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PAPER

Objects, numbers, fingers, space: clustering of ventral and dorsal functions in young children and adults

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Abstract

In the primate brain, sensory information is processed along two partially segregated cortical streams: the ventral stream, mainly coding for objects' shape and identity, and the dorsal stream, mainly coding for objects' quantitative information (including size, number, and spatial position). Neurophysiological measures indicate that such functional segregation is present early on in infancy, and that the two streams follow independent maturational trajectories during childhood. Here we collected, in a large sample of young children and adults, behavioural measures on an extensive set of functions typically associated with either the dorsal or the ventral stream. We then used a correlational approach to investigate the presence of inter-individual variability resulting in clustering of functions. Results show that dorsal- and ventral-related functions follow two uncorrelated developmental trajectories. Moreover, within each stream, some functions show age-independent correlations: finger gnosis, non-symbolic numerical abilities and spatial abilities within the dorsal stream, and object and face recognition abilities within the ventral stream. This pattern of clear within-stream cross-task correlation seems to be lost in adults, with two notable exceptions: performance in face and object recognition on one side, and in symbolic and non-symbolic comparison on the other, remain correlated, pointing to distinct shape recognition and quantity comparison systems.

Introduction

In the primate brain, sensory information is processed along two partially segregated cortical streams: the ventral stream, along the inferior occipito-temporal cortex, mainly coding for objects' shape and identity (important for recognition), and the dorsal stream, through the occipito-parietal cortices, mainly coding spatial and quantitative information (including size, number, distance, position) from the self and the environment (important for planning actions).

Each stream seems to be further characterized by complex patterns of anatomo-functional parcellation of sub-regions, each preferentially involved in specific functions: within the ventral stream, different regions respond preferentially to different categories of visual stimuli (objects, faces, scenes, or letter strings; Cohen & Dehaene, 2004; Golarai, Ghahremani, Whitfield-Gabrieli, Reiss, Eberhardt, Gabrieli & Grill-Spector, 2007; Haxby, Gobbini, Furey, Ishai, Schouten & Pietrini, 2001). Within the dorsal stream, parietal cortex also appears parcellated into sub-regions involved preferentially in grasping, pointing, eye movements and visuo-spatial attention, approximate numerical quantity processing, but also higher-level cognitive functions such as calculation (for a review, see Hubbard, Piazza, Pinel & Dehaene, 2005).

Some macroscopic aspects of cortical organization, namely the segregation between ventral vs. dorsal functions, seem to be present quite early in life. For example, already at about 6 months of age, researchers have observed a preferential involvement of the ventral stream in visual shape coding and of the dorsal stream in numerical and spatio-temporal information coding (Izard, Dehaene-Lambertz & Dehaene, 2008; Wilcox, Haslup & Boas, 2010). Morphologic measures of brain maturation (grey matter thickness, myelinization, and synaptic pruning) also support an early segregation between dorsal and ventral streams, indicating that they

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mature following different trajectories, the parietal regions peaking at about the age of 10–12 years old, while the occipito-temporal regions much later, from 16 to 20 years old (Gogtay, Giedd, Lusk, Hayashi, Greenstein, Vaituzis, Nugent, Herman, Clasen, Toga, Rapoport & Thompson, 2004; Shaw, Kabani, Lerch, Eckstrand, Lenroot, Gogtay, Greenstein, Clasen, Evans, Rapoport, Giedd & Wise, 2008; Yakovlev & Lecours, 1967). Finally, there are genetically controlled clear-cut boundaries in the patterns of cortical expansion of the parietal and temporal cortices: in adults, the sizes of different parietal cortex sub-regions exhibit high genetic correlations (are highly correlated in monozygotic twins compared to dizigotic twins), and are decorrelated with the cortical surface size of temporal regions, suggesting that the development of parietal and temporal cortical areas are influenced by different genes with region-specific expression patterns (Chen, Panizzon, Eyler, Jernigan, Thompson & Fennema-Notestine, 2011).

However, developmental neuroimaging studies describing the time course of the emergence of cortical specialization within each stream and their relation to behavioural performance in the different domains during the lifespan are still very scarce. Within the ventral stream, an important study (Golarai *et al.*, 2007) has shown that activity in the occipito-temporal cortex in children as young as 7 years of age already shows an adult-like spatial organization in domain-specific sub-regions, each preferentially responding to faces, places, or objects. The size and selectivity of the activation in these regions increases with age and is tightly and selectively correlated with behavioural performance in each domain. Conversely, for parietal cortex, we still largely ignore how the cortical specialization for grasping, pointing, eye movement, attention, quantity processing and calculation emerges and develops, and what is its relation with behavioural performance. A few studies have investigated the neural basis of numerical abilities (but not their relation with the other parietal functions), and have shown, for example, an early parietal cortex response to numerical quantity, which appears mostly right lateralized in babies and young children (Hyde, Boas, Blair & Carey, 2010; Izard, Sann, Spelke & Streri, 2009). It also appears that, in children as well as in adults, the cortical activation to numerical quantity is tightly related to behavioural performance in magnitude comparison but also in symbolic calculation, in both children and adults (Mussolin, De Volder, Grandin, Schlögel, Nassogne & Noël, 2010; Price, Holloway, Rasanen, Vesterinen & Ansari, 2007; Molko, Cachia, Riviere, Mangin, Bruandet, Le Bihan, Cohen & Dehaene, 2003; Paulsen, Woldorff & Brannon, 2007). A single recent fMRI study reports a parcellation of parietal sub-regions involved preferentially in saccades, finger pointing and calculation already in a group of children between 5 and 10 years of age (Krinzinger, Koten, Horoufchin, Kohn, Arndt, Sahr, Konrad & Willmes, 2011). However, the study did not include a direct comparison between children's and adults' activation patterns, nor did it investigate the effect of age and/or education on such functional organization, thus remaining uninformative both with respect to the time course of the emergence of such specialization during development and to its functional role in behaviour.

Brain imaging data in adults and behavioural measures in both adults and children also indicate important interactions between functions pertaining to parietal cortex, maybe suggestive of an early cross-talk between these different systems. For example, finger representations seem to be automatically associated with numerical representations in calculation and identification tasks in adults (Andres, Seron & Oliver, 2007; Di Luca, Grana, Semenza, Seron & Pesenti, 2006; Sato, Cattaneo, Rizzolatti & Gallese, 2007). Indeed, the parietal cortex activation during calculation shows some overlap with that related to the mental representation of the position of one's fingers (Andres, Michaux & Pesenti, 2012). In children, finger gnosis (defined as the internal schema of one's own fingers) successfully predicts mathematical achievements (Fayol, Barrouillet & Marinthe, 1998), and it is also often impaired in dyscalculia (Benson & Geschwind, 1970).

The fine visuo-motor co-ordination and control of finger posture during grasping movements is also associated with number processing and calculation in adults and children. For example, in adults, the magnitude of perceived numbers automatically influences the magnitude of grip aperture during grasping (Andres, Davare, Pesenti, Olivier & Seron, 2004; Andres *et al.*, 2007; Lindemann, Abolafia, Girardi & Bekkering, 2007; Moretto & di Pellegrino, 2008; Song & Nakayama, 2008). In children, impairments in grasping, as for example in dyspraxia, are also quite often associated with calculation disabilities, even in cases of overall preserved general intelligence (Yeo, 2003).

Finally, visuo-spatial attention seems to be associated with numerical abilities (Hubbard *et al.*, 2005). For example, in adults, processing numbers automatically induces eye movements as well as spatial attention shifts (Ranzini, Dehaene, Piazza & Hubbard, 2009; Loetscher, Bockisch & Brugger, 2008). A posterior parietal region for eye movement control is also implicated in calculation (Knops, Thirion, Hubbard, Michel & Dehaene, 2009). During childhood, visuo-spatial abilities (for example, visuo-spatial span, as measured by different variants of the Corsi test) are also good predictors of numerical performance (De Smedt, Janssen, Bouwens, Verschaffel, Boets & Ghesquière, 2009; Holmes, Adams & Hamilton, 2008). Visuo-spatial abilities are also often severely impaired in developmental dyscalculia (for a review, see Wilson & Dehaene, 2007).

The exact nature and origin of these reported associations is, however, poorly understood. It is possible that such behavioural links simply reflect the fact that cortical regions which are spatially close in adults undergo common developmental trajectories during brain formation, infancy or childhood (Dehaene, 2009; Penner-Wilger & Anderson, 2008; Rusconi, Pinel, Dehaene & Kleinschmidt, 2010). Under this hypothesis, there would be no causal relation between these functions, just a correlation due to synchronous cortical development, presumably under joint genetic or hormonal forces. However, it is also possible that there are causal links between some or all of these functions in the course of development. For instance, the implementation of cultural practices such as finger counting and the use of spatially oriented number lines may both positively impact on arithmetic development, thus imposing a strong functional association between these domains.

To date it has been difficult to disentangle the role of culture-based training from the role of common developmental trajectories in the emergence of these behavioural associations. Most published studies reported interactions between number, finger and space-related functions either in adults or in children in the initial primary school years, in a period where children have already undergone or are currently undergoing highly intensive training specifically aimed at creating links across these domains (Fayol *et al.*, 1998; Gracia-Bafalluy & Noel, 2008). Indeed, during the first years of primary 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 spatially oriented number line and measurement procedures) may contribute to create (or reinforce) the associations between numbers, fingers, and visuo-spatial attention, thus confounding the effects of pre-existing neuro-functional correlations with those induced by specific learning procedures.

In the literature, even among the very few studies run on young children, it is often difficult to exclude such cultural factors. For example, Fayol and colleagues (Fayol *et al.*, 1998), showed that finger knowledge correlates with numerical abilities in kindergarteners between 5 and 6 years of age. However, the numerical tests used in their experiment included arithmetical calculation, which, especially at that age, is often solved using finger counting procedures. It is possible that the use of finger counting jointly improves both finger gnosis, via increasing awareness of the fingers and their relative position in space, and symbolic calculation skills. Thus, the correlation between finger gnosis and symbolic number processing observed in that study could be a result of training in finger counting.

In order to verify the presence of pre-existing associations among numerical and other non-numerical functions associated to both parietal and occipito-temporal cortex, prior to formal school-based training, we tested preschoolers from 3 to 6 years of age, prior to formal education in mathematics, using tests devoid of any symbolic content, and which are not the subject of direct and explicit training during preschool. In the number domain, we measured accuracy with a non-symbolic large numerical quantity comparison task; finger gnosis was measured with a cross-modal tactile-to-visual finger matching task; visuo-spatial abilities were measured with a visuo-spatial short-term memory task; grasping precision was assessed by measuring the adequacy of in-flight grip aperture during grasping objects of different sizes; face and object recognition abilities were measured by a short-term recognition memory task. In order to evaluate the potential impact of preschool education in our tested children, it is important to notice that in the Italian educational system schooling becomes compulsory only at 1st grade, and that children might enrol in 1st grade only at the end of the 6th year of age. Enrolment to preschool is still an optional choice for parents as well as the numbers of years of attendance (one to three). For this reason, the Ministry of Education does not give strict directives on the topics, goals and knowledge to be reached by the end of preschool. In the case of maths, teachers are invited to introduce simple numerical concepts by creating numerical 'experiences' usually by using games and songs to teach number words and simple counting. In general, training practices in the number domain remain very poor, especially because common expectations of children's numerical abilities prior to formal schooling are very low (the ministerial document that gives indications related to maths for preschoolers claims that 'only around 6 years, the child, by operating on objects becomes able to count them …' (from 'Orientamenti dell'attività educativa nelle scuole materne', Decreto Ministeriale del 3 giugno 1991, Italy).

In the present study we thus investigated, in young children, a large set of functions tentatively associated with different cortical streams, dorsal and ventral, and capitalized on inter-individual differences to isolate clusters of correlations among functions that would indicate the presence of early associations across domains prior to formal and school-based training. For comparison, and to investigate how the relations between these functions develop from childhood to adulthood, we also administered the tests to a group of adults.

Methods

Participants

We obtained a signed informed consent from the parents or the legal representatives of 109 kindergarteners from two schools in Rovereto (TN), 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 because either they did not speak Italian sufficiently to understand the tasks' instructions (n = 7), or did not complete any of the proposed tasks (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 ethics committee.

General testing procedure

Children were tested in a quiet room in the school during school hours. They completed five tests in two separate sessions (mean inter-session time: 6 days), each one lasting for about 30 minutes. Task order was randomly varied across children with the only constraint being that the SPAN test was always the first test proposed during the first session because it did not involve unfamiliar external devices other than the wooden colored blocks, and because it required continuous interaction with the experimenter. Children could take breaks between two tasks 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 at a distance of approximately 40 cm from a 15-inch LCD monitor.

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

Numerosity comparison

Pairs of dot arrays (black, on a white background) were shown on a computer screen, laterally to a central fixation point. The 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 presentation of the two arrays. Subjects were given an unlimited amount of time to produce their response, but they were instructed not to count.

The number of dots in the two arrays was varied in order to estimate the discrimination threshold (Weber fraction). On each trial, one array contained a fixed numerosity (N1, 16 for half the trials, 32 for the other half), and the other array (N2) varied among eight possible values, 5-9-12-15-17-20-23-27 dots for the pairs where n1 was 16, and double those values for the pairs where n1 was 32. This method is a variant of the classical psychophysical method of constant stimuli, and we used it to estimate the psychometric function. Each pair was repeated eight 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 for the effect of dot size and array area. For each pair, half of the trials were controlled for dot size and the other half for dot area, so that response to number could not be attributed to any single non-numerical visuo-spatial parameter. Before starting the experiment, subjects performed eight practice trials. The trial order was randomized both within and across subjects.

Symbolic number comparison (adults only)

This task was the symbolic version of the numerosity comparison task. Subjects had to choose the larger among two visually presented two-digit Arabic numbers. Adults performed a total of 256 trials (each pair being repeated sixteen times). Trial order was randomized both within and across subjects.

Finger 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 hid the subject's hand from sight by putting a white vertical panel at the level of their wrist. Then the experimenter started the stimulation, which consisted of 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 (such that overall each finger was stimulated twice) and 10 for the two-finger conditions (all 10 finger pairs were stimulated once, with the order of stimulation randomly assigned to each pair). For adults we also added a three-finger condition (10 additional trials) to avoid ceiling effects. 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 ($40 \times 40 \times 18$ mm) mounted on a white-coloured board (420×300 mm). The digits 1 to 9 were printed on one side of the blocks, visible to the experimenter only. Subjects sat in front of the examiner and 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 subject was requested to repeat the action using his/her index finger. Subjects were given three trials for each number of touched blocks. If the subject succeeded on two out of three trials, the experimenter increased the number of touched blocks by a unit. The test was terminated if the subject failed to reproduce at least two sequences of a given number. Only complete and correct sequences were scored as correct; 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: 10×8 mm, 1 g) to three microphones built into the measuring sensor. It gives spatial coordinates in 3-D space with a resolution of 1/10 mm.

Subjects sat in front of a table with the two Zebris markers wrapped around the tip of the thumb and index finger of their dominant hand by a soft leather strip. Their task consisted of grasping a wooden cylinder that was placed 13 cm 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’), children grasped the cylinder, put it in a box located on the table on the opposite side of the dominant hand (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.

Face and object recognition

This task (whose stimuli and method are directly derived from a previous imaging study on the cortical response to objects and faces in children; Golarai *et al.*, 2007) comprises a study phase and a test phase. During the study phase, children were shown 16 grey-scale pictures (7×7 cm), representing eight different Caucasian male faces and eight novel objects, one after the other, for 10 seconds each (images courtesy of Golijeh Golarai and Kalanit Grill-Spector). Some seconds 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 images) 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 stimuli in the test phase.

Results

The results from children and adults were analyzed separately.

Experiment 1A: Children

For each task, we first describe the average results and main effects, and then we report the developmental trajectory during the studied age period (from 3 to 6 years of age). Developmental trajectories are reported in two ways: first, by comparing performance in children grouped into three different age groups as defined by the kindergarten class they belong to[1] (young class: from 37 to 52 months, average = 45 months (3.8 years of age), $n = 32$; medium class: from 51 to 65 months, average = 58 (4.8 years), $n = 34$; old class: from 62 to 76, average = 70 (5.8 years), $n = 28$), and second by performing regressions with age. Finally, we describe the correlations among tasks using correlation, regression, and cluster analysis.

Numerosity comparison

The overall accuracy was 63% (chance level 50%, $t(93) = 18.51$, $p < .000$), well above chance. On average, children from all age groups performed above chance

[1] Children are usually assigned to the class on the basis of the year of birth, with some very few exceptions for the kids born in the beginning of the year (January-March), who, upon parents’ request, may be admitted to school one year earlier. This explains a small overlap between the ages in the three groups, which is due to 7 kids (2 in the medium, and 5 in the old class) who requested early admission.

(young group mean accuracy = 59%, $t(32) = -9.31$, $p < .000$; medium group accuracy = 63%, $t(34) = 18.63$, $p < .000$; old group accuracy = 67%, $t(28) = 11.41$, $p < .000$). Response times were on average very short (group average = 2.3 sec, $SD = 2.9$; young = 2.8 sec; medium = 2.1 sec; old = 2.1 secs), incompatible with exact counting. We first analyzed the average psychometric functions (the % response 'larger' for each level of n2 and n1) and verified that they followed a sigmoid curve. The slope of the curve was approximately twice as large for trials where the stimuli were twice as large, replicating earlier findings of Weber's law for numbers. The curves became parallel when plotted on a log scale, and overlapping once expressed as a function of the log ratio of n1 and n2. Across age ranges, the slope of the central portion of the sigmoid became steeper, indicating a progressive refinement in numerosity discrimination during the lifespan. On the basis of these data, for each participant, we estimated the Weber fraction (hereafter w), calculated as the standard deviation of the random variable whose cumulative distribution function best fits (using nonlinear least-squares fitting) the individual subjects' psychometric data (Piazza, Izard, Pinel, Le Bihan & Dehaene, 2004). The data were thus fit with a normal cumulative distribution function with two free parameters: the mean, indicating the point of subjective equality (the ratios at which the two sets are perceived as equally numerous), and the standard deviation, indicating the Weber fraction. The latter parameter provides a measure of how rapidly performance changes with changes in numerosity and can thus be taken as a sensitive index of the precision of the numerosity discrimination. Importantly, we were able to estimate the Weber fraction independently from the underestimation bias that characterized performance with the current stimuli (see below). Seven out of the 94 children initially tested were excluded because performance was not meaningfully modulated by ratio level and was thus quasi-random, as indicated by the fact that a sigmoid function could not fit the data (the least mean square fitting algorithm did not converge). The data from the remaining 87 children were used to calculate the average w, which was equal to 0.71 (group model fit: $R^2 = 0.96$). This value appears to be twice as large as the one reported in previous studies on children of the same age range (Halberda & Feigenson, 2008; Piazza & Izard, 2009). This effect comes from the fact that, for the most difficult trials, and especially for stimuli where the individual dot size decreased with number, children made more errors, and performed their comparison on the basis of the dot size instead of the actual number (see error rate analysis). Irrespective of this bias, however, the overall w decreased with age [$F(2, 81) = 15.36$, $p < .000$; all planned comparisons ps < .020], starting from an average of 0.95 for the youngest ($R^2 = 0.92$ for the group data), 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 ($\beta = -.52$, $p < .000$, see Figure 1), denoting a progressive improvement in numerosity discrimination abilities during development, as previously reported by Piazza, Facoetti, Trussardi, Berteletti, Conte and Lucangeli (2010) and Halberda, Mazzocco and Feigenson (2008).

In order to further characterize performance in this task, we also carried out a more classical analysis of variance on error rate. As a first step, we searched for subjects whose performance would not statistically differ from chance. Because by design we expected that children would be around chance for the condition where stimuli were most similar, we only considered performance on the eight (of 16) most extreme ratios (larger than a 4:3 ratio), corresponding to what would theoretically be the most discriminable pairs of numerosities. Note that this analysis is highly conservative, especially given the biases that we observe with the current stimuli (see Table 1). For each individual subject, we thus performed a chi-square analysis on the average performance over the selected large ratio conditions. According to this criterion, 12 out of 94 subjects were excluded (five in common with those excluded on the basis of the analysis of the psychometric function analysis). Data for the remaining 82 children were entered in a mixed $3 \times 8 \times 2$ ANOVA with age group as between-subjects factor and the variables n2/n1 ratio (eight levels) and control type (two levels, area vs. size) as within-subjects factors. Performance increased as a function of the age group [$F(2, 79) = 8.73$, $p < .000$], and was also modulated by the n2/n1 ratio [$F(7, 553) = 268.6$, $p < .000$] (see Table 1 for mean accuracy for each ratio level) and control type (71.7% correct ($SE = 0.71$) for stimuli controlled for area, and 55.13% ($SE = 0.83$) for stimuli controlled for item size) [$F(1, 79) = 354.6$, $p < .000$]. As expected, ratio was modulated by age group [$F(14, 553) = 2.05$, $p < .01$] such that in larger n2/n1 ratios young children made more errors than older ones. Ratio was also modulated by control type [$F(7, 553) = 128.9$, $p < .000$], such that in the most difficult ratio levels errors were especially high for stimuli controlled for item size. This effect, however, did not vary as a function of age group (no triple interaction age*ratio*control-type [$F(14, 553) = 1.20$, $p = .27$]). 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

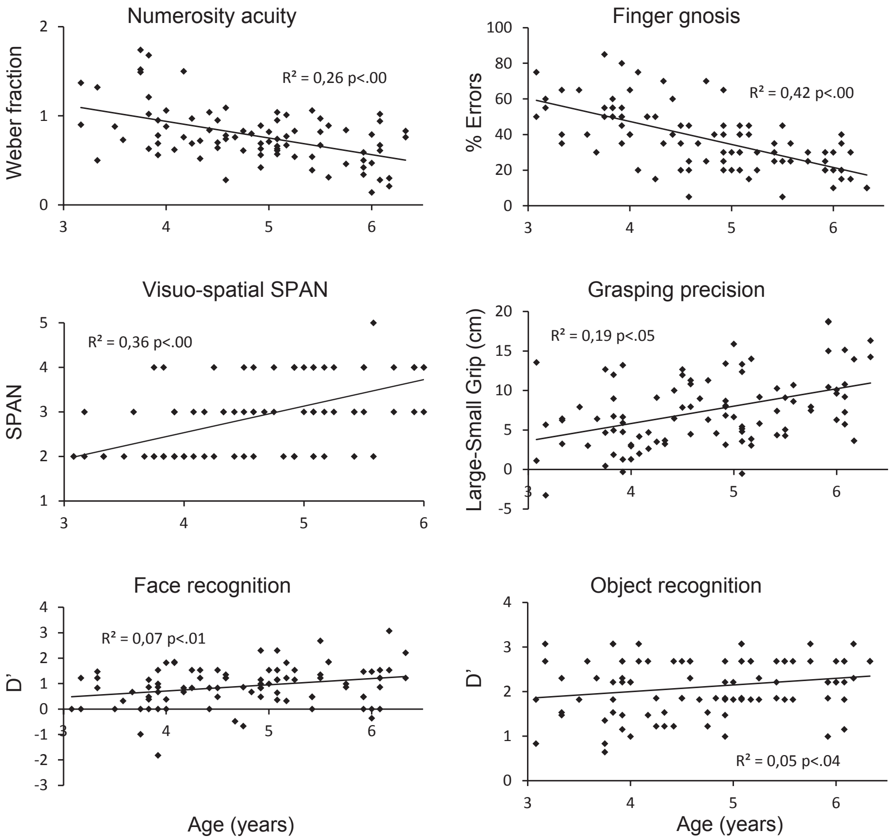

Figure 1 *Indexes used to characterize performance level in each task (Weber fraction for numerosity comparison, SPAN, accuracy for finger gnosis and sensitivity for face and object recognition) as a function of age in preschoolers.*

Table 1 *Accuracy (and standard error) as a function of N2/N1 ratios*

N1/N2 ratio	Mean accuracy (%)	Standard error
0.3	92.6	0.7
0.6	87.0	1.1
0.7	75.8	1.1
0.9	67.5	1.4
1.1	37.0	1.4
1.2	46.5	1.3
1.4	49.9	1.5
1.7	51.1	1.5

bigger, irrespective of their number (see Discussion). It also suggests that such bias was equally present in all age ranges.

Finger gnosis

The overall mean accuracy was 75% for one finger (chance level 20% $t(93) = 8.43$, $p < .000$) and 25% for two fingers (chance level 5% $t(93) = 23.73$, $p < .000$). Overall accuracy increased across ages starting from an average of 48% for the youngest up to 65% for the medium and 75% for the oldest kindergarteners [$F(2, 91) = 29.91$, $p < .000$; 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 incorrect discrimination of one or two fingers (hereafter 'discrimination errors', 83%, 76%, and 83% for the three groups), while 19% were due to incorrect report of the order in which 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 representation abilities progressively improved as a function of age ($\beta = -.65$, $p < .000$, see Figure 1). This effect was confirmed when trials were separated on the basis of the number of stimulated fingers ($\beta = -.46$, $p < .000$ and $\beta = -.64$, $p < .000$, for one vs. two fingers stimulated, respectively). Both discrimination and inversion errors also linearly decreased with age ($\beta = -.55$, $p < .000$, and $\beta = -.29$,

$p < .010$, for discrimination and inversion errors, respectively).

Visuo-spatial SPAN

The overall SPAN (index of the capacity of visuo-spatial short term memory) was 3 ($\pm$ 0.9). It increased 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 [($F(2, 91) = 22.81$, $p < .000$; all ps $< .002$], as also confirmed by linear regression ($\beta = .60$, $p < .000$, see Figure 1).

Grasping

As expected, the maximal grip aperture during grasping was modulated by the size of the to-be-grasped cylinders: it was 9.8 cm for small cylinders and 10.8 cm for big cylinders [$F(1, 91) = 503.52$, $p < .000$] (Castiello, 2005). As a measure of the impact of object size on grip aperture, we took the difference between the maximum grip aperture for the large and the small objects. This difference progressively increased with age (it was 0.7 cm in 3-year-old, 1 cm in 4-year-old, and 1.1 cm in 5-year-old children [main effect of age range on max grip aperture size modulation $F(2, 91) = 10.27$, $p < .000$; all planned comparisons ps $< .000$], also confirmed by linear regression ($\beta = .44$, $p < .000$, see Figure 1).

This difference was mostly, but not entirely, due to an increase in the maximum grip aperture with age for the large object ($\beta = .21$, $p < .050$). Indeed, hierarchical regressions showed that the increased difference between the maximum 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.

Face and object recognition

Due to informatic problems we could not collect performance for three children in this task. For the remaining 91 children, the overall mean accuracy was 85% for objects and 64% for faces. In order to quantify face and object 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 (in z-scores) 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 [$F(2, 88) = 3.69$, $p < .050$] and was higher for objects than for faces [$F(1, 88) = 239.42$, $p < .000$]. Linear regressions confirmed that recognition ability improved with age, and that this improvement was steeper and more significant for faces ($\beta = .27$, $p < .010$) than for objects ($\beta = .22$, $p < .040$; see Figure 1).

Interactions among tasks

The main goal of the present experiment was to identify the presence of clusters of correlations among the dorsal and ventral functions tested, and their development during the lifespan. To this end, we selected the most significant index of each task to describe each subject's performance. The chosen indexes were overall accuracy for the finger gnosis task, SPAN for visuo-spatial memory, the impact of object size on finger aperture in grasping, d' for face and object recognition memory, and the Weber fraction for the numerosity judgments (results remain substantially unchanged if we used average accuracy instead of the Weber fraction). For each subject we extracted these indexes, and we investigated their pattern of relations using correlations as well as a principal component analysis (thereafter PCA). PCA requirements of sampling adequacy (Kaiser-Meyer-Olkin measure = 0.63), and sphericity (Bartlett's test chi-square (15) = 79.4, $p < .000$) were met. In order to better separate (and thus interpret) the isolated factors, we also applied varimax rotation to the PCA loadings (Jolliffe, 2002). Unless otherwise stated, in the PCA analysis we adopted a standard criterion for adding clusters to the model, which is of an eigenvalue >1. The analysis revealed a clear two-cluster solution, accounting for 58% of the variance (Figure 2 and Table 2). The two factors sharply separated dorsal from ventral functions: the first included non-symbolic comparison, fingers gnosis, visuo-spatial SPAN and grasping, and the second included face and object recognition. Paired correlations among the individual tasks within the two factors confirmed the presence of significant correlations among the dorsal and ventral functions and the absence of consistent correlations across dorsal and ventral tasks (see Table 4 for the full correlation matrix).

We then performed partial correlations to control for the effect of age. Correlations that remained significant once age was controlled were: face and object recognition (partial correlation Pearson's $r = .393$, $p < .000$), finger gnosis and visuo-spatial SPAN ($r = .237$, $p = .02$), and numerosity comparison and finger gnosis ($r = .276$, $p = .01$; see Figure 3 and Table 4). The presence of

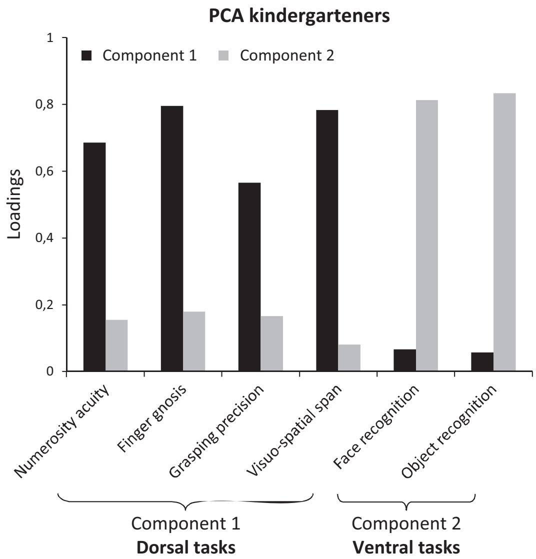

Figure 2 *Principal component analysis reveals that the entire set of kindergarteners' data can be accounted for by two components, a 'dorsal' and a 'ventral' one. Coefficients of linear correlation (loadings) express the impact of each task on the component.*

Table 2 *Factor loadings (PCA) for each task in children*

Task	Component 1	Component 2
Numerosity comparison	**.69**	.15
Finger discrimination	**.80**	.18
Grasping	**.57**	.17
SPAN	**.78**	.08
Face recognition	.07	**.81**
Object recognition	.06	**.83**

age-independent clusters grouping together finger gnosis, numerical abilities and visuo-spatial span on one side, and face and object processing on the other was also confirmed by a supplementary PCA analysis, whereby a two-cluster solution was searched for on the age-controlled residual data. In this data reduction analysis (which accounted for 48% of the total variance) ventral and dorsal components clearly separated, with the exception of grasping, which loaded onto the 'ventral' component, even though with the lowest weight (see Table 3). In order to verify the robustness of our results, in particular the presence of two separate functional clusters (including finger and numerosity comparison on one side, and object and face recognition on the other), we performed the same analysis as described above (simple correlations, partial correlation, and PCA), both excluding the data from those seven additional subjects whose error rate analysis indicated chance-level performance on the numerosity comparison task, and using error rate instead of the Weber fraction measure as the index of proficiency in approximate numerosity comparison. In all cases we replicated the same pattern of results as reported in the main analysis.

Table 3 *Factor loadings (PCA) for each task on age-corrected data in children*

Task	Component 1	Component 2
Numerosity comparison	.12	**.70**
Finger discrimination	.09	**.73**
SPAN	.11	**.61**
Grasping	**.44**	.14
Face recognition	**.78**	.19
Object recognition	**.78**	.05

Experiment 1B: Adults

Numerosity comparison

The overall accuracy was 83%. The classical sigmoid response distributions, of the psychometric functions, were recovered. On the basis of individual performance we calculated the Weber fraction for each participant. Overall, the mean w was equal to 0.19 (model fit: $R^2 = 0.99$), a value that is slightly higher than that reported in previous studies (0.14, (Pica, Lemer, Izard & Dehaene, 2004), 0.15 (Piazza & Izard, 2009), and 0.11 (Halberda & Feigenson, 2008)).

As with the analysis of the children's data, an 8 × 2 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 the n2/n1 numerical ratio [$F(7, 245) = 105.37$, $p < .000$] and control type [$F(1, 35) = 42.61$, $p < .000$]. Separate analyses for each control type revealed that error rate increased when total occupied area was kept fixed, especially for larger ratios [$F(7, 245) = 3.63$, $p < .000$]. This pattern was in line with the one that emerged in the same experiment with children, indicating that adults also may be, under certain stimuli conditions, misled by individual dot size in estimating numerical quantity.

Symbolic number comparison

The overall accuracy was 96%. Two 2 × 4 repeated measures ANOVAs were carried out on both RTs and accuracy with n1 magnitude (16 or 32) and distance level (four levels: close, medium, far, very far). Results showed the classical magnitude and distance effects: first, responses to pairs with smaller magnitudes (n1 = 16) were faster than those to pairs with larger magnitudes (n1 = 32) [$F(1, 35) = 85.69$, $p < .000$; accuracy *ns*].

Table 4 *Correlations between the different measures of tasks in children (beta and p-value)*

	Numerosity comparison	Finger discrimination	Grasping	SPAN	Face recognition	Object recognition
Numerosity comparison	**1**					
Finger discrimination	**β = -.516 *p* = .000 ****	**1**				
Grasping	β = −.104 *p* = .337	**β = .296 *p* = .004**	**1**			
SPAN	**β = −.399 *p* = .000**	**β = .534 *p* = .000 ****	**β = .353 *p* = .000**	**1**		
Face Recognition	β = −.100 *p* = .366	β = .149 *p* = .159	β = .031 *p* = .769	β = .031 *p* = .770	**1**	
Object Recognition	β = −.174 *p* = .109	β = .151 *p* = .149	β = −.006 *p* = .952	β = .190 *p* = .068	**β = .423, *p* = .000 ****	**1**

Note: In bold are significant correlations ($p < .05$). Asterisks (**): significant correlations after partialling out age. Grey shading shows functions agglomerated by the PCA.

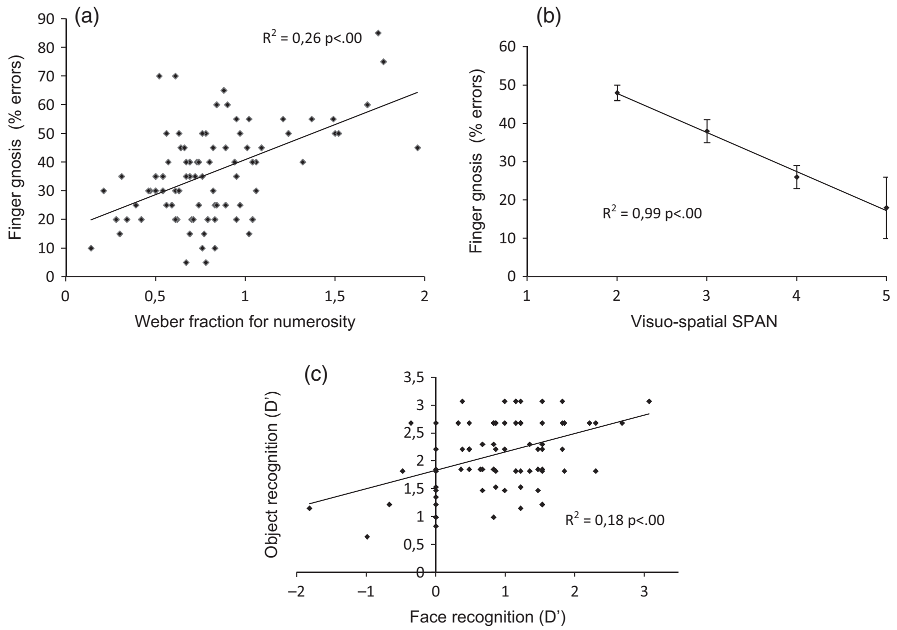

Figure 3 *Correlations between (a) Weber fraction of numerosity comparison and accuracy in symbolic number comparison, (b) accuracy in finger gnosis and SPAN, and (c) recognition memory (d′) for faces and objects.*

Second, both RT and error rate decreased with increasing distance level [$F(3, 105) = 175.78$, $p < .000$, and $F(3, 105) = 18.56$, $p < .000$, for RTs and errors, respectively]. The two effects were additive (no distance level * magnitude interaction). See Figure 5 for a direct comparison between ratio-modulated accuracy in the symbolic and non-symbolic number comparison task.

Finger gnosis

The overall mean accuracy was 89%. All errors related to finger discrimination. No inversion errors were made. Errors were modulated by the number of fingers stimulated [$F(1, 35) = 23.25$, $p < .000$]. The three-finger trials represented the most difficult condition (67% of overall errors) compared to two-finger trials [33%; three- versus two-finger trails: $t(35) = -4.82$, $p < .000$]. No one-finger errors were observed.

Visuo-spatial SPAN

The overall SPAN was 6 with a range from 4 to 7 across subjects.

Grasping

The maximum grip aperture was positively modulated by the size of the objects, being larger for the big cylinder than for the small cylinder [10.9 cm vs. 9.6 cm; $t(35) = 1.86$, $p = .07$].

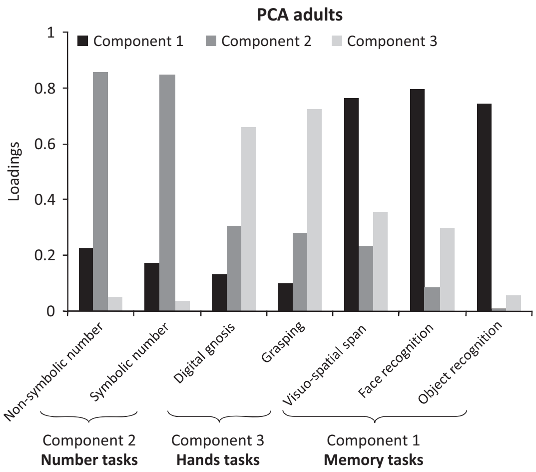

Figure 4 *Principal component analysis reveals that the set of adults data can be accounted for by three components: a numerical quantity component, comprising symbolic and non-symbolic number acuity, a finger-related component, comprising finger gnosis and grasping precision, and a visual memory component, comprising visual identity and location memory abilities. Coefficients of linear correlation (loadings) express the impact of each task on the component.*

Face and object recognition

The overall mean accuracy was 82% for objects and 82% for faces. Mean *d′* for faces and objects was 2.04 and 2.05, respectively, a non-significant difference.

Interactions among tasks

In order to explore the presence of clusters of functions, we first performed a correlation analysis on the same indexes used for the children data analysis, with the addition of the symbolic number comparison task, for which we used overall accuracy as the proficiency index. Paired correlations indicated significant links between face and object recognition memory and visuo-spatial short-term memory on one side, and non-symbolic and symbolic number comparison abilities on the other (see Figure 6). As can be seen from figure 6, the correlation between symbolic and non symbolic numerical comparison was mainly driven by the difference in performance between the main group of subjects and two very low performing ones. However, these two subjects were not just generically low performers: they performed well within the norms in all other non-numerical tasks. Indeed, the correlation remained significant even after controlling for performance in all the remaining tasks (partial correlation Beta = .61, p = .000). As for the other reported correlations (faces and objects recognition and visuo-spatial short term memory), they resulted from a continuous variation within the tested population.

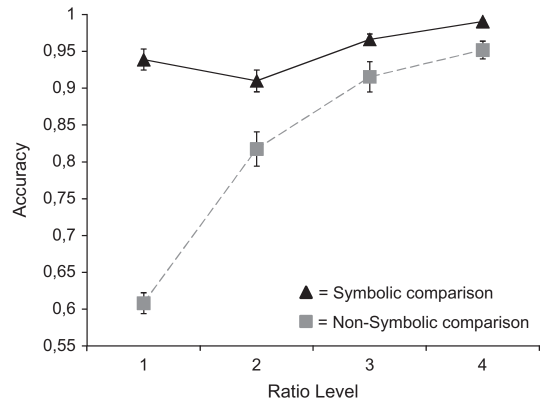

Figure 5 *Mean accuracy for the four ratio levels in the symbolic and non-symbolic number comparison task in adults. Error bars are SEM.*

We then entered the data into a PCA applying varimax rotation. Sampling was just about adequate according to the standard Kaiser-Meyer-Olkin measure (0.51), and the sphericity assumption was met (Bartlett's test chi-square (15) = 42, p < .000). However, because of the low sampling adequacy score and the relatively small sample size in the adult group compared with children, we should stress that this PCA analysis is to be taken as being highly exploratory. A three-cluster solution was obtained, accounting for 68% of the variance among variables (see Figure 4 and Table 5).

The first cluster included the three memory-related tasks (visuo-spatial memory SPAN and face and object recognition memory). The second cluster included the two numerical abilities (symbolic and non-symbolic), while the third involved the two finger-related tasks (grasping and finger gnosis). However, because the last cluster explains only 16% of the total variance and the tasks loading onto it

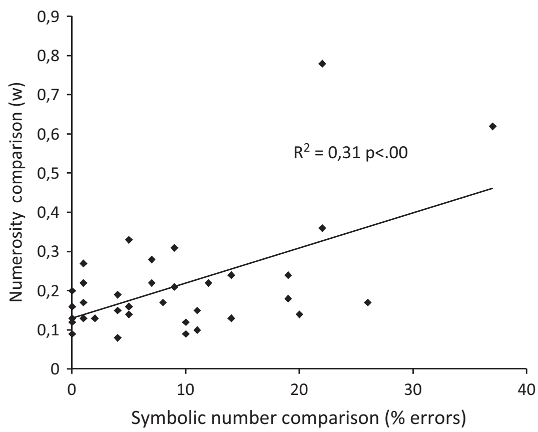

Figure 6 *Correlations between symbolic and non-symbolic number comparison proficiency in adults.*

Table 5 *Correlations between the different measures of tasks in adults (beta and p-value)*

	Numerosity comparison	Symbolic number comparison	Finger discrimination	Grasping	SPAN	Face recognition	Object 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		
Face Recognition	β = −.148 *p* = .388	β = .189 *p* = .271	β = .058 *p* = .735	β = .153 *p* = .373	**β = .392 *p* = .018**	**1**	
Object 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**

Note: In bold are significant correlations ($p < .05$). Grey shading shows functions agglomerated by the PCA.

(finger gnosis and grasping) do not show significant correlations, this component might not be very reliable. As a final data reduction analysis, in order to be able to more directly compare between adult and children data, we performed the PCA analysis excluding the symbolic number comparison data. A three-cluster component solution is individuated, whereby span, object, and face memory make the first functional group. The second component groups together the non-symbolic number comparison abilities with finger gnosis, while the third one isolates grasping from all other tasks.

Discussion

This study compared the inter-individual variability of behavioural performance in a set of tasks probing visuo-spatial, numerical, and shape recognition skills in young preschoolers, from 3 to 6 years of age, to verify the presence of clusters of correlations among cognitive functions prior to formal school-based education. Previous work indicates a tight link between calculation, finger-related skills, and visuo-spatial skills in educated children and adults: finger gnosis and visuo-spatial memory are deficient in children with developmental dyscalculia and co-vary with calculation abilities in normally developing children; numerical, finger-related, and visuo-spatial tasks also interfere with each other in adults. Finally, in adults, these functions activate spatially close sub-regions of the parietal cortex. It is unclear, however, whether these reported correlations result from school-based practices (such as the use of finger counting and of spatially oriented number lines as teaching supports for calculation), or from early and spontaneous (e.g. non education-based) clustering of functions, possibly reflecting that the subtending neural networks, lying in close cortical space within the parietal cortex, are inherently variable across subjects. In order to investigate this hypothesis, we also added tests tapping functions related to a different cortical stream, namely shape recognition memory, pertaining to ventral occipito-temporal regions.

Results first show that in all tasks there was a general age-related improvement. Non-symbolic numerosity acuity (indexed by the internal Weber fraction) continues the process of progressive refinement that starts from birth (Halberda & Feigenson, 2008; Izard *et al.*, 2009). The rate of decrease that we observe, i.e. a 42% decrease from 3 to 6 years of age, is in perfect agreement with previous reports (e.g. 40% reported in Halberda & Feigenson, 2008, and Piazza *et al.*, 2010). Visuo-spatial CORSI span also increases with age, almost linearly, with an enlargement in memory capacity of 0.6 elements per year in kindergarteners, confirming previous reports (Pickering, 2001). Finger gnosis also improved, probably because of increased proficiency in visuo-tactile integration and/or in the representation of the 'body schema', a high-level internal map of the body in space (Lefford, Birch & Green, 1974; Benton, Hutcheon & Seymour, 1951; Maravita, Spence & Driver, 2003). Finally, grasping also became better adapted to the target object during these years, such that, across ages, the grip aperture during grasping was increasingly influenced by the to-be-grasped object size.

Among ventral functions, both face and object recognition abilities improved with age, but at different rates. Face processing seemed overall less precise than object processing, but underwent a faster process of refinement compared to object processing. Interpolating from this pattern, one might tentatively predict that the overall performance (at least on this particular set of stimuli) should reverse during the first 3–4 years of schooling, with faces eventually being processed more efficiently than objects. This prediction is actually in line with previous reports documented in a combined behavioural and fMRI study on children aged from 7 to 16 years of age, using the same stimuli as we used in our experiment (Golarai *et al.*, 2007). This study showed that face processing improves faster than object processing during the 7 to 16 year period, and that this trend was related to the different anatomical maturation and functional specialization of the fusiform face area (FFA) for faces and the lateral occipital complex (LOC) for objects (Golarai *et al.*, 2007).

Correlations as well as data reduction analysis allowed us to explore the relations among all these tasks. Results show that, in young children, functions presumably related to the ventral and the dorsal stream are completely unrelated, and presumably follow separate and independent developmental trajectories. In fact, we observed a clear separation *between* dorsal and ventral functions, together with important correlations *within* both dorsal and ventral functions (dorsal functions correlated with each other, and ventral functions correlated with each other, in the absence of consistent dorsal–ventral correlations). This was true even without correcting the data for possible common age effects.

The dorso–ventral behavioural dissociation that we observe here is in line with previous observations: first, the two cortical streams mature along different trajectories (Gogtay *et al.*, 2004; Shaw *et al.*, 2008; Yakovlev & Lecours, 1967). Second, the cortical expansion of the two streams is influenced by different regionally specific genetic factors (Chen *et al.*, 2011). The relative independence of the two streams is also evident from the existence of double dissociations in neurodevelopmental genetic disorders, whereby on one side, Williams syndrome, associated with poor visuo-spatial and numerical competences but intact object recognition abilities, is accompanied by hypo-activation and grey matter density reduction in parietal cortex but intact occipito-temporal cortex, while on the other side, developmental prosopagnosia (a developmental deficit with a high genetic component), associated with poor visual object and face processing but intact spatial abilities, is accompanied by altered functional activation and connectivity of the occipito-temporal cortex but intact parietal cortex (Avidan & Behrmann, 2009; Duchaine, Germine & Nakayama, 2007; Meyer-Lindenberg, Kohn, Mervis, Kippenhan, Olsen & Morris, 2004). Among the correlated functions, some remained significantly related after accounting for age-related effects, indicating the presence of genuine age-independent inter-domain connections. In particular, we observed an age-independent correlation between numerosity comparison abilities and finger gnosis, and between finger gnosis and visuo-spatial abilities on one side, and between face and object recognition on the other. Thus, children who can easily mentally represent their own fingers will also perform well in approximate numerosity comparison, and also have a high short-term visuo-spatial memory span. Those children, however, may perform well or poorly at face and object recognition tasks. On the other hand, face recognition abilities strongly predict object recognition abilities, and are totally unrelated to quantity, space, and finger-related tasks.

There are at least two possible interpretations for these age-independent correlations. The first is a 'functional' interpretation, for which a third factor jointly influences the different domains (number, space, and fingers on one side, and objects and faces on the other). For the dorsal stream functions, this factor could be, for example, finger counting. The use of finger counting in fact could jointly improve finger gnosis, via increasing awareness of the fingers and their relative position in space, spatial abilities, via practice in tracking multiple items in parallel, and, at the same time, the mental representation of numerical quantity. As a result, children with high finger gnosis would also have a high visuo-spatial span, as well as high numerical competences. However, in this study we did not test symbolic calculation or counting abilities, but the ability to compare large approximate numerosities (arrays of five to 54 dots). This task, which children perform without counting, seems unlikely to be directly influenced by finger counting practices.

For this reason, we favour the alternative interpretation for these age-independent correlations that subregions of the dorsal visual stream subtending finger, numerical quantity, and visuo-spatial processing are inherently variable across subjects and that this has a determinant effect on behavioural performance. Under this interpretation, these correlations are implemented at the *neural architectural* level, over and above explicit training with finger counting. There are several potential and non-exclusive neuronal mechanisms that may underlie the observed behavioural correlations: first, the parietal sub-regions coding for finger, space, and numerical operations may show a smaller degree of domain specificity in children compared to adults (for a similar scenario in the ventral stream response for faces, objects, and symbols, see Cantlon, Pinel, Dehaene & Pelphrey, 2011; Golarai *et al.*, 2007). A second possibility is that the parietal functional parcellization is already well in place in young children but the different sub-regions are highly connected such that maturation of one region would entrain maturation in the others. Finally, the sub-regions could be functionally segregated and not necessarily hyper-connected, yet their surface and/or grey matter thickness and/or other neurobiological features affecting their neural coding efficacy might be determined by a third common possibly genetic region-specific factor which likely affects the entire parietal lobe (or the entire occipito-temporal lobe, in the case of the ventral stream) (see Rimol, Panizzon, Fennema-Notestine, Eyler, Fischl & Franz, 2010; Chen *et al.*, 2011). In the long term, our data suggest that in the case of the dorsal stream maturation, experience and education drive these domains apart. Indeed, in the present study, the three domains (numerical, spatial, and finger) cease to correlate in adults. Recent functional imaging studies indicate that the brain activation maps of finger or spatial tasks versus number-related tasks, in human adults, lie next to each other but show relatively little spatial overlap (Knops *et al.*, 2009; Rusconi *et al.*, 2010). The results from the present study may predict a higher degree of overlap at the neural level in young children than in adults, a prediction that remains to be tested.

The present results also suggest that it might be possible to improve performance in one domain (e.g. numerical estimation) by training the correlated abilities (e.g. finger knowledge), and that this transfer of training should especially occur in children. This second highly tentative hypothesis also remains to be tested.

The two ventral abilities tested (object and face recognition) also remained correlated after controlling for age in children. The functional specialization of the ventral visual system is a slow process which has been described with fMRI (Golarai *et al.*, 2007). Our work suggests that it might be inherently variable across children, and has a determinant effect on both object and face recognition abilities. Another possible interpretation would be that both our face and object memory tasks tapped a common system for recognition memory (e.g. relying on the hippocampus) which shows a significant variation across children, over and above the mere effects of age. Interestingly, however, an important recognition memory component is also present in the finger gnosis task we used, but finger gnosis did not correlate with either face or object recognition, making the memory factor hypothesis less plausible.

In adulthood, the pattern of correlations across functions appeared quite different from that of children. Visuo-spatial memory correlated with object and face processing, while the number tasks (non-symbolic and symbolic number comparison) did not correlate significantly with either the finger (grasping and finger gnosis) or the visuo-spatial task. Thus, it appears as if development entails a progressive decorrelation process, possibly due to greater specialization and cortical segregation, even among functions which are correlated early in life. However, not all parietal functions eventually segregate in adults within the number domain, symbolic and non-symbolic number processing were correlated in adults: subjects who performed particularly bad in Arabic digits comparison also showed poor ability in numerosity comparison, in the context of average performance in all other tasks. This finding supports the presence of mutual and long-lasting cross-talk between symbolic exact and non-symbolic approximate number abilities, as also previously revealed by behavioural (Halberda *et al.*, 2008; Lipton & Spelke, 2005) and brain-imaging studies (Eger, Michel, Thirion, Amadon, Dehaene & Kleinschmidt, 2009; Piazza, Pinel, Le Bihan & Dehaene, 2007). The role of the other parietal functions in symbolic number processing seems different. While the present data do not exclude spatial and finger processing being of crucial importance during numeracy acquisition, they suggest that they might play a scaffolding role: once symbolic numbers are constructed, finger and space processing abilities do not influence, and are no longer influenced by symbolic numerical thinking (De Cruz, 2008; Spelke, 2000).

In sum, our correlational and data reduction analyses show that the tested dorsal-related functions follow similar developmental trends, which are different from the developmental trends characterizing ventral-related function development in young children. Moreover, they show that the inter-individual differences in finger and space on one side, and finger and non-symbolic number estimation abilities on the other side, correlate in young children over and above an age-related maturational trajectory. While a large set of factors, including education, experience, and personal preferences, can exert strong influence in shaping each individual's pattern of strengths and weakness in different cognitive domains, the present data show that in early childhood the patterns of abilities in different cognitive domains are not randomly distributed across individuals but follow coherent relations which are partially predictable from knowledge of brain function as inferred from adult studies. The present results may be relevant for educational programmes that could capitalize on the reported early and spontaneous association between functions to design efficient teaching programmes, especially in the domain of mathematics.

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