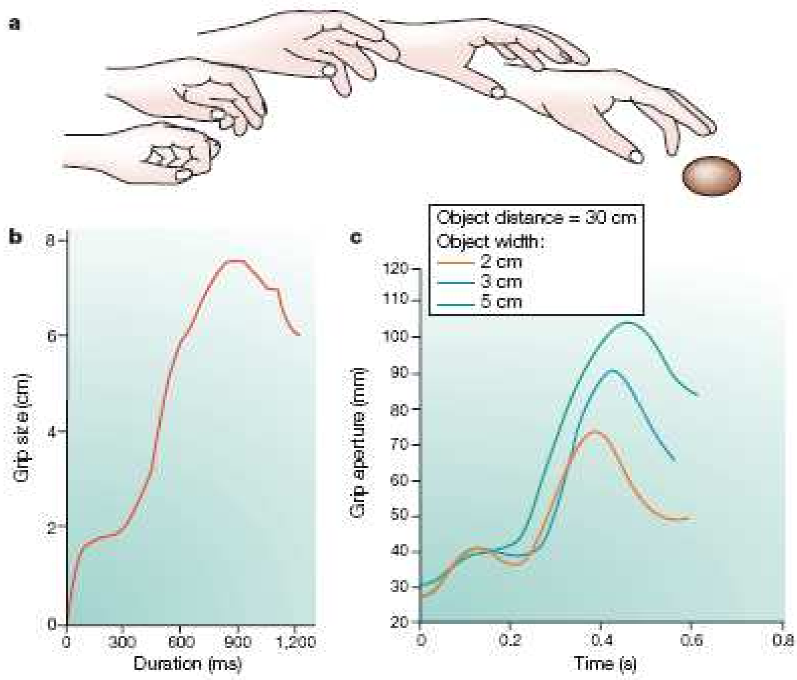


Fig. 14. Kinematics of grasping. a) The hand preshapes during its journey to the target object. b) Maximal grip aperture (distance between the tip of thumb and the tip of index finger) typically occurs within 70% of movement completion. c) Representation of traces demonstrating the scaling of maximum grip aperture with respect to object size (from Castiello, 2005).

In monkey, three specific regions are responsible of grasping: the primary motor cortex (F1), the premotor cortex (PML/F5) and the anterior intraparietal sulcus (AIP; see

(Castiello, 2005) for a review). The integrity of F1 is obviously fundamental for performing successful grasping. The role of AIP and F5 is more complex and the neural response properties of these two regions show striking similarities as well as important differences. For instance, both AIP and F5 regions code for actions related to the type of objects to be grasped during precision grip movements. By contrast, while AIP neurons are able to represent the entire action, F5 neurons are specifically involved in the selection of the patter of movement of the hand and fingers (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Rizzolatti, et al., 1998; Sakata & Taira, 1994; Sakata, Taira, Murata, & Mine, 1995). Moreover, as suggested by a study by Sakata et al. (1995; see also Murata et al., 2000), F5 selects and sends back the information regarding the selected motor command to area AIP.

Single-unit recordings tried to clarify the visual and somato-sensory contributions of grasping, and showed that AIP activity is influenced by the shape of the target object, while somato-sensory cortex classically responded later than AIP region while/after the hand touched the object (Gardner, Debowy, Ro, Ghosh, & Babu, 2002).

In humans, neuroimaging data documented the role of primary motor cortex (PMC) and posterior parietal cortex (PPC) in grasping. In comparison with touching, grasping actions increased the regional cerebral blood flow (rCBF) in wide regions of the bilateral PMC, the PPC and the prefrontal cortex PFC (Matsumura, et al., 1996). Another study confronted pointing, grasping, and matching conditions (Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997). In this last condition subjects had to compare the shape of the target objects with the previous one. While grasping-pointing contrast showed an increased activation of the anterior part of PPC, the grasping-matching contrast showed an increased activation in the cerebellum, left and medial frontal cortex and left IPS. In summary, primary motor, premotor, and AIP areas were found to be involved in grasping circuits. However, other regions may be involved, including for example prefrontal, superior parietal and cerebellar areas (Castiello, 2005).

Interestingly, some studies showed the influence of numerical magnitude on grasping actions. A recent study investigated on the electromyographic (EMG) recordings of hand muscles activity during a parity judgment task with Arabic digits. The participants had to open or close (and vice versa) their hand according to the parity status of the number (odd or even). Data showed larger grip apertures in case of large digits, and the opposite for small digits (Andres, Davare, Pesenti, Olivier, & Seron, 2004). Again, another behavioral study shows a modulation of grasping kinematics regarding an enlarged maximum grip aperture in the presence of large numbers (Lindemann, Abolafia, Girardi, & Bekkering, 2007).

In another study, participants had to judge whether they can grasp a rod lengthways between their thumb and index finger. Each presentation of the rod was anticipated by Arabic digits. When a small digit preceded the rod, participants overestimated their grasp; conversely, when a large digit preceded the rods, they underestimated their grasp. Control experiments allowed to exclude that the weight on the performance on other effect, such as perceptual factors (Badets, Andres, Di Luca, & Pesenti, 2007). Thus, since grasping requires the estimation of object size in order to determine a precise and correct hand shaping, both coding number magnitude and grasping may share common processes (Andres, et al., 2004). On this wave, Walsh proposed a model by which number magnitude and the size of objects to grasp take place in the dorsal visual pathway on the basis of a common system of magnitude (Walsh, 2003).

Anatomically, objects manipulations (Binkofski, et al., 1999), grasping (Culham, et al., 2003), reaching (Cohen & Andersen, 2002), and visual pointing (Connolly, Andersen, & Goodale, 2003) rely on the same parieto-premotor networks co-activated even during numerical tasks, such as additions, subtractions, multiplications and magnitude comparisons (Dehaene, et al., 2003).

For example, human dorsal premotor cortex (F2), an area plays a crucial role in programming and controlling proximal movements based on somatosensory information (Shen & Alexander, 1997) also is also found active in subjects performing additions, subtractions and numerical comparisons (Chochon, et al., 1999; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Menon, Rivera, White, Glover, et al., 2000). The fronto-parietal connectivity is represented by the connections between the F2 areas and the medial intraparietal areas (MIP) in the IPS region. In particular, MIP represents an important component of the parietal reach region involved in preparation, execution and monitoring of reaching movements. Thus, the MIP-F2 circuit integrates both the visual and somatosensory information to coordinate hand movements toward a visual target (Cohen & Andersen, 2002; Colby & Duhamel, 1991; Eskandar & Assad, 1999).

Furthermore, the AIP activity is invariant to spatial location of objects (Sakata, et al., 1995) and it is connected to F5 throughout the premotor ventral regions. Thus, the anterior intraparietal region (AIP) exhibits a neural selectivity while grasping objects and the AIP-F5 circuits are thought to be responsible of the object manipulations on the basis of their visual and physical features (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). The neurons of AIP can be divided into two groups: “object type” and “non-object type”. The former plays a role during object observation in absence of grasping movement, while the latter is related to the shape of handgrip, irrespective to object observation (Murata, et al., 2000). Clinically, patients with parietal lesions exhibit impairments in matching the grip aperture with object size (Jeannerod, 1986).

In summary, on the basis of neuropsychological studies, we can delineate the role of MIP-F2 and AIP-F5 circuits. On one hand, the circuit MIP-F2 seems to contribute to the coding of spatial location of objects, even during enumeration tasks.

On the other hand, the circuit AIP-F5 is crucial for shaping the handgrip to grasp objects (in line with the presence of a shared mechanism for coding number magnitude and object size (Castiello, 2005)). However, other investigations are necessary to better understand if the human homologues of AIP and MIP are located in the anterior and medial parts of the IPS coherently with the neural structure of monkey brain. On this wave, anatomical coordinates of recent neuroimaging studies suggest a partial overlap of these regions (Culham & Kanwisher, 2001; Koyama, et al., 2004; Simon, et al., 2002).

Overall, these findings suggest a clear interplay between numerical processing with other parietal functions such as spatial, digital and action processes. These relations are both explained on the basis of anatomical connections and proximity of parietal regions, but even on the basis of functional contributions mediated by educational and cultural factors (e.g. finger counting, grasping, displaying numbers on an oriented line). However some questions remain open, in particular regarding the processes that allow these interactions to emerge during childhood and the relative contribution of maturational and functional factors.

Chapter 4

CLINICAL EVIDENCES OF PARIETAL IMPAIRMENTS IN NUMBER PROCESSING

In this chapter I consider evidences coming from two clinical disorders, the developmental dyscalculia and Gerstmann's syndrome, that present deficits in both the number domain and in other domains related to parietal cortex functions. These two disorders have different origins. In the case of "dyscalculia", this deficit appears during the cognitive development from childhood, in contrast with the term "acalculia" generally used for acquired lesions determining impairments in numerical domain and calculation.

4.1 Developmental dyscalculia

Developmental dyscalculia (hereafter DD) concerns a disorder of numerical competence and arithmetical abilities in children who fail to achieve adequate proficiency in the number domain despite normal IQ, proper schooling, emotional stability, adequate social relations and motivation (Shalev & Gross-Tsur, 2001; Temple, 1992). The term "developmental dyscalculia " was introduced by Ladislav Kosc (Kosc, 1974), even if nowadays other terminologies are considered to describe this disorder on the base of selection criteria, such as "arithmetical learning disabilities", "mathematical disabilities" or "specific arithmetic learning difficulties" (Jordan, Hanich, & Kaplan, 2003a; McLean & Hitch, 1999). Recent epidemiological studies showed that this deficit afflicts approximately the 6% of school-age children (Gross-Tsur, Manor, & Shalev, 1996; Lewis, Hitch, & Walker, 1994). It was also demonstrate the co-occurrence of other disorders in DD cases: 25% of children with mathematical disabilities showed an occurrence of attention deficit hyperactivity disorder ADHD (Gross-Tsur, et al., 1996)) and roughly the 40-60% of DD children exhibit reading difficulties (Lewis, et al., 1994). The reason of these relations remains still unclear.

Even genetic studies demonstrated that 58% of monozygotic twins and 39% of dizygotic twins had developmental dyscalculia (Alarcon, DeFries, Light, & Pennington, 1997). The genetic susceptibility for DD was also found in some genetic disorders such as velo-cerdio-facial syndrome (Eliez, et al., 2001), fragile-X syndrome (Mazzocco, 2001), Turner's syndrome (Bruandet, Molko, Cohen, & Dehaene, 2004), and Down's syndromes (Paterson, 2001).

Difficulties in learning and remembering basic arithmetical facts are consistently reported in children with mathematical difficulties (Geary, 1990; 1993; Ostad, 1997). Apparently, the arithmetical facts retrieval from long-term memory remains stable across elementary ages in these children, suggesting the presence of a persistent cognitive deficit rather than a delayed development (Geary, 1993). The classical development of calculation in children concerns the transition from digital-verbal strategies to memory-based ones. Interestingly, DD children do not exhibit this shift and they persist in using immature strategies (Geary, Brown, & Samaranayake, 1991; Jordan, et al., 2003a; Ostad, 1997), showing difficulties not only in the knowledge of facts, but also in arithmetical procedures (Russell & Ginsburg, 1984). Moreover, children with mathematical difficulties showed slower verbal counting ability (e.g. counting from 45 to 65 and backwards) and lack of some counting principles, such as order irrelevance principle (Landerl, et al., 2004).

Two different streams of research have proposed alternative interpretations of this disorder: one point towards a more general cognitive deficit while the other to a specific impairment of core number system.

On one hand, the difficulties of DD children may derive from a general dysfunction affecting processing speed (Bull & Johnston, 1997), working memory (Bull & Scerif, 2001), general information retrieval (Geary, 2000), spatial disabilities (Rourke & Conway, 1997) or finger agnosia (Fayol, et al., 1998). Indeed slow RTs while naming letters of numbers (Geary, Hoard, Byrd-Craven, Nugent, & Numtee, 2007), reduced digit and visuo-spatial span (McLean & Hitch, 1999) were found in children with mathematical difficulties. On this wave, many evidences suggest the presence even of a form of "developmental Gerstmann's syndrome" in which dyscalculia is associated to a corollary of other parietal deficits such as dysgraphia, finger agnosia and right-left disorientation (Kinsbourne, 1968; PeBenito, Fisch, & Fisch, 1988).

Recently most of researches have been focused on the role of spatial abilities and finger gnosis in DD. On the basis of the presence/absence of co-morbid reading difficulties, Rourke (Rourke & Conway, 1997) suggested that the cause of this disorder was due to a lateralized hemispheric dysfunction: a left hemisphere dysfunction may be responsible of both mathematical and reading impairment. Alternatively, right hemisphere dysfunctions may be associated to specific problems in mathematics. However, some recent studies fail to find consistent differences between DD children and children with DD and reading deficits (Jordan, Hanich, & Kaplan, 2003b). Moreover, some developmental studies support the role of finger gnosis in number acquisition, showing for example that accuracy of finger gnosis at the age of 5 predicts a significant proportion of variance in arithmetical tests administered 1 year later (Fayol, et al., 1998; Noel, 2005).

On the other hand, some authors considered the DD as the result of a specific core deficit in the numerical domain (Butterworth, 1999; Dehaene, 1997). A “number defective module” or an impaired “number sense” were suggested to describe the incapacity to manipulate and understand numbers and numerical quantities. Indeed dyscalculic children showed consistent deficits in numerical task including symbolic quantities compared to age-matched controls despite their phonological processing, information retrieval, language abilities and psychomotor development were all in the normal range or above average (Landerl, et al., 2004).

Additionally, dyscalculic children exhibit a defective sensibility and a less precise internal representation for numerosity as showed by a higher Weber fraction compared to healthy counterpart (Fig. 15). Specifically, 10 years old dyscalculic children show a 5 years delay in numerical sensibility, which is similar to what found in 5 years-old non-dyscalculic children (Piazza, et al., 2010).

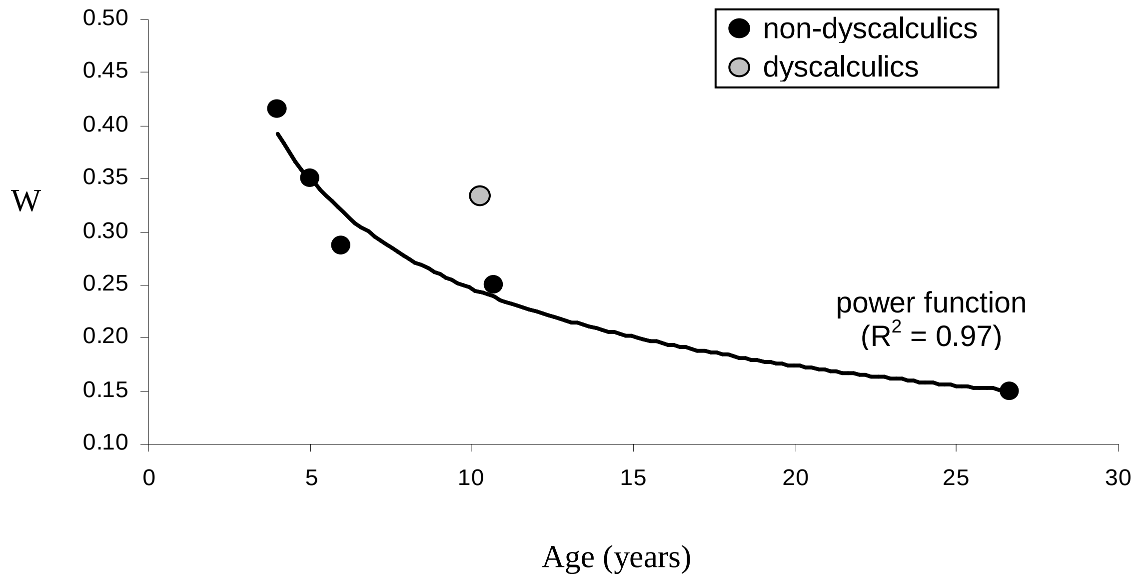


Fig. 15. Developmental trajectory of internal w. The graph represents mean w as a function of mean age and group (in black: non-dyscalculic group, in red: dyscalculic group; adapted from Piazza et al., 2010)

In a physical number line task, participants have to estimate the position of a number on a line, for example, from 0 to 100. Typically, during the development, children shifted from a logarithmic-based estimation (with small numbers compressed on the left side and big numbers on the right side) to a linear representation. Generally, this transition happens between 6 and 8 years for 0 to 100 numbers (Siegler & Booth, 2004), and between 8 and 11 years for 0 to 1000 numbers (Siegler & Opfer, 2003). Children with mathematical difficulties are less accurate than their counterparts and they used more often a logarithmic strategy rather than a linear one (Geary, et al., 2007).

All these data support the idea of a basic numerical deficit for DD, as the result of a defective number sense. Indeed, compared to age-matched controls, children with mathematical difficulties had poor performance in identifying small and large numerosities (Mandler & Shebo, 1982; Piazza, Price, Mechelli, & Butterworth, 2001), calculation (Jordan & Hanich, 2000) and placing a number on a physical line (Geary, et al., 2007).

Even neuro-anatomical and neuro-functional data suggest structural abnormalities in the dyscalculic IPS as compared to non-dyscalculic controls. For instance, adults with genetic problems (e.g. Turner's syndrome in (Molko, et al., 2003) and adolescents with very low birth weight (Isaacs, Edmonds, Lucas, & Gadian, 2001) frequently showed arithmetical difficulties, associated with reduced grey matter volume in the IPS (Isaacs, et al., 2001; Rotzer, et al., 2008). Functionally, fMRI studies showed a lack of IPS modulation during non-symbolic comparison and symbolic comparison in children with mathematical difficulties which was interpreted as either a weaker parietal representation of number magnitude, or a limited access to numerical information (Price, Holloway, Rasanen, Vesterinen, & Ansari, 2007; Soltesz, Szucs, Dekany, Markus, & Csepe, 2007).

The interpretations regarding the etiology of developmental dyscalculia are multiple. On one hand, a "core deficit" idea was suggested by those studies that have reveal a defective number sense, impaired transition from a non-symbolic to a symbolic representation and structural/functional abnormalities of IPS in dyscalculic children. On the other hand, scientific literature shows the presence of variegated sub-types of dyscalculia based on a defective verbal symbolic representation (deficits in learning and retrieving arithmetical facts and counting sequence), executive dysfunctions (inefficient strategies and arithmetical procedures) or impaired spatial attention (defective subitizing skills).

4.2 Gerstmann's syndrome

Acalculia represents one of the tetrad of symptoms that characterize the syndrome described by the neurologist Gerstmann (Gerstmann, 1927). The other deficits consist in left-right disorientation, finger agnosia and agraphia. This syndrome was initially found in patients with lesions of the left parietal cortex, precisely of the AG (Butterworth, 1999; J. Gerstmann, 1940, 1957). Subdural stimulations of AG produce the emerging of all of the four characteristic deficits, alternatively called as the "angular syndrome" (Mazzoni, Pardossi, Cantini, Giorgetti, & Arena, 1990). Gerstmann's clinical interpretation was based on the presence of a selective disorder of the hand area and its body schema representation, "the finger sense". A cascade of impairments was associated by observing that: calculation and fingers share the ten-base system, hands are used as reference of left-right orientation, and writing implies a good finger praxia. In particular, acalculia may emerge as the result of impossibility to relate numbers and fingers by using finger counting strategies (J. Gerstmann, 1957).

Here, I briefly report the main characteristics of each symptom:

Finger gnosis is frequently impaired in patients with Gerstmann's syndrome especially in finger naming and verbal identification (Jung, et al., 2001; Moore, Saver, Johnson, & Romero, 1991; Tucha, Steup, Smely, & Lange, 1997). In particular, the accuracy decreases in case of lack of visual control while performing the task (Mayer, et al., 1999; Tucha, et al., 1997). This deficit afflicts not only the own fingers but also the identification of the corresponding fingers of the examiner's hand (Carota, Di Pietro, Ptak, Poglia, & Schnider, 2004; Mayer, et al., 1999).

Even the representational structure of the hand seems disrupted with the inability to know the number of fingers between two fingers touched by the examiner. Higher error rates were documented for index, middle and ring fingers compared with thumb and little finger

(Mayer, et al., 1999; Mazzoni, et al., 1990). In several cases, a toe agnosia was described suggesting the idea of a more general disorder in the body schema (Tucha, et al., 1997).

Left-right confusion emerges while asking to identify specific body parts. Patients make more errors in absence of visual control (Levine, Mani, & Calvanio, 1988; Mayer, et al., 1999; Mazzoni, et al., 1990) or when asked to point the examiner's body, (Carota, et al., 2004; Tucha, et al., 1997) especially if he/she faces the patients. Even crossed commands (e.g. "touch your left eye with your right hand") were executed less precisely than uncrossed ones (Jung, et al., 2001; Mayer, et al., 1999)).

Two main types of peripheral deficit in handwriting (**agraphia**) afflict these patients. On one hand, the writing can be slow and illegible with misaligned and scrawled letters (Jung, et al., 2001), in particular for cursive letters (Mazzoni, et al., 1990). This deficit may sometimes afflict also the drawing of geometrical shapes (Levine, et al., 1988), taking the form of apraxic agraphia, as the result of a disruption in motor graphic patterns in memory (Zesiger, Martory, & Mayer, 1997). On the other hand, letters are omitted, repeated or, more often, substituted with other similar letters, e.g. p-b, q-d (Carota, et al., 2004) that shared the same motor segments. This deficit may reflect impairments at the allographic level where letter identity is accessed from motor production, as also confirmed by the lack in the visual imagery for letter forms (Rapp & Caramazza, 1992).

Acalculia constitutes the most variegated deficit among the tetrad of symptoms.
Syntactic difficulties frequently characterize the comprehension and production of Arabic numbers (Kinsbourne, 1968; Martory, et al., 2003), especially while reading three-digits numbers versus one- or two- digits ones (Varney, 1984). Even syntactical relationship among number words can be impaired (Martory, et al., 2003).
The spatial disorganization of digits often induces errors in writing calculation, suggesting the presence of a spatial acalculia (Strub & Geschwind, 1974). The effects of this syndrome on arithmetic and calculation are more debated.

In accordance with the interpretation of Gerstmann, this syndrome should involve basic arithmetical difficulties due to their intimate link with the finger counting in childhood (J. Gerstmann, 1940).

Alternatively, Dehaene and colleagues (2003) predict that number processing and complex operation should be disrupted in contrast with arithmetical facts (e.g. small additions or multiplications) retrieval relying on language areas. Moreover, the presence of deficits in arithmetical facts in some patients can be imputed to larger lesions involving the AG, a fundamental area for the verbal processing of numbers. Probably, verbal processing does not represent the core of the problem, considering that those patients did not exhibit aphasic disorders. An extensive study contributed to clarify the consequences of angular lesion, concerning impaired simple and complex calculation and semantic knowledge of numbers (Martory, et al., 2003), indeed patients are unable to place numbers on a straight line and to recite numbers series (Cipolotti, Butterworth, & Denes, 1991; Delazer & Benke, 1997; Varney, 1984).

Although the existence of this syndrome was occasionally questioned (Poeck & Orgass, 1966) and despite an uncertain localization on cortical or subcortical substrates, the left angular gyrus lesion may represent a sufficient condition for the syndrome onset. Not surprisingly, angular gyrus seems to be responsible for the initialization of bimanual finger movements (Roux, et al., 2003), which are thought to be typically used during finger counting.

Furthermore, other non- Gerstmann deficits were reported in clinical studies, together with some heterogeneity in the neural localization. Extensive studies on brain-damaged patients documented the presence of other symptoms, such as constructional apraxia and reading difficulties that correlated with the typical tetrad of Gerstmann's syndrome (Kinsbourne, 1968). In particular, the agnosia, left-right confusion, agraphia and acalculia were mostly associated to aphasic patients than to non-aphasic ones (Poeck & Orgass, 1966; Poeck & Orgass, 1975)). Thus, these cardinal symptoms may be the consequence of language disorder and verbal comprehension of the task contents. However this hypothesis was ruled out by two studies (Strub & Geschwind, 1974) where the majority of Gerstmann patients did not exhibit language disorders.

In this view, Roeltgen and colleagues (Roeltgen, Sevush, & Heilman, 1983) firstly asserted that the territory of the left AG and SMG were responsible of the syndrome in case of patients without aphasia, normal IQ and preserved memory, spatial processing and constructional apraxia. Again, TMS over the left AG in adults is associated to impairments in both numerical and digital tasks (Rusconi, et al., 2005). Taken together, these data support the idea that the neural territory of the left AG represents the sufficient condition for emerging the syndrome.

Recently, Dehaene et al. (2003) suggest another interpretation of the syndrome. The co-occurrence of the tetrad of symptoms was the result of anatomical proximities of the regions involved in calculation, manual tasks and visuo-spatial processing in the IPS.

All these regions are irrigated by the middle cerebral territory. Thus, the common vascularisation determines a conjunction of the deficits of different parietal subregions.

However this explanation does not account clinical cases where IPS is not involved in the etiology of the syndrome, such as in patients with non-angular lesions, such as in hiv-1 encephalopathy (Cirelli, Ciardi, Salotti, & Rossi, 1994) and diffuse cerebral atrophy (Jung, et al., 2001). This non-converging data may suggest the idea of a wider network in the AG of cortical and subcortial regions responsible of the Gerstmann’s syndrome. To address this point, the incidence of Gerstmann’s deficits in Alzheimer patients was considered. Surprisingly the Gerstmann’s symptoms did not cluster together during the cortical degeneration supporting the idea of distinct neural networks for each function in the AG (Jung, et al., 2001).

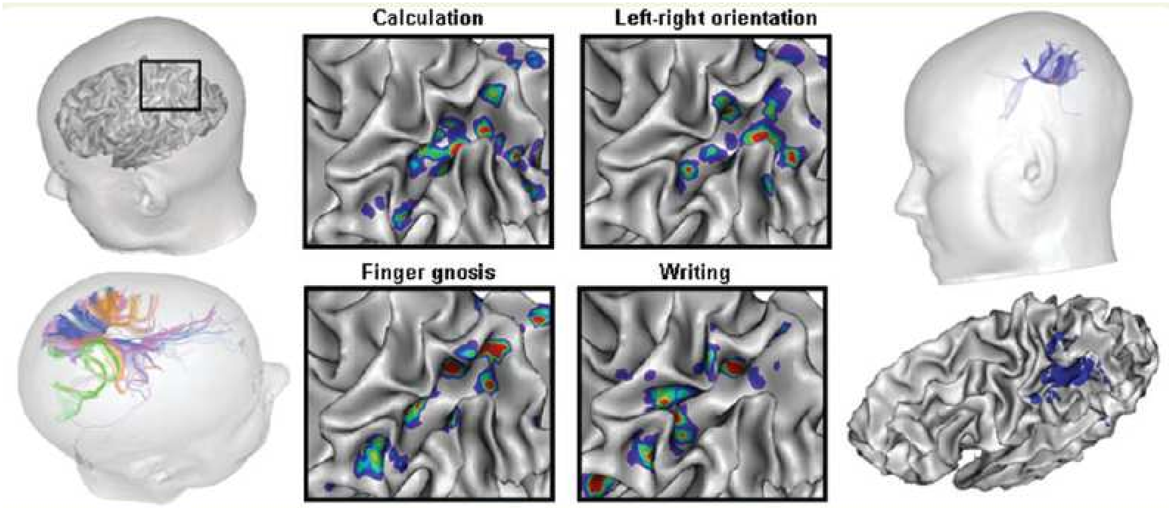


Fig. 16. Functional and structural imaging results of left parietal lobe organization in the human brain. The upper left-hand picture provides a rendering of the left hemisphere cortical surface for reference. The four middle panels show functional activation results superimposed onto a left parietal zoom of this surface rendering. Activations are from experiments separately probing the four domains as labelled in the figure. These different task-related activation zones do not show significant overlap across all four domains. Taking these activation foci as seeding points permits tracking fibres connected with these cortical zones, as shown in the lower left-hand panel by different colours for the different domains of the tetrad. The upper right-hand panel tracks fibres from a bottleneck in parietal white matter and the lower right-hand panel shows the disconnection effect from such a 'virtual' lesion on the cortical surface (from Rusconi et al., 2009).

More recently, Rusconi and colleagues ((Rusconi, et al., 2009); Fig. 16) clarified the organization of the fiber tracts of the classical tetrad by using fMRI with high spatial resolution. Curiously, a great subcortical overlap was found among fiber bundles activated for numerical, spatial, writing and digital tasks. Their interpretation consists in considering the Gerstmann's pure forms a sort of "syndrome by disconnection". In other terms, its cause is not determined by a lesion to a shared cortical substrate, but due to an intraparietal disconnection between segregated cortical regions in parietal cortex to their related regions in the frontal cortex. Thus, Gerstmann's syndromes more likely emerge after damage to subcortical white matter region.

Together, developmental dyscalculia and Gerstmann's syndrome represent the main clinical evidences regarding the role of abnormal parietal structures and functions in the etiology of numerical deficits. Interestingly, both there pathologies showed a tight relation of number cognition with other parietal domains involved in the processing of space, finger representation and action, based on the anatomical proximities among these regions within the parietal cortex.

EXPERIMENTAL SECTION

Chapter 5
EXPERIMENTAL QUESTIONS

The present thesis investigates the developmental trajectories of several both number-related and non-number related parietal functions during the preschool years, with the aim of identifying clusters of associations across functions and their relative role as functional predictors of arithmetical abilities during the first year of primary school. In particular, within the number domain, we were interested in better understanding the relation between pre-existing non-symbolic quantity system and the culturally mediated symbolic number system. Second, we were interested in measuring the relative contributions of both quantity-related and non quantity related functions to the development of arithmetical skills.

Developmental trajectories of the pre-symbolic and symbolic numerical systems

In humans, two different systems can be recruited for the manipulation of numerical information. On one hand, an innate, approximate and non-symbolic system for numerosity represents the natural sensitivity for numerical quantity shared by both humans and non-human animals. On the other hand, an exact and symbolic system for number is progressively acquired during development on the basis of cultural factors, such as mathematical education at school. Previous research has suggested an interplay across these two systems. Here, we investigated the maturation of these systems in preschool age and capitalize on the study of their relative developmental trajectories to better understand the nature of their interplay. The questions were: Can the inter-individual difference between children in these two domains reveal something about the development of the relation between the pre-symbolic and the symbolic system? Can the analysis of the development of such relation reveal something about the direction of the causality link between the pre-symbolic and the symbolic systems?

Contributions of spatial, digital and sensory-motor processes to number processing

Studies on children and adults showed interactions of numerical abilities with other parietal non-numerical domains, such as finger gnosis, visuo-spatial processing and sensory-motor abilities. These non-numerical functions are thought to be relevant for the acquisition of an exact and abstract concept of number and for arithmetical procedures. Here, we investigated the pattern of correlations across these parietal functions in preschoolers, in order to isolate functional clusters that could be more safely interpreted as pre-determined (or pre-existing) associations vs. culturally mediated associations due to explicit training. For comparison, we also considered the associations among all these parietal functions in adulthood after a long period of familiarization and practice with numbers, in order to see whether the adult pattern of functional correlations showed similar functional clusterization and cross-domain interactions as well as in children.

Predictive power for arithmetical achievement

The last section of the present thesis is dedicated to investigate the predictive power of both quantity and non-quantity related (i.e. space, finger gnosis, grasping abilities) factors measured in preschool, for arithmetical achievement one year later, at the end of the first year of primary school. In the literature only few studies have adopted a longitudinal and extensive approach to explore which cognitive functions can predict the subsequent arithmetical performance, especially during the transition from kindergarten to school. Our aim was to determine whether and which quantity or non quantity-related function, measured during the last year of kindergarten, can predict the subsequent number processing and the arithmetical outcome 1 year later, at the end of the first year of primary school.

Chapter 6

NUMBER ACUITY CLUSTERIZES WITH OTHER PARIETAL FUNCTIONS IN PRESCHOOLERS AND ADULTS

6.1 ABSTRACT

Parietal cortex is the major component of the dorsal stream supporting several different functions mainly involved in perception for action. In particular, the integrity of parietal cortex is fundamental for visuo-spatial, sensory-motor and quantity-related skills. In numerical cognition, during development, all these functions are thought to play an important role, especially in the construction of the concepts of exact numbers and their governing principles. Previous developmental research has focused on a restricted number of functions (mainly sensitivity to non-symbolic numerical quantity and finger gnosis in school age children). This study explores an extensive set of parietal (presymbolic and symbolic numerical abilities, finger gnosis, visuo-spatial span, grasping abilities) as well as ventral (faces and objects recognition) functions in a large sample of preschoolers and of human adults, with the aim of determining clusters of correlations among these functions and their development during life-span.

Firstly, our data show a general improvement in all tasks during development between 3 and 6 years of age. In preschoolers, our findings suggest that anatomical proximity is a strong predictor of behavioural correlations across cognitive functions with a clear segregation of dorsal and ventral functions. In contrast, data from adults reveal a higher degree of specialization within parietal functions and the presence of some dorso-ventral functional correlations. Concerning the relation between pre-symbolic and symbolic numerical abilities, our results show that the two start from a general independency in preschool age to a close relation in adulthood. Finally, our data also point towards a particularly strong correlation between numerosity and finger processing, which, being strongest in young children, allows us to conclude for the presence of important anatomo-

functional links between the two domains in childhood even prior to the formal use of procedure (like finger counting) that may eventually strengthen this link.

6.2 INTRODUCTION

Parietal cortex is the major component of the dorsal stream supporting several different functions mainly involved in perception for action (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). Data from macaque monkeys and humans (based on cytoarchitectonic, patterns of connectivity and neural response properties) converge in revealing a complex anatomo-functional parcellisation of parietal cortex in sub-regions.

This parcellisation is organized along a caudal-to-rostral functional gradient by which information is coded with a systematic transformation from sensory to effector-specific properties. Caudal regions (LIP in monkeys and its human homologue hLIP) are involved in the control of eye movements and of attention in the *extrapersonal* space, code information mainly unimodally (either visual or auditory) and in eye-centered reference frames (Sereno et al., 2002). Medial regions (VIP and hVIP) are involved in complex co-ordinate transformation and multi-modal integration crucial in motion and quantity processing (Bremmer, et al., 2001; Duhamel, Colby, & Goldberg, 1992; Piazza & Dehaene, 2004) (Nieder & Miller, 2003) and the control of attention in *peripersonal* space (Colby & Goldberg, 1999). In these regions neural responses are massively multimodal (audio-visual, visuo-tactile, visuo-vestibular) (Grefkes, et al., 2004; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005) and mainly centered on head co-ordinates (Vallar, Bottini, & Paulesu, 2003) (Duhamel, Colby, & Goldberg, 1998). Finally, more anterior regions (AIP) are involved in programming hand-related actions and particularly *grasping*, code space in hand-centered co-ordinates (Iwamura, Iriki, & Tanaka, 1994), and mainly proprioceptive and visuo-motor information, thus tuned to the motor-component of hand-actions (Bodegard, Geyer, Grefkes, Zilles, & Roland, 2001; Bushara, et al., 1999) (Jancke, Kleinschmidt, Mirzazade, Shah, & Freund, 2001).

Whether this pattern of anatomo-functional specialization already exists at birth or whether and to what extent it develops as a function of experience and/or brain maturation is still unknown. However, it is well known that during the first several years of life the human brain undergoes a long process of maturation. In particular, in the case of parietal cortex, maturation follows a cubic-like developmental trajectory, with a progressive increase in cortical thickness during infancy, reaching its peak around 10 years of age, declining during adolescence, and stabilizing in adulthood (Gogtay, et al., 2004; Shaw, et al., 2008). A similar pattern of synaptic pruning and of increased myelinization of cortico-cortical associative fibers is observed during the first 10 years of life (Huttenlocher, 1990) (Yakovlev & Lecours, 1967). Given that maturation implies at least some degree of functional specialization it is highly probable that the pattern of functional specialization observed in adults is laid down within the 10 initial years after birth.

Among the different parietal cortex functions reviewed above, in this study we were particularly interested in quantity and number-related functions. Number processing has been associated to parietal cortex by a vast number of studies hinging upon different methodologies, from neuropsychology to functional imaging. Parietal cortex is the major site for both acquired and developmental dyscalculia, a disability that selectively affects number processing and calculation (Rotzer, et al., 2008; Temple, 1992), and it is systematically activated in subjects performing mental arithmetic tasks as well as many other number-related task (e.g. comparing numbers, detecting numbers, judging the parity of numbers; for a review, see (Dehaene, et al., 2003)).

Moreover, a system for extracting and internally manipulation approximate non-symbolic numerical quantities (i.e. the number of elements in a collection) is based on neural populations localized precisely around the medial horizontal segment of the intraparietal sulcus (Knops, et al., 2009; Piazza, et al., 2004; Venkatraman, et al., 2005). This system is evolutionary ancient, shared with other animals (Dehaene, 1997), and deployed by humans spontaneously at birth (Izard, et al., 2009). This system is considered as one of the most basic building blocks on which culturally mediated knowledge of symbolic numbers builds upon. Indeed, its “acuity” (the precision of the numerosity estimate) is an excellent predictor of the success in arithmetical tasks in children and adolescents (Gilmore, et al., 2007; Halberda, et al., 2008), and also predicts the severity of the dyscalculic disease in developmental dyscalculia (Piazza, et al., 2010).

Over and above this basic pre-symbolic numerical ability, however, a series of other cognitive functions have been seen as crucial in shaping the development of numeracy. These functions comprise finger gnosis, fine visuo-motor co-ordination, and visuo-spatial abilities. Finger gnosis, for example (defined as the intact internal schema of one own fingers), also successfully predicts mathematical achievements in first and second grade children (Fayol, et al., 1998; Marinthe, et al., 2001). As numerosity discrimination ability, it is also often impaired in children with dyscalculia (Benson & Geschwind, 1970). Finally, the strong association between fingers and numbers is also reflected in automatic number-finger associations in human adults (Andres, Seron, & Oliver, 2007; Di Luca, et al., 2006; Sato, Cattaneo, Rizzolatti, & Gallese, 2007).

A secondary, even thought not less important aspect of the number-finger interaction is the fine visuo-motor co-ordination and control of finger posture during grasping movements. Planning to grasp an object depends to a large extent on magnitude processing, since it requires a translation of physical magnitude information (i.e., object size) into an appropriate grip aperture. Indeed, considerable behavioral evidences indicate a tight and automatic link between number and the and size of grip aperture during grasping in adult subjects (Andres, et al., 2004; Andres, et al., 2007; Lindemann, et al., 2007; Moretto & di Pellegrino, 2008; Song & Nakayama, 2008). Little is known on the relation between grasping abilities and mathematical abilities in children. However, it is well known that impairments in grasping abilities, very common for example in dyspraxia, are also quite often associated with calculation disabilities, even in cases of overall preserved general intelligence (Yeo, 2003).

Finally, another function that seems to be of substantial relevance in developing of mathematical skills seems to be the ability to internally represent visuo-spatial information. During childhood, visuo-spatial span (as measured by variants of the Corsi test) represents another good predictor of numerical performance in children (De Smedt, et al., 2009;

Holmes, Adams, & Hamilton, 2008; Rasmussen & Bisanz, 2005). Visuo-spatial abilities are also often severely impaired in developmental dyscalculia (for a review, see (Wilson & Dehaene, 2007)). Finally, in adults, several types of number-space interactions occur (Hubbard, et al., 2005).

It is possible that the parietal cortex subregions specialized for the representation of fingers and their control during grasping, the representation of spatial information, and the representation of numerical quantity, are strongly interconnected and undergo common developmental trajectories due to anatomical proximity(Penner-Wilger & Anderson, 2008) (Dehaene, 2009). However, it is also possible that the implementation of cultural practices such as finger counting and ordering numbers on an oriented number-line greatly influence the functional associations between these domains.

To date it is not possible to disentangle the role of culture-based training from the role of anatomical proximity in the emergence of these associations because most studies reporting interactions between number and other parietal functions either test adults or children in the initial primary school years, in a period where children undergo intensive training specifically aimed at creating links across these domains. Notably, during the first years of school, the intensive use of new procedures (i.e. finger-counting, finger use in simple arithmetical operations, number-to-space association with the use of the number line) may contribute to create or reinforce the associations between number and fingers and number and space, thus confounding what is due to common neuro-functional maturational processes from the effect of learning procedures. In order to verify the presence of genuine (non-culturally driven) associations among functions prior to formal training one needs to test younger children who did not yet undergo formal teaching aiming at boosting these associations.

The present study investigates a large set of parietal functions in preschoolers, traces and compares their developmental trajectories, and capitalizes on the inter-individual differences to isolate clusters of correlations among functions indicating the presence of early connections prior to school-based training of associations across domains. We also tested some non-parietal functions (face and object processing) to test the hypothesis that dorsal and ventral streams undergo different developmental trajectories.

6.3 METHODS

6.3.1 Participants

We obtained a signed informed consent from the parents or the legal representatives of 109 kindergarteners from two schools in Rovereto, Italy, and from 36 adults without neurological or psychiatric disorders, and normal or corrected-to-normal vision. The data from 15 children were not included in the analysis either because they did not speak Italian sufficiently to understand the tasks instructions (N=7), or did not complete any of the proposed task (N=8). The final sample consisted of 94 children (mean age= 56±11 months, range = 37-76 months; right-handed= 91.5 %; males= 54.3 %) and 36 adults (mean age= 27 years, range= 20-45; right-handed= 91.7%; males=50%). The study was approved by the local ethical committee.

6.3.2 General testing procedure

Children were tested in a quiet room in the school during school hours. They carried out 6 tests in two separate sessions (mean inter-session time: 6 days), each lasting for about 30 minutes. The tasks-order randomly varied across child with the only constraints that the SPAN test was always the first test proposed during the first session because it did not involve unfamiliar external devices other then the wooden colored blocks and because it required continuous interaction with the experimenter. Children could take breaks between each task and anytime during testing, upon request. For the PC-based tasks (based on MATLAB psychotoolbox – MathWorks MA:USA software for both stimuli presentation and response recording), children were seated approximately 40 cm from a 15-inch LCD monitor.

Adults were tested in a quiet room in the Laboratory of Experimental Psychology of the Center for Mind/Brain Center in Rovereto, Italy. All tests were performed, in randomized order, in one session lasting approximately 1 hour.

Numerosity comparison

Subjects were presented with pairs of arrays of dots were on a computer screen. Their task was to choose the array containing more dots. Children made their choice by pointing to the chosen array, while adults pressed the button corresponding to the chosen array. Every trial started with a fixation cross for 1 sec. followed by the appearance of two lateralized arrays. Subjects were given an unlimited amount of time to produce their response, but they were asked not to perform exact counting.

The number of dots of the two arrays was varied in order to modulate the comparison difficulty. One of the two arrays always included 16 or 32 dots (n1), while the other could contain 5-9-12-15-17-20-23-27 dots (or 10-18-24-30-34-40-46-54 dots respectively, n2). Each pair was repeated 8 times for children and 12 times for adults, for a total of 128 trials for children and 192 for adults. Dot arrays were generated by a computerized program controlling the effect of dot size and array area. For each pair, half of the trials were controlled for dots size and the other half for dots area, so that response to number could not be attributed to any single non-numerical visuo-spatial parameter. Before starting the experiment subjects performed 8 practice trials. The trial order was randomized both within and across subjects.

Symbolic number comparison

This task was the symbolic version of the previous task. Subjects had to choose the larger among two two-digits numbers, which were presented in the auditory modality in children (as most of them could not read Arabic digits –e.g., the experimenter would say "what is the largest number between 16 and 25?") and in the visual modality in adults (on a computer screen). The ratio between the numbers of dots in the two arrays spanned 4 values: 0.4, 0.5, 0.6, or 0.8, while for adults we used the same ratios and digits used in the numerosity comparison task. Additionally, only for children, we introduced eight supplementary digit pairs (16-11, 40-15, 60-31, 30-12, 28-22, 23-18, 20-10, 21-13), with the same ratio as the "standard pairs" but controlled for word length. Children performed 24 trials, whereby each digit pair was presented only once. Indeed, in order to keep the experiment short the order of the numbers (large number first or second) was not counterbalanced but randomly assigned to each trial. This was not the case for adults, who performed a total of 256 trials (each pair being repeated eight times). The trial order was randomized both within and across subjects.

Fingers gnosis

Subjects sat on a chair in front of a table, and were asked to place their dominant hand (DH), palm down on the table, in front of the experimenter. The experimenter then covered the subjects' DH to their sight by putting a white vertical panel at the level of their wrist. Then the experimenter started the stimulation, which consisted in touching either one or two fingers (in sequence). The experimenter then removed the panel and asked the subject to point to the finger(s) that were previously touched, maintaining the same order. Children performed 10 trials for the one finger condition (each finger was stimulated twice) and 10 for the two fingers conditions (all 10 finger pairs were stimulated once), while for adults we also added a three-fingers condition (10 additional trials) to avoid ceiling effects. The trial order was randomized both within and across subjects.

Visuo-spatial SPAN

In order to measure visuo-spatial short term memory abilities we used a standard measure of capacity (SPAN) using the Corsi block-tapping task (Corsi, 1972). The test material consisted of nine blue wooden blocks (40×40×18 mm) mounted on a white-colored board (420×300 mm). The digits 1 to 9 were printed on one side of the blocks, visible to the experimenter only. Subjects, set in front of the examiner, observed him/her tapping the blocks with his/her index finger, at a rate of approximately 1 block per second. The experiment always started with a sequence of two blocks. Once the experimenter terminated the sequence the subjects was requested to repeat the action using his/her index finger. Subjects were given 3 trials for each number of touched blocks. If the subject succeeded on 2 out of 3 trials, the experimenter increased the number of touched blocks by a unit. The test was terminated if the subject failed to reproduce at least 2 sequences (out of

3) of a given number. Only complete and correct sequences were scored as correct; and self-corrections were allowed.

Grasping

We measured grip aperture during grasping objects of different sizes using the Zebris CMS20S system (ZEBRIS, Medizintechnik-GmbH, Germany), which is based on the travel time measurement of ultrasonic pulses (40 kHz) transmitted by miniature transmitters (markers: 10 x 8 mm, 1 g) to three microphones built into the measuring sensor. It gives spatial coordinates in the 3-D space with a resolution of 1/10 mm.

The subject sat in front of a table with the two Zebris markers wrapped around the tip of the thumb and index fingers of his/her DH by a soft leather stripe. Their task consisted in grasping a wooden cylinder that was placed 13 cm away in front of them. They started from a "neutral" position, with their hand lying on the table close to them, and with the index-thumb distance of 0 cm. After the experimenter's verbal input ("Go"), the children grasped the cylinder, put it in a box located on the table on the opposite side of the DH (cylinder-box distance of about 25 cm) and, then returned to the "neutral" position. Cylinders were of two different sizes (3.1 and 5.1 cm diameter). Subjects performed 10 trials with each cylinder size, in random order, for a total of 20 trials.

Faces and objects recognition

This experiment comprises a study phase and a test phase. During the study phase, children were shown 16 gray scale images (7 x 7 cm), representing 8 different Caucasian male faces and 8 novel 3-D objects, one after the other, for 10 seconds each (images courtesy of (Golarai, et al., 2007)). Some second after the end of the study phase, the test phase started. In this phase, the children were asked to classify 32 images (consisting of 16 old and 16 new) as already seen or not. For adults, in order to avoid ceiling effects, there were 28 stimuli in the study phase (14 faces and 14 objects) and 56 in the test phase.

6.4 RESULTS

The results from children and adults were analyzed separately.

6.4.1 Experiment 1A: CHILDREN

For each task, we first describe the average results and main effects, and then we report their developmental trajectory during the studies age period (from 3 to 6 years of age). Finally, we describe the interactions among tasks using correlations and cluster analysis.

Numerosity comparison

Overall, “larger” responses to n2 followed a classic sigmoid curve. The slope was approximately twice as large for trials where the stimuli were twice larger, replicating earlier findings of Weber’s law for numbers (Figures 1A). The curves became parallel when plotted on a log scale (Figures 1B), and super-imposable once expressed as a function of the log ratio of the two numbers (Figures 1C). Across age ranges, the slope of the central portion of the sigmoid became steeper, indicating a progressive refinement in the internal representation of numerosity during the life-span (compare the columns in figure 1). On the basis of these accuracy distributions we then estimated the internal Weber fraction (thereafter w), a measure of the precision of the underlying numerical representation. This measure corresponds to the standard deviation of the estimated Gaussian distribution (on a log scale) of the internal representation of numerosity that generates the observed performance (a method previously described in the Supplemental Data from (Piazza, et al., 2004), and also used in (Halberda & Feigenson, 2008)). We first fitted the individual subjects’ data to exclude subjects with too variable (quasi-random) response distributions. 10 out of 94 children were excluded, either because the fitting procedure using to derive w did not converge (N=7), or the R^2 of the fit was very low (<.2; N=3). The data from the remaining 84 children was used to calculate the average w, which was equal to 0.71 (model fit: $R^2 = 0.96$), a value twice as large as the one reported in previous studies on children of the same age range (Halberda & Feigenson, 2008; Piazza & Izard, 2009).

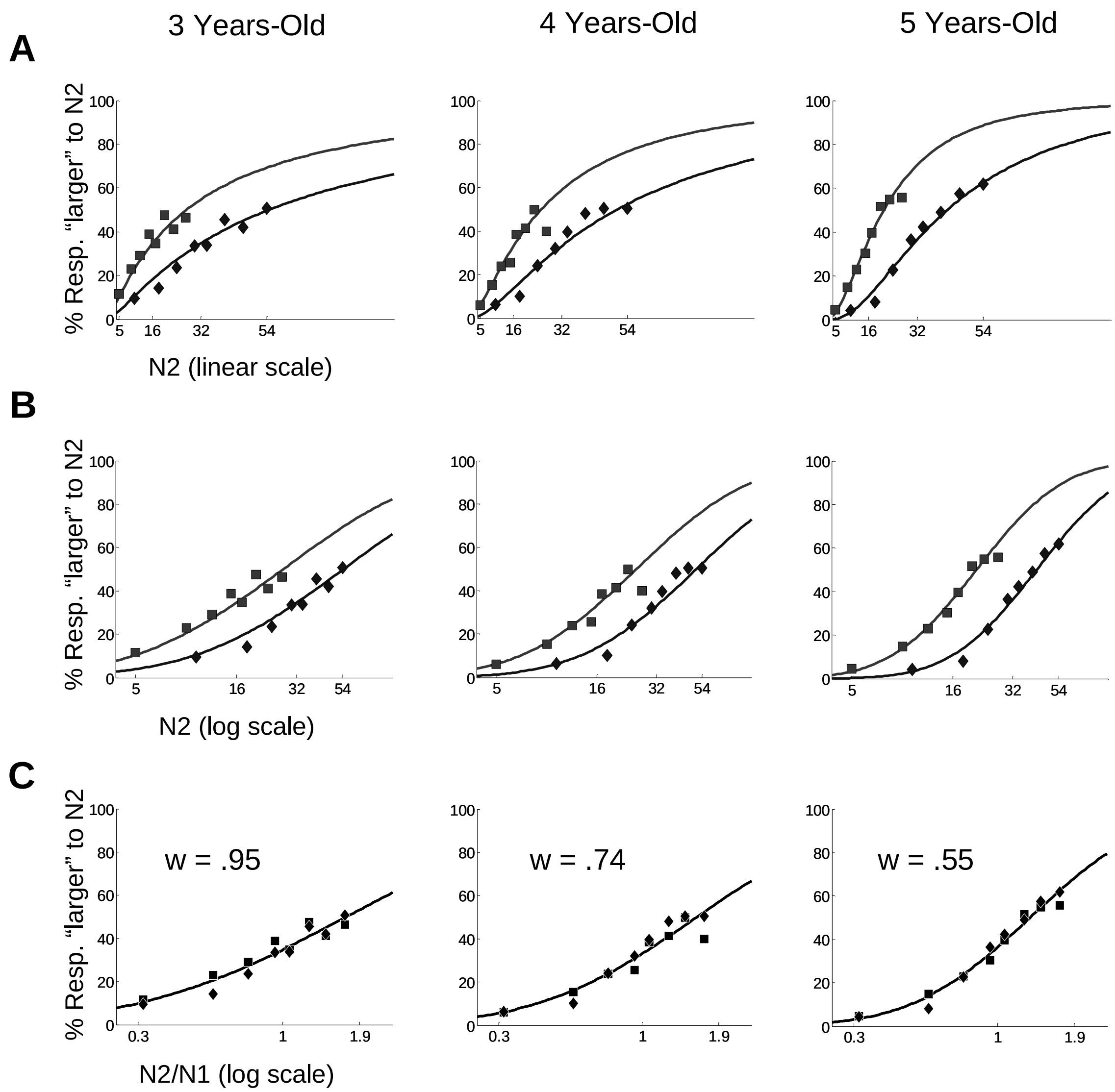


Fig. 1. Performance in the numerosity comparison task as a function of age group. Graphs represent the proportion of the trials in which participants responded that n2 was more numerous than n1. Performance is plotted as a function of n1 on a linear scale (A), logarithmic scale (B) and on the logarithm of the numerical ratio (C; see Piazza et al., 2004)

Close inspection of response distributions indicated that children made more errors that what expected on the basis of previous reported data in particular when the total occupied area was kept constant across numerosities, thus when the individual dot size increased with number (see figure 2A), and especially in those conditions where n2 was larger than n1 and. To address this effect statistically, we run a mixed 3x8x2 ANOVA on the accuracy with age group as between-subjects factor and the variables ratio (8 levels) and control type (2 levels, area vs. size) as within-subjects factors. Results showed a main effect of age group [$F(2,91)=16.4$, $p<.000$], ratio [$F(7,637)=270.1$, $p<.000$] and control type [$F(1,91)=397.5$, $p<.000$]. As expected, ratio was modulated by age group [$F(14,637)=2.9$, $p<.000$], and control-type [$F(7,637)=145.0$, $p<.000$]: in larger N2/N1 ratios young children made more errors then older. Ratio was also modulated by control-type: errors in large ratios errors were especially large for trials controlled for area. This effect did not vary as a function of age group (as evident in no triple interaction age*ratio*control-type). This pattern of results suggests that for the present stimuli and setting children were often misled by the size of the individual dots, selecting the array where the dots were bigger, irrespective of their number (see discussion). Since this response bias was identical across age groups (see figure 2B), we could be sure that this effect was not responsible for the observed difference in w across groups.

Irrespective of the bias to choose the set with larger individual dot size, as expected, the overall w decreased with age [$F(2,81)=15.4$, $p<.000$; all planned comparisons $ps<.020$], starting from an average of 0.95 for the youngest ($R^2=0.92$), down to 0.74 for the medium ($R^2=0.91$), and to 0.55 for the oldest kindergarteners ($R^2=0.98$). Linear regression between w and age as a continuous variable indicated that w continuously decreased as a function of age (β =-.51, $p<.000$), denoting a progressive improvement in numerosity discrimination abilities during development (see figure 3).

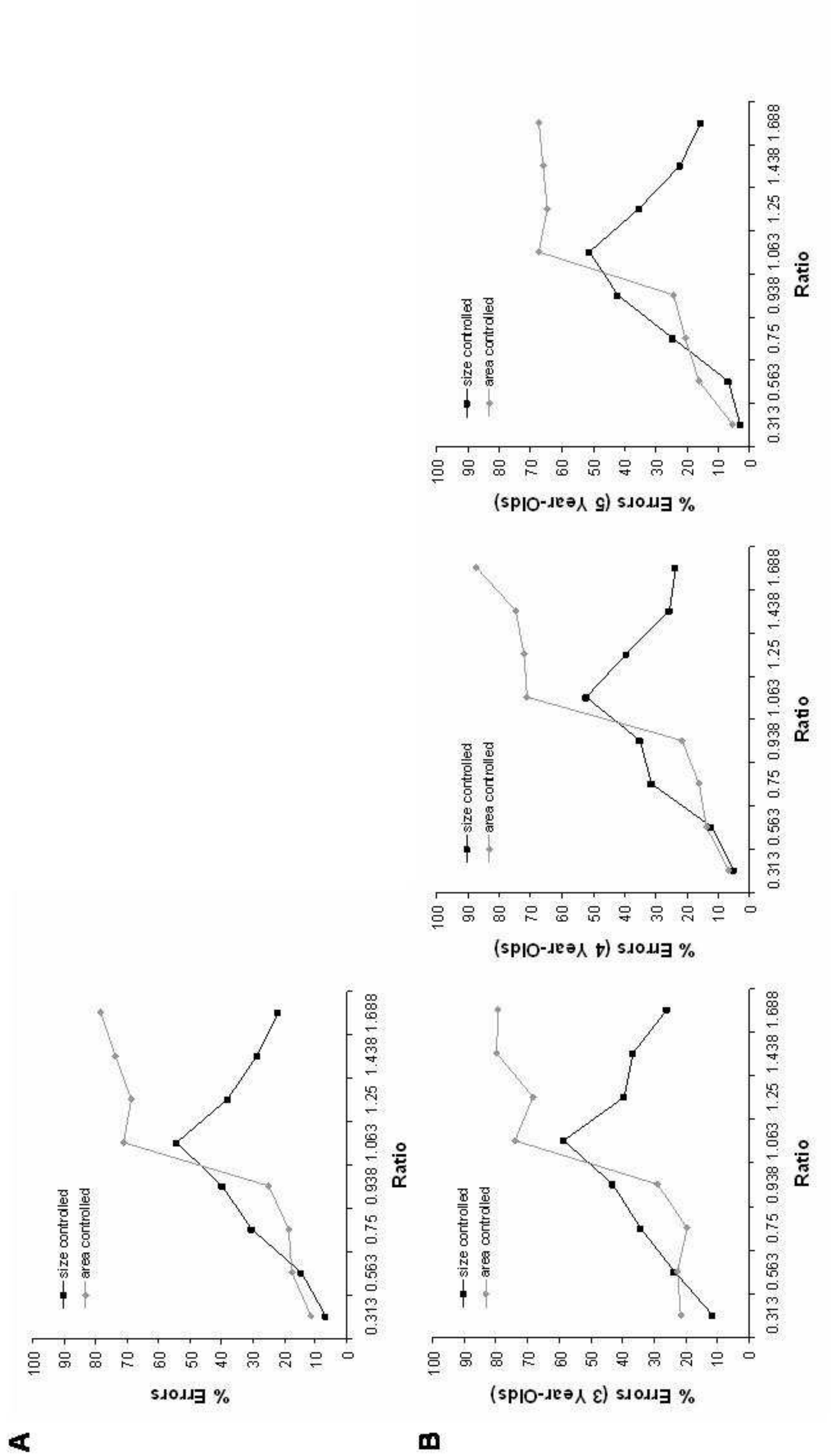


Fig. 2. Distribution of errors (%) separated for control-type (size vs. area) overall (A) and for age group (B).

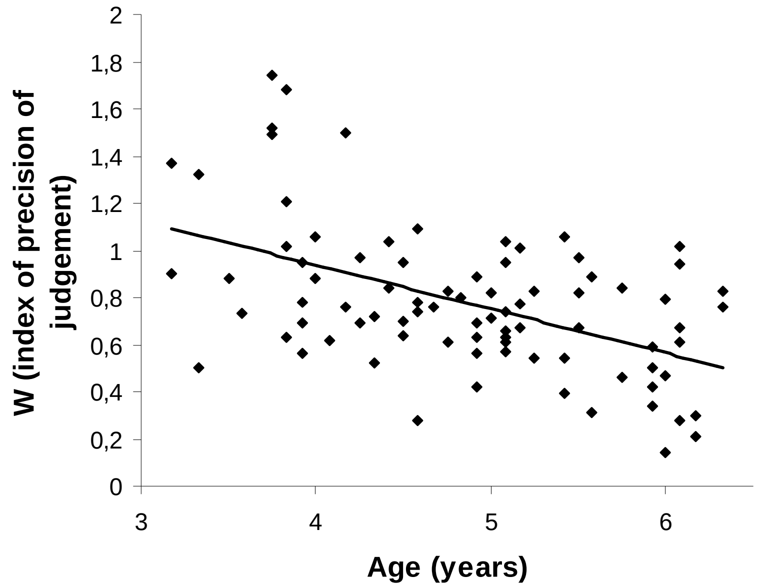


Fig. 3. Distribution of Weber fraction (w) as a function of age.

Symbolic number comparison

Some children, in particular among the youngest, found this task very difficult, as they never encountered the large two digits numbers used in the experiment before. Indeed, the experimenter noticed that some children overcome this difficulty by almost systematic employing the strategy of choosing the second number of the pair whatever its magnitude (the last number pronounced by the experimenter). In order to exclude the trials in which children used such “chose the last number” strategy, since the stimuli order was not counterbalanced neither within nor across subjects, we restricted our analysis to the trials where the first number was the larger. Performance in these trials would not be “polluted” by particular response strategies, but would rather reflect a genuine ability to perform numerical comparisons. Errors in these trials decreased with age [main effect of age range $F(2,91)=10.8$, $p<.000$] going from 74 % to 69% and 40% in 3, 4, and 5-years old children. Moreover, they were modulated by the ratio between the numbers [main effect of ratio $F(3,273)=3.2$, $p<.050$] and this modulation increased with age [age range * ratio interaction $F(6,273)=2.3$, $p<.050$]. Linear regression between overall errors and age as a continuous variable indicated that error rate for numerical comparison continuously decreased as a function of age (β =-.488, $p<.000$), denoting a progressive improvement of number abilities during development (see figure 4).

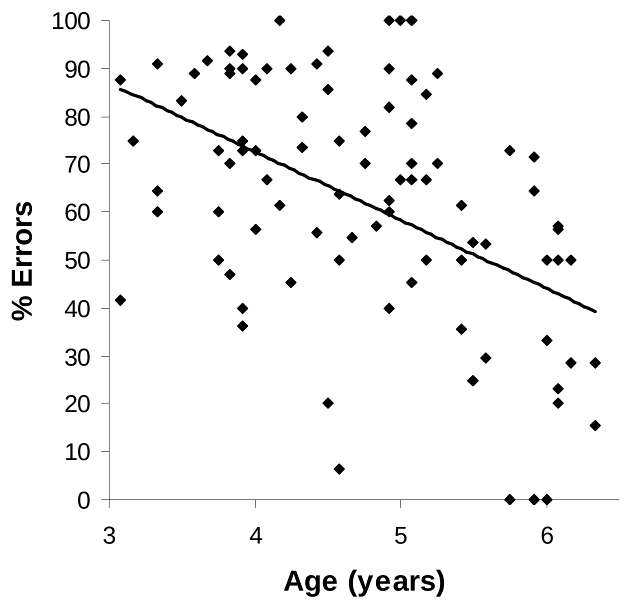


Fig. 4. Distribution of the performance in symbolic number comparison (% errors) as a function of age.

Finger gnosis

The overall mean error rate was 38% and it declined across ages starting from an average of 52% for the youngest down to 35% for the medium and 25% for the oldest kindergarteners [$F(2,91)=29.9$, $p<.000$; all planned comparisons ps<.010]. On average, 77% of the errors corresponded to trials where two fingers were stimulated (85%, 77%, and 75% for the young, medium, and old group, respectively). Of those errors, 81% were due to an incorrect discrimination of one or two fingers (hereafter 'discrimination errors' 83%, 76%, and 83% for the three groups), while 19% were due to an incorrect report of the order in which the fingers were stimulated (hereafter 'inversion errors' 17%, 24%, and 17% for the three groups).

Linear regression between the overall error rate and age indicated that finger discrimination progressively increased as a function of age (β =-.65, $p<.000$, see figure 5). This trend was confirmed even when trials were separated on the basis of the number of stimulated fingers (β =-.46, $p<.000$ and β =.-64, $p<.000$ for one vs. two fingers stimulated respectively). Both discrimination and inversion errors also linearly decreased with age (β =-55, $p<.000$, and β =-.29, $p<.010$ for discrimination and inversion errors respectively).

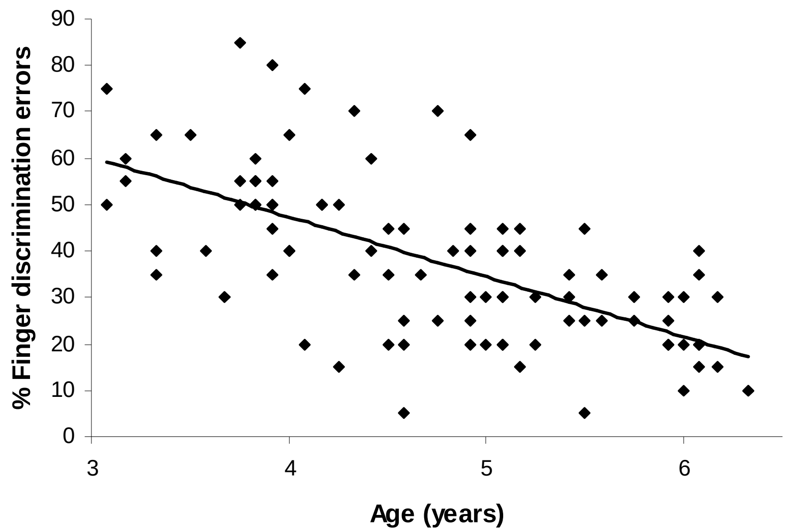


Fig. 5. Distribution of errors (%) in fingers discrimination as a function of age

Visuo-spatial SPAN

The overall SPAN (index of the capacity of visuo-spatial short term memory) was 3 (±0.9). It increases with age, starting from an average of 2.4 for the youngest, 3.0 for the medium and to 3.6 for the oldest kindergarteners [(F(2,91)=22.8, $p<.000$; all p.s <.002] (see figure 6), as also confirmed by linear regression (β =.60, $p<.000$).

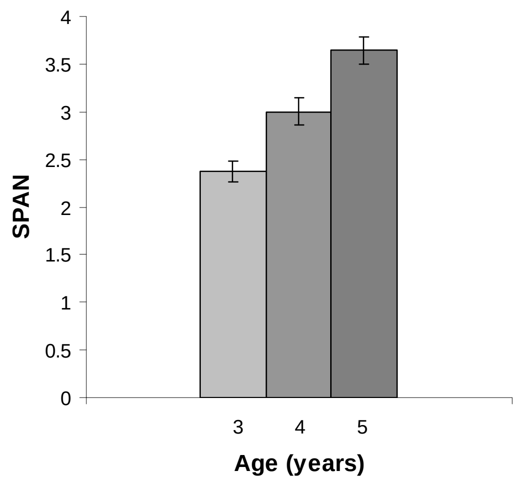


Fig. 6. Mean visuo-spatial SPAN for age group.

Grasping

The maximal grip aperture was modulated by the size of the to-be-grasped cylinders: it was 9.8 cm for small and 10.8 cm for big cylinders [$F(1,91)=503.5$, $p<.000$]. The difference between the max grip aperture for the large and the small objects, indicating the ability to modulate the grip aperture on the basis of the size of the to-be-grasped object progressively increased with age (it was 0.7 cm in 3 years old, 1 cm in 4 years old, and 1.1 cm in 5 years old children [main effect of age range on max grip aperture size modulation (large object max grip aperture – small object max grip aperture) $F(2,91)=10.3$, $p<.000$; all planned comparisons ps <.000], also confirmed by linear regression (β =.44, $p<.000$) (see figure 7).

This difference was mostly, but not entirely due to an increase of the maximum grip aperture with age for the large object (β = .21, $p<.050$). Indeed, hierarchical regressions showed that the increased difference between the max grip aperture for the large and the small objects with age remained significant even after partialling out the effect of the increasing grip aperture to large objects (potentially associated to pure "hand enlargement") (r = .513, $p<.005$, r^2=.247). Indeed, both cylinders' sizes were way below the children's maximum grip aperture.

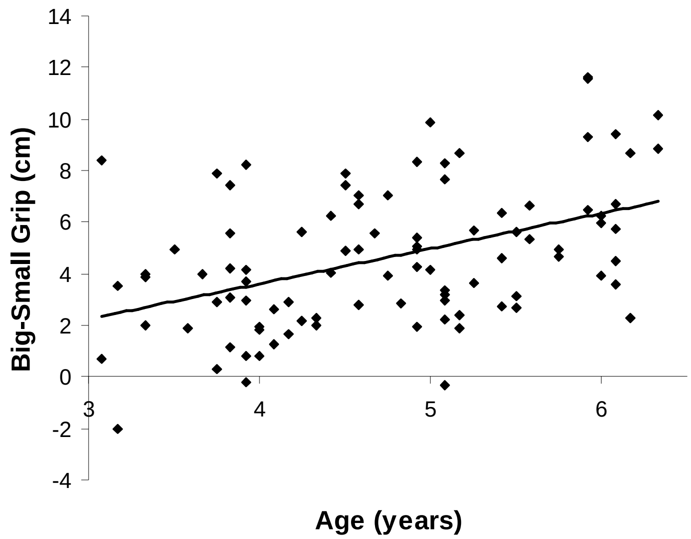


Fig. 7. The difference between the max grip aperture for the large and the small objects was plotted as a function of age.

Faces and Objects recognition

In order to quantify recognition abilities excluding the effects due to response biases (e.g., tendency to consistently respond “no” or “yes” to the question “have you seen this image before?”) we used d’, a measure commonly used in signal detection theory, calculated as the difference between the hit rate (old images correctly categorized as old) and the false alarm rate (new images incorrectly categorized as old), for faces and objects separately (Green & Swets, 1966; Macmillan & Creelman, 1991). Sensitivity improved with age [$F(2,88)=3.7$, $p<.050$] and was higher for objects then to faces [$F(1,88)=239.4$, $p<.000$]. Linear regressions confirmed that recognition ability improved with age, and that this improvement was steeper and more significant for faces (β =.27, $p<.010$) than for objects (β = .22, $p<.040$) (see figure 8A and 8B, respectively).

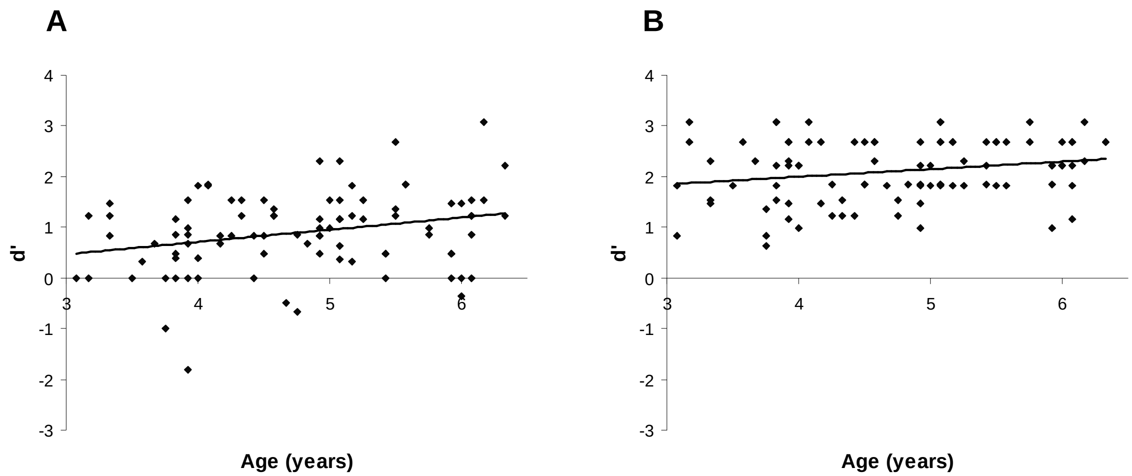


Fig. 8. Sensitivity for faces (A) and objects (B) as a function of age.

Interactions among Tasks

The main goal of the present experiment was to indentify clusters of correlations among the tested functions. Towards this aim, we selected the most significant index of each task to describe subjects' performance. The chosen indices were w for the numerosity judgments, overall accuracy for both the symbolic number processing task and the finger gnosis task, SPAN for the visuo-spatial memory, the difference in aperture for large vs. small objects in grasping, and d' for faces and objects recognition memory. For each subjects we extracted these indexes, and we investigated the patter of relations using a Principal Component Analysis (thereafter PCA). In order to better separate (and thus interpret) the isolated factors we also applied Varimax rotation to the PCA loadings (Jolliffe, 2002). A very clear two-cluster solution, accounting for 56% of the variance emerged (figure 9). The two factors sharply separated dorsal from ventral functions: the first included number related tasks (symbolic and non-symbolic comparison), as well as fingers gnosis, visuo-spatial SPAN and grasping, and the second included faces and objects recognition. Paired correlations among the individual tasks within the two factors confirmed the presence of significant correlations among the dorsal and the ventral functions and the absence of consistent correlations across dorsal and ventral tasks (see table 1 for the full correlation matrix).

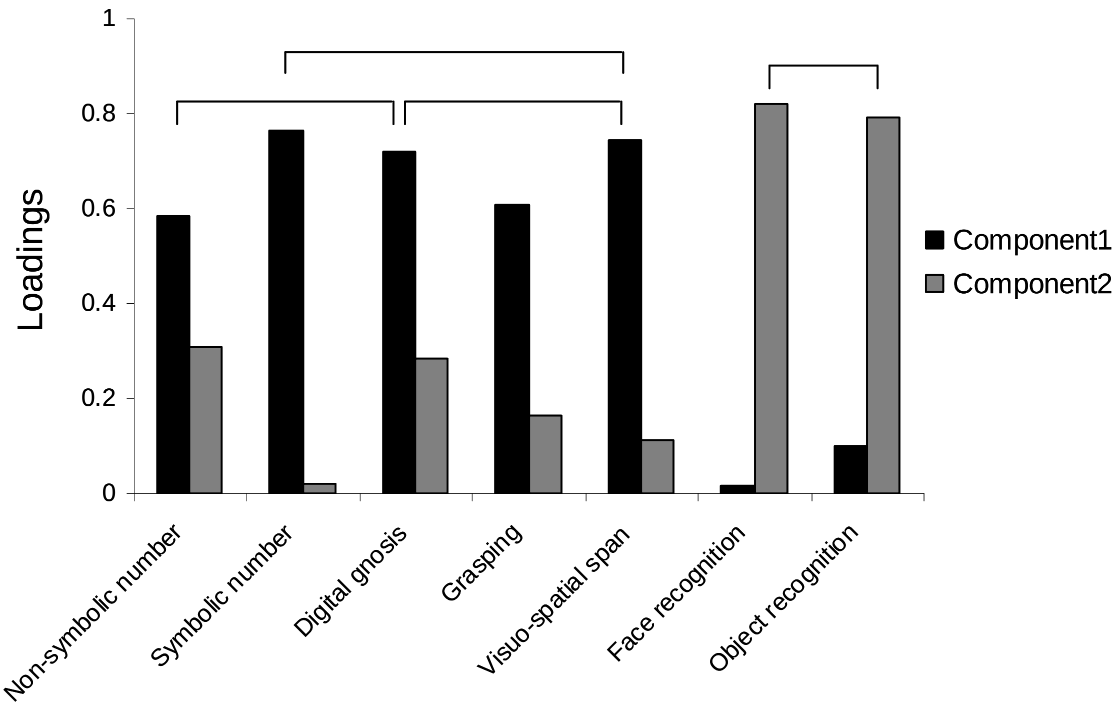


Fig. 9. PCA among the tasks. Coefficients of linear correlation (loadings) express the degree of influence of each variable on the component. Lines show significant interactions between tasks partialling out the effect of age.

We then focused on the pattern of correlations among tasks, and performed hierarchical regressions partialling out the effect of age. This analysis aimed at isolating functions that characterize individual differences over and above the presence of similar developmental trajectories (those cases are indicated by a star in Table 1). These were: finger gnosis and numerosity comparison (r^2=.427, p<.030; see Fig. 10); finger gnosis and visuo-spatial SPAN (r^2=.439, p<.030); symbolic number comparison and visuo-spatial SPAN (r^2=.382, p<.050, and, finally, faces and objects recognition (r^2=.199, p<.000). All these correlations are reported in fig. 9 (lines).

Table 1

	Numerosity comparison	Symbolic number comparison	Finger discrimination	Grasping	SPAN	Faces recognition	Objects recognition
Numerosity comparison	**1**						
Symbolic number comparison	**β=.322 p<.005**	**1**					
Finger discrimination	**β=.484 p<.000 ***	**β=.433 p<.000**	**1**				
Grasping	β=-.153 p=.164	**β=-.318 p<.005**	**β=-.296 p<.005**	**1**			
SPAN	**β=-.345 p=.001**	**β=-.452 p<.000 ***	**β=-.534 p<.000 ***	**β=.353 p<.000**	**1**		
Faces recognition	β=-.152 p=.172	β=.072 p=.499	β=-.149 p=.159	β=.031 p=.769	β=.031 p=.770	**1**	
Objects recognition	**B=-.240 p=.029**	β =-.115 p=.272	β=-.151 p=.149	β=-.006 p=.952	β=.190 p=.068	**β=.423, p<.000 ***	**1**

* Significant relation even excluding the effect of age

To better explore the relation between finger gnosis and numerosity comparison we carried out separate data analyses considering the number of stimulated fingers and the types of errors. Concerning the former, while both 1-finger errors (β=.415, p<.000) and 2-fingers errors (β=.404, p<.000) significantly correlated with the ability to discriminate numerosities (w), only 1-finger errors only survived the correction for the effect of age (r^2=.223, p<.050). We performed the same analysis to investigate the relation between finger gnosis and SPAN, and show that wile both 1-finger errors (β=-.315, p<.005), and 2-fingers errors (both discrimination (β=-.389, p<.000) and inversion (β=-.415, p<.000) errors) correlated with SPAN, only 2-fingers inversion errors (r=.417, p<.005, r^2=.156)) remained significant after controlling for the effect of age.

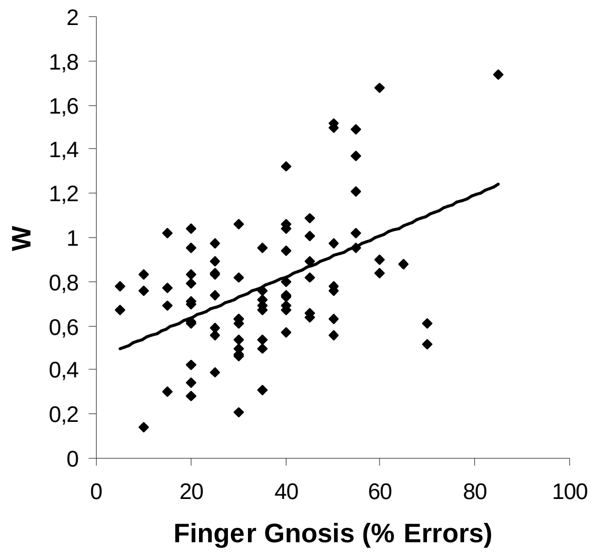


Fig. 10. Distribution of Weber fraction (numerosity comparison task) as a function of (%) errors in finger discrimination task.

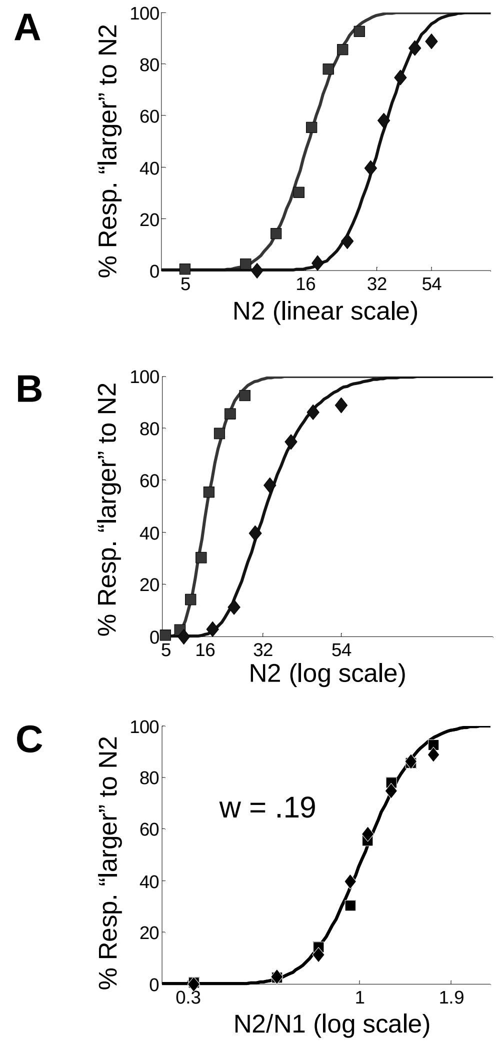
6.4.2 Experiment 1B: ADULTS

Numerosity comparison

The classical sigmoid response distributions, well accounted for by the Weber's law were recovered. On the basis of individual performance we calculated w for each participant. Overall, the mean w was equal to 0.19 (model fit: $R^2 = 0.99$; fig. 11), a value that is slightly higher compared to what reported in other studies (0.14, Pica et al., 2004; 0.15 in Piazza et al. 2009, 0.11 in Halberda et al. 2008).

Similarly to children, an 8x2 ANOVA with ratio and control type (size vs. area) as within-subjects factors was performed on error rate. The analysis showed the main effects of numerical ratio [$F(7,245)=105.4$, $p<.000$] and control type [$F(1,35)=42.6$, $p<.000$]. Separate analysis for each control type revealed that error rate increased when total occupied area was kept fixed, especially for larger ratios [$F(7,245)=3.6$, $p<.000$; see fig.12]. This pattern was coherent with what showed in Exp. 1, underling that dot size represented relevant information for numerical processing, especially with the current set of stimuli.

Fig. 11. Performance in the numerosity comparison task (adults). Graphs represent the proportion of the trials in which participants responded that n2 was more numerous than n1. Performance is plotted as a function of n1 on a linear scale (A), logarithmic scale (B) and on the logarithm of the numerical ratio (C).



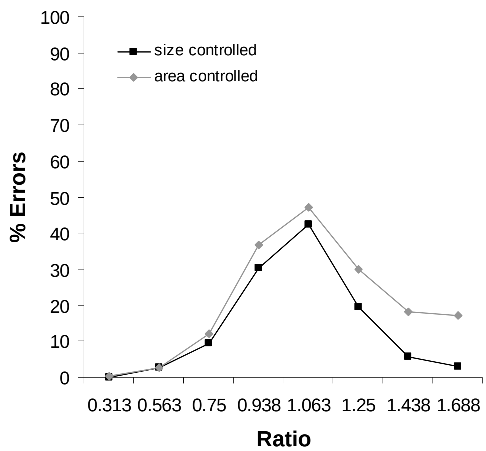


Fig. 12. Distribution of errors (%) separated for control-type (size vs. area).

Symbolic number comparison

Two 2x4x2 repeated measures ANOVAs were carried out on both RTs and accuracy with n1 magnitude (16 o 32), ratio (4 levels), and side of the larger number (left vs. right). Results showed the classical magnitude and distance effects: first, pairs with smaller magnitudes (n1=16) were responded faster to than pairs with larger magnitudes (n1=32) [$F(1,35)=85.7$, $p<.000$; accuracy n.s.]. Second, both RT and error rate decreased with increasing ratio [$F(3,105)= 175.8$, $p<.000$ and $F(3,105)=18.6$, $p<.000$ for RTs and errors, respectively].

Fingers gnosis

The mean error rate was 11%. All error related to finger discrimination. No inversion errors were made. Errors were modulate by the number of fingers stimulated ($F(1,35)=23.2$, $p<.000$). The three-fingers trials significantly represented the most difficult condition (67% of overall errors) compared to two-fingers trials [33%; three- versus two-fingers trails: $t(35)=-4.8$. $p<.000$]. No one-fingers error reported.

Visuo-spatial SPAN

The overall SPAN was 6 (±1) with a range from 4 to 7 across subjects.

Grasping

The maximum grip aperture was modulated by the size of the objects, being higher for the big cylinder than the small cylinder's aperture [10.9 cm vs. 9.6 cm; $t(35)=1.9$, $p=.07$ (0.04 one tail)].

Faces and objects recognition

Mean d-prime for faces and objects were of 2.04 and 2.05 respectively, a non significant difference (p = n.s.).

Interactions among tasks

In order to explore the presence of clusters of function we entered one index for each function (w in numerosity judgments, accuracy in symbolic number processing and in finger gnosis, SPAN in visuo-spatial memory, difference in aperture for large vs. small objects in grasping, d' in faces and objects recognition memory) into a PCA applying a Varimax rotation. A three-cluster solution was obtained, accounting for 68% of the variance among variables (figure 13).

The first cluster included the numerical tasks (symbolic and non-symbolic comparison). A second cluster involved grasping abilities and finger gnosis and the last one included visuo-spatial SPAN, faces and objects recognition. Paired correlations among the individual tasks within the three clusters confirmed the presence of significant correlations (see table 2).

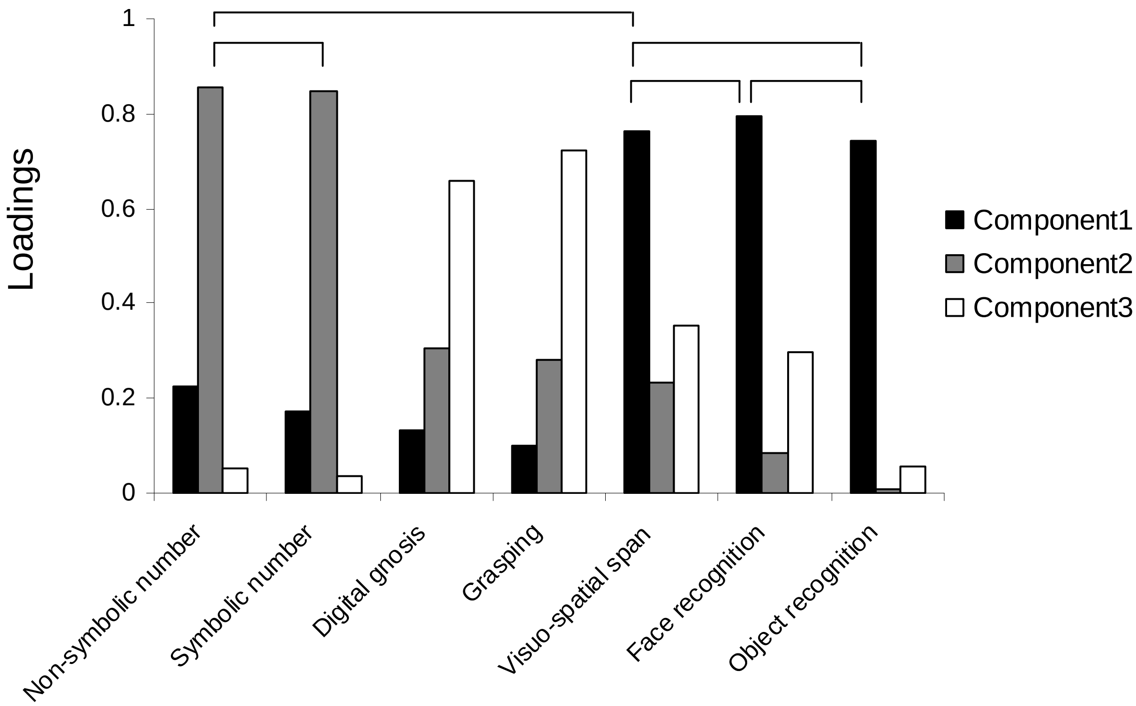


Fig. 13. PCA among tasks. Coefficients of linear correlation (loadings) express the degree of influence of each variable on the component. Lines show significant interactions between tasks.

Table 2

	Numerosity comparison	Symbolic number comparison	Finger discrimination	Grasping	SPAN	Faces recognition	Objects recognition
Numerosity comparison	**1**						
Symbolic number comparison	**β=.557 p<.000**	**1**					
Finger discrimination	β=.235 p=.168	β=.053 p=.760	**1**				
Grasping	β=-.113 p=.510	β=-.081 p=.638	β=.033 p=.848	**1**			
SPAN	**β=-.343 p=.041**	β=-.032 p=.851	β=-.319 p=.058	β=-.051 p=.769	**1**		
Faces Recognition	β=-.148 p=.388	β=.189 p=.271	β=.058 p=.735	β=.153 p=.373	**β=.392 p=.018**	**1**	
Objects Recognition	β=-.085 p=.622	β=-.022 p=.899	β=-.023 p=.895	β=-.027 p=.876	**β=.455 p=.005**	**β=.369, p=.027**	**1**

6.5 DISCUSSION

The aim of this study was to trace developmental trajectories of the sensitivity of numerical quantity (measured by numerosity and number comparison tasks) and other parietal functions such as visuo-spatial SPAN (Corsi test), finger gnosis (measured by a finger agnosia test) and grip aperture (measured by the index-thumb distance while grasping objects) in preschoolers and adults. As control tasks, we also tested face and object processing abilities (measured by a recognition task), which are related to the functioning of occipito-temporal regions.

Firstly, our data showed a general improvement in all tasks during development between 3 and 6 years of age.

Among parietal functions, numerosity acuity (w) continues the process of progressive refinement that starts from birth (Halberda & Feigenson, 2008; Izard, et al., 2009). While in absolute terms the estimated Weber's fraction values departed from those reported in previous studies, the rate of decrease across the preschool ages that we observed, fitted with previous reports (e.g. 40%, compared to 42% of the present study respectively from 3 to 6 years of age (Halberda & Feigenson, 2008; Piazza & Izard, 2009)). The factors liable for the reduction of w with age are still unknown; although maturational processes are more likely to play a significant role from birth up to before schooling, arithmetic education may account for later and further refinements.

Finger gnosis also improved. Two factors can be taken into account in explaining this trend. On one hand, our digital task involved a tactile-to-visual integration and parietal maturation that can determine more precise cross-modality interplay. On the other hand, "one factor that determines a correct movement of one part of the body to another is the sensory differentiation of the point or locus which is the goal of the movement" (Lefford, Birch, & Green, 1974). Thus, the development of fingers sensibility is related with the concept of body schema and body image (Benton, Hutcheon, & Seymour, 1951) and their modifications during the development. Thus, improvements in both the pure sensory representation and/or in the higher level representation at the level of the body schema can account for the observed improvement.

Visuo-spatial span increased linearly with age with an enlargement of 0.6 elements every year, confirming previous reports (Pickering, 2001).

Grasping also becomes more rigorous and object-specific during these years. Indeed, across ages, the maximum grip aperture is progressively more influenced by the objects size: small objects determine a reduced aperture while big objects determine bigger aperture in the initial moments of grasping action. This result suggested a refinement of grasping ability in terms of a more precise modulation of grip aperture based on the physical magnitude of objects.

Among ventral functions, processes such as faces and objects recognition improved with age. This result is also in line with previous reports as documented by in a combined behavioral and fMRI study on older children (ages 7-11) showing that face, but not objects, processing improved during the development and this trend was strictly related to the anatomical maturation of fusiform face area - FFA (Golarai, et al., 2007). In this way, the refinement of faces sensitivity seems to involve throughout a longer period when compared to objects sensitivity.

Data reduction analysis allowed us to explore the relations among these tasks. Results showed that in young children anatomical proximity was a strong predictor of behavioural correlations across cognitive functions. Indeed, we observed a clear separation between dorsal and ventral functions. In this respect, data from adults showed a quite different picture: a much higher degree of specialization within parietal functions, and the presence of correlations between dorsal and ventral functions, suggesting that experience and education act by modifying the pre-existing pattern of functional (and maybe also anatomical) connections.

In children, hierarchical regression analysis showed that while some correlations between tasks were due to common developmental trajectories, a correlation was present even when the effect of common developmental trends was controlled for. Thus, the presence of even stronger associations within subjects is evident between some functions.

The first strong correlation observed was the one between finger gnosis and non-symbolic numerical acuity. Given that this part of the correlation was not accounted by common maturational factors, it would be tempting to attribute it to common functional factors, such as finger counting. Indeed, even when preschool children do not receive formal teaching at finger counting, it is possible that some of them have already started using finger-counting in quantification tasks. On one hand, the use of finger counting would improve finger gnosis via increasing awareness of one's finger and their relative position in space. On the other hand, it is also possible that this operation would produce some degree of refinement of the internal representation of magnitude (Verguts & Fias, 2005). As a result, children with high finger gnosis would also have high number acuity (functionalist account). An alternative interpretation is the presence of high functional connections among regions related to finger gnosis and quantity processing, present at the architectural level, and irrespective of training finger counting. In order to disentangle these two interpretations, we explored the numerosity-finger interplay within each age group. Contrary to the predictions from the functionalist hypothesis, we found that the strongest association between finger and numerical discrimination was present in 3 years-old children (β=539, $p<.010$), and that, even among the youngest children, this correlation remained significant after partialling out the effect of age ($r=.554$, $p<.020$, $r^2=.237$). Due to a limited influence of functional factors (e.g. finger counting) in early childhood, this finding supported the view that the strong interplay between numerosity and fingers discrimination is mostly driven by anatomo-functional connections which are not modulated by experience. On the contrary, it seems that education and experience determine a distinct specialization of these two domains; indeed, the two abilities did not correlate in adults.

On the other hand, symbolic number processing seemed to be more related to spatial abilities in preschoolers. Indeed, the idea of ordered spatial distribution of numbers on a line and the mental number line could contribute to solve the relative task easier. Furthermore, spatial span memory interacted with finger gnosis, especially in the case of correct discrimination of fingers, but with an inverted sequence (inversions). Indeed, children with lower spatial span had the highest tendency -when solving the digital task- to start from the last stimulated finger rather than the first one (although instructed to avoid this strategy). Probably, the use of this strategy may help low-span children to solve the task with less mental load.

Experiment 2 gave us the possibility to explore the same cognitive functions in adulthood when maturational processes linked to development are concluded, or limited.

Interestingly, symbolic (number words) and non-symbolic (dots) number processing exhibited a peculiar trend in early childhood and adulthood. These two abilities seemed to converge during the development, from a general independency in preschool age to an intimate relation in adulthood. A possible cause of this phenomenon derived from the effect of the exact numerical manipulation that contributed to the mapping of the symbolic representation on a preexisting representation of numerosity. In other terms, the acquisition of symbolic knowledge for numbers may determine a refinement of the numerosity acuity, as suggested by Verguts & Fias (2005).

Spatial memory is considered more important for adults during the processing of numerical information. Dot arrays (vs. Arabic digits) may imply higher contributions of spatial processing during the phase of visualization and comparisons of the array pairs due to different spatial complexity of these stimuli. In contrast to preschool data, in adults SPAN is more related to ventral memory-based tasks. Probably, this is due to a stronger impact of common and shared memory-related processes of working memory for visuo-spatial information retention.

In summary, our findings contributed to disentangle of the developmental trajectories of dorsal and ventral functions. In particular, we showed the relation of number domain with space, finger gnosis and action among parietal components. Interestingly, this extensive approach gave the possibility to investigate a large set of parietal functions in preschool age, comparing their developmental trajectories, and capitalizing on their inter-individual differences in order to isolate functional clusters of correlations across domains.

Chapter 7

INDIVIDUAL DIFFERENCES IN FINGER, SPATIAL AND QUANTITY REPRESENTATIONS CORRELATE WITH MATH ACHIEVEMENT IN FIRST GRADERS

7.1 ABSTRACT

Previous studies have shown the existence of associations between single abilities (e.g. numerosity estimation, subitizing skills, finger gnosis, linear number to space mapping) and calculation. Curiously, few studies adopted a larger perspective measuring all these important functions at the same time. Thus, it is unknown how both numerical and non-numerical abilities interact with each other and support formal arithmetical calculation.

This study aims at overstepping these limitations, and considers the pattern of relations across several different cognitive domains related to the numeracy development such as numerosity estimation, number comparison, finger gnosis, subitizing, number to space mapping and simple mental arithmetic in 6 year-old children, at the end of the first year of primary school.

Functional clusterization shows three distinct components that respectively include subitizing skills, quantity processing and arithmetic-space-finger domains.

Subitizing skills do not correlate with any other numerical abilities, supporting the non-numerical interpretation of subitizing as an independent mechanism for parallel estimation of small numerosity.

The strong relation between symbolic and non symbolic number comparison is dependent on the fact that both these tasks are thought to share a common cortical representation of quantity on the basis of a “cortical remapping” of the preexisting neural system for numerosity during the acquisition of symbolic numbers.

Performance in addition and subtraction problems is strongly associated with symbolic number comparison, finger gnosis and with the degree of linearity in the mapping numbers

to a line, suggesting the role of all these factors in calculation. In particular, a mixed anatomo-functional interpretation regarding the arithmetic-finger association is suggested as a function of a higher influence of educational factors across ages.

7.2 INTRODUCTION

Humans, as well as other human primates, come to life equipped with a system, based on parietal cortex circuitry (Piazza & Izard, 2009), for estimating and internally manipulating numerical information (the approximate number of objects in a collection). Thanks to this system they can match, compare and perform simple calculation like additions and subtractions on sets of items. This system is approximate in nature and in humans it appears to be complemented by a second system that allows a direct apprehension of the exact small number of up to three or four items (called “subitizing” or “object file system”). For some time subitizing and estimation were thought to reflect a common system for approximate numerosity, which precision decreases as the number of items increases, according to Weber’s law (Dehaene & Changeux, 1993; Gallistel & Gelman, 1991). Recently, however, it is becoming clearer that subitizing reflects a truly separate mechanism which is non-numerical in nature, limited in capacity, and based on indexing multiple objects in parallel ((Revkin, et al., 2008; Trick & Pylyshyn, 1994); see (Feigenson, et al., 2004) for a review).

Both subitizing and estimation are thought to act as start-up-tools for the development of further mathematical knowledge (Butterworth, 1999; Dehaene, 1997). However, while much empirical research have focused on the relation between symbolic numerical abilities and the pre-verbal approximate estimation system, little is known on the role of subitizing during numeracy development.

Indeed, to date we have convincing empirical evidence for the foundational role played by the approximate number system: first, its acuity correlates with symbolic number comparison in adults and children ((Gilmore, et al., 2007), and see the results of chapter 5 of this thesis), second, it predicts mathematical achievements in normally developing children and adolescent (Gilmore, et al., 2007; Halberda, et al., 2008), and finally, it is impaired in dyscalculic children (Piazza, et al., 2010). On the contrary, while some researchers have proposed that subitizing is even more crucial then estimation abilities in the development of number processing (Butterworth, 1999), we still lack strong evidence in favour of the foundational role of subitizing in numeracy development (but see (Landerl, et al., 2004)).

A key step in numeracy development is the acquisition of symbolic numbers as arbitrary signs for exact numerical quantity (cardinality). This important acquisition is achieved thanks to several strategies. The first one is certainly the implementation of counting. Counting (at least in our society) is very often performed with the aid of fingers, used as "abstract" place holders. Indeed, even if fingers are themselves concrete objects, they can be used to represent physical objects of any nature (sounds, visual objects, movements, ideas). Moreover, given their fixed spatial configuration, they help the access to exact quantities even when their number exceeds the subitizing limit (e.g., if all fingers of a hand are raised we do not need to count them to know that there are exactly 5, and this is because we recognise a specific spatial configuration). This "handy" tool is spontaneously recruited by children not only to count objects but also to solve simple arithmetical problems (Jordan, et al., 2008). Indeed, finger gnosis (the ability to mentally representing one's own fingers and their spatial relations) is a good predictor of symbolic arithmetical abilities in children in the first years of schools, and it is often severely impaired in dyscalculic children (Fayol, et al., 1998).

A second and probably also very important strategy towards a full understanding of exact number concepts is the establishment of spatial metaphors for numbers. Indeed, the introduction of the idea that numbers can be ordered in space, along an oriented number line is part of the educational program of the first year in Italian elementary school. This linear number to space mapping helps children reshaping their internal representation of numerical quantity which is initially approximate and compressed (logarithmic) towards an exact and linear one. Indeed, by using the number-to-space task, where children are asked to position different numbers on a line representing a given continuum, researchers have shown that during development there is a shift from a logarithmic to a linear number-to-space mapping (Berteletti, Lucangeli, Piazza, Dehaene, & Zorzi, 2009; Siegler & Opfer, 2003), and that this shift occurs between the last year of preschool and the first year of elementary school. This mentalized number line is then used by children for calculation and measurements. Indeed, the degree of linearity of the number-to-space mapping correlates with mental arithmetic scores (Berteletti, et al., 2009) and is immature in dyscalculic children (Wilson & S., 2007).

While we now know that both number-to-finger and the number-to-space associations play important roles in the transition between presymbolic to symbolic number processing, the exact steps underlying this transition are still very little understood. In particular, little is known about the *relative* contributions and the interplay between numerical and non-numerical functions in numeracy development. In fact, previous studies report the existence of associations between single abilities and calculation, but never approached the question from a large perspective measuring all these important functions at the same time.

As a result, it is unknown how both numerical and non-numerical abilities, such as estimation, subitizing, finger gnosis, and the ability to attribute numbers to linear positions in space interact with each other and support arithmetical calculation.

This study aims at overstepping these limitations, and considers several tasks tackling several different cognitive domains relevant in numeracy development: numerosity estimation, finger gnosis, subitizing, number to space mapping, number comparison, and simple mental arithmetic. We propose those tasks to 6 years old children in the end of the first year of primary school in order to investigate the pattern of relations across these tasks and their role in predicting performance in mental arithmetic.

7.3 METHODS

7.3.1 Participants

The study recruited 19 children (age=84 ±4 months; right-handed= 89.5%; males= 52 .7%) attending Grade1 classes in Rovereto (Italy). Before starting the study, we obtained the approval by the local ethical committee and a signed informed consent from the parents (or the legal representatives). The testing took place in April-May 2009 towards the end of the school year.

7.3.2 General testing procedure

Children were tested in a quiet room while seated at a table, in front of a familiar examiner and approximately 40 cm from a 15-inch LCD monitor. Children were given breaks between each task and anytime during testing, upon request. Computerized tasks were based on MATLAB psychotoolbox software (MathWorks MA:USA) for both stimuli presentation and response recording (reaction times, RTs). The overt use of fingers counting was recorded by the experimenter. Each child carried out 7 tasks in one session lasting about 50 minutes. The tasks order was randomly assigned to each child.

Numerosity comparison

Children were presented with pairs of arrays of dots on a computer screen. Their task was to point to the array containing more dots. Every trail started with a fixation cross for 1 sec. followed by the appearance of two lateralized arrays. Children were given an unlimited amount of time to produce their response, but were urged to avoid exact counting. One of the two arrays always included 16 or 32 dots (n1), while the other could contain 12-13-14-15-17-18-19-20 (or 24-26-28-30-34-36-38-40 dots respectively, n2). Each pair was repeated 8 times, for a total of 128 trials. Dot arrays were generated by a computerized program controlling the effect of dot size and array area, so that response to number could not be attributed to any single non-numerical visuo-spatial parameter. Indeed, for each pair, half of the trials were controlled for dots size and the other half for dots area. Before starting the experiment, children performed 8 practice trials, followed by 128 trials. The trial order was randomized both within and across subjects.

Number comparison

In this task, children were presented with pairs of lateralized two digit Arabic numbers, black on a white screen, and had to press the button corresponding to the numerically larger number (buttons: 'D' and 'L' of the keyboard). Trials started with a fixation cross for 1 sec. followed by the stimuli. The children had an unlimited amount of time to give their solution. The numbers used were identical to the ones used in the numerosity comparison task. Each pair was showed twice for counterbalanced left-right stimuli assignment, and repeated 2 times for a total of 64 trials. The trial order was randomized both within and across subjects.

Fingers gnosis

Children sat on a chair in front of a table, and were asked to place their dominant hand (DH), palm down on the table, in front of the experimenter. The experimenter then covered the children's hand to their sight by putting a white vertical panel at the level of their wrist. Then the experimenter started the stimulation, which consisted in touching one, two, or three fingers (in sequence). The experimenter removed the panel and asked the child to point to the finger(s) that were previously touched, maintaining the same order. For the one finger condition, each finger was touched twice (10 trials), for the two fingers condition, all finger pairs were touched once (10 trials), while for the three fingers conditions 10 random triplets of fingers were touched. The trial order was randomized both within and across subjects.

Additions

Children were asked to solve orally 20 simple additions showed on a Pc screen. As soon as the children gave their answer the experimenter collected their responses and press on a key to record the approximate RTs. The addends were one-digit numbers (between 1 and 9). In order to modulate difficulty, in half of the problems the result was inferior to 10, while in the remaining half it was superior to 10. The children had an unlimited amount of time to give their solution. The trial order was randomized both within and across subjects.

Subtractions

18 subtractions were solved orally by children without time restrictions for responses. As for the addition problems, the experimenter collected the children's responses and the relative RTs. The subtractions were divided for difficulty level on the basis of the magnitude of the minuend: simple (with 4/5), medium (8/9) and difficult (14/15). The subtrahend was 2, 3, or 4. The trial order was randomized both within and across subjects.

Number-to-line task (thereafter "Line")

Children were shown a horizontal white segment in the middle of a black screen labeled with "1" on the left and "10" on the right side. For each trial, children had to indicate the position on the segment of a top-centered target-number (Arabic digit). The children placed the number by using the arrow of the mouse. All the target-numbers from 2 to 9 were showed three times, avoiding repetitions. The trial order was randomized both within and across subjects.

Enumeration

Children were presented dots arrays and instructed to name the number of dots as accurately and quickly as possible using a microphone. The dots were black on a white disc, appearing on a black background of the display. Each trial began with a double flashed fixation cross, to announce the arrival of the dots. Then a flicker mask was displayed, and finally a black screen (see fig. 1). Children performed 4 practice trials, followed by three blocks of 16 trials each one (for a total of 48 valid trials). For each dots pattern, half of the trials were controlled for dots size and the other half for dots area (cfr. (Revkin, et al., 2008)). The trial order was randomized both within and across subjects.

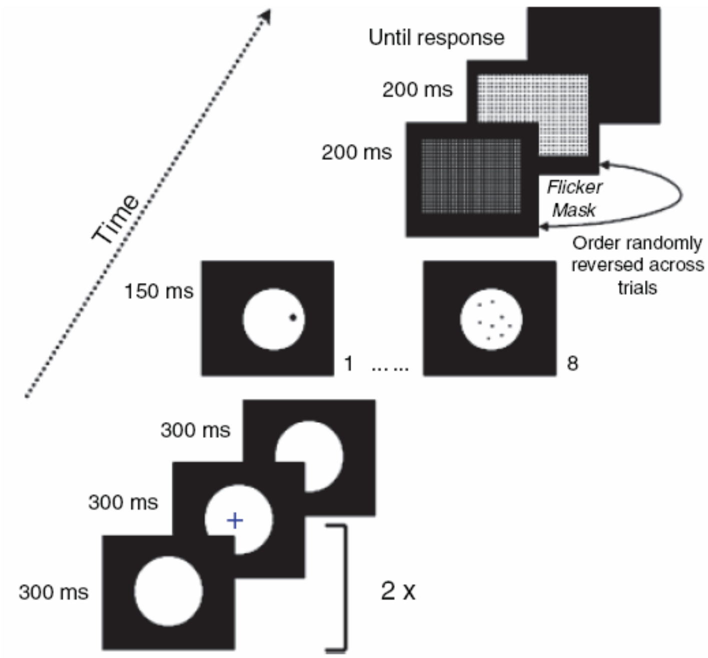


Fig. 1. In the 1–8 naming task, after a fixation cross flashed twice, participants were shown a group of 1 to 8 dots, followed by amask; the task was to name the presented numerosity as quickly as possible using the labels ‘‘1’’ through ‘‘8.’’ (from Revkin et al., 2008)

7.4 RESULTS

Here we first report the results in each individual task, end the then pattern of correlations across tasks. About half of our sample (N= 10/19) used intensively fingers to count in solving both addition and subtraction problems. We thus run a t-test comparison for each task to check for significant difference between finger-counters and non-counters. No comparison was significant. Thus we collapsed the data from counters and non-counter for all analysis. For all RTs analyses, we considered the mean RT (±2 s.d.) as cutoff.

Numerosity comparison

Overall, “larger” responses to n2 followed a classic sigmoid curve. With the aim to measure the precision of the numerical judgment, the internal Weber fraction (thereafter w) was estimated for each subject. This measure corresponds to the standard deviation of the estimated Gaussian distribution (on a log scale) of the internal representation of numerosity that generates the observed performance. Three subjects were excluded because the psychophysical model did not converge (one subject), or the R^2 of the model was too low (<.2, two subjects). The data from the remaining 16 children was used to calculate the average w, which was equal to 0.27 (model fit: $R^2 = 0.65$; fig. 2).

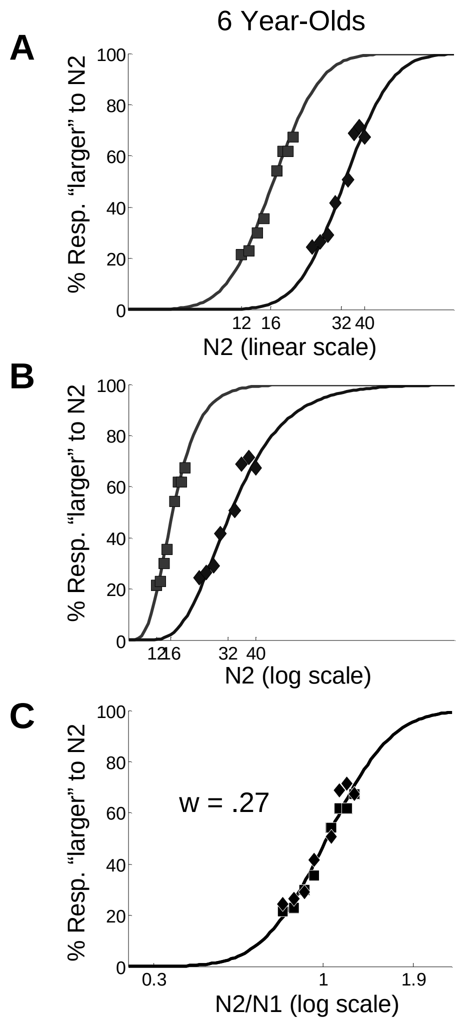


Fig. 2. Performance in the numerosity comparison task (first graders). Graphs represent the proportion of the trials in which participants responded that n2 was more numerous than n1. Performance is plotted as a function of n1 on a linear scale (A), logarithmic scale (B) and on the logarithm of the numerical ratio (C).

Number comparison

We carried out two separated 2x4 ANOVAs on RTs [cutoff=7 sec. (57 data points out)] and accuracy with n1 (16 or 32) and ratio as within-subjects factors. Only main effects were significant: magnitude (pairs around 16 elicited fewer errors and faster responses in comparison with pairs around 32 [$F(1,18)=11.3$, $p<.010$; $F(1,18)=43.1$, $p<.000$ for error and RTs respectively], and ratio (reaction times increased linearly with the ratio between paired numbers [$F(3,54)=6.4$, $p<.000$], no effect for accuracy).

Finger gnosis

The error rate increased from 9% to 41%, and 54% (all t-tests ps<.030; see fig. 3) with the number of touched digits.

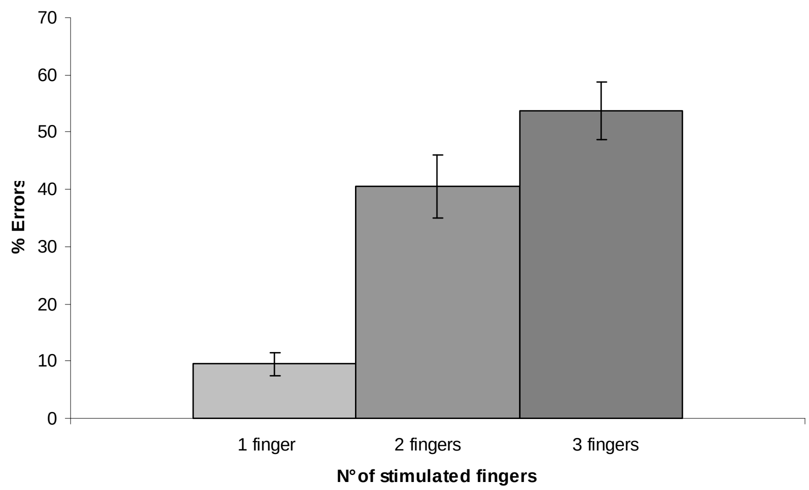


Fig. 3. Mean distribution of errors (%) as a function of the number of stimulated fingers.

Additions

Two ANOVAs on RTs [cutoff=27sec. (20 out)] and accuracy, with task difficulty (results above/below 10) as within-subjects factor, confirmed that additions below-10 were the fastest [6.3 vs. 10.8 sec.; $F(1,18)=66.2$, $p<.000$] and with the lowest error rate [6 vs. 18 %; $F(1,18)=36.3$, $p<.000$].

Subtractions

Two ANOVAs on RTs [cutoff=30 sec. (19 out)] and accuracy, with difficulty (simple, medium, difficult) as within-subjects factor, confirmed a significant increase of both RTs [7.6, 9.7 and 12.1 sec. respectively; $F(2,36)=7.4$, $p<.010$] and error rate [3, 9 and 8 %; $F(2,36)=5.0$, $p<.050$] from simple to difficult task conditions.

Number-to-Line

We calculated the goodness of fit (R^2) of the linear regressions on the estimated number positions for each subject. Data showed a linear representation of numbers (mean $R^2=.97$) in all children, even thought there was an overall tendency to overestimate the spatial position of the number on the line, exhibiting a right-sided bias (Fig. 4).

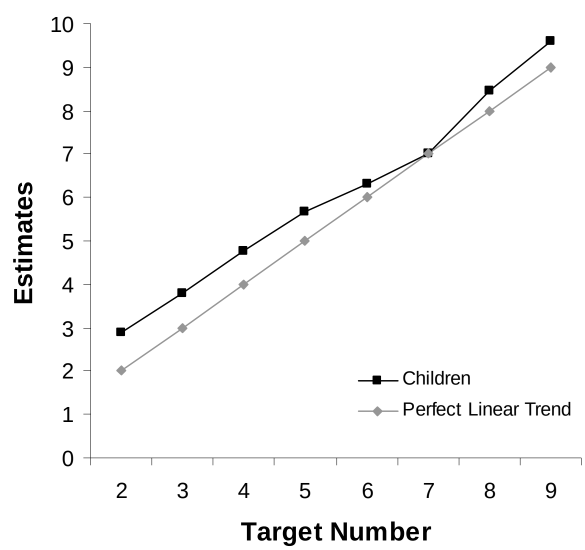


Fig. 4. Location of each target number (from 2 to 9) on the spatial line from 1 to 10.

Enumeration

The errors distribution followed a sigmoid curve with a stable high accuracy for the first three numbers (mean Error= 4%) and a progressive error increase from 4 to 5 (respectively, mean Error= 28% and 50%) and a stabilization from 6 to 8 (Mean Error= 73%; fig. 5). We calculated the subitizing range for each participant by fitting the full accuracy curve with a sigmoid function of numerosity and considering its inflexion point (Revkin, et al., 2008). The model was highly accurate in all subjects (model fit: mean R^2=.82) with a mean subitizing range of 4.8. Comparable results were found when considering the RTs distribution with a mean subitizing range of 4.5 (R^2=.79).

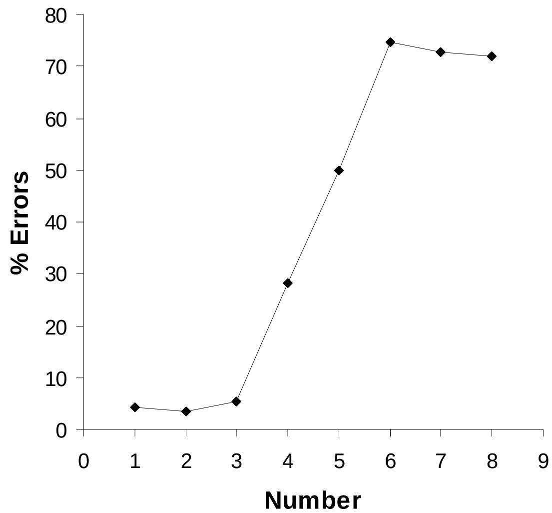


Fig. 5. Error rates (%) as a function of the presented number (stimuli)

Correlations

For each task and each subject we considered one index representing proficiency in the different tasks: w for numerosity comparison, accuracy for Arabic number comparison, finger gnosis, additions and subtractions, the R^2 of the linear model for the number-to-line task, accuracy based subitizing range for subitizing (we obtain comparable results using RTs based subitizing range). This analysis showed a strong correlation between numerosity and numbers comparisons (β =.585, $p<.02$ with 3 subjects out), and between additions and subtractions (β=.835, $p<.00$). Additions and subtraction correlated with both number comparison (β= .559, $p<.03$, and β=.504, $p<.03$ respectively) and finger gnosis (β=.684, $p<.01$ and β=.449, p=.054). (See table 1 for the full correlation matrix).

Table 1

	Numerosity comparison	Symbolic number comparison	Finger discrimination	Additions	Subtractions	Number To Line	Enumeration
Numerosity comparison	**1**						
Symbolic number comparison	**β=.585 p=.017**	**1**					
Finger discrimination	β=.432 p=.095	β=.305 p=.204	**1**				
Additions	β=.185 p=.492	**β=.559 p=.013**	**β=.684 p=.001**	**1**			
Subtractions	β=-.005 p=.987	**β=.504 p=.028**	β=.449 p=.054	**β=.835 p<.000**	**1**		
Number-to-Line	β=.269 p=.314	β=.243 p=.316	β=.425 p=.070	β=.431 p=.065	β=.200 p=.411	**1**	
Enumeration	β=-.076 p=.780	β=-.150 p=.539	β=-.275 p=.225	β=.082 p=.738	β=.053 p=.829	β=.008 p=.975	**1**

Interactions among Tasks

Given our interest in exploring the global pattern of relations among the different tasks, we decided to use a Hierarchical clustering approach. Hierarchical algorithms find successive clusters using previously established clusters. These algorithms begin with each element as a separate cluster and merge them into successively larger clusters. We used this method to explore the possibility of finding hierarchical patterns reflecting the typical step-by-step educational procedure to teach mathematic in Italian Grade1 classes. Thus, all the relations among tasks were explored by using a Buttom-Up Hierarchical clustering on all the Pearson's correlations among individual measures for each task (on 16/19 subjects) (see fig. 6). Results show a clear segregation of subitizing skills from the other numerical and arithmetical abilities. We found a functional parcellisation of the pure basic numerical abilities from more and more complex tasks and procedures, which are acquired and practiced progressively during the first year of school (fig. 7).

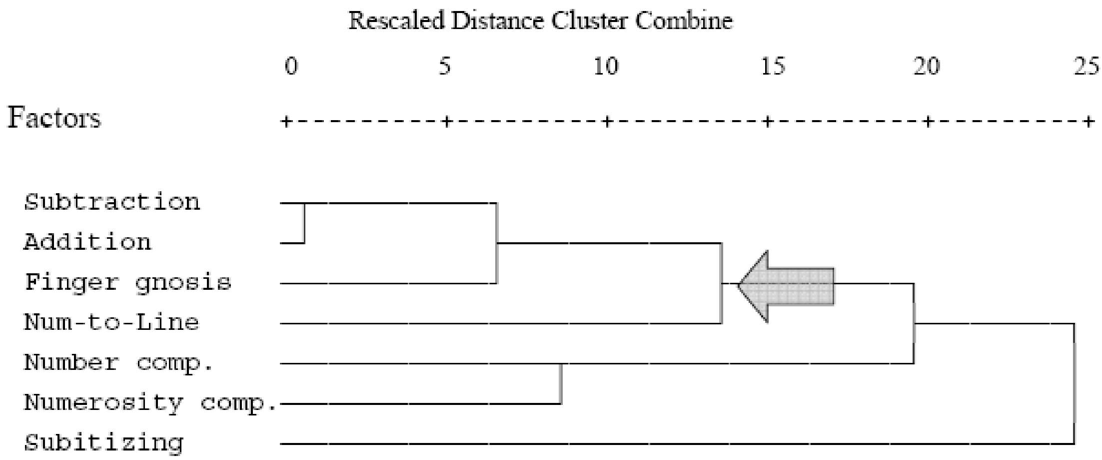


Fig. 6. Dendrogram of Hierarchical Clustering on Pearson's correlations among individual measures for each task.

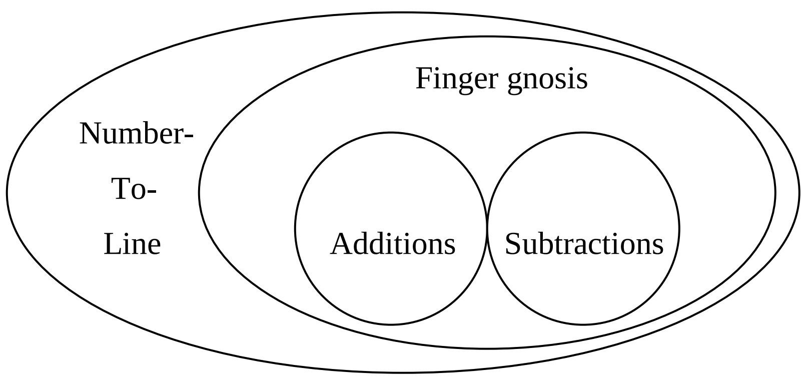


Fig. 7. Graphical representation of the hierarchy of tasks related to calculation (indicated by the arrow in fig. 6).

Moreover, the presence of functional clusters were investigated entering one index for each task (w in numerosity judgments, accuracy for symbolic number processing, finger gnosis, subtractions and additions; the goodness of fit (R^2) for number-to-line task and the subitizing range) into a PCA applying a Varimax rotation. A three-cluster solution was obtained, accounting for 81% of the variance among variables (figure 8).

The first cluster included subitizing skills alone. Then, the second cluster involved the numerical tasks (symbolic and non-symbolic comparison). The last cluster included number-to-line task, finger gnosis, additions and subtractions.

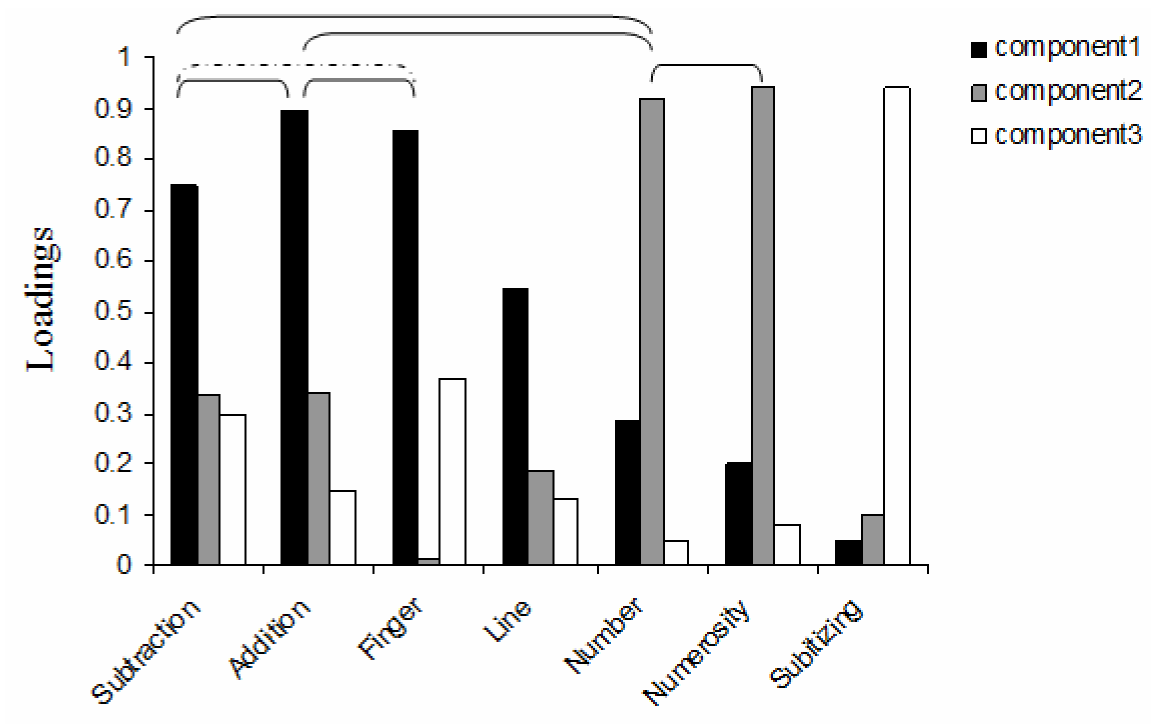


Fig. 8. PCA among tasks. Coefficients of linear correlation (loadings) express the degree of influence of each variable on the component. Lines represent significant interactions between tasks (dashed line: trend - p=.054)

7.5 DISCUSSION

Correlational results together with cluster analysis methods suggested a high degree of correlations as well as segregations among the investigated functions. Three main functional components, representing distinct domains, emerged: one concerned only subitizing, while the other two components - only partially segregated - concerned quantity representations as well as arithmetic, finger gnosis, and spatial processing.

The fact that the acuity of the system for apprehending a limited number of items in parallel (subitizing) did not correlate with any other numerical abilities supported the non-numerical interpretation of subitizing which has already been suggested by previous studies (Revkin, et al., 2008). However, it disconfirmed the hypothesis that subitizing is fundamental for the development of symbolic numerical abilities (Butterworth, 1999).

In contrast to subitizing, the other two domains showed more inter-cluster and intra-cluster interactions. The strong relation between symbolic and non-symbolic number comparison is coherent with functional imaging studies that showed a convergence across the symbolic and non-symbolic modalities towards a common cortical representation of quantity (Piazza, et al., 2007). This convergence was also predicted by the models of Dehaene and Changeaux (1993) and of Verguts and Fias (2005), according to which the acquisition of symbolic numbers determines a progressive cortical remapping of the preexisting neural system for numerosity. According to this slow “recycling” process, the correlation between symbolic and non-symbolic numerical comparison abilities is much stronger in first graders compared to preschoolers (see Experiment 1 of this thesis).

Interestingly, the ability to compare Arabic numbers also highly correlated with the success in solving arithmetical problems such as additions and subtractions. Indeed, in all these problems, Arabic numbers constituted the typical vehicle of numerical information for their solution. Performance in addition and subtraction problems is also strongly associated with finger gnosis. This correlation did not differ significantly between children that explicitly and overtly used finger-counting compared to those who did not use finger-counting.

Indeed, we did not find significant differences contrasting finger counters versus non-counters in all the investigated functions in first graders.

Considering the findings on preschoolers (Exp. 1), we can define two separate contributions of finger gnosis to the numerical domain. On one hand, before going to school, finger discrimination abilities are related to numerosity acuity possibly because of the existence of important connections among neighboring parietal regions supporting these two different functions (see Exp. 1). At the same time, no relation clearly emerged between finger gnosis and symbolic number comparison. This pattern is completely reversed in first graders: finger gnosis clusterizes with symbolic calculation abilities but became more independent than approximate number processing. These findings suggested a functional association between finger gnosis and arithmetical procedures (e.g. in additions, subtractions) which was mediated by the use of finger to count (finger-counting) that is explicitly taught during school ages.

The correlation data suggested that the degree of linearity in mapping numbers to a line seemed to be independent from the other numerical abilities, even if there was an almost significant correlation with both additions (p=.065) and finger gnosis (p=.070). Indeed, the PCA analysis associated it to the calculation component, indicating an early recruitment of spatial strategies for solving arithmetical problems such as the number line. Hierarchical clustering places this ability in between the calculation and the number domains, again confirming this idea. The use of spatial strategies in mental calculation, and especially in additions and subtractions (versus multiplications, which are mainly retrieved by memory (Dehaene, et al., 2003)) was demonstrated by the use of interference paradigms (Lee & Kang, 2002).

Another source of evidence for an automatic number-to-space mapping is the phenomenon of “operational momentum”. Empirically, this effect revealed the solving additions in which incorrect results was systematically overestimated when compared to the correct solution, and the subtractions, where the incorrect results was systematically underestimated compared to the correct solution (McCrink & Wynn, 2009).

In conclusion, cultural factors like the use of fingers and the association between ordered sequences to spatial positions allowed children to partially reshape their innate quantity representations so as to generate discrete representations of numerical quantities attached to symbolic numbers. The link between these factors was evident very early in development, as early as the end of the first grade, and therefore it was not surprising to observe it even in adult subjects.

Chapter 8

PREDICTIVE POWER OF NUMERICAL AND NON-NUMERICAL ABILITIES FOR ARITHMETIC: A LONGITUDINAL STUDY

8.1 ABSTRACT

Both quantity-related (e.g. number acuity) and non-quantity related abilities (e.g. finger gnosis, visuo-spatial processing) were previously shown to play an important role during the acquisition of formal arithmetic and number processing. However, the relation between these abilities and math achievement is often made by testing each of these functions individually.

In the present study, we take a more comprehensive approach and contrast the relative power of a large set of functions in predicting later achievements in number processing and mental arithmetic. We thus perform a longitudinal study on a group of children from kindergarten (T1) to the end of first grade (T2). The measures used for predictions (T1 measures) were numerosity comparison, symbolic number comparison, finger gnosis, visuo-spatial SPAN, grasping abilities and, as control tasks, face and object recognition. At T2 we additionally measured additions, subtractions, spatial mapping of numbers and subitizing skills.

Results indicate a strong continuity of non-symbolic number and finger acuity in time as a contrast to a discontinuity in symbolic number processing. It suggests an important functional reorganization of the internal representation of numerical quantity during first grade. In terms of predictions, we find that good predictors of performance in arithmetical tasks are verbal number processing, visuo-spatial abilities and finger gnosis. Moreover, hierarchical multiple regressions reveal a relative independent contribution of finger gnosis at T1 and at T2 in influencing arithmetical abilities.

8.2 INTRODUCTION

The acquisition of abstract concepts of exact numbers during school ages is a long process that involves the contributions of preexisting numerical and non-numerical abilities.

Within the number domain, the innate sensitivity for approximate numerical information (called Number Sense) is thought to constitute the functional and neural base on which we build an exact representation of number and to compute arithmetical problems (Dehaene, 1997). However, other non-numerical abilities may play a crucial role in the transition from an approximate to an exact representation of number and even for calculation such as finger gnosis, fine visuo-motor coordination, and visuo-spatial abilities (Butterworth, 1999). Finger discrimination is based on an intact internal schema of one own fingers and it represents a good predictor of the subsequent mathematical achievements in first and second grade children (Fayol, et al., 1998; Marinthe, et al., 2001), in contrast with other cognitive skills such as reading abilities.

Moreover, finger counting constitutes a frequent strategy used by children to count and to create discrete representations of numerical quantities (Jordan, et al., 2008). Interestingly, repeated training sessions on finger gnosis in first graders have beneficial and indirect effects on processing of Arabic digits (Gracia-Bafalluy & Noel, 2008). As numerosity discrimination ability, impairments regarding finger gnosis are reported in dyscalculic children (Benson & Geschwind, 1970). Automatic finger-number associations were also reported in human adults as a developmental trace of finger-related strategies during numerical tasks (Andres, et al., 2007; Di Luca, et al., 2006; Sato, et al., 2007). More recently, a TMS study in adults revealed impairments in both digital and numerical tasks after the stimulation of angular gyrus suggesting the anatomical proximities of the regions involved in numerical and finger discriminations (Rusconi, et al., 2005). On this regard, both VIP and AIP areas (involved in quantity and finger –related processes, respectively) lie in close proximity within the intraparietal sulcus, suggesting a high probability of shared circuits between a quantity-related circuit and the processing of proprioceptive and visuo-motor information of hand-related actions (Bodegard, et al., 2001; Bushara, et al., 1999;

Hubbard, et al., 2005; Jancke, et al., 2001). Despite some evidences during primary school, little is known about the predictive power of finger gnosis on match achievement in preschool age, when the effect of functional factors (e.g. finger counting) is limited.

Another important aspect of the finger-number interactions regards the fine visuo-motor co-ordination during grasping movements. Indeed, the precision of grip aperture while grasping depends, among other parameters, on the estimation of the physical magnitude of objects (Pryde & Roy, 1998). At the behavioral level, a modulation of the numerical magnitude on the size of grip aperture during grasping was found in both adult and children (Andres, et al., 2004; Lindemann, et al., 2007; Moretto & di Pellegrino, 2008; Pryde & Roy, 1998; Song & Nakayama, 2008). Interestingly, manual tasks such as objects manipulations (Binkofski, et al., 1999), grasping (Culham, et al., 2003), reaching (Cohen & Andersen, 2002), and visual pointing (Connolly, et al., 2003) rely on the same parieto-premotor networks that is also active during numerical tasks, such as additions, subtractions, multiplications and magnitude comparisons (Dehaene, et al., 2003). On this line, some studies showed that the motor components of some actions, such as pointing and grasping movements seem to be modulated by numerical information (Andres, et al., 2004; Song & Nakayama, 2008). Again, patients with iimpairments in grasping abilities quite often also exhibit calculation disabilities (Yeo, 2003). However, to our knowledge nothing is known on the relation between grasping abilities and mathematical abilities in children.

Another non-numerical ability that is thought to play an important role in numeracy development is the ability to deal with spatial information (Hubbard, et al., 2005). The interplay between space and number seems may derive from the culturally mediated tools, such as the number line (where numbers are associated to precise spatial positions ordered on a left-to-right oriented line), the Cartesian axis, the measurement systems (such as the meter and/or the thermometer). These cultural constructions may elicit and contribute to an automatic association between the representations of number and space (Berch, et al., 1999; Hubbard, et al., 2005). Interestingly, during childhood, visuo-spatial span (as measured by variants of the Corsi test) represents another good predictor of subsequent numerical performance in children (De Smedt, et al., 2009; Holmes, et al., 2008; Rasmussen &

Bisanz, 2005). In fact, visuo-spatial deficits are often found in children with developmental dyscalculia (for a review, see (Wilson & Dehaene, 2007)). In adults, a vast body of evidence showed several types of number-space interactions such as SNARC (Spatial Numerical Association of Response Codes) effect (Dehaene, et al., 1993; Hubbard, et al., 2005).

Considering the pattern of interactions and contributions of quantity-related (numerosity acuity) and non-quantity-related (finger, space, grasping) abilities to the development of arithmetical abilities, we performed a longitudinal study on a group of children from kindergarten (T1) to the end of first year if primary school (T2). The tasks used for predictions (T1 measures) were numerosity comparison, symbolic number comparison, finger gnosis, visuo-spatial SPAN, grasping abilities and, as control tasks, face and object recognition. At T2, we consider also the children performance in additions, subtractions, spatial mapping of numbers and subitizing skills.

8.3 METHODS

8.3.1 Participants

This longitudinal study was initially based on 28 preschoolers attending the last year of preschool, recruited from two kindergartens in Rovereto (T1). Of this initial group, only 19 children (mean age=84 ±4 months; right-handed= 89.5%; males= 52 .7%) took part in the study one year later (T2) after attending Grade1 classes. The study was approved by the local ethical committee. For each child we obtained signed informed consent from the parents (or the legal representatives).

8.3.2 General testing procedure

Each child was tested twice, in two sessions separated by one year on average. During the first session (T1 phase), which took place in quiet rooms of two kindergarten schools in Rovereto (IT), each child was administered a set of cognitive tasks exploring several non-verbal functions (quantity comparisons, finger gnosis, spatial short term memory, grasping, faces and objects recognition). During the second session (T2 phase), which took place in the experimental psychology laboratories of the University of Trento, in Rovereto (IT), the same children performed another set of tasks, some of which were identical to the ones performed one year before (quantity comparisons and finger gnosis), while others were different and tapped on newly acquired numerical and calculation abilities (enumeration, calculation, and number-to-space mapping, table 1). Here, we simply report a reminder with the main details for each task (for more detailed descriptions see Experiment 1 and 2 of the present thesis), their relative administration phase and indexes used for the longitudinal correlations.

Numerosity comparison (pre-symbolic): T1&T2

In this test, children were presented pairs of dots arrays on a computer screen. Their task was to point to the array containing more dots. The numerosity of the paired arrays was ratio-controlled. On the basis of accuracy distribution we extracted for each child the internal Weber's fraction, an index of the precision of the judgment (Piazza & Izard, 2009). The internal Weber fraction was taken as the index of numerosity comparison ability.

Number comparison (symbolic): T1&T2

This test is the symbolic version of the numerosity comparison test: children were presented with two digits symbolic numbers and were asked to choose the numerically large one. In T1 stimuli were presented in the auditory modality, while in T2 they were presented visually, as Arabic digits. The ratio between the numbers was manipulated. Mean accuracy for each child was taken as the index of number comparison ability.

Fingers gnosis: T1&T2

In this test children sat on a chair in front of a table with their dominant hand placed on the table covered by a panel from their sight. The experimenter then touched one or two (in T1), or one, two, or three (T2) fingers in sequential order. After removing the panel, the children were asked to point to the finger(s) that were previously touched, maintaining the same order. Mean accuracy for each child was taken as the index for finger representation ability.

Visuo-Spatial SPAN: T1

The “Corsi block-tapping” task was administered. The SPAN (the higher number of blocks correctly identified by children) of each child was taken as the index of visuo-spatial abilities.

Grasping abilities: T1

The kinematic analysis of grasping allowed us to obtain the maximum grip aperture while children were grasping objects of either small or big size. This measure that is known to correlate with object size and it reflects high precision grasping. Thus, we used the difference between the maximal grip aperture during large object grasping and the maximal grip aperture during small object grasping as a measure of the ability to modulate grasping on the basis of objects’ size (thus indirectly grasping precision).

Faces and Objects recognition: T1

Cards representing faces and objects were showed to child, one at a time, for some seconds. Then, the experimenter mixed the familiar stimuli with cards representing novel faces and objects, and presented them to the child, who had to identify the cards already seen. D’ (defined as hits-false alarms recognition performance) for each child was taken as the index of faces and objects recognition abilities.

Additions: T2

Children had to solve orally 20 additions problems (addends between 1 and 9) showed on a Pc screen. The experimenter noted the children’s responses. Mean accuracy for each child was taken as the index of the ability to solve additions.

Subtractions: T2

Children had to solve orally 18 simple subtractions showed on a Pc screen. The experimenter collected the children's responses (accuracy). Mean accuracy for each child was taken as the index of the ability to solve subtractions.

Number-to-line test (thereafter "Line"): T2

Children were shown a horizontal white segment of a black screen labeled with "1" on the left and "10" on the right side. For each trial, children had to indicate the position on the segment of a top-centered target-number (Arabic digit). The children placed the number by using the arrow of the mouse. For each child, we performed a linear regression on the estimated and the correct positions, and took the goodness of the linear fit (R^2) as a measure of the linearity of the number-to-space mapping.

Enumeration: T2

Sets of 1 to 8 dots were flashed on a screen and subsequently masked. Children were asked to report the number of dots by saying that number out loud. For each child, we fit the full accuracy distribution with a sigmoid function, and took the inflection point as a measure of the subitizing range.

Table 1

T1: 5 years old	T2: 6 years old (1 year later)
Numerosity comparison	Numerosity comparison
Symbolic Number comparison	Symbolic Number comparison
Finger gnosis	Finger gnosis
Visuo-spatial SPAN	Additions
Grasping abilities	Subtractions
Face recognition	Line
Objects recognition	Subitizing

8.4 RESULTS

8.4.1 Single tasks results

For a full description of the results in each of the proposed tasks, please see chapter 5 and 6 of the present thesis.

8.4.2 Correlation from T1 to T2

To start exploring the data in a longitudinal perspective, we first performed simple correlations between the tasks' indices at T1 and the tasks indices at T2. Three subjects were excluded from this analysis because the R^2 of the fitting procedure used to derive w (at T2) did not converge (N=1) or was very low (<.07, N=2). In order to help the reader, we report two correlation matrices, one for the "pure longitudinal" tasks only, i.e. tasks for which we acquired one measure in T1 and one measure in T2 (Table 2), and the other including all tasks in T1 and their correlations with all "new" tasks in T2 (Table 3). As for the pure longitudinal measures, we observed strong correlations between analogous tasks performed in T1 and T2 only for numerosity comparison (β =.676, p<.005) and finger gnosis (β =.597, p<.020) but not for symbolic number comparison (β=.069, p=.800). As for the pattern of correlations between the measures in T1 and the new measures in T2, we observe that accuracy in solving additions and subtractions is directly predicted by accuracy in symbolic number comparison and by the visuo-spatial SPAN one year earlier. Second, the linearity of the number-to-space mapping is also predicted by accuracy in symbolic number comparison one year earlier. Finally, subitizing is not predicted by any numerical or non-numerical ability one year earlier.

Table 2

T1 / T2	Numerosity comparison	Symbolic number comparison	Finger discrimination
Numerosity comparison	**β=.676** **p=.004**	β=.158 p=.559	β=.381 p=.146
Symbolic number comparison	β=.216 p=.421	β=.069 p=.800	β=.187 p=.488
Finger discrimination	β=.059 p=.827	**β=.716** **p=.002**	**β=.597** **p=.015**

Table 3

T1 / T2	Numerosity comparison	Symbolic number comparison	Finger discrimination	Grasping	SPAN	Faces recognition	Objects recognition
Additions	β=-.126 p=.642	**β=.612** **p=.012**	β=.182 p=.499	β=-.338 p=.201	**β=-.590** **p=.016**	β=.039 p=.886	β=.205 p=.446
Subtractions	β=-.175 p=.516	β=.310 p=.242	β=.101 p=.710	β=-.214 p=.426	**β=-.621** **p=.010**	β=.063 p=.817	β=.342 p=.195
Number-to-line	β=-.108 p=.689	**β=.621** **p=.010**	β=.230 p=.392	β=.075 p=.781	β=.020 p=.942	β=-.328 p=.214	β=-.427 p=.099
Enumeration	β=-.249 p=.352	β=-.245 p=.360	β=-.350 p=.183	β=.436 p=.071	β=.238 p=.375	β=-.051 p=.850	β=-.145 p=.592

8.4.3 Hierarchical Models

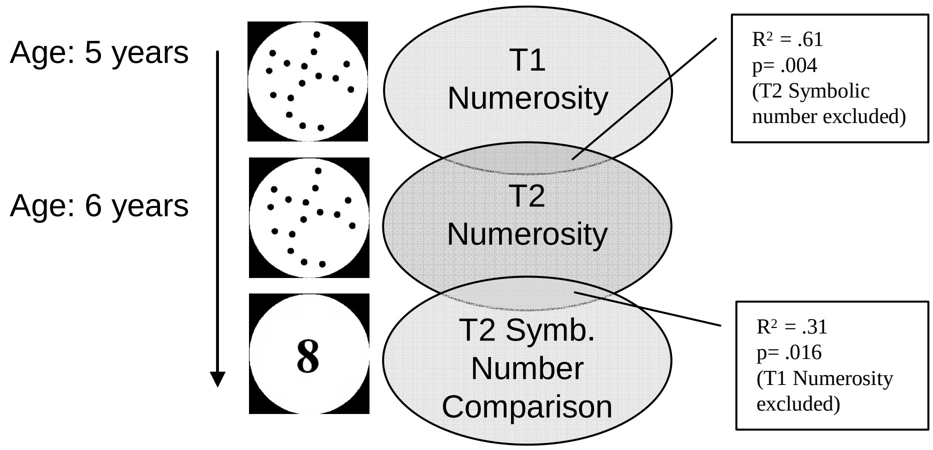
In our longitudinal simple correlational analysis, we did not observe the expected correlations between finger gnosis and numerosity acuity at T1 on one side and symbolic number processing (number comparison and mental arithmetic) at T2 on the other. However, previous findings (see Exp. 1 and 2) showed strong interactions between these abilities in both preschoolers and first graders. In preschoolers, finger gnosis, number comparison, and numerosity acuity were part of the same functional cluster, while in first graders finger gnosis, number comparison and mental arithmetic were heavily correlated. However, using a longitudinal approach, it is possible that functional discontinuity during development masks the presence of genuine but more complex correlations between these functions. Here we thus considered the most relevant discontinuities.

The relation between non-symbolic and symbolic number processing during development

Considering the strong correlation between numerosity acuity and symbolic number comparisons found in first graders (T2: $\beta=.59$, $p<.020$) and between numerosity acuity at T1 and T2 ($\beta=.68$, $p<.005$), we expected that numerosity acuity at T1 would predict symbolic number processing at T2. However, no significant relation was found between these two factors in the longitudinal analysis (see table 2). We reasoned that the absence of correlation could indicate the presence of a developmental discontinuity in numerosity acuity between kindergarten and first grade. This discontinuity would indicate that the presence of cultural factors (the introduction of symbolic numbers and arithmetic) may account for (part) of the refinement of numerosity acuity in first graders.

Thus, we carried out three hierarchical multiple regressions among the numerosity acuity (measured with the Weber's fraction) at T1, at T2 and the Arabic number processing at T2, taken two at the time and excluding the effect of the remaining factor of the triad. The results first confirmed an absence of a direct predictive power of numerosity acuity at T1 for the symbolic number processing at T2, even partialling out the effect of numerosity acuity at T2. Second they show that numerosity acuity at T2 still correlated with symbolic number processing at T2 even after partialling out the effect of numerosity acuity at T1 ($r^2= .31$; $p< .020$). Taken together these results suggest that part of the refinement of numerosity acuity during first grade is due to maturation, while part is due to the acquisition of symbolic numbers.

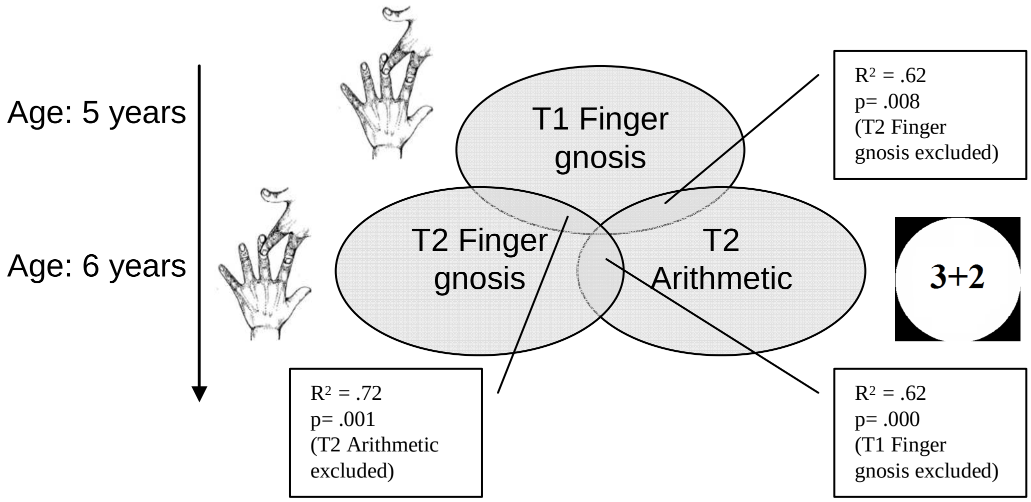
Model 1



The relation between finger gnosis and arithmetic during development

Analysis of correlations across tasks in our group of first graders (see chapter 6), revealed correlations between finger gnosis at T2 and arithmetical proficiency (β=.68, p<.005, and β=.45, p=.054, for additions and subtractions respectively). Longitudinal analysis between finger gnosis at T1 and T2 also revealed a significant correlation (β=.60, p<.020). However, surprisingly, longitudinal correlations of finger gnosis at T1 and arithmetical proficiency at T2 were not significant. Thus, in order to better explore the unclear predictive role between finger gnosis and arithmetical performance, we applied three hierarchical multiple regressions among finger gnosis at T1 and T2 and arithmetical outcome for additions in T2, taken two at the time and excluding the effect of the remaining factor of the triad. Results revealed a relative independent contribution of finger gnosis at T1 (r^2= .62; p< .010) and at T2 (r^2= .62; p< .000) in influencing arithmetical abilities. Indeed, finger gnosis at T1 became a significant predictor of arithmetic only when the shared variance with finger gnosis at T2 was excluded. This suggests that even finger gnosis may exhibit a qualitative change during the development under the intense effect of functional factors (finger counting) that support the relation with arithmetical abilities.

Model 2



8.5 DISCUSSION

The transition from kindergarten to school determines implicitly important new functional associations, which sometimes can create discontinuities during the cognitive development. Considering that the first year of school represents an intensive period for the acquisition of arithmetical operations and the symbolic number system, we tried to delineate the principal contributions of each preexisting abilities to numerical and arithmetical domains.

Continuities and discontinuities during development

Firstly we considered the relations among those tasks that we repeateded at T1 and T2: numerosity comparison, number comparison and finger gnosis. While we observed a strong continuity in time indicating consistency in children's abilities to discriminate dot arrays, and to correctly identify their fingers, we found a discontinuity (absence of correlation) in the ability to compare symbolic numbers between the last year of preschool and the end of first grade. In other words, performance at T1 did not significantly predict performance on the same task at T2. As depicted in figure 1, the improvement from T1 to T2 for the number comparison task was not homogenous among children. Some of them improved more than others, and curiously, few of them (N=3) exhibited even an inverse trend (showed worst performance in T2 compared to T1). It would be tempting to speculate that this discontinuity is due to a major reorganization of the internal representation of numbers during first grade, and that this reorganization may not be strongly influenced by the pre-training intuitions that children have on symbolic numbers. Indeed, a key change during first grade is the introduction of Arabic digits, which are not formally taught (at least in Italy) during preschool. Moreover, the introduction of Arabic digits is also accompanied with procedures such as finger counting and spatial mapping of numbers. It is possible that these procedures affect the children's internal representation of numbers in a way that is idiosyncratic.

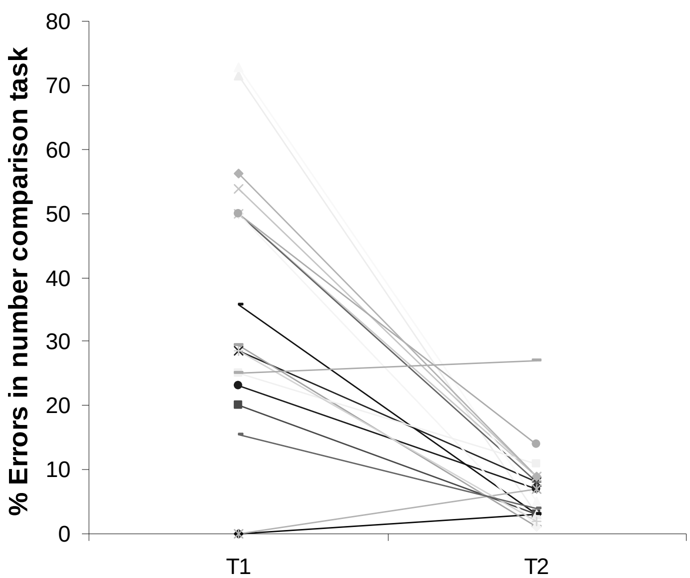


Fig. 1. Error rates for the symbolic number comparison respectively in T1 and T2 for each participant.

However, we should consider a caveat in the interpretation of these results, which relates to the fact that while in T1 the stimuli were presented as verbal numbers, in T2 they were presented visually as Arabic digits. While we ensured that all children could correctly read the Arabic digit numbers by asking them to read them aloud before making their comparative judgment, it is possible that the difference in the input modality may have masked a potential convergence across modalities towards internal representation of numerical quantity. Thereofore, this difference may have negatively influenced the correlation between T1 and T2 in number comparison scores. Indeed, while several results reported a convergence between the different types of modalities towards a common representation of magnitude (Dehaene & Akhavein, 1995), other studies found that Arabic and verbal numbers were processed in a notation-dependent manner, suggesting that Arabic and verbal codes are represented separately even at the semantic level (Cohen Kadosh, Henik, & Rubinsten, 2008).

Processing symbolic and non-symbolic quantity

Since previous research have reportied an important relation between non-symbolic and symbolic numerical abilities, we further explored the relation regarding the link between them (Gilmore, et al., 2007; Halberda, et al., 2008). By using hierarchical regressions, we observed that the precision of the internal representation of numerical quantity in first graders resulted from independent contributions of the previous ability to discriminate numerosity (one year before), and also the acquisition of a new system to represent and manipulate exact numerosity (Arabic digits). Indeed, the hierarchical regression showed that the independent portions of variance of the non-symbolic acuity in T2 were accounted for by the previous numerosity sensibility in T1, and the precision of symbolic number comparison in T2. In other words, these results suggested that the observed refinement of number acuity (at least in first grade) was partially due to the acquisition of symbolic Arabic numbers. Such partial remapping of non-symbolic number representations during the symbol acquisition was previously predicted by a computational model (Verguts & Fias, 2005).

Grasping abilities at T1 also seemed to predict the ability to perform Arabic digits comparison at T2 (β =-.512, p=.043). Indeed, grasping ability as defined by our measure is the ability to modulate grip aperture on the size of the to-be-grasped objects during the execution of grasping movement. This modulation is only possible when a correct estimation of the objects' magnitude is performed. Behaviorally, the effect of Arabic magnitude of grip aperture while grasping objects was demonstrated in a recent study (Badets, et al., 2007) in which the small versus big magnitude of numbers was able to modulate the grip aperture determining, respectively, an overestimation vs. underestimation of the object size to grasp. Our results thus confirmed that numerical and non-numerical magnitude processing is deeply related to each other and influences one another even during development.

Arithmetic, finger and spatial processing

Coherently with previous research pointing towards an important relation between finger processing and arithmetical abilities (Noel, 2005), we observed a strong correlation between finger discrimination abilities at T1 and arithmetical abilities at T2. Nevertheless this correlation emerged only when the finger discrimination abilities at T2 was partialled out.

This suggested the existence of a partial refinement of finger gnosis in first graders which was not directly explained by the preexisting finger gnosis in T1. This discontinuity, masking the predictive power of finger gnosis at T2 for the subsequent arithmetical performance was possibly due to an increasing influence of cultural factors, (like finger counting).

Then, we also observed that spatial memory (SPAN) predicted the arithmetical performance one year later, confirming previous observations that spatial processing is a key component in mental arithmetic. Indeed the contributions of space in the numerical domain even during simple calculation are well-known (see "Operational momentum", (McCrink, et al., 2007)). Specifically, spatial influences on numerical processing - consistent with the orientation of the mental number line- can emerge during the solution of arithmetical problems.

Chapter 9

GENERAL DISCUSSION

From the results of these experiments, it is possible to trace the main contributions of this thesis to cognitive development, specifically on numerical cognition.

9.1 Developmental trajectories of numerosity acuity and symbolic numbers

Numerosity sensitivity represents one of the functions present at birth (Izard, et al., 2009). Despite some knowledge about its modifications across the life-span (Halberda & Feigenson, 2008), little is known about its interplay with the system for representing exact numerical quantities that emerges during the development as the result of a long process of symbolization of numerosity into discrete quantities through the use of symbolic numbers. In particular, while it has always been suggested that the approximate number system has a causal role in determining maths achievement, the results to date are still equally compatible with the opposite interpretation which states that the ability to manipulate symbolic numbers and perform calculation is not the consequence but the cause of the refinement in the acuity of the approximate number system (Halberda, et al., 2008; Verguts & Fias, 2005).

Our data concerning the developmental trajectory of numerosity acuity (measured by the internal Weber's fraction) are in favor of a maturational interpretation of the refinement of numerosity acuity during development before schooling. It is in line with previous observations pointing towards a dramatic refinement during the first years of life (Piazza & Izard, 2009), which cannot be explained by cultural factors. The maturational interpretation seems also to be in line with recent cross-cultural studies showing that, even in cultures with limited number lexicon and with absence of formal mathematical education, adult number acuity appears to be quite similar to adults from educated western society (Pica, et al., 2004). However, it is possible that the published research in those pre-numerical cultures lacks the necessary sensitivity to reveal potential differences across cultures.

Indeed, our data supports the idea that part of the observed refinement of the numerosity acuity during the first year of primary school is also accounted by the introductions of symbols for numbers and arithmetic. Indeed a qualitative change (partial recycling) of the numerosity acuity was found in children at the end of the first year of primary school. In this way, the impact of educational and cultural factors on numerosity acuity increases, and becomes additionally relevant, especially in school age when education influences robustly the experience and the practice with numerical quantity.

In the same manner, also the symbolic verbal representation of numbers (number words) is subject to refinement during development. From the age of 3 to 5 years, the ability to compare verbal numbers increases from a random choice (52%) up to 25% of error rates.

It is probable that the verbal numbers knowledge and counting can play a role in the improvement of representation of numbers, contributing to provide an insight about the numerical organization at least for the first few numbers (e.g. one, two, three etc.) based on their order relations and on the understanding of recursive aspects (e.g. the linguistic transparence) of verbal numerical sequence. It is particularly evident for larger numbers (e.g. twenty-three, thirty-three, forty-three).

Using a cross-sectional approach, the interplay between presymbolic (dots) and symbolic (number words, Arabic digits) numerical representations was investigated from childhood to adulthood. In preschoolers, even though data clustering analysis (PCA) associated the two functions, we observed no significant correlations across children, suggesting that these representations are only very slightly linked in preschoolers. Interestingly, other non numerical variables (such as length, luminance) followed the Weber’s law, accordingly to a ratio-based modulation on the behavioral performance (Dayan & Abbott, 2001). Due to this shared Weber-like behavior for both numerical and non-numerical variables, ratio-dependent performance cannot be considered per se as an evidence of converging development between numerosity acuity and symbolic number system. On the contrary, stronger evidences can be taken from correlational studies. In this respect, the data presented in this thesis showed that at preschool age, presymbolic and symbolic number processing follows partially separated developmental trajectories. Successively, the first evidence for strong converging trajectories between presymbolic and symbolic numerical representations emerges behaviorally from the first year of primary school. During this long period, characterized by an intensive arithmetical education, the manipulation of exact numbers could additionally contribute to the formation of a deeper association between numerical symbols (e.g. Arabic digits) and an innate and approximate sensitivity for numerosity.

Thus, the progressive effect of symbolic numbers on the preexisting numerosity acuity can be elicited on the basis of an intense manipulation of precise numerical quantities from the initial verbal numbers and during the first years of school with the introduction of a new symbolic system for numbers, the Arabic digits.

Moreover, behavioral data shows that this cortical recycling does not concern the overall system dedicated to numerosity acuity, but just a part of it. Indeed different proportions of the inter-subjects variability in numerosity acuity at 6 years of age are correlated to the pre-existing numerosity acuity and to the recently acquired symbolic number processing. The fact that the numerosity acuity in preschool does not directly predict the symbolic number processing after 1 year can support the idea of a partial qualitative change (in terms of retuning) within the numerical sensitivity during the first year of primary school. Thus, the manipulation of symbolic numbers (in the form of Arabic digits) can determine a quite important change in the internal representation of quantity, strengthening the link between a preexisting ability to process numerosity and a precise symbolic system for numbers.

9.2 Finger gnosis and its relation to number domain

During early childhood, finger gnosis, as well as numerosity acuity, develop on base of maturation processes involving the hand schema and the integration of visuo-tactile inputs.

In our digital task, since we asked preschoolers to point to the finger(s) that were previously touched, both these factors can play a relevant role. On one hand, the correct movement of a body part to another one is influenced by the sensory differentiation of the locus or place which is the target of the movement. Second, fingers are stimulated tactically, but the children's response is based on a visual-guided movement of the hand that implicitly involves two-sense integration. The effects of manual practice and manipulations over time can affect the chronological organization, integration and interpretation of sensory inputs during the development (Lefford et al., 1974).

A relevant result from our experiments concerns the curious trajectory of finger gnosis in relation to the number domain. This relation appears early in both preschool and school age, but shows relevant peculiarities.

Before going to school, children exhibit a genuine relation between fingers and numerosity discrimination. Due to a limited effect of cultural/educational factors at this age, the anatomical proximity of numerical and digital regions within the IPS can be suggested to explain this relation. This view is also supported by the presence of a strong and early number-finger relation particularly in 3-year old children.

Then the interplay between number and digital domains changes during the first year of primary school. In first graders, this relation takes the form of a functional association involving finger gnosis and arithmetical abilities. At this age, thanks to its contributions to calculation, finger counting is thought to play a mediator role in shaping this relation.

Taken together, localizationist and functionalist interpretations on the development of digital and numerical interplay in childhood were considered (for a review see (Penner-Wilger & Anderson, 2008)). Indeed, in the early preschool age, this association is mostly driven by anatomo-functional connections not modulated by experience. Therefore, before going to school, the existence of important connections among close parietal regions supports the relation between finger discrimination abilities and numerosity acuity. Curiously, in first graders, this pattern is modified by the functional use of finger to count (finger-counting) that is explicitly taught during school ages. Indeed, finger gnosis correlates robustly with symbolic calculation abilities (versus approximate number processing), suggesting a functional association between finger gnosis and arithmetical procedures (e.g. additions, subtractions).

9.3 Contributions of quantity-related functions to arithmetical achievement

From longitudinal and cross-sectional data, symbolic number comparison seems to be directly related to arithmetical abilities. Accuracy in symbolic number comparison tasks in both preschoolers and first graders correlates with arithmetical abilities. This finding supports the idea that formal arithmetical procedures recruit the manipulation of exact numbers, and that knowledge of numbers predicts achievement in arithmetic. This finding is not trivial if one considers that while the number comparison tasks involved large two digits numbers, most arithmetical problems involved the manipulation of much smaller numbers. Thus, the relations does not simply reveal knowledge of the precise numbers involved, but a more general phenomenon in which proficiency in manipulating symbolic numerical quantities in preschool is a good predictor on achievement in simple arithmetic in first grade. Moreover, our data shows that (verbal) number comparison abilities in preschoolers predict the precision of the linearity of the (Arabic) numbers to space mapping in first graders, suggesting that a refined knowledge of magnitude relations between numbers influences the linearization of the internal representation, irrespective of the symbolic notation used (verbal or Arabic)

Quite surprisingly, neither in preschooler nor in first graders, numerosity acuity is directly involved in the arithmetical achievement. Despite the lack of a direct link between an innate system for numerosity and the arithmetical abilities, numerosity acuity seems to support more strongly the symbolic exact representation of numbers which, in turn, has a fundamental role for arithmetical outcome.

9.4 Contributions of non quantity-related functions to arithmetical achievement

A last important point concerns the predictive power of non-numerical parietal functions on the number domain and arithmetical abilities in primary school.

Visuo-spatial memory represents the most relevant contribution to arithmetical domain. Indeed, spatial working memory is implied in the solution of addition and subtraction problems. However, the role of space in problem solving is not new. A spatial representation of numbers was suggested and conceptualized as a mental line with left-to-right increasing numbers. This spatial metaphor of numbers is also used in arithmetical procedures. On this regard, an example of spatial influence is represented by the presence of an "operational momentum" while solving arithmetical problems (McCrink & Wynn, 2009).

Subitizing skill (here considered as a visuo-spatial function because it represents the result of our ability to detect precisely and rapidly a limited number of visual items) constitutes a separated component from the number and arithmetical domains supporting the non-numerical interpretation of this ability, thought to be more dependent on the visual parallel processing of small numerosities. As a matter of fact, our visual system can select a fixed number of about four objects or can encode their details, based on their spatial information. It explains the limited capacity of working memory to process visual information (Xu & Chun, 2009). However contradictory evidences emerge from clinical evidence in which children with dyscalculia seem to count sets of items even within the typical subitizing range (<4), exhibiting a progressive increase of response times for each additional item (Koontz & Berch, 1996. Moreover, coherent with Butterwoth's proposal (Butterworth, 1999, 2005), in a vast study of first graders (Penner-Wilger, et al. 2007), subitizing skills predict directly calculation skills.. In this regard, three main independent components can support the human numerical representation and processing: an innate capacity to process small numerosities (e.g. subitizing), secondly the functional use of fingers (fine motor ability), and the precision of mental finger representation (finger gnosis).

In addition, a second important contribution in explaining the achievement in arithmetic in first graders seems to be finger knowledge. Indeed, in first graders, finger knowledge strongly correlate with arithmetical achievement. Specifically, not only finger gnosis correlates but also partially predicts the subsequent arithmetical achievement. Indeed independent contributions of finger gnosis at T1 and at T2 influence arithmetical abilities.

This data is in accordance with a very well documented fact that finger counting represents a useful and spontaneous strategy used by children to solve the problems. Again, counting with fingers is thought to be an important step from a continuous representation of numerosity to discrete numbers (Jordan et al., 2008). Curiously, the performance in addition and subtraction problems does not significantly differ between children that explicitly and overtly used finger-counting compared to those who did not use finger counting. Actually, we did not find any significant differences contrasting finger counters versus non-counters in all the investigated functions in first graders. It is likely that the result is due to the fact that, in our case, both finger-counters and non finger-counters respectively use explicit or implicit finger-related processes to count.

9.5 Practical implications

All these findings represent an important input within the rising framework of "educational neuroscience", regarding new prospective for mathematical education at school. Following this line, innovative teaching methods should include not only typical numerical components (such, as numerosity acuity) but also take into considerations the cognitive contributions of other non-numerical parietal functions (e.g. finger gnosis, space processing, grasping abilities) with the aim to improve the arithmetical learning of symbolic numbers and arithmetical procedures in first graders.

Meanwhile, new educational plans about "proto-mathematic" should be introduced from preschool age so as to strengthen and boost the early numerical abilities. In this way, preschool children may have a robust numerical knowledge and processing that will help them during the acquisition of the formal arithmetic at school.

Finally, these findings allow us to trace additional evidences regarding the complex pattern of arithmetical deficits during childhood (developmental dyscalculia) and the role of non-numerical functions for new approaches about the rehabilitation of numerical impairments.

9.6 Limits and future directions

Although these studies render a clearer cognitive panorama of preschool cognitive development, the kindergarten-to-school transition appears more uncertain and confusing.

Indeed, despite typical linear trends of cognitive functions during the preschool age, important and relevant behavioral discontinuities can be found in first graders. These changes may represent the result of the educational influence on the functional reorganization of the brain that can elicit quantitative and qualitative modifications in the behavioral performances in various tasks and in their interrelations across ages. For these reasons, it seems highly necessary to understand better this transition phase with further investigations.

Moreover, a critical observation from the literature concerns the paucity of scientific evidences regarding preschoolers compared to school age children, in particular their cognitive development of numerical abilities and educational implications.

Specifically, additional investigations could test the real functional association between functions (e.g. number processing and finger gnosis) through cognitive training at school. An example on this line derives from a recent study (Gracia-Bafalluy & Noel, 2008) regarding the functional link between finger gnosis and number skills. Surprisingly, these authors found that training in finger discrimination increases not only finger gnosis but it improves indirectly numerical performance in school age children. Taken together, cognitive training on specific functions can represent an interesting research line of educational neuroscience to improve learning and teaching methods in both preschool and school age children.

Chapter 10
APPENDIX

Gender differences and cognitive development

In the study on preschoolers (Exp. 1), we consider also the possible effect of gender on cognitive development contrasting male versus female performance, especially regarding the developmental trajectories of parietal functions.

Results

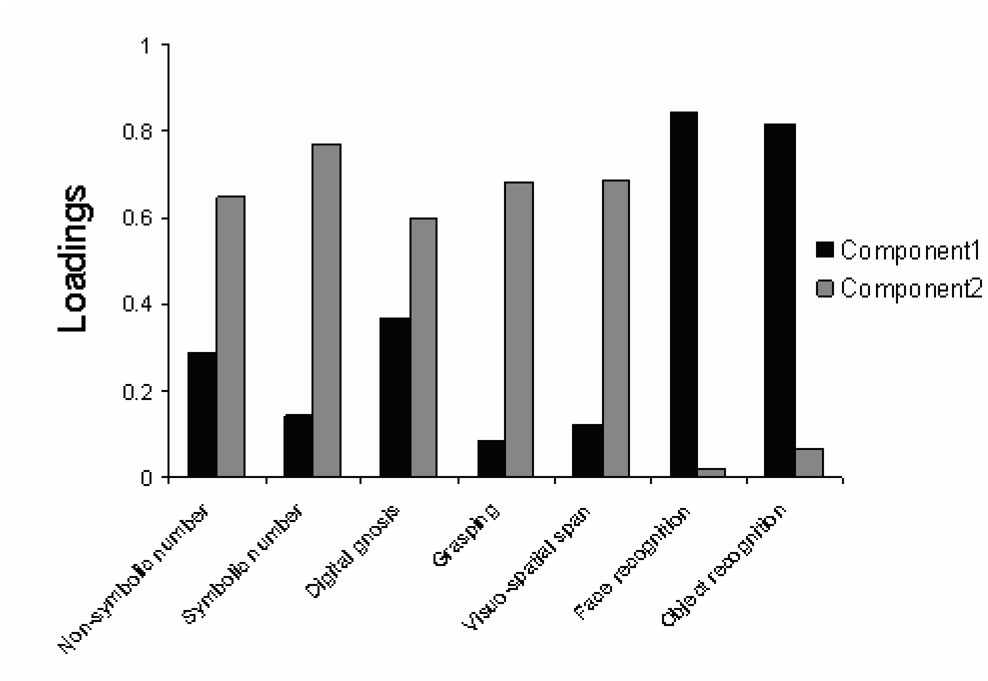
The two samples do not show relevant differences in terms of either age distribution [t(42)=-1.3; p=.197] or task performance (all comparisons n.s.). Here, we report briefly the significant correlations between tasks (p<.050).

Table 1

	Numerosity comparison	Symbolic number comparison	Finger discrimination	SPAN	Grasping	Faces recognition	Objects recognition
Numerosity comparison							
Symbolic number comparison	♂ - ♀(.06)						
Finger discrimination	♂-♀	♂(.06) - ♀					
SPAN	♂-♀	♂-♀	♂-♀				
Grasping		♂	♂	♂			
Faces Recogn.							
Objects Recogn.						♂-♀	

Significant correlations for ♀ female ♂ male

Correlations analysis and PCA (fig. 1) showed similar developmental trajectories of the parietal and ventral functions in male and female children from 3- to 6-years old. The only cross-gender difference concerns the stronger interaction of grasping abilities with most of parietal functions in male children compared to female counterpart (see table 1).



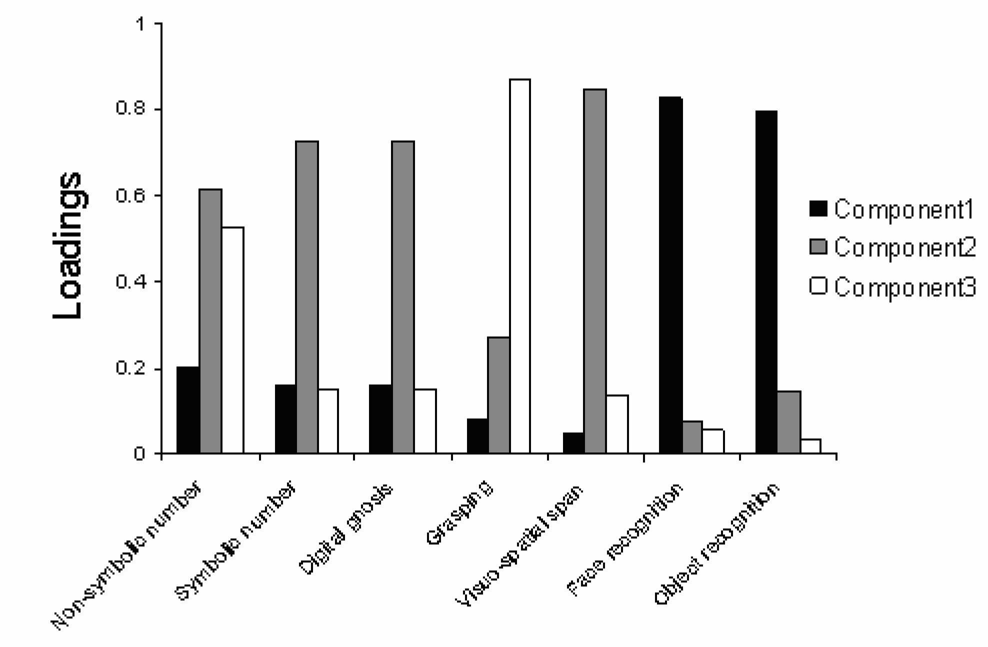


Fig. 1. PCA among tasks and divided for gender (on top: male, below: female). Coefficients of linear correlation (loadings) express the degree of influence of each variable on the component.

Chapter 11
REFERENCES

Alarcon, M., DeFries, J. C., Light, J. G., & Pennington, B. F. (1997). A twin study of mathematics disability. *J Learn Disabil, 30*(6), 617-623.

Andres, M., Davare, M., Pesenti, M., Olivier, E., & Seron, X. (2004). Number magnitude and grip aperture interaction. *Neuroreport, 15*(18), 2773-2777.

Andres, M., Seron, X., & Oliver, E. (2007). Contribution of hand motor circuits to counting. *Journal of cognitive neuroscience, 19(4)*, 563-576.

Andres, M., Seron, X., & Olivier, E. (2005). Hemispheric lateralization of number comparison. *Brain Res Cogn Brain Res, 25*(1), 283-290.

Ansari, D., Dhital, B., & Siong, S. C. (2006). Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes. *Brain Res, 1067*(1), 181-188.

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

Aron, A. R., Behrens, T. E., Smith, S., Frank, M. J., & Poldrack, R. A. (2007). Triangulating a cognitive control network using diffusion-weighted magnetic resonance imaging (MRI) and functional MRI. *J Neurosci, 27*(14), 3743-3752.

Ashcraft, M. H. (1982). The development of mental arithmetic: A chronometric approach. *Developmental review, 2*, 213-236.

Ashcraft, M. H., & Battaglia, J. (1978). Cognitive arithmetics: evidence for retrieval and decision processes in mental addition. *Journal of Experimental Psychology : Human Learning and Memory, 4*, 527-538.

Bachtold, D., Baumuller, M., & Brugger, P. (1998). Stimulus-response compatibility in representational space. *Neuropsychologia, 36*(8), 731-735.

Badets, A., Andres, M., Di Luca, S., & Pesenti, M. (2007). Number magnitude potentiates action judgements. *Exp Brain Res, 180*(3), 525-534.

Banister, C. M., & Tew, B. (1991). *Current concepts in spina bifida and hydrocephalus*. Cambridge: Cambridge Press.

Barnes, M. A., Smith-Chant, B. L., & Landry, S. (2005). Number processing in neurodevelopmental disorders: Spina bifida myelomenigocele. In J. Campbell (Ed.), *Handbook of mathematical cognition*. NY: Psychology Press.

Baroody, A. J. (1987). *Children's mathematical thinking: A developmental framework for preschool, primary, and special education teachers*. NY: US: Teachers College Press. .

Barth, H., La Mont, K., Lipton, J., Dehaene, S., Kanwisher, N., & Spelke, E. (2006). Non-symbolic arithmetic in adults and young children. *Cognition*, *98*(3), 199-222.

Barth, H., La Mont, K., Lipton, J., & Spelke, E. S. (2005). Abstract number and arithmetic in preschool children. *Proc Natl Acad Sci U S A, 102*(39), 14116-14121.

Ben Hamed, S., Duhamel, J. R., Bremmer, F., & Graf, W. (2001). Representation of the visual field in the lateral intraparietal area of macaque monkeys: a quantitative receptive field analysis. *Exp Brain Res, 140*(2), 127-144.

Benoita, L., Lehalle, H., & Jouenb, F. (2004). Do young children acquire number words through subitizing or counting? *Cognitive Development, 19 (3)* 291-307.

Benson, D. F., & Geschwind, N. (1970). Developmental Gerstmann syndrome. *Neurology, 20,* 293-298.

Benton, A. L., Hutcheon, J. F., & Seymour, E. (1951). Arithmetic ability, finger-localization capacity and right-left discrimination in normal and defective children. *Am J Orthopsychiatry, 21*(4), 756-766.

Berch, D. B., Foley, E. J., Hill, R. J., & Ryan, P. M. (1999). Extracting parity and magnitude from Arabic numerals: developmental changes in number processing and mental representation. *J Exp Child Psychol, 74*(4), 286-308.

Berteletti, I., Lucangeli, D., Piazza, M., Dehaene, S., & Zorzi, M. (2009). Numerical representations in preschoolers. *Developmental Science, In press*.

Binkofski, F., Buccino, G., Posse, S., Seitz, R. J., Rizzolatti, G., & Freund, H. (1999). A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *Eur J Neurosci, 11*(9), 3276-3286.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., et al. (1998). Human anterior intraparietal area subserves prehension: a combined lesion and functional MRI activation study. *Neurology, 50*(5), 1253-1259.

Bodegard, A., Geyer, S., Grefkes, C., Zilles, K., & Roland, P. E. (2001). Hierarchical processing of tactile shape in the human brain. *Neuron, 31*(2), 317-328.

Boysen, S. T., & Capaldi, E. J. (Eds.). (1993). *The development of numerical competence: Animal and human models.* Hillsdale N.J.: Erlbaum.

Brannon, E. M., & Gautier, T. (2003). Continuous versus discrete represenations of quantity in infancy *Biennal meeting of the Society of Research in Child Development*.

Brannon, E. M., & Terrace, H. S. (1998). Ordering of the numerosities 1 to 9 by monkeys. *Science, 282*(5389), 746-749.

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*, 31-49.

Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K., et al. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron, 29*(1), 287-296.

Brown, T. T., Lugar, H. M., Coalson, R. S., Miezin, F. M., Petersen, S. E., & Schlaggar, B. L. (2005). Developmental changes in human cerebral functional organization for word generation. *Cereb Cortex, 15*(3), 275-290.

Bruandet, M., Molko, N., Cohen, L., & Dehaene, S. (2004). A cognitive characterization of dyscalculia in Turner syndrome. *Neuropsychologia, 42*(3), 288-298.

Brysbaert, M. (1995). Arabic number reading: On the nature of the numerical scale and the origin of phonological recoding. *Journal of Experimental Psychology: General, 124*, 434-452.

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

Bull, R., & Johnston, R. S. (1997). Children's arithmetical difficulties: contributions from processing speed, item identification, and short-term memory. *J Exp Child Psychol, 65*(1), 1-24.

Bull, R., Johnston, R. S., & Roy, J. A. (1999). Exploring the roles of the visual-spatial sketch pad and central executive in children's arithmetical skills: Views from cognition and developmental neuropsychology. *Developmental Neuropsychology, 15*, 421-442.

Bull, R., & Scerif, G. (2001). Executive functioning as a predictor of children's mathematics ability: inhibition, switching, and working memory. *Dev Neuropsychol, 19*(3), 273-293.

Burbaud, P., Camus, O., Guehl, D., Bioulac, B., Caille, J. M., & Allard, M. (1999). A functional magnetic resonance imaging study of mental subtraction in human subjects. *Neurosci Lett, 273*(3), 195-199.

Bushara, K. O., Weeks, R. A., Ishii, K., Catalan, M. J., Tian, B., Rauschecker, J. P., et al. (1999). Modality-specific frontal and parietal areas for auditory and visual spatial localization in humans. *Nat Neurosci, 2*(8), 759-766.

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

Butterworth, B. (2005). The development of arithmetical abilities. *J Child Psychol Psychiatry, 46*(1), 3-18.

Calabria, M., & Rossetti, Y. (2005). Interference between number processing and line bisection: a methodology. *Neuropsychologia, 43*(5), 779-783.

Caminiti, R., Ferraina, S., & Johnson, P. B. (1996). The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. *Cereb Cortex, 6*(3), 319-328.

Campbell, J. I. D. (1987). Network interference and mental multiplication. *Journal of Experimental Psychology: Learning, 13*, 109-123.

Carota, A., Di Pietro, M., Ptak, R., Poglia, D., & Schnider, A. (2004). Defective spatial imagery with pure Gerstmann's syndrome. *Eur Neurol, 52*(1), 1-6.

Casey, B. J., Giedd, J. N., & Thomas, K. M. (2000). Structural and functional brain development and its relation to cognitive development. *Biol Psychol, 54*(1-3), 241-257.

Castiello, U. (2005). The neuroscience of grasping. *Nat Rev Neurosci, 6*(9), 726-736.

Cermak, S. A., & Larkin, D. (2001). *Developmental coordination disorder.* NY: Delmar.

Chafee, M. V., & Goldman-Rakic, P. S. (2000). Inactivation of parietal and prefrontal cortex reveals interdependence of neural activity during memory-guided saccades. *J Neurophysiol, 83*(3), 1550-1566.

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

Chugani, H. T., Phelps, M. E., & Mazziotta, J. C. (1987). Positron emission tomography study of human brain functional development. *Ann Neurol, 22*(4), 487-497.

Church, R. M., & Meck, W. H. (1984). The numerical attribute of stimuli. In H. L. Roitblat, T. G. Bever & H. S. Terrace (Eds.), *Animal Cognition*. Hillsdale N.J.: Erlbaum.

Cipolotti, L., & Butterworth, B. (1995). Toward a multiroute model of number processing: impaired number transcoding with preserved calculation skills. *Journal of Experimental Psychology: General, 124*, 375-390.

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

Cirelli, A., Ciardi, M., Salotti, A., & Rossi, F. (1994). An unusual neurological feature of HIV-1 encephalopathy: Gerstmann's syndrome. *Acta Neurol (Napoli), 16*(3), 110-113.

Clearfield , M. W., & Mix, K. S. (1999). Number versus contour length in infants' discrimination of small visual sets. *Psychological Science, 10(5)*, 408-411

Cohen Kadosh, R., Henik, A., & Rubinsten, O. (2008). Are Arabic and verbal numbers processed in different ways? *J Exp Psychol Learn Mem Cogn, 34*(6), 1377-1391.

Cohen, L., Dehaene, S., Chochon, F., Lehéricy, S., & Naccache, L. (2000). Language and calculation within the parietal lobe: A combined cognitive, anatomical and fMRI study. *Neuropsychologia, 38*, 1426-1440.

Cohen, Y. E., & Andersen, R. A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nat Rev Neurosci, 3*(7), 553-562.

Colby, C. L., & Duhamel, J. R. (1991). Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia, 29*(6), 517-537.

Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annu Rev Neurosci*, *22*, 319-349.

Connolly, J. D., Andersen, R. A., & Goodale, M. A. (2003). FMRI evidence for a 'parietal reach region' in the human brain. *Exp Brain Res, 153*(2), 140-145.

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

Cordes, S., Gelman, R., Gallistel, C. R., & Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychon Bull Rev, 8*(4), 698-707.

Corsi, P. M. (1972). *Human memory and the medial temporal region of the brain. Unpublished Thesis.* Montreal: McGill University.

Coull, J. T., Frith, C. D., Buchel, C., & Nobre, A. C. (2000). Orienting attention in time: behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia, 38*(6), 808-819.

Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *J Neurosci, 18*(18), 7426-7435.

Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: what have we learned from neuroimaging? *Neuropsychologia, 44*(13), 2668-2684.

Culham, J. C., Danckert, S. L., DeSouza, J. F., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Exp Brain Res, 153*(2), 180-189.

Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Curr Opin Neurobiol, 11*(2), 157-163.

Dayan, P., & Abbott, L. F. (2001). *Theoretical Neuroscience: Computational and mathematical modeling of neural systems.* Cambridge, Mass.: MIT Press.

de Hevia, M. D., Girelli, L., & Vallar, G. (2006). Numbers and space: a cognitive illusion? *Exp Brain Res, 168*(1-2), 254-264.

de Hevia, M. D., Vallar, G., & Girelli, L. (2008). Visualizing numbers in the mind's eye: the role of visuo-spatial processes in numerical abilities. *Neurosci Biobehav Rev, 32*(8), 1361-1372.

De Smedt, B., Janssen, R., Bouwens, K., Verschaffel, L., Boets, B., & Ghesquière, P. (2009). Working memory and individual differences in mathematics achievement: A longitudinal study from first grade to second grade *Journal of Experimental Child Psychology, 103(2),* 186-201

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition, 44*, 1-42.

Dehaene, S. (1997). *The number sense*. New York: Oxford University Press.

Dehaene, S. (2003). The neural basis of the Weber-Fechner law: a logarithmic mental number line. *Trends Cogn Sci, 7*(4), 145-147.

Dehaene, S. (2007). Symbols and quantities in parietal cortex: elements of a mathematical theory of number representation and manipulation *Attention and Performance Vol XXII* (Press HU ed., pp. 527-574).

Dehaene, S. (2009). Origins of mathematical intuitions: the case of arithmetic. *Ann N Y Acad Sci*, *1156*, 232-259.

Dehaene, S., & Akhavein, R. (1995). Attention, automaticity and levels of representation in number processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 314-326.

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

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

Dehaene, S., & Cohen, L. (1995). Towards an anatomical and functional model of number processing. *Mathematical Cognition, 1*, 83-120.

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neuroscience*, *21*, 355-361.

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

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

Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., & Tsivkin, S. (1999). Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science, 284*(5416), 970-974.

Dehaene, S., Tzourio, N., Frak, V., Raynaud, L., Cohen, L., Mehler, J., et al. (1996). Cerebral activations during number multiplication and comparison: a PET study. *Neuropsychologia, 34*, 1097-1106.

Delazer, M., & Benke, T. (1997). Arithmetic facts without meaning. *Cortex, 33*(4), 697-710.

Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., et al. (2003). Learning complex arithmetic--an fMRI study. *Brain Res Cogn Brain Res, 18*(1), 76-88.

Deloche, G., & Seron, X. (1987). Numerical transcoding: A general production model. In G. Deloche & X. Seron (Eds.), *Mathematical Disabilities: A cognitive neuropsychological perspective* (pp. 137-170). Hillsdale New Jersey: Lawrence Erlbaum Associates.

Di Luca, S., Grana, A., Semenza, C., Seron, X., & Pesenti, M. (2006). Finger-digit compatibility in Arabic numeral processing. *Q J Exp Psychol (Colchester), 59*(9), 1648-1663.

Diamond, A. (1996). Evidence for the importance of dopamine for prefrontal cortex functions early in life. *Philos Trans R Soc Lond B Biol Sci, 351*(1346), 1483-1493; discussion 1494.

Donlan, C., Bishop, D. V., & Hitch, G. J. (1998). Magnitude comparisons by children with specific language impairments: evidence of unimpaired symbolic processing. *Int J Lang Commun Disord, 33*(2), 149-160.

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science, 255*, 90-92.

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1998). Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *J Neurophysiol, 79*(1), 126-136.

Duncan, E. M., & McFarland, C. E. (1980). Isolating the effects of symbolic distance and semantic congruity in comparative judgments: an additive-factors analysis. *Memory and Cognition, 8*, 612-622.

Durston, S., & Casey, B. J. (2006). What have we learned about cognitive development from neuroimaging? *Neuropsychologia, 44*(11), 2149-2157.

Durston, S., Davidson, M. C., Tottenham, N., Galvan, A., Spicer, J., Fossella, J. A., et al. (2006). A shift from diffuse to focal cortical activity with development. *Dev Sci, 9*(1), 1-8.

Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., & Kleinschmidt, A. (2009). Deciphering cortical number coding from human brain activity patterns. *Curr Biol, 19*(19), 1608-1615.

Eidelberg, D., & Galaburda, A. M. (1984). Inferior parietal lobule. Divergent architectonic asymmetries in the human brain. *Arch Neurol, 41*(8), 843-852.

Eliez, S., Blasey, C. M., Menon, V., White, C. D., Schmitt, J. E., & Reiss, A. L. (2001). Functional brain imaging study of mathematical reasoning abilities in velocardiofacial syndrome (del22q11.2). *Genet Med, 3*(1), 49-55.

Eskandar, E. N., & Assad, J. A. (1999). Dissociation of visual, motor and predictive signals in parietal cortex during visual guidance. *Nat Neurosci, 2*(1), 88-93.

Facoetti, A., Trussardi, A. N., & Zorzi, M. (2007). *Is the Right Parietal Cortex Impaired in Developmental Dyscalculia? Evidence from Inhibition of Return (poster)*: NUMBRA.

Faillenot, I., Toni, I., Decety, J., Gregoire, M. C., & Jeannerod, M. (1997). Visual pathways for object-oriented action and object recognition: functional anatomy with PET. *Cereb Cortex, 7*(1), 77-85.

Farrer, C., Frey, S. H., Van Horn, J. D., Tunik, E., Turk, D., Inati, S., et al. (2008). The angular gyrus computes action awareness representations. *Cereb Cortex, 18*(2), 254-261.

Fayol, M., Barrouillet, P., & Marinthe, X. (1998). Predicting arithmetical achievement from neuropsychological performance: A longitudinal study. *Cognition, 68*, B63-B70.

Fayol, M., & Seron, X. (2005). About numerical representations: Insights from neuropsychological, experimental, and developmental studies In J. Campbell (Ed.), *Handbook of mathematical cognition*. NY: US: Psychology Press.

Feigenson, L., Carey, S., & Hauser, M. (2002). The representations underlying infants' choice of more: object files versus analog magnitudes. *Psychol Sci, 13*(2), 150-156.

Feigenson, L., Carey, S., & Spelke, E. (2002). Infants' discrimination of number vs. continuous extent. *Cogn Psychol, 44*(1), 33-66.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends Cogn Sci, 8*(7), 307-314.

Fias, W. (2001). Two routes for the processing of verbal numbers: evidence from the SNARC effect. *Psychol Res, 65*(4), 250-259.

Fias, W., Lammertyn, J., Reynvoet, B., Dupont, P., & Orban, G. A. (2003). Parietal representation of symbolic and nonsymbolic magnitude. *J Cogn Neurosci, 15*(1), 47-56.

Fiez, J. A., & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences USA, 95*(3), 914-921.

Fischer, M. H. (2001). Number processing induces spatial performance biases. *Neurology, 57*(5), 822-826.

Fischer, M. H., Castel, A. D., Dodd, M. D., & Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience, 6*(6), 555-556.

Flavell, J. H., Beach, D. R., & Chinsky, J. M. (1966). Spontaneous verbal rehearsal in a memory task as a function of age. *Child Dev, 37*(2), 283-299.

Foltz, G. S., Poltrock, S. E., & Potts, G. R. (1984). Mental comparison of size and magnitude: size congruity effects. *Journal of Experimental Psychology: Learning, 10*, 442-453.

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 Am J Neuroradiol, 21*(6), 1048-1054.

Fuson, K. C. (1982). An analysis of the counting-on solution procedure in addition. In C. T. P., M. J. M. & R. T. A. (Eds.), *Addition and subtraction: A cognitive perspective* (pp. 67-81). Hillsdale NJ: Lawrence Erlbaum.

Fuson, K. C. (1988). *Children's counting and concepts of number*. New York: Springer-Verlag.

Fuson, K. C., Richards, J., & Briards, D. J. (1982). The acquisition and elaboration of the number word sequence. In B. C. J. (Ed.), *Children's logical and mathematical cognition* (pp. 33-92). New York: Springer Verlag.

Gaillard, W. D., Hertz-Pannier, L., Mott, S. H., Barnett, A. S., LeBihan, D., & Theodore, W. H. (2000). Functional anatomy of cognitive development: fMRI of verbal fluency in children and adults. *Neurology, 54*(1), 180-185.

Gallistel, C. R., & Gelman, I. I. (2000). Non-verbal numerical cognition: from reals to integers. *Trends Cogn Sci, 4*(2), 59-65.

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

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

Galton, F. (1880). Visualised numerals. *Nature, 21*, 252-256.

Gardner, E. P., Debowy, D. J., Ro, J. Y., Ghosh, S., & Babu, K. S. (2002). Sensory monitoring of prehension in the parietal lobe: a study using digital video. *Behav Brain Res, 135*(1-2), 213-224.

Geary, D. C. (1990). A componential analysis of an early learning deficit in mathematics. *Journal of Experimental Child Psychology, 49*, 363-383.

Geary, D. C. (1993). Mathematical disabilities: Cognitive, neuropsychological and genetic components. *Psychological Bulletin, 114*, 345-362.

Geary, D. C. (1996). The Problem-size Effect in Mental Addition: Developmental and Cross-national Trends. *Mathematical Cognition 2(1)*, 63-93.

Geary, D. C. (2000). From infancy to adulthood: the development of numerical abilities. *Eur Child Adolesc Psychiatry, 9 Suppl 2*, II11-16.

Geary, D. C., Brown, S. C., & Samaranayake, V. A. (1991). Cognitive addition: A short-longitudinal study of strategy choice and speed-of-processing differences in normal and mathematically disabled children. *Developmental Psychology, 27*, 787-797.

Geary, D. C., Frensch, P. A., & Wiley, J. G. (1993). Simple and complex mental subtraction: strategy choice and speed-of-processing differences in younger and older adults. *Psychol Aging, 8*(2), 242-256.

Geary, D. C., Hoard, M. K., Byrd-Craven, J., Nugent, L., & Numtee, C. (2007). Cognitive mechanisms underlying achievement deficits in children with mathematical learning disability. *Child Dev, 78*(4), 1343-1359.

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

Gerstmann. (1927). Finger-Agnosie und insolierte Agraphie; ein neues Syndrom. *Z. ges. Neurol. Psychiat., 108*, 152-177.

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

Gerstmann, J. (1957). Some notes on the Gerstmann syndrome. *Neurology, 7*(12), 866-869.

Gescheider, G. A. (1997). *Psychophysics: the fundamentals*. Mahwah, NJ, US: Lawrence Erlbaum Associates Publishers.

Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., et al. (1999). Brain development during childhood and adolescence: a longitudinal MRI study. *Nat Neurosci, 2*(10), 861-863.

Gilmore, C. K., McCarthy, S. E., & Spelke, E. S. (2007). Symbolic arithmetic knowledge without instruction. *Nature, 447*(7144), 589-591.

Girelli, L., Lucangeli, D., & Butterworth, B. (2000). The development of automaticity in accessing number magnitude. *Journal of Experimental Child Psychology, in press*.

Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proc Natl Acad Sci U S A, 101*(21), 8174-8179.

Golarai, G., Ghahremani, D. G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J. L., Gabrieli, J. D., et al. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nat Neurosci, 10*(4), 512-522.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience, 15*, 20-25.

Gracia-Bafalluy, M., & Noel, M. P. (2008). Does finger training increase young children's numerical performance? *Cortex, 44*(4), 368-375.

Grafman, J., Passafiume, D., Faglioni, P., & Boller, F. (1982). Calculation disturbances in adults with focal hemispheric damage. *Cortex, 18*, 37-50.

Grafton, S. T., Fagg, A. H., Woods, R. P., & Arbib, M. A. (1996). Functional anatomy of pointing and grasping in humans. *Cereb Cortex, 6*(2), 226-237.

Grana, A., Girelli, L., & Semenza, C. (2003). Writing and rewriting arabic numerals: dissociated processing pathways? *Neurocase*, *9*(4), 308-318.

Green, D., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Krieger Publishing Company.

Grefkes, C., Ritzl, A., Zilles, K., & Fink, G. R. (2004). Human medial intraparietal cortex subserves visuomotor coordinate transformation. *Neuroimage, 23*(4), 1494-1506.

Groen, G. J., & Parkman, J. M. (1972). A chronometric analysis of simple addition. *Psychological Review, 79*, 329-343.

Gross-Tsur, V., Manor, O., & Shalev, R. S. (1996). Developmental dyscalculia: prevalence and demographic features. *Dev Med Child Neurol, 38*(1), 25-33.

Gruber, O., Indefrey, P., Steinmetz, H., & Kleinschmidt, A. (2001). Dissociating neural correlates of cognitive components in mental calculation. *Cereb Cortex*, *11*(4), 350-359.

Halberda, J., & Feigenson, L. (2008). Developmental change in the acuity of the "Number Sense": The Approximate Number System in 3-, 4-, 5-, and 6-year-olds and adults. *Dev Psychol*, *44*(5), 1457-1465.

Halberda, J., Mazzocco, M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature, 455*(7213), 665-668.

Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proc R Soc Lond B Biol Sci, 267*(1445), 829-833.

Hauser, M. D., Dehaene, S., Dehaene-Lambertz, G., & Patalano, A. L. (2002). Spontaneous number discrimination of multi-format auditory stimuli in cotton-top tamarins (Saguinus oedipus). *Cognition, 86*(2), B23-32.

Hauser, M. D., MacNeilage, P., & Ware, M. (1996). Numerical representations in primates. *Proceedings of the National Academy of Sciences USA*, *93*, 1514-1517.

Hauser, M. D., Tsao, F., Garcia, P., & Spelke, E. (2003). Evolutionary foundations of number: spontaneous representation of numerical magnitudes by cotton-top tamarins. *Proc R Soc Lond B Biol Sci, 270*, 1441-1446.

He, S. Q., Dum, R. P., & Strick, P. L. (1993). Topographic organization of corticospinal projections from the frontal lobe: motor areas on the lateral surface of the hemisphere. *J Neurosci, 13*(3), 952-980.

He, S. Q., Dum, R. P., & Strick, P. L. (1995). Topographic organization of corticospinal projections from the frontal lobe: motor areas on the medial surface of the hemisphere. *J Neurosci, 15*(5 Pt 1), 3284-3306.

Hinrichs, J. V., Berie, J. L., & Mosell, M. K. (1982). Place information in multidigit number comparison. *Memory & Cognition, 10,* 487-495.

Holloway, I. D., & Ansari, D. (2008). Mapping numerical magnitudes onto symbols: The numerical distance effect and individual differences in children's mathematics achievement. *J Exp Child Psychol*.

Holmes, J., Adams, J. W., & Hamilton, C. J. (2008). The relationship between visuospatial sketchpad capacity and children’s mathematical skills. *European Journal of Cognitive Psychology, 20*, 272–289.

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

Hughes, M. (1986). *Children and number: difficulties in learning*. NY: Basic Blackwell.

Hurford, J. R. (1987). *Language and Number.* Oxford: Basil Blackwell.

Huttenlocher, J., Jordan, N., & Levine, S. C. (1994). A mental model for early arithmetic. *Journal of Experimental Psychology: General, 123*, 284-296.

Huttenlocher, P. R. (1979). Synaptic density in human frontal cortex - developmental changes and effects of aging. *Brain Res, 163*(2), 195-205.

Huttenlocher, P. R. (1990). Morphometric study of human cerebral cortex development. *Neuropsychologia, 28*(6), 517-527.

Ifrah, G. (1981). *Histoire Universelle des Chiffres*. Paris: Seghers.

Isaacs, E. B., Edmonds, C. J., Lucas, A., & Gadian, D. G. (2001). Calculation difficulties in children of very low birthweight: A neural correlate. *Brain, 124*(Pt 9), 1701-1707.

Ischebeck, A., Zamarian, L., Siedentopf, C., Koppelstatter, F., Benke, T., Felber, S., et al. (2006). How specifically do we learn? Imaging the learning of multiplication and subtraction. *Neuroimage, 30*(4), 1365-1375.

Ito, Y., & Hatta, T. (2004). Spatial structure of quantitative representation of numbers: evidence from the SNARC effect. *Mem Cognit, 32*(4), 662-673.

Iwamura, Y., Iriki, A., & Tanaka, M. (1994). Bilateral hand representation in the postcentral somatosensory cortex. *Nature, 369*(6481), 554-556.

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proc Natl Acad Sci U S A, 106*(25), 10382-10385.

Jancke, L., Kleinschmidt, A., Mirzazade, S., Shah, N. J., & Freund, H. J. (2001). The role of the inferior parietal cortex in linking the tactile perception and manual construction of object shapes. *Cereb Cortex, 11*(2), 114-121.

Jeannerod, M. (1984). The timing of natural prehension movements. *J Mot Behav, 16*(3), 235-254.

Jeannerod, M. (1986). The formation of finger grip during prehension. A cortically mediated visuomotor pattern. *Behav Brain Res 19(2)*, 99-116.

Jeannerod, M. (1997). *The cognitive neuroscience of action*. New York: Blackwell.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci, 18*(7), 314-320.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in Neurosciences, 18,* 314-320.

Jernigan, T. L., & Tallal, P. (1990). Late childhood changes in brain morphology observable with MRI. *Dev Med Child Neurol, 32*(5), 379-385.

Jolliffe, I. T. (2002). *Principal component analysis*. NY: Springer.

Jordan, N. C., & Hanich, L. B. (2000). Mathematical thinking in second-grade children with different forms of LD. *J Learn Disabil, 33*(6), 567-578.

Jordan, N. C., Hanich, L. B., & Kaplan, D. (2003a). Arithmetic fact mastery in young children: a longitudinal investigation. *J Exp Child Psychol, 85*(2), 103-119.

Jordan, N. C., Hanich, L. B., & Kaplan, D. (2003b). A longitudinal study of mathematical competencies in children with specific mathematics difficulties versus children with comorbid mathematics and reading difficulties. *Child Dev, 74*(3), 834-850.

Jordan, N. C., Kaplan, D., Ramineni, C., & Locuniak, M. N. (2008). Development of number combination skill in the early school years: when do fingers help? *Dev Sci, 11*(5), 662-668.

Jordan, N. C., Levine, S. C., & Huttenlocher, J. (1995). Calculation abilities in young children with different patterns of cognitive functioning. *J Learn Disabil, 28*(1), 53-64.

Jung, R. E., Yeo, R. A., Sibbitt, W. L., Jr., Ford, C. C., Hart, B. L., & Brooks, W. M. (2001). Gerstmann syndrome in systemic lupus erythematosus: neuropsychological, neuroimaging and spectroscopic findings. *Neurocase, 7*(6), 515-521.

Kaufmann, L., Koppelstaetter, F., Delazer, M., Siedentopf, C., Rhomberg, P., Golaszewski, S., et al. (2005). Neural correlates of distance and congruity effects in a numerical Stroop task: an event-related fMRI study. *Neuroimage, 25*(3), 888-898.

Kawashima, R., Naitoh, E., Matsumura, M., Itoh, H., Ono, S., Satoh, K., et al. (1996). Topographic representation in human intraparietal sulcus of reaching and saccade. *Neuroreport, 7*(7), 1253-1256.

Keating, D. P., Keniston, A. H., Manis, F. R., & Bobbitt, B. L. (1980). Development of the search-processing parameter. *Child Dev, 51*(1), 39-44.

Keus, I. M., Jenks, K. M., & Schwarz, W. (2005). Psychophysiological evidence that the SNARC effect has its functional locus in a response selection stage. *Brain Res Cogn Brain Res, 24*(1), 48-56.

Kilian, A., Yaman, S., von Fersen, L., & Gunturkun, O. (2003). A bottlenose dolphin discriminates visual stimuli differing in numerosity. *Learn Behav, 31*(2), 133-142.

Kinsbourne, M. (1968). Developmental Gerstmann syndrome. *Pediatr Clin North Am, 15*(3), 771-778.

Klingberg, T., Forssberg, H., & Westerberg, H. (2002). Increased brain activity in frontal and parietal cortex underlies the development of visuospatial working memory capacity during childhood. *J Cogn Neurosci, 14*(1), 1-10.

Knops, A., Thirion, B., Hubbard, E. M., Michel, V., & Dehaene, S. (2009). Recruitment of an area involved in eye movements during mental arithmetic. *Science, 324*(5934), 1583-1585.

Koontz, K. L., & Berch, D. B. (1996). Identifying simple numerical stimuli: processing inefficiencies exhibited by arithmetic learning disabled children. *Mathematical Cognition, 2*, 1-24.

Kosc, L. (1974). Developmental dyscalculia. *Journal of Learning Disabilities, 7*, 165-177.

Koyama, M., Hasegawa, I., Osada, T., Adachi, Y., Nakahara, K., & Miyashita, Y. (2004). Functional magnetic resonance imaging of macaque monkeys performing visually guided saccade tasks: comparison of cortical eye fields with humans. *Neuron, 41*(5), 795-807.

Landerl, K., Bevan, A., & Butterworth, B. (2004). Developmental dyscalculia and basic numerical capacities: a study of 8-9-year-old students. *Cognition, 93*(2), 99-125.

Le Clec'H, G., Dehaene, S., Cohen, L., Mehler, J., Dupoux, E., Poline, J. B., et al. (2000). Distinct cortical areas for names of numbers and body parts independent of language and input modality. *Neuroimage, 12*(4), 381-391.

Le Corre, M., & Carey, S. (2007). One, two, three, four, nothing more: an investigation of the conceptual sources of the verbal counting principles. *Cognition, 105*(2), 395-438.

Le Corre, M., & Carey, S. (2008). Why the verbal counting principles are constructed out of representations of small sets of individuals: a reply to Gallistel. *Cognition, 107*(2), 650-662.

Le Corre, M., Van de Walle, G., Brannon, E. M., & Carey, S. (2006). Re-visiting the competence/performance debate in the acquisition of the counting principles. *Cogn Psychol, 52*(2), 130-169.

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

Lee, K. M., & Kang, S. Y. (2002). Arithmetic operation and working memory: differential suppression in dual tasks. *Cognition, 83*(3), B63-68.

Lefford, A., Birch, H. G., & Green, G. (1974). The perceptual and cognitive bases for finger localization and selective finger movement in preschool children. *Child Dev, 45*(2), 335-343.

Levine, D. N., Mani, R. B., & Calvanio, R. (1988). Pure agraphia and Gerstmann's syndrome as a visuospatial-language dissociation: an experimental case study. *Brain Lang, 35*(1), 172-196.

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

Lindemann, O., Abolafia, J. M., Girardi, G., & Bekkering, H. (2007). Getting a grip on numbers: numerical magnitude priming in object grasping. *J Exp Psychol Hum Percept Perform, 33*(6), 1400-1409.

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

Lipton, J. S., & Spelke, E. S. (2006). Preschool children master the logic of number word meanings. *Cognition, 98*(3), B57-66.

Lochy, A., Pillon, A., Zesiger, P., & Seron, X. (2002). Verbal structure of numerals and digits handwriting: new evidence from kinematics. *Q J Exp Psychol A, 55*(1), 263-288.

Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. Cambridge: Cambridge University Press.

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

Marinthe, C., Fayol, M., & P., B. (2001). Gnosies digitales et développement des performances arithmétiques. In A. v. Hout, C. Melijac & J. P. Fisher (Eds.), *Troubles du calcul et dyscalculie chez l'enfant*. Paris: Masson.

Martory, M. D., Mayer, E., Pegna, A. J., Annoni, J. M., Landis, T., & Khateb, A. (2003). Pure global acalculia following a left subangular lesion. *Neurocase, 9*(4), 319-328.

Matsumura, M., Kawashima, R., Naito, E., Satoh, K., Takahashi, T., Yanagisawa, T., et al. (1996). Changes in rCBF during grasping in humans examined by PET. *Neuroreport, 7*(3), 749-752.

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*(Pt 6), 1107-1120.

Mazzocco, M. M. (2001). Math learning disability and math LD subtypes: evidence from studies of Turner syndrome, fragile X syndrome, and neurofibromatosis type 1. *J Learn Disabil, 34*(6), 520-533.

Mazzoni, M., Pardossi, L., Cantini, R., Giorgetti, V., & Arena, R. (1990). Gertsmann syndrome: A case report. *Cortex, 26*, 459-467.

McCloskey, M., Caramazza, A., & Basili, A. (1985). Cognitive mechanisms in number processing and calculation: Evidence from dyscalculia. *Brain and Cognition, 4*, 171-196.

McCloskey, M., Macaruso, P., & Whetstone, T. (1992). The functional architecture of numerical processing mechanisms: Defending the modular model. In J. I. D. Campbell (Ed.), *The nature and origins of mathematical skills* (pp. 493-537). Amsterdam: Elsevier.

McComb, K., Packer, C., & Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, Panthera leo. *Animal Behaviour, 47*, 379-387.

McCrink, K., Dehaene, S., & Dehaene-Lambertz, G. (2007). Moving along the number line: operational momentum in nonsymbolic arithmetic. *Percept Psychophys, 69*(8), 1324-1333.

McCrink, K., & Wynn, K. (2009). Operational momentum in large-number addition and subtraction by 9-month-olds. *J Exp Child Psychol, 103*(4), 400-408.

McLean, J. F., & Hitch, G. J. (1999). Working memory impairments in children with specific arithmetic learning difficulties. *J Exp Child Psychol, 74*(3), 240-260.

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

Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *J Neurosci, 23*(15), 6209-6214.

Menon, V., Rivera, S. M., White, C. D., Eliez, S., Glover, G. H., & Reiss, A. L. (2000). Functional optimization of arithmetic processing in perfect performers. *Brain Res Cogn Brain Res, 9*(3), 343-345.

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.

Miller, K., Smith, C. M., Zhu, J., & Zhang, H. (1995). Preschool origins of cross-national differences in mathematical competence: The role of number-naming systems. *Psychological Science, 6*, 56-60.

Miura, I. T., Okamoto, Y., Kim, C. C., Chang, C.-M., Steere, M., & Fayol, M. (1994). Comparisons of children's cognitive representation of number: China, France, Japan, Korea, Sweden, and the United States. *International Journal of Behavioral Development, Vol 17(3)*, 401-411.

Molko, N., Cachia, A., Riviere, D., Mangin, J. F., Bruandet, M., Le Bihan, D., et al. (2003). Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. *Neuron, 40*(4), 847-858.

Moore, M. R., Saver, J. L., Johnson, K. A., & Romero, J. A. (1991). Right parietal stroke with Gerstmann's syndrome. Appearance on computed tomography, magnetic resonance imaging, and single-photon emission computed tomography. *Arch Neurol, 48*(4), 432-435.

Moretto, G., & di Pellegrino, G. (2008). Grasping numbers. *Exp Brain Res, 188*(4), 505-515.

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

Mühlau, M., Hermsdörfer, J., Goldenberg, G., Wohlschläger, A. M., Castrop, F., Stahl, R., et al. (2005). Left inferior parietal dominance in gesture imitation: an fMRI study. *Neuropsychologia, 43(7)*, 1086-1098.

Mundy, E., & Gilmore, C. K. (2009). Children's mapping between symbolic and nonsymbolic representations of number. *J Exp Child Psychol, 103*(4), 490-502.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *J Neurophysiol, 83*(5), 2580-2601.

Mussolin, C., & Noel, M. P. (2007). The nonintentional processing of Arabic numbers in children. *J Clin Exp Neuropsychol, 29*(3), 225-234.

Mussolin, C., & Noel, M. P. (2008). Automaticity for numerical magnitude of two-digit Arabic numbers in children. *Acta Psychol (Amst), 129*(2), 264-272.

Nieder, A. (2005). Counting on neurons: the neurobiology of numerical competence. *Nat Rev Neurosci, 6*(3), 177-190.

Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annu Rev Neurosci, 32*, 185-208.

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

Nieder, A., Freedman, D. J., & Miller, E. K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. *Science, 297*(5587), 1708-1711.

Nieder, A., & Miller, E. K. (2003). Coding of cognitive magnitude. Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron, 37*(1), 149-157.

Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proc Natl Acad Sci U S A, 101*(19), 7457-7462.

Noel, M. P. (2005). Finger gnosia: a predictor of numerical abilities in children? *Child Neuropsychol, 11*(5), 413-430.

Noël, M. P. (2001). Le transcodage chez l'enfant. In A. v. Hout, C. Melijac & J. P. Fisher (Eds.), *Troubles du calcul et dyscalculie chez l'enfant*. Paris: Masson.

Noel, M. P., & Seron, X. (1993). Arabic number reading deficit: A single case study. *Cognitive Neuropsychology, 10*, 317-339.

Nuerk, H. C., Weger, U., & Willmes, K. (2001). Decade breaks in the mental number line? Putting the tens and units back in different bins. *Cognition, 82*(1), B25-33.

Orban, G. A., Fize, D., Peuskens, H., Denys, K., Nelissen, K., Sunaert, S., et al. (2003). Similarities and differences in motion processing between the human and macaque brain: evidence from fMRI. *Neuropsychologia, 41*(13), 1757-1768.

Orban, G. A., Van Essen, D., & Vanduffel, W. (2004). Comparative mapping of higher visual areas in monkeys and humans. *Trends Cogn Sci, 8*(7), 315-324.

Ostad, S. A. (1997). Developmental differences in addition strategies: a comparison of mathematically disabled and mathematically normal children. *Br J Educ Psychol, 67 (Pt 3)*, 345-357.

Paterson, S. (2001). Language and number in Down syndrome: the complex developmental trajectory from infancy to adulthood. *Downs Syndr Res Pract, 7*(2), 79-86.

Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of the verbal component of working memory. *Nature, 362*, 342-345.

PeBenito, R., Fisch, C. B., & Fisch, M. L. (1988). Developmental Gerstmann's syndrome. *Arch Neurol, 45*(9), 977-982.

Penner-Wilger, M., & Anderson, M. L. (2008). *An alternative view of the relation between finger gnosis and math ability: redeployment of finger representations for the representation of number*. Paper presented at the Proceedings of the 29th Annual Conference of the Cognitive Science Society, Austin: TX.

Penner-Wilger, M., Fast, L., LeFevre, J., Smith-Chant, B. L., & et al. (2007). *The foundations of numeracy: Subitizing, finger gnosia, and fine-motor ability*. Paper presented at the Proceedings of the 29th Annual Conference of the Cognitive Science Society, Mahwah, NJ: Erlbaum.

Pesenti, M., Thioux, M., Seron, X., & De Volder, A. (2000). Neuroanatomical substrates of arabic number processing, numerical comparison, and simple addition: A PET study. *J Cogn Neurosci, 12*(3), 461-479.

Pesenti, M., Zago, L., Crivello, F., Mellet, E., Samson, D., Duroux, B., et al. (2001). Mental calculation in a prodigy is sustained by right prefrontal and medial temporal areas. *Nat Neurosci, 4*(1), 103-107.

Piazza, M., & Dehaene, S. (2004). From number neurons to mental arithmetic: the cognitive neuroscience of number sense. In M. Gazzaniga (Ed.), *The cognitive neurosciences, 3rd edition.* (pp. 865-875). New York: Norton.

Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., Lucangeli, D., et al. (2010). Developmental trajectories of number sense in normal and dyscalculic children. *Cognition, in press*.

Piazza, M., Giacomini, E., Le Bihan, D., & Dehaene, S. (2003). Single-trial classification of parallel pre-attentive and serial attentive processes using functional magnetic resonance imaging. *Proc R Soc Lond B Biol Sci, 270*(1521), 1237-1245.

Piazza, M., & Izard, V. (2009). How humans count: numerosity and the parietal cortex. *Neuroscientist, 15*(3), 261-273.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron, 44*(3), 547-555.

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

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

Piazza, M., Pinel, P., & Dehaene, S. (2006). Objective correlates of an unusual subjective experience: a single-case study of number-form synaesthesia. *Cognitive Neuropsychology, 23*(8), 1081–1082.

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron, 53*(2), 293-305.

Piazza, M., Price, C., Mechelli, A., & Butterworth, B. (2001). Symbolic and non-symbolic number processing: an fMRI study.

Pica, P., Lemer, C., Izard, W., & Dehaene, S. (2004). Exact and approximate arithmetic in an Amazonian indigene group. *Science, 306*(5695), 499-503.

Pickering, S. J. (2001). The development of visuo-spatial working memory *Memory*. Hove: Lawrence Erlbaum.

Pinel, P., Dehaene, S., Riviere, D., & LeBihan, D. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *Neuroimage, 14*(5), 1013-1026.

Pinel, P., Le Clec, H. G., van de Moortele, P. F., Naccache, L., Le Bihan, D., & Dehaene, S. (1999). Event-related fMRI analysis of the cerebral circuit for number comparison. *Neuroreport, 10*(7), 1473-1479.

Poeck, K., & Orgass, B. (1966). Gerstmann's syndrome and aphasia. *Cortex, 2*, 421–437.

Poeck, K., & Orgass, B. (1975). Gerstmann syndrome without aphasia: comments on the paper by Strub and Geschwind. *Cortex, 11*(3), 291-295.

Poltrock, S. E., & Schwartz, D. R. (1984). Comparative judgments of multidigit numbers. *Journal of Experimental Psychology: Learning, 10*, 32-45.

Pouget, A., Deneve, S., & Duhamel, J. R. (2002). A computational perspective on the neural basis of multisensory spatial representations. *Nat Rev Neurosci, 3*(9), 741-747.

Price, G. R., Holloway, I., Rasanen, P., Vesterinen, M., & Ansari, D. (2007). Impaired parietal magnitude processing in developmental dyscalculia. *Curr Biol, 17*(24), R1042-1043.

Pryde, K. M., & Roy, E. A. (1998). Prehension in children and adults: the effects of objects size. *Human Movement Science, 17*, 743-752.

Quintana, J., & Fuster, J. M. (1999). From perception to action: temporal integrative functions of prefrontal and parietal neurons. *Cereb Cortex, 9*(3), 213-221.

Rakic, P., Bourgeois, J. P., & Goldman-Rakic, P. S. (1994). Synaptic development of the cerebral cortex: implications for learning, memory, and mental illness. *Prog Brain Res, 102*, 227-243.

Ranzini, M., Dehaene, S., Piazza, M., & Hubbard, E. M. (2009). Neural mechanisms of attentional shifts due to irrelevant spatial and numerical cues. *Neuropsychologia, 47*(12), 2615-2624.

Rapp, B., & Caramazza, A. (1992). On the distinction between deficits of access and deficits of storage: A question of theory. In Caramazza & W. A. H. (Eds.), *Theoretical and methodological issues in cognitive neuropsychology*: in press.

Rasmussen, C., & Bisanz, J. (2005). Representation and working memory in early arithmetic. *J Exp Child Psychol, 91*(2), 137-157.

Revkin, S. K., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (2008). Does subitizing reflect numerical estimation? *Psychol Sci, 19*(6), 607-614.

Reynvoet, B., & Brysbaert, M. (1999). Single-digit and two-digit Arabic numerals address the same semantic number line. *Cognition, 72*(2), 191-201.

Rivera, S. M., Reiss, A. L., Eckert, M. A., & Menon, V. (2005). Developmental changes in mental arithmetic: evidence for increased functional specialization in the left inferior parietal cortex. *Cereb Cortex, 15*(11), 1779-1790.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annu Rev Neurosci, 27*, 169-192.

Rizzolatti, G., Fogassi, L., & Gallese, V. (1997). Parietal cortex: from sight to action. *Curr Opin Neurobiol, 7*(4), 562-567.

Rizzolatti, G., Luppino, G., & Matelli, M. (1998). The organization of the cortical motor system: new concepts. *Electroencephalogr Clin Neurophysiol, 106*(4), 283-296.

Roeltgen, D. P., Sevush, S., & Heilman, K. M. (1983). Pure Gerstmann's syndrome from a focal lesion. *Arch Neurol, 40*(1), 46-47.

Roitman, J. D., Brannon, E. M., & Platt, M. L. (2007). Monotonic coding of numerosity in macaque lateral intraparietal area. *PLoS Biol, 5*(8), e208.

Rotzer, S., Kucian, K., Martin, E., von Aster, M., Klaver, P., & Loenneker, T. (2008). Optimized voxel-based morphometry in children with developmental dyscalculia. *Neuroimage, 39*(1), 417-422.

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

Roux, F. E., Boetto, S., Sacko, O., Chollet, F., & Tremoulet, M. (2003). Writing, calculating, and finger recognition in the region of the angular gyrus: a cortical stimulation study of Gerstmann syndrome. *J Neurosurg, 99*(4), 716-727.

Rubinstein, O., Henik, A., Shahar-Shalev, S., & Berger, A. (2000). The development of internal representations of magnitude and their association with Arabic numerals. *submitted*.

Rueckert, L., Lange, N., Partiot, A., Appollonio, I., Litvar, I., Le Bihan, D., et al. (1996). Visualizing cortical activation during mental calculation with functional MRI. *NeuroImage, 3*, 97-103.

Rusconi, E., Pinel, P., Dehaene, S., & Kleinschmidt, A. (2009). The enigma of Gerstmann's syndrome revisited: a telling tale of the vicissitudes of neuropsychology. *Brain*.

Rusconi, E., Walsh, V., & Butterworth, B. (2005). Dexterity with numbers: rTMS over left angular gyrus disrupts finger gnosis and number processing. *Neuropsychologia, 43*(11), 1609-1624.

Russell, R. L., & Ginsburg, H. P. (1984). *Cognitive Analysis of Children's Mathematics Difficulties.* (Vol. 1 (2)): Lawrence Erlbaum Associates

Sakata, H., & Taira, M. (1994). Parietal control of hand action. *Current Biology, 4,* 847-856.

Sakata, H., Taira, M., Murata, A., & Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cereb Cortex, 5*(5), 429-438.

Sato, M., Cattaneo, L., Rizzolatti, G., & Gallese, V. (2007). Numbers within our hands: modulation of corticospinal excitability of hand muscles during numerical judgment. *J Cogn Neurosci, 19*(4), 684-693.

Sawamura, H., Shima, K., & Tanji, J. (2002). Numerical representation for action in the parietal cortex of the monkey. *Nature, 415*(6874), 918-922.

Schlack, A., Sterbing-D'Angelo, S. J., Hartung, K., Hoffmann, K.-P., & Bremmer, F. (2005). Multisensory Space Representations in the Macaque Ventral Intraparietal Area. *The Journal of Neuroscience, 25(18),* 4616-4625.

Schwarz, W., & Keus, I. M. (2004). Moving the eyes along the mental number line: comparing SNARC effects with saccadic and manual responses. *Percept Psychophys, 66*(4), 651-664.

Sereno, M. I., Pitzalis, S., & Martinez, A. (2001). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science, 294*(5545), 1350-1354.

Seron, X., Pesenti, M., Noël, M. P., Deloche, G., & Cornet, J.-A. (1992). Images of numbers or when 98 is upper left and 6 sky blue. *Cognition, 44,* 159-196.

Shalev, R. S., & Gross-Tsur, V. (2001). Developmental dyscalculia. *Pediatr Neurol, 24*(5), 337-342.

Shaw, P., Kabani, N. J., Lerch, J. P., Eckstrand, K., Lenroot, R., Gogtay, N., et al. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *J Neurosci, 28*(14), 3586-3594.

Shen, L., & Alexander, G. E. (1997). Neural correlates of a spatial sensory-to-motor transformation in primary motor cortex. *J Neurophysiol, 77*(3), 1171-1194.

Shikata, E., Hamzei, F., Glauche, V., Koch, M., Weiller, C., Binkofski, F., et al. (2003). Functional properties and interaction of the anterior and posterior intraparietal areas in humans. *Eur J Neurosci, 17*(5), 1105-1110.

Siegler, R. S. (1988). Individual differences in strategy choices: good students, not-so-good students, and perfectionists. *Child Dev, 59*(4), 833-851.

Siegler, R. S. (1988). Strategy choice procedures and the development of multiplication skill. *Journal of Experimental Psychology: General, 3,* 258-275.

Siegler, R. S., & Booth, J. L. (2004). Development of numerical estimation in young children. *Child Dev, 75*(2), 428-444.

Siegler, R. S., & Jenkins, E. A. (1989). *How children discover new strategies.* Hillsdale N.J.: Lawrence Erlbaum Associates.

Siegler, R. S., & Opfer, J. E. (2003). The development of numerical estimation: evidence for multiple representations of numerical quantity. *Psychol Sci, 14*(3), 237-243.

Siegler, R. S., & Shrager, J. (1984). Strategy choices in addition: How do children know what to do? In C *Sophian (Ed* (Vol. 229).

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.

Soltesz, F., Szucs, D., Dekany, J., Markus, A., & Csepe, V. (2007). A combined event-related potential and neuropsychological investigation of developmental dyscalculia. *Neurosci Lett, 417*(2), 181-186.

Song, J. H., & Nakayama, K. (2008). Numeric comparison in a visually-guided manual reaching task. *Cognition, 106*(2), 994-1003.

Sowell, E. R., Peterson, B. S., Thompson, P. M., Welcome, S. E., Henkenius, A. L., & Toga, A. W. (2003). Mapping cortical change across the human life span. *Nat Neurosci, 6*(3), 309-315.

Sowell, E. R., Thompson, P. M., Holmes, C. J., Jernigan, T. L., & Toga, A. W. (1999). In vivo evidence for post-adolescent brain maturation in frontal and striatal regions. *Nat Neurosci, 2*(10), 859-861.

Spelke, E. S., & Tsivkin, S. (2001). Language and number: a bilingual training study. *Cognition, 78*(1), 45-88.

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, 123*, 2240-2255.

Stevenson, H. W., & Stigler, J. W. (1992). *The learning gap.* New York: Simon & Schuster.

Strub, R., & Geschwind, N. (1974). Gerstmann syndrome without aphasia. *Cortex, 10*(4), 378-387.

Takayama, Y., Sugishita, M., Akiguchi, I., & Kimura, J. (1994). Isolated acalculia due to left parietal lesion. *Archives of Neurology, 51*, 286-291.

Temple C..M. (1992). *Developmental dyscalculia*. In I. R. S.J. Segalowitz, F. Boller and J. Grafman (Ed.), *Handbook of Neuropsychology* (Vol. 6, pp. 93-114)

Thioux, M., Pesenti, M., Costes, N., De Volder, A., & Seron, X. (2005). Task-independent semantic activation for numbers and animals. *Brain Res Cogn Brain Res, 24*(2), 284-290.

Thompson, J. C., Abbott, D. F., Wheaton, K. J., Syngeniotis, A., & Puce, A. (2004). Digit representation is more than just hand waving. *Brain Res Cogn Brain Res, 21*(3), 412-417.

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

Toga, A. W., Thompson, P. M., & Sowell, E. R. (2006). Mapping brain maturation. *Trends Neurosci, 29*(3), 148-159.

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

Tucha, O., Steup, A., Smely, C., & Lange, K. W. (1997). Toe agnosia in Gerstmann syndrome. *J Neurol Neurosurg Psychiatry, 63*(3), 399-403.

Turkeltaub, P. E., Gareau, L., Flowers, D. L., Zeffiro, T. A., & Eden, G. F. (2003). Development of neural mechanisms for reading. *Nat Neurosci, 6*(7), 767-773.

Uller, C., Jaeger, R., Guidry, G., & Martin, C. (2003). Salamanders (Plethodon cinereus) go for more: rudiments of number in an amphibian. *Anim Cogn, 6*(2), 105-112.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale & R. J. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549-586). Cambridge: MIT Press.

Vallar, G., Bottini, G., & Paulesu, E. (2003). Neglect syndromes: the role of the parietal cortex. *Advances in neurology, 93*, 293-319.

Van Essen, D. C., Lewis, J. W., Drury, H. A., Hadjikhani, N., Tootell, R. B., Bakircioglu, M., et al. (2001). Mapping visual cortex in monkeys and humans using surface-based atlases. *Vision Res, 41*(10-11), 1359-1378.

Vanduffel, W., Fize, D., Peuskens, H., Denys, K., Sunaert, S., Todd, J. T., et al. (2002). Extracting 3D from motion: differences in human and monkey intraparietal cortex. *Science, 298*(5592), 413-415.

Varney, N. R. (1984). Gerstmann syndrome without aphasia: a longitudinal study. *Brain Cogn, 3*(1), 1-9.

Venkatraman, V., Ansari, D., & Chee, M. W. (2005). Neural correlates of symbolic and non-symbolic arithmetic. *Neuropsychologia, 43*(5), 744-753.

Verguts, T., & Fias, W. (2005). Representation of Number in Animals and Humans: A Neural Model. *Journal of Cognitive Neuroscience*.

Vuilleumier, P., Ortigue, S., & Brugger, P. (2004). The number space and neglect. *Cortex, 40*(2), 399-410.

Walsh, V. (2003). A theory of magnitude: common cortical metrics of time, space and quantity. *Trends Cogn Sci, 7*(11), 483-488.

Watkins, K. E., Paus, T., Lerch, J. P., Zijdenbos, A., Collins, D. L., Neelin, P., et al. (2001). Structural asymmetries in the human brain: a voxel-based statistical analysis of 142 MRI scans. *Cereb Cortex, 11*(9), 868-877.

Wellman, H. M., & Miller, K. F. (1986). Thinking about nothing: Development of concepts of zero *British Journal of Developmental Psychology, Vol 4(1)*, 31-42

Wiese, H. (2003). Iconic and non-iconic stages in number development: the role of language. *Trends Cogn Sci, 7*(9), 385-390.

Wilson, A. J., & Dehaene S. (2007). Number sense and developmental dyscalculia. In D. Coch, G. Dawson & K. Fischer (Eds.), *Human behavior, learning and the developing brain: Atypical development.* NY: Guilford Press.

Wise, S. P., Boussaoud, D., Johnson, P. B., & Caminiti, R. (1997). Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. *Annu Rev Neurosci, 20,* 25-42.

Wood, J. N., & Spelke, E. S. (2005). Infants' enumeration of actions: numerical discrimination and its signature limits. *Dev Sci, 8*(2), 173-181.

Wynn, K. (1990). Children's understanding of counting. *Cognition, 36*, 155-193.

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

Wynn, K. (1992b). Children's acquisition of the number words and the counting system. *Cognitive Psychology, 24*, 220-251.

Xia, L., Emmerton, J., Siemann, M., & Delius, J. D. (2001). Pigeons (Columba livia) learn to link numerosities with symbols. *J Comp Psychol, 115*(1), 83-91.

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition, 74*(1), B1-B11.

Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human infants. *Dev Sci, 8*(1), 88-101.

Yakovlev, P. I., & Lecours, A. R. (1967). *Regional development of the brain in early life.* Oxford: Blackwell.

Yeo, D. (2003). *Dyslexia, Dyspraxia and Mathematics*. London: Whurr

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.

Zebian, S. (2005). Linkages between number concepts, spatial thinking, and directionality of writing: The SNARC effect and the REVERSE SNARC effect in English and Arabic monoliterates, biliterates, and illiterate Arabic speakers. *Journal of Cognition and Culture, 5,* 165-190.

Zesiger, P., Martory, M.-D., & Mayer, E. (1997). Writing without graphic motor patterns: A case of dysgraphia for letters and digits sparing shorthand writing. *Cognitive Neuropsychology.*, *14(5)*, 743-763.

Zorzi, M., Priftis, K., Meneghello, F., Marenzi, R., & Umilta, C. (2006). The spatial representation of numerical and non-numerical sequences: evidence from neglect. *Neuropsychologia*, *44*(7), 1061-1067.

Zorzi, M., Priftis, K., & Umilta, C. (2002). Brain damage: neglect disrupts the mental number line. *Nature*, *417*(6885), 138-139.