CHAPTER 2

Cerebral correlates of number processing

What does neuroimaging tell about numbers? Current research on brain-imagery allows us to investigate which areas are involved when computing 9-2 or 6×8, or when comparing 7 and 5. This chapter provides a detailed view of the cerebral implication in number processing. Studies on brain-damaged patients and healthy adults converge to show a crucial role of the parietal cortex in calculation and number comparison. However, the question of whether the intraparietal sulcus contains a number-module or rather a general system of magnitude representation is still debated. In the first and second parts of this chapter, we explore the criteria of a potential number-specific role of the intraparietal sulcus, and confront them with the recent brain imaging results. The contribution of neuroimaging studies on number development is addressed in the third part. While most of them examined the difference in brain activation between adults and children, other investigation focused on cerebral changes on the same participants after short-term training.

1. The IPS as the core representation of number magnitude

Over a hundred years ago, Galton (1880) proposed the idea of a language-independent spatial representation of numbers in the human brain. This view is still present in most current theories (Butterworth, 1999b; Dehaene, 1997; Gallistel & Gelman, 1992). Recent advances in brain-imaging techniques have made it possible to precise the role of the different areas implicated in number processing. Evidence from neuropsychological studies of brain-damaged patients indicates that acalculia, the impaired ability to perform arithmetic calculations, often results from lesions of the parietal cortex of the left (dominant) hemisphere, particularly in the inferior lobule (Benson & Weir, 1972; Cohen, Dehaene, Cochon, Lehericy, & Naccache, 2000; Dehaene & Cohen, 1991; Grafman, Passafiume, Faglioni, & Boller, 1982; Henschen, 1920; Kahn & Whitaker, 1991; Takayama, Sugishita, Akiguchi, & Kimura, 1994). Moderate numerical deficits following right parietal damage have been occasionally reported (Langdon & Warrington, 1997; Mayer et al., 2003; Rosselli &

Ardila, 1989). Beyond the parietal cortex, lesions to prefrontal (Fasotti, Eling, & Bremer, 1992; Lucchelli & De Renzi, 1993; Tohgi et al., 1995), fronto-parietal (Cipolotti, Butterworth, & Denes, 1991), and subcortical structures, particularly the thalamus (Corbett, McCusker, & Davidson, 1986; Hittmair-Delazer et al., 1994; Ojemann, 1974), were also found to be associated with impaired arithmetic abilities.

Brain-imaging studies have been conducted in healthy human adults to measure cerebral blood flow during number processing. In a pioneering experiment, Roland and Friberg (1985) were the first to report bilateral inferior parietal and prefrontal blood flow increases during subtraction relative to rest periods using the Xe intracarotid method. More recently, cerebral bases of number processing in normal individuals were investigated by other neuroimaging methods. Dehaene and collaborators (1996) used positron emission tomography (PET) to measure regional cerebral blood flow when adults performed multiplication and comparison on pairs of Arabic numerals. Brain activation was observed in the inferior parietal lobule and in the precentral gyrus during both tasks. These localisations were confirmed by functional magnetic resonance imaging (fMRI). The first experiments showed that adults activated left prefrontal and posterior parietal cortices during complex calculation tasks, such as counting backward by sevens from a three-digit number (Rueckert et al., 1996), or multiply numbers presented serially (Fulbright et al., 2000). Furthermore, the left and right parietal areas were implicated in number comparison to the same extent as in a multiplication verification task (Rickard et al., 2000). The time course of brain activation dedicated to mental calculation was also examined using event-related potentials (ERPs). When participants had to perform a verification task on single-digit multiplication problems, a difficulty effect was found on left and right parietal electrodes sites, irrespective of whether the operands were presented as Arabic numerals or number words (Kiefer & Dehaene, 1997). The simple problems (e.g., 2×4=8 or 10?) elicited an early activation in the left parietal cortex while the more complex problems (e.g., 6×7=42 or 36?) required longer activation in both left and right parietal cortices. The role of the parietal cortex in the number representation was investigated by temporarily interfering with brain activation during numerical tasks using repetitive transcranial magnetic stimulation (rTMS). In this technique, a coil is held over the scalp of the participants generating magnetic pulses. The logic is as follows: if the stimulated area is necessary for the cognitive task, then performance will be impaired and slower; by contrast, if the area is not important then TMS either will have no effect or even could facilitate task performance (Marzi et al., 1998; Oliveri et al., 1999; Walsh, Ellison, Battelli, & Cowey, 1998). When adults had to compare two Arabic numerals separated by a either small or a large distance, stimulation on the left inferior parietal lobule induced slower RTs relative to right or sham stimulation[3] (Sandrini, Rossini, & Miniussi, 2004). There was also a trend for greater numerical distance effect after left rTMS.

All together, functional magnetic resonance imaging, positron emission tomography, and electrophysiological studies show the prefrontal and parietal cortices to be regularly activated not only in mental calculation (Appolonio et al., 1994; Burbaud et al., 2000; Burbaud et al., 1999; Burbaud et al., 1995; Dehaene et al., 1999; Gruber, Indefrey, Steinmetz, & Kleinschmidt, 2001; Kazui, Kitagaki, & Mori, 2000; Menon, Mackenzie, Rivera, & Reiss, 2002; Menon, Rivera, White, Glover, & Reiss, 2000; Rickard et al., 2000; Rueckert et al., 1996), but also in simpler tasks like number comparison (Pesenti et al., 2000; Pinel, Dehaene, Riviere, & LeBihan, 2001; Pinel et al., 1999).

1.1. Dehaene's proposal

Amongst the various brain regions aforementioned, neuroimaging studies have found the intraparietal sulcus to be activated in a wide range of numerical tasks, such as number comparison (Chochon, Cohen, van de Moortele, & Dehaene, 1999), approximation (Stanescu-Cosson et al., 2000; Venkatraman, Ansari, & Chee, 2005), simple calculation (addition: Pesenti et al., 2000; subtraction: Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002; multiplication: Zago et al., 2001), complex calculation (Delazer et al., 2005; Ischebeck et al., 2006), and counting (Piazza, Mechelli, Butterworth, & Price, 2002).

Eighteen years ago, Dehaene and Cohen (1991) proposed that the intraparietal sulci (IPS) play an important role in number processing and might underlie an abstract representation of number magnitude. Based on a recent meta-analysis of eight fMRI studies using various tasks and methods, Dehaene, Piazza, Pinel, and Cohen (2003) showed that the horizontal segment of the IPS (hIPS) bilaterally, in particular, is consistently implicated in

[3] Sham stimulations were used to control for unspecific TMS effects. In these trials, the magnetic field was not directed towards the brain tissue, but reproduced the coil noise.

numerical tasks, with a reproducibility of 5-7 mm in standardised coordinates. Whereas the hIPS could specifically contribute to the processing of number magnitude, two other parietal circuits would also be involved in both numerical and non-numerical domains (see Fig. 2-1). The angular gyrus, which is involved in language-based processes such as phoneme detection (Simon et al., 2002), is thought to support verbal aspects of number processing (Stanescu-Cosson et al., 2000). This area could mediate exact and highly automatized calculation, especially multiplication and small addition problems (Chochon et al., 1999; Duffau et al., 2002; Lee, 2000). Finally, the posterior superior parietal lobule would contribute to number processing in a non-specific way to support visuospatial processes, attention and spatial working memory (Dehaene et al., 2003; Simon et al., 2002). All together, these three brain regions differently participate to the cerebral networks activated when adults process numbers.

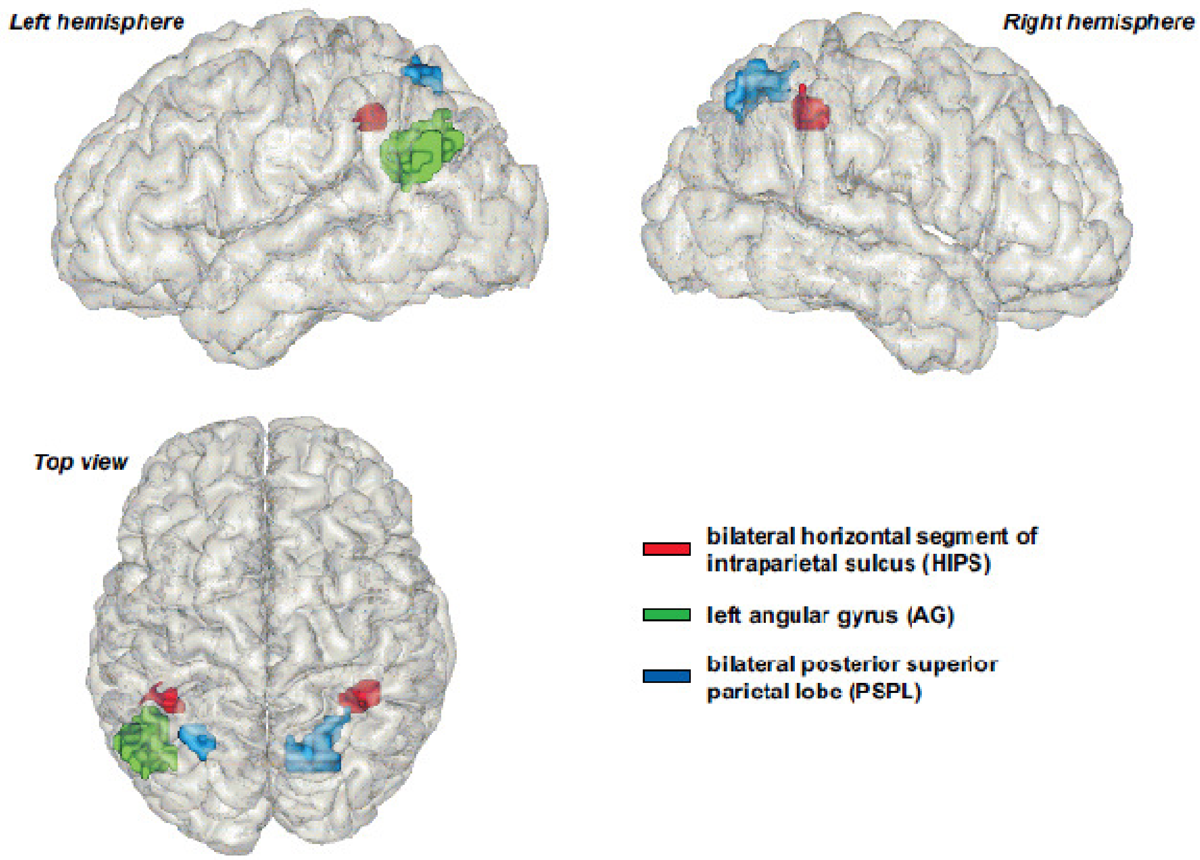

Figure 2-1. Three-dimensional representation of parietal brain activation during number processing in the hIPS (red), the angular gyrus (green), and the posterior superior parietal lobule (blue). Clusters included voxels activated in at least 40% of studies in a given group (reproduced from Dehaene et al., 2003).

1.2. Criteria for a number module in the IPS

A large body of evidence supports the hypothesis of a number module localised in the IPS. Several brain-imaging studies report higher brain activation of this area in numerical relative to non-numerical tasks. This could be seen as a relative specifity for number processing. Moreover, the involvement of the IPS in numerical tasks is observed regardless of the format of number presentation. Furthermore, the modulation of brain activity in this area reflects the nature of the number magnitude representation. In a number comparison task, the IPS activation increases as the numerical distance between the numbers decreases. Finally, this brain region could be activated even in the lack of explicit processing of number magnitude. Each of the aforementioned criteria has given rise to a detailed discussion presented in the subsequent sections.

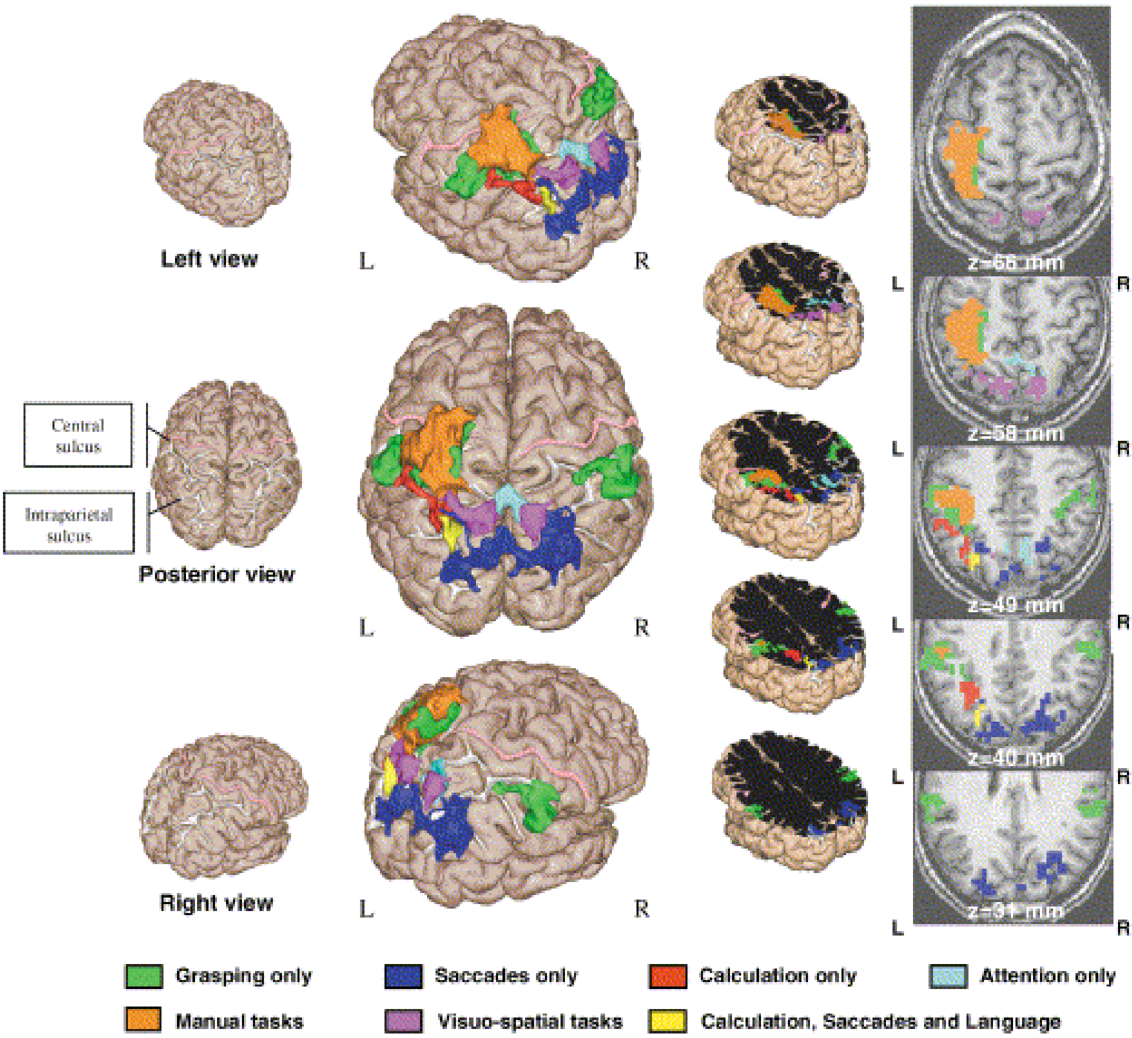

Figure 2-2. Localisation of task-specific and task intersection activations related to grasping, pointing, saccades, attention, calculation, and phoneme detection (reproduced from Simon et al., 2002).

First, the activation of some part of the IPS was found to be *specific* to number processing as opposed to other semantic categories. It appears that the left and right IPS were more activated for numbers than for animals in comparison and classification tasks (Thioux, Pesenti, Costes, De Volder, & Seron, 2005). When adults had to perform a comparison task on names of numbers (decide whether the number was larger or smaller than 12) or body parts (decide whether the part was higher or lower than the shoulders when a person is standing), more activation for numbers was observed in the right IPS (Le Clec'H et al., 2000). Furthermore, it seems that, amongst the various functions subserved by the parietal cortex, the calculation was related to specific activation of the IPS. Adults performed different tasks related to parietal activation, including grasping, pointing, saccades, attention, calculation, and phoneme detection (Simon et al., 2002). Compared to other tasks, calculation (i.e., subtracting each presented number from a fixed standard) yielded unique activation in the left hIPS, and another activation shared with phoneme detection in the left posterior segment of the IPS beneath the left angular gyrus (see Fig. 2-2). This fits well with the hypothesis of two different systems of number representation: a nonverbal representation in the IPS and a verbal representation in the left angular gyrus (Dehaene & Cohen, 1991; Dehaene & Cohen, 1997).

Second, the implication of the IPS in number processing seems to be *notation independent*. A large amount of studies have shown an activation of this region when participants performed numerical tasks on single- (Kadosh, Kadosh, Kaas, Henik, & Goebel, 2007) or two-digit Arabic numbers (Pinel et al., 2001; Pinel et al., 1999; Wood, Nuerk, & Willmes, 2006). Similar findings were found with written (Le Clec'H et al., 2000; Naccache & Dehaene, 2001a) or spoken number words (Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003). The IPS was also activated during the estimation of numerosity of dot patterns using an adaptation-recovery paradigm (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza, Pinel, Le Bihan, & Dehaene, 2007), or during the estimation of sequences of items with visual or auditory presentation (Piazza, Mechelli, Price, & Butterworth, 2006). Regarding more elaborate numerical processes, it has been shown that addition problems presented in symbolic (Arabic numerals) or non-symbolic (canonical dot patterns) formats shared common activations in the left and right anterior IPS, even after controlling for a matching (control) task on the same numbers (Venkatraman et al., 2005). Together, this indicates that the IPS could hold a supramodal representation of number magnitude.

Third, the activation of the IPS could reflect the internal properties of the magnitude representation, especially the *numerical distance effect*. When adults had to compare single- (Pinel et al., 1999) or two-digit numbers (Pinel et al., 2001) to a fixed memorised reference number (5 or 65) in Arabic or spelled-out forms, it was found that brain activation in the left and right IPS was modulated by the distance between the numbers to be compared regardless of the input notation: there is an inverse relationship between numerical distance and levels of IPS activation. Similar results were obtained in comparing pairs of Arabic numerals (Kaufmann et al., 2005), or pairs of square arrays (Ansari & Dhital, 2006). However, the distance effect was also found in non-numerical contexts (e.g., Moyer, 1973; Paivio, 1975). It is thus questioned whether the activation of the IPS is modulated by the numerical distance only, or by any distance related to other dimensions. An interesting study (Pinel, Piazza, Le Bihan, & Dehaene, 2004) tested this possibility by presenting pairs of Arabic numerals that differed in numerical value, physical size and luminance (e.g., 2 **7**). Participants had to perform comparisons on identical stimuli, focusing successively on each dimension. Their behavioural performance was matched across the tasks by adjusting the stimuli during a training period. For each task, only the relevant dimension induced a distance effect on RTs. This effect yielded activation in the IPS bilaterally during the three tasks. Pairwise comparisons did not show any regions with significantly greater distance effect for one dimension than for the other. Furthermore, the analysis of interference effects by contrasting incongruent and congruent trials in each task revealed a common cerebral substrate between size and number on the one hand, and between size and luminance on the other hand. Another experiment (Kadosh et al., 2005) used the same dimensions (numerical value, physical size, and luminance) in three different comparison tasks to investigate the specificity of the IPS for number magnitude. For each task, pairs of Arabic numerals were varied only in the relevant dimension in order to avoid any automatic processing of the irrelevant dimensions. Relative to size and luminance comparisons, the numerical comparison yielded higher activation in the IPS, particularly in the left hemisphere. Moreover, only a region in the left anterior IPS showed a distance-specific effect for numbers while an overlap of the three distance effects was observed in the posterior part of the left IPS.

Fourth, the recruitment of the IPS in number processing is relatively *automatic*. When adults had to detect the occurrence of a target item within three categories (numbers, letters, or colours), the left and right IPS were more activated by numbers than by colours or letters. Further evidence was provided by the adaptation paradigm (Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998; Grill-Spector & Malach, 2001; Grill-Spector, Sayres, & Ress, 2006). In this paradigm, the blood oxygenation level-dependent (BOLD) response decreases when the same stimulus is presented repeatedly due to neural adaptation. The recovery of the BOLD response after a new stimulus is introduced reflects that different neuron populations are sensitive to this change. When participants passively viewed square arrays varying in numerosity, the left and right IPS showed a decrease of activation as the numerical distance increased (Ansari, Dhital, & Siong, 2006). In another study (Piazza et al., 2007), once adults were adapted to a fixed set of numerical quantities presented as either dot patterns or Arabic numbers, activation in the hIPS regions showed recovery whenever a new numerical quantity was presented, irrespective of notation changes. Moreover, overall activation was higher when the numerical distance between deviant and adaptation values was large than when it was small. This suggests that the activation of the IPS was correlated with the numerical distance even if no explicit processing of the number magnitude was required.

2. Data challenging this view

As reported earlier, Dehaene (1997) as well as other researchers (Butterworth, 1999b; Gallistel & Gelman, 1992) argue in favour of a number module internally implemented in the parietal regions along the IPS. However, despite the amount of evidence for a crucial role of the IPS in numerical tasks, whether or not this area contains a domain-specific representation of number magnitude is still debated (for a review, see Kadosh, Lammertyn, & Izard, 2008). The IPS is activated not only in numerical tasks, but also in various non-numerical processes like grasping (Culham et al., 2003), object manipulation (Binkofski et al., 1999), visual pointing (Connolly, Andersen, & Goodale, 2003), and more generally in attention (for a review, see Behrmann, Geng, & Shomstein, 2004), and working memory (Knops, Nuerk, Fimm, Vohn, & Willmes, 2006; Owen, McMillan, Laird, & Bullmore, 2005). This led some authors to argue in favour of a non-specific role of the IPS for numbers. Walsh (2003) proposed a theory of magnitude (ATOM) which suggests that the IPS is used for coding magnitude in general, to represent quantity, space and time. In line with this view, several non-numerical dimensions share the psychophysical properties with numbers, especially the distance (e.g., Johnson, 1939; Moyer, 1973), size (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003), and SNARC effects (e.g., Gevers, Reynvoet, & Fias, 2004; Rusconi, Kwan, Giordano, Umilta, & Butterworth, 2006). It is thus possible that a similar network of cerebral regions is equally involved when dealing with these dimensions and number magnitudes. The question is whether there is only one common representation for magnitude in the brain, or whether different dimensions are represented by different neuronal populations in the IPS. Here under, we report recent neuroimaging studies that challenge the "specificity" of the IPS for number processing. In particular, we investigate the extent to which the number-related activation in the IPS might reflect an involvement in general magnitude comparisons, in ordinal information processing, in general spatial processing, or in the difficulty of the task. Finally, we address the issues of the hemispheric lateralisation and the abstract number-coding in the IPS.

2.1. The involvement of the IPS in general magnitude comparisons

Up to now, it is unclear whether or not a part of the IPS is related to number processing only. On the one hand, the IPS could be implicated in many tasks requiring magnitude processing, but more strongly for numbers. On the other hand, the IPS might be equally involved in numerical and non-numerical tasks that share some semantic properties with numbers. While the former hypothesis favours a specificity for numbers in the IPS, the latter suggests that this area would contribute to general rather than specific magnitudes processing.

Fias and his colleagues (2003) tested this question by comparing different symbolic and non-symbolic quantities characterised by the same mechanisms for representing and processing the magnitudes. Adults participated in three comparison tasks in which the quantitative information was presented as angles, lines, or two-digit Arabic numbers. A conjunction analysis between each comparison task and its control one revealed a left IPS region involved in quantitative comparison irrespective of stimulus format. A contrast between the number comparison task and the two other comparison tasks showed an activation in a more anterior area in the left IPS. This region was activated in all conditions relative to rest periods, but more strongly in number comparison. These results reflect a different contribution of the IPS in quantity comparison: an anterior region reflecting general processes not specific for number processing, and a posterior region reflecting specific processes related to the abstract processing of number magnitude.

As previously reported, the hIPS reacted almost identically when numbers were processed according to their numerical value, physical size, or luminance (Kadosh et al., 2005; Pinel et al., 2004). More support for common substrates comes for another experiment which analysed brain activation during numerical and physical size comparisons on the same pairs of Arabic numerals (Kaufmann et al., 2005). Although some areas were more activated in numerical comparisons than in physical size comparisons, no significant differences related to the distance effect were observed between both tasks in any region of the parietal lobe. This lack of IPS specificity could be due to either common cerebral substrates for both numerical and physical magnitudes, or to an involvement of the IPS during physical size comparisons reflecting an automatic activation of the number magnitude.

These recent data offer a more balanced view on the relative degree of specialisation of the IPS for number processing. Indeed, although the anterior part of the IPS shows higher activation when comparing number magnitude relative to perceptual dimensions, there is a strong overlap in IPS activation during numerical and non-numerical tasks. In the same vein, it has been shown that the IPS was involved in both discrete (numerosities) and continuous quantities processing, but more strongly for discrete than for continuous quantities (Castelli, Glaser, & Butterworth, 2006). Participants were presented with either different numbers of blue and green squares (discrete, numerical quantities) or with the same display transformed into smoothly changing distributions of green and blue hues (continuous, non-numerical quantities), and were asked to judge whether there was more blue or more green. Continuous and discrete stimuli were presented in spatial and temporal modalities. A greater bilateral activation of the IPS was found during discrete than during continuous quantity judgments irrespective of temporal or spatial presentation, suggesting that at least some parts of the IPS are specific to the representation of discrete quantity.

Nevertheless, some other findings cast more doubt on the IPS specificity for numbers. Throughout three fMRI experiments (Shuman & Kanwisher, 2004), no specific activation for non-symbolic numerical quantities was found in any of the parietal regions (including the hIPS) previously identified as involved in number processing when both experimental and control tasks were controlled for difficulty and cognitive demands. In Experiment 1, participants were scanned while comparing sequentially presented pairs of dot arrays according to either the number or colour of the dots. Contrary to what was expected, the average level of response in IPS was higher during the colour comparison task than during the number comparison task. Experiment 2 was based on an fMRI adaptation design in which participants passively viewed sequences of arrays that were either constant or randomly varied in the numerosity or in the shape of the elements. No significant number adaptation effect was found in any region of interest. In Experiment 3, participants were presented with dot arrays followed by dot flash sequences and asked to judge either which had more elements/flashes or whether the dots in the two sets were of the same or different colour. Once again, the difficulty effect was more pronounced for the colour task than for the number task in the IPS activation. This suggests that the IPS is involved in number representation and processing but that this area is not domain specific for number.

However, these findings have been criticised. In Experiments 1 and 3, the fact that colours were compared according to their luminance level, which might activate the IPS as for numbers (see Kadosh et al., 2008), could account for the lack of difference in IPS activation between numbers and colours. Dehaene's group also pointed out that the adaptation period used in the Experiment 2 could be too short to observe a possible number adaptation effect. The design included blocks of 16 seconds with a fixed numerosity while other paradigms engaged long blocks of several minutes to observe numerosities adaptation (Cantlon, Brannon, Carter, & Pelphrey, 2006; Piazza et al., 2004).

2.2. The involvement of the IPS in ordinal information processing

Numbers do not only represent magnitude information, they also refer to ordinal assignments reflecting the position of an item within an ordered set. Therefore, it could be questioned whether the IPS contains only magnitude information, or whether this area can also represent order. Since comparisons of non-numerical ordered items like letters or months are influenced by distance (months of the year: Gevers, Reynvoet, & Fias, 2003; days of the week: Gevers et al., 2004; letters of the alphabet: Taylor, Kim, & Sudevan, 1984) and SNARC effects (months: Gevers et al., 2003; days: Gevers et al., 2004) like numbers, all ordered series may share mechanisms that could be reflected by common IPS activation. Indeed, as for numbers, activation within the IPS was negatively correlated with distance in an order memory task with letters (Marshuetz, Reuter-Lorenz, Smith, Jonides, & Noll, 2006). Yet, some data from brain-damaged patients have revealed possible double dissociations between quantity and order information (Delazer & Benke, 1997; Turconi & Seron, 2002).

An ERPs study investigated whether quantity and order information rely on common or separate underlying processes (Turconi, Jemel, Rossion, & Seron, 2004). Adults had to compare a two-digit Arabic number to a fixed standard according to either its numerical value (smaller or larger than the standard 15) or its position (before or after the standard 15). In addition, participants performed an alphabetic task in which they had to decide if a letter came before or after the standard letter M in the alphabet. Although both quantity and order showed similar behavioural patterns including the numerical distance effect, they were associated with different time courses and lateralisation. The numerical distance appeared earlier and was larger on the left hemisphere for quantity processing, while it was delayed and bilateral for order processing. Moreover, the order task on numbers elicited a larger prefrontal distance effect relative to the quantity and alphabetic order tasks.

This question was further investigated by comparing IPS functional response to numbers relative to other non-numerical ordered series. It has been observed that the involvement of hIPS was similar when adults had to compare pairs of two-digit numbers according to their magnitude or two letters with respect to their position in the alphabet (Fias, Lammertyn, Caessens, & Orban, 2007). Another fMRI experiment analysed IPS activity during the processing of ordered series like months and numbers, as well as during the processing of non ordered verbal materials (Ischebeck et al., 2008). Participants performed a covert word generation task on canonical sequence of numbers (i.e., counting from 1 to 12), canonical sequence of months (i.e., reciting the months of the year from January to December), random sequence of numbers and months, and word sequence of animals. Although ROIs analyses revealed that the IPS was more activated for months and numbers than for animals, no difference in IPS activity was found between months and numbers during either canonical or random generation. This suggests that the IPS not only hosts a representation of quantity but also a representation of ordinal information that is not number-specific.

2.3. Number-related versus general spatial processing in the IPS

The way human beings represent numbers is most probably based on spatial processes. Behavioural investigation in healthy adults (e.g., Dehaene et al., 1993) and neglect patients (e.g., Zorzi, Priftis, Meneghello, Marenzi, & Umiltà, 2006) provides support for the spatial nature of the number magnitude representation. Furthermore, cerebral bases of numbers and space are closely linked (for a review, see Hubbard, Piazza, Pinel, & Dehaene, 2005). Therefore, one could investigate whether similar brain regions are involved in number processing and in non-numerical tasks requiring spatial processing, or whether some areas are specifically dedicated to the (spatial) processing of numbers.

This issue was addressed in a fMRI experiment (Fink et al., 2001). Participants were presented with three, four, or five dots which appeared in different spatial positions along an imaginary square. They had to judge either whether the number of dots was equal to four (i.e., the numerosity condition), or whether the dots formed a square (i.e., the shape condition). Common activation for numerosity and shape judgments was found in a widespread cerebral network including bilateral parietal regions close to the IPS. More importantly, stronger activation for the numerosity judgment than for the shape judgment was found neither in the inferior nor in the superior parietal cortices. Similarly, another experiment using PET reported no IPS activation when an orientation judgment task on Arabic numerals was compared with the same task on non-numerical characters (Pesenti et al., 2000). By contrast, the left IPS was more activated in a number comparison task relative to an orientation task on numerical or non-numerical symbols. Together, these findings indicate that spatial mechanisms involved during number processing could also be recruited by other non-numerical tasks. Nonetheless, specific activations in the IPS were observed in comparison tasks, suggesting that the involvement of the IPS might depend on the level of requirements on number magnitude processing.

2.4. Brain activation of the IPS with the task difficulty

Most imaging studies on number processing consist in the comparison between a numerical task and a non-numerical (control) task which is generally easier as indexed by faster processing speed (e.g., Kadosh et al., 2005). For instance, calculation which was found to activate a unique region in the hIPS relative to various tasks yielded the longer RTs (Simon et al., 2002). In the same vein, the numerical distance effect, which is seen as an internal feature of the number representation, is confounded with the overall difficulty of response selection. Therefore, changes in IPS activity may reflect the difficulty of selecting responses rather than the nature of the number representation itself.

A fMRI study (Göbel, Johansen-Berg, Behrens, & Rushworth, 2004) directly tested whether or not the IPS activation repeatedly found in number comparison was due to a general task component, such as response selection or task difficulty. Participants had to compare one- and two-digit Arabic numbers to a fixed standard (5 or 65). Two control tasks matched for response selection were used and consisted in detecting the presence of a vertical line in numerical or non-numerical stimuli. The whole-brain analysis failed to find brain areas varying with the judgment type, the distance effect, or the number size effect. By contrast, several parietal regions, including the left supramarginal gyrus extending into the lateral bank of the IPS and the left superior parietal lobule, were modulated by RTs irrespective of judgment type. ROIs analyses revealed that brain activation in the left IPS increased with the distance between the numbers to be compared, reflecting a reverse distance effect. These findings suggest that it is difficult to identify changes in the IPS related to number magnitude when numerical and non-numerical tasks are matched for difficulty and response selection. However, one cannot exclude the possibility that the lack of task-related differences in IPS activation is due to the involvement of common spatial processes in numerical and non-numerical tasks. Moreover, other brain-imaging studies found no such relationship between task difficulty and brain activation in the IPS. For instance, while this area was more activated in number comparisons relative to orientation judgments on the same numerals, RTs were faster in the comparison task than in the orientation task (Pesenti et al., 2000).

2.5. Hemispheric lateralisation and abstract number-coding in the IPS

As originally proposed by Dehaene (1992; see also Dehaene & Cohen, 1991), the abstract number magnitude would be represented in the IPS of both hemispheres. While this view is confirmed in split-brain patients (Cohen & Dehaene, 1996; Seymour, Reuter-Lorenz, & Gazzaniga, 1994), lesion studies in acalculic patients (e.g., Grafman et al., 1982; Jackson & Warrington, 1986) have identified an advantage of the left parietal cortex. Later, neuroimaging studies in healthy adults have provided evidence for predominantly left parietal activations during mental calculation (Chochon et al., 1999; Pesenti et al., 2000; Zago et al., 2001). In contrast, right-sided lesions could lead to particular difficulties in the processing of Arabic numerals, as reflected by the impaired performance of patients in reading and written calculation tasks (Langdon & Warrington, 1997; Mayer et al., 2003; Rosselli & Ardila, 1989). The dominant role of the right hemisphere in the identification of Arabic numerals is corroborated by a recent visual half field experiment with healthy individuals (Ratinckx, Brysbaert, & Reynvoet, 2001). However, although a small right-hemispheric preference was found for Arabic numerals, numbers were equally well compared in the left and right hemisphere, regardless of whether they were presented as Arabic numerals, word numbers, or bar graphs.

Current brain-imaging data are inconclusive about the hemispheric localisation of parietal regions involved during number comparison. The first studies reported bilateral activation of the areas in and around the IPS (Chochon et al., 1999; Pinel et al., 2001; Pinel et al., 1999). On the contrary, more recent results observed either left or right activation in the IPS according to the symbolic or non-symbolic format of the numbers. However, as reported here below, no clear association between the lateralisation of activations and the format of numbers was consistently found. Using rTMS to temporarily interfere with the activity in the inferior parietal lobule during the comparison of Arabic numerals, it was found that RTs were significantly longer after left but not right stimulations relative to RTs after a sham stimulation (Sandrini et al., 2004). In a fMR adaptation study (Kadosh, Kadosh, Kaas et al., 2007), healthy adults passively viewed two successive numbers presented as Arabic numerals, number words, or mixed notations. The adaptation effect was investigated by extracting individual ROIs within the parietal cortices. While the left-lateralised regions showed a main effect of adaptation that did not interact with notation, the right-lateralised regions showed a significant adaptation effect in the Arabic format only. These findings seriously challenge the idea of an abstract number representation in both parietal lobes. Rather, they suggest distinct representation of numbers, one notation-independent representation in the left parietal lobe, and one notation-dependent representation for Arabic numbers in the right parietal lobe. Conversely, another experiment (Piazza et al., 2007) reported cross-notation adaptation and recovery whenever numbers presented as Arabic numerals or dot patterns changed, particularly in the right parietal cortex. Therefore, this area could share neural populations encoding both non-symbolic and symbolic quantities. The apparent conflict in the data could be due to gender or interindividual differences in the way numbers are represented in parietal cortices. It has been recently shown that the impact of rTMS on the left hIPS differently influenced the numerical distance effect in female and male participants (Knops et al., 2006). Furthermore, it is possible that a relative hemispheric specialisation appears in the first stages of the development (see section 3 of the present chapter), but disappears in adults as experiences with symbolic numbers increase.

In summary, what emerges from the above experiments is that some parts of the IPS, particularly in the horizontal segment, are involved in number processing. Nevertheless, it is not clear whether these brain activations are specific to numbers (see Table 2-1). While Dehaene's group reported specific hIPS response to numbers relative to various control tasks, other studies found only small differences (Fias et al., 2003; Kadosh et al., 2005) or even no difference (Shuman & Kanwisher, 2004). Several non-numerical stimuli sharing semantic characteristics with numbers also activate the IPS, leading to the postulation for a common representation of general magnitudes (Walsh, 2003).

Can these findings be taken as evidence for a non-specifity of number in the brain? It is possible, but very unlikely. The IPS consists of a mosaic of distinct specialised areas which are involved not only in number processing, but also in spatial attention, working memory, or response selection. Given the strong overlap between parietal functions, the capacity to demonstrate domain specificity for numbers is limited due to the weak spatial resolution of fMRI. It may be that subpopulations of neurons in the IPS differently contribute to number processing. Separate sets of neurons would respond specifically to numbers while others would be involved in domain-general magnitudes (see Kadosh et al., 2008). In line with this view, the heterogeneity in the tasks used to control for non-numerical factors could account for the lack of specificity observed in several studies. This could also explain why ERPs data showed that processing quantity and order had different time courses in the IPS (Turconi et al., 2004), while common underlying mechanisms was observed for these both numerical properties using fMRI (Fias et al., 2007; Ischebeck et al., 2008).

Table 2-1. Different reports of specific and non-specific activation of the IPS for numbers (inspired by Kadosh et al., 2008)

Studies	Task			Are numbers specific?	Talaraich coordinates of maxima					
	Numerical		Control		left			right		
					x	*y*	*z*	*x*	*y*	*z*
Dehaene et al. (1996)	Number comparison	vs.	Multiplication	No		n.s.			n.s.	
Fias et al. (2003)	Number comparison	and	Angle or line comparison	No	-36	-68	58		n.s.	
Göbel et al. (2004)	Number comparison	and	Vertical line judgment	No	-28	-48	50		n.s.	
Fias et al. (2008)	Number comparison	and	Letter comparison	No	-39	-39	36	45	-36	48
Pesenti et al. (2000)	Number orientation	vs.	Character orientation	No		n.s.			n.s.	
Kaufmann et al. (2005)	Numerical distance	and	Size distance	No	-24	-60	52	28	-44	48
Kadosh et al. (2005)	Numerical distance	and	Size or luminance distance	No	-24	-58	38		n.s.	
Pinel et al. (2004)	Size congruity (number)	and	Size congruity (physical size)	No	-52	-32	56	47	-25	42
Kadosh et al. (2007)	Size congruity (number)	and	Size congruity (physical size)	No	-37	-37	43	38	-44	45
Shuman & Kanwisher (2004)	Number processing	vs.	Shape/colour processing	No		n.s.			n.s.	
Ischebeck et al. (2008)	Number counting	vs.	Months reciting	No		n.s.			n.s.	
Fias et al. (2003)	Number comparison	vs.	Angle or line comparison	Yes	-32	-56	54	34	-64	40
Pesenti et al. (2000)	Number comparison	vs.	Number orientation	Yes	-24	-68	50			
Pinel et al. (1999)	Small numerical distance	vs.	Large numerical distance	Yes	-48	-66	21		n.s.	
Pinel et al. (2001)	Small numerical distance	vs.	Large numerical distance	Yes	-40	-44	36	44	-56	48
Ansari et al. (2006)	Small numerical distance	vs.	Large numerical distance	Yes	-32	50	44	32	-49	46
Kadosh et al. (2005)	Numerical distance	vs.	Size or luminance distance	Yes	-24	-55	42		n.s.	
Stanescu et al. (2000)	Approximate calculation	vs.	Exact calculation	Yes	-56	-44	52	44	-36	52
LeClech et al. (2000)	Number words comparison	vs.	Body parts	Yes		n.s.		30	-54	60
Simon et al. (2002)	Calculation (subtraction)	vs.	Various tasks[a]	Yes	-36	-60	36	40	-56	52
Chochon et al. (1999)	Numerical tasks[b]	vs.	Letter naming	Yes	-45	-42	39	39	-42	-42
Piazza et al. (2002)	Counting	vs.	Subitizing	Yes		n.s.		28	-68	50
Eger et al. (2003)	Number detection	vs.	Letter or colour detection	Yes	-32	-48	32	32	-58	30
Thioux et al. (2005)	Number names	vs.	Animal names	Yes	-28	-56	48	42	-40	38
Castelli et al. (2006)	Discrete quantity	vs.	Continuous quantity	Yes	-24	-48	48	33	-57	51

[a] The tasks included grasping, pointing, saccades, attention, and phoneme detection, and were supposed to depend on the parietal cortex
[b] The tasks included numeral naming, comparison, subtraction, and multiplication tasks

Suggestive evidence for this number-neuron subpopulation comes from the recent discovery of numerosity-selective neurons concentrated in the IPS in non-human primates. Nieder and Miller (2003) trained two rhesus monkeys on a delayed matching numerosity task that required them to judge whether two successive visual patterns contained the same number of dots varying in disposition and appearance. In subsequent testing on unmatched numerosities, monkeys' errors increased as numerical distance between two displays decreased ("distance effect), and this effect was more important for larger numerosities ("size effect"). Moreover, the distribution of performances was asymmetric when plotted on a linear scale, but symmetric when plotted on a logarithmic scale. As predicted by Weber-Fechner law, the variance of each numerosity distribution was constant when data was plotted on a nonlinear scale. The analyses of the activity of neurons from the lateral prefrontal cortex reported similar results. In both the acquisition and the test phases, the neural response decreased with increasing numerical distance from a preferred numerosity, and was more symmetric when plotted on a logarithmic scale than on a linear scale. As observed at the behavioural level, the variance of neural distributions was relatively constant regardless the size of numbers when plotted on a logarithmic scale.

A subsequent study investigated the respective contributions of the prefrontal and parietal cortices in mapping visual shapes to small numerical quantities at the single-cell level in monkeys (Diester & Nieder, 2007). Using a delayed match-to-sample task, two monkeys were trained to match either a set of dots with another set of dots, or a visual Arabic numeral with a set of dots. While many neurons in the IPS encoded either the visual shapes or the numbers of dots separately, only very few IPS neurons (8/437) were selectively tuned to numerosity irrespective of whether Arabic numerals or multi-dot were displayed. By contrast, many association neurons (157/692) were observed in the prefrontal cortex that discharged more strongly to specific numerical values regardless of the presentation format. All together, these findings suggest plausible homologies between the prefronto-parietal network reported in human and in monkeys. Differences in the respective implication of prefrontal and parietal regions could be due to potential inter-species divergence or maybe to training duration, as monkeys were trained for few months whereas humans acquire symbols meaning over years.

3. Number-related changes in brain activity during development or learning

Recent brain-imaging research has begun to examine the role of brain regions in the development of numerical abilities. The first goal is to test whether specific brain response to numbers could appear in children or even in infants. In particular, the IPS should be more activated for numerical relative to non-numerical tasks, since it has been postulated that this region contains a specialised system for number manipulation (Butterworth, 1999b; Dehaene, 1997). The second aim is to trace developmental changes in areas involved in number processing, and to examine the extent to which they reflect an increasing activation of number-related parietal circuits. In the following section, we describe neuroimaging studies which address these issues. We will start by presenting the few data that reveal functional changes after short-term training on calculation in healthy adults, and then we will review experiments that focus on the differences in brain activation between adults and children during number comparison and simple arithmetic.

3.1. Training-related changes

A few studies used short-term training to investigate the relative plasticity in brain activation related to calculation. Adult students were trained on complex multiplication problems over one week until they had mastered all of them perfectly (Delazer et al., 2003). In a subsequent fMRI test session, participants were presented with the trained problems as well as with novel (untrained) problems. Compared to trained problems, higher activation was observed in the left IPS and inferior frontal gyrus for the untrained set. On the contrary, activation in the left angular gyrus was stronger for the trained relative to the untrained problems. These results suggest that learning of arithmetic facts is reflected by a shift from frontal to parietal regions and, within the parietal lobe, from the IPS to the angular gyrus. This was taken as evidence that the IPS is involved in novel problems requiring number magnitude manipulation (Dehaene et al., 1998) whereas the angular gyrus could play a crucial role in representing and retrieving arithmetic facts (e.g., Chochon et al., 1999).

In a following study (Delazer et al., 2005), adults were trained on two new arithmetic operations during five days, one set of problems was learned by pure drill and repetition, and the other set was learned by applying an algorithm. Then, brain activation was analysed on problems previously learned by drill or by strategy, and on new problems which could be resolved by the application of the same algorithm. Compared to a (control) number-matching task, all three conditions showed stronger brain activation in bilateral parietal areas including the IPS. Contrasting trained and untrained problems solved by strategy, new problems activated more strongly a large right parietal area, especially the IPS. Other foci of activation were found in both inferior frontal gyri. Regarding the effect of training method, the IPS was not more activated for problems learned by strategy than for those learned by drill. The bilateral precuneus extending to the left angular gyrus were the only parietal regions showing more activation for drill than for strategy condition.

Another fMRI experiment from the same research group (Ischebeck et al., 2006) investigated whether an identical training for both multiplication and subtraction arithmetic operations, supposed to be differently represented in the human brain (Dagenbach & McCloskey, 1992; Dehaene & Cohen, 1995; McCloskey, 1992), led to similar or different modifications of cerebral activation patterns. Adult students were trained on ten multiplication and ten subtraction problems during one week. Then, trained and untrained problems were presented to participants during fMRI session. In both operations, untrained items elicited more fronto-parietal activation than trained items. Contrasting untrained and trained multiplication problems revealed higher activation in the IPS bilaterally, the inferior frontal gyrus, the precentral gyrus, and the supplementary motor area. Contrasting untrained and trained subtraction problems showed significant left and right parietal activations along the IPS and in the inferior frontal gyri bilaterally. In the reverse contrast between trained and untrained problems, only multiplication yielded a significant cluster of activation in the left angular gyrus. In fact, the left angular gyrus was deactivated in all conditions except for the trained multiplication problems. This confirms that untrained problems required more IPS activation than trained problems. These findings suggest that trained multiplication, but not trained subtraction, showed a shift from quantity-based processing (supported by the areas in and around the IPS) to more automatic retrieval (supported by the left angular gyrus).

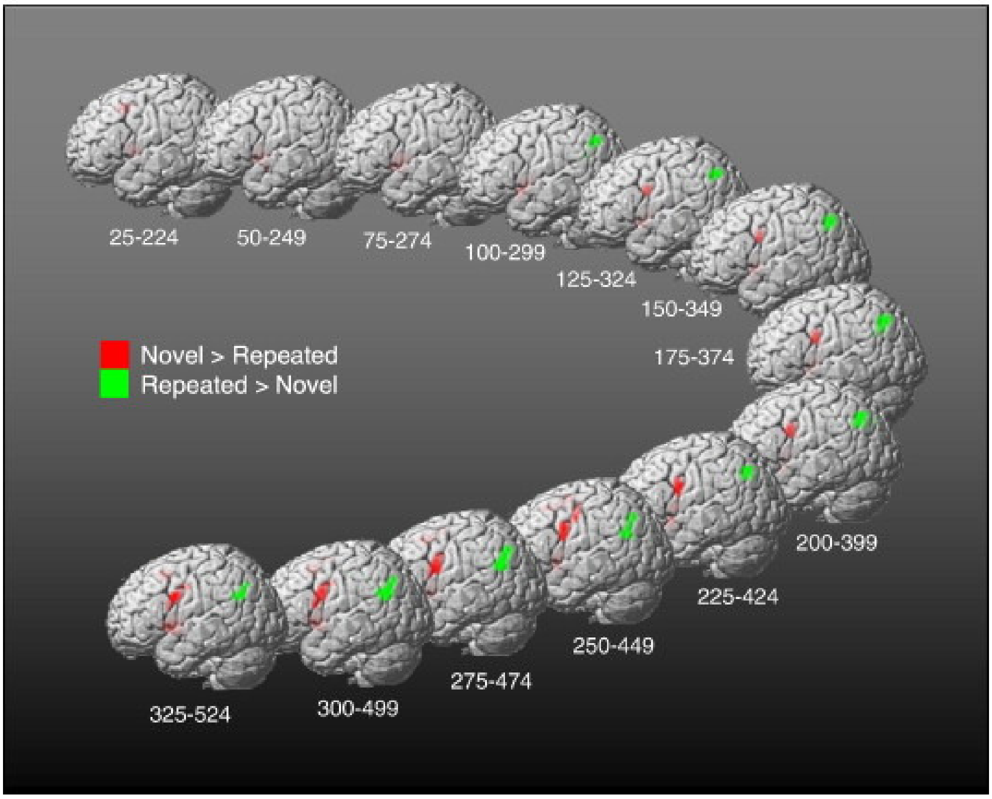

Figure 2-3. Activation changes due to practice over the course of the experiment. For repeated compared to novel problems, a significantly stronger activation first appeared in the left angular gyrus from scans 100 to 299. For novel compared to repeated problems, an area in the middle frontal gyrus became significantly more activated from scans 125 to 324 (reproduced from Ischebeck et al., 2007).

Contrarily to previous experiments in which training was provided prior scanning, a recent study examined the activation change due to practice over the course of the learning (Ischebeck, Zamarian, Egger, Schocke, & Delazer, 2007). Adults were presented with multiplication problems, and had to choose amongst two alternatives the closest to the solution. A subset of three problems was highly repeated (24 times) during the experiment, while the remaining problems were repeated only three times, and could be therefore considered as novel. The analysis by time window (see Fig. 2-3) indicated a training effect from scans 100 to 299, corresponding to a significantly stronger activation within the left angular gyrus for repeated compared to novel problems. In the reverse contrast, more activation for novel than repeated was observed in the middle frontal gyrus. Moreover, activation correlating positively with training (i.e., the number of repetitions) was found in the left angular and middle temporal gyri, and in the right supramarginal/angular gyrus. By contrast, several areas including the left inferior frontal and precentral gyri, as well as the left and right precuneus and superior parietal lobule showed negative correlation with training. In line with previous results after training, a repetition effect was associated with a decrease of activation within the parieto-frontal areas, and an increase of activation within the left angular gyrus.

Together, the adult data pointed out an important role of the IPS in the learning of new arithmetic problems. Yet, one could question whether or not similar effects might be found earlier in the development. To the best of our knowledge, only one study examined the effect of short-term training related to calculation on teenagers' brain activation (Qin et al., 2004). Young adolescents aged between 12 and 15 years learned to solve complex algebraic equations (e.g., 7χ+1=29) during a training period of five days. Cerebral activity was recorded on day 1 and day 5 to analyse the improvement on brain activation. During pre-training, areas activated in teenagers did not differ from adults' ones (Anderson, Qin, Sohn, Stenger, & Carter, 2003), and included the left parietal and the left prefrontal. The only difference was that the left parietal cortex showed a practice effect in teenagers, corresponding to a lower activation on day 5 than on day 1 (see Fig. 2-4), but not in adults. Moreover, similar results appeared when focusing on teenagers and adults with a matched behavioural practice effect, suggesting that age rather than performance caused the significant learning effect in the parietal region.

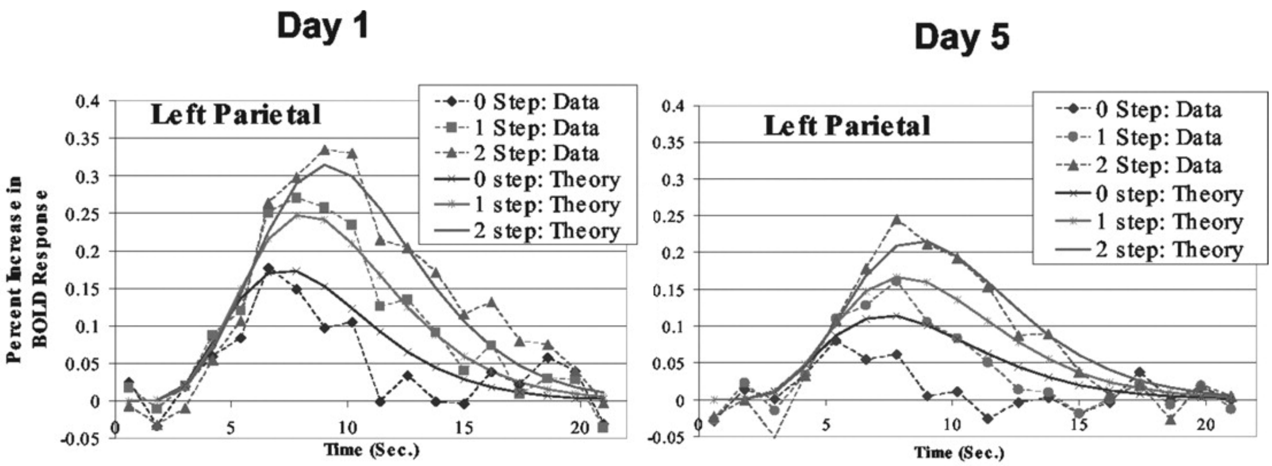

Figure 2-4. Teenagers' brain activation in the left parietal cortex (-27, -64, 35) for both days 1 and 5 in the three types of equations, and the predictions of the model based on adult performances (reproduced from Qin et al., 2004).

3.2. Age-related changes

A few experiments have examined differences in brain activation between various age groups during number/numerosity processing. Infants and young children were assessed using habituation paradigm in which they were habituated to a specific numerosity and then were presented with a deviant numerosity. The variation in brain activation related to this change was taken as evidence for a processing of the numerosity-related difference.

Brain electrical activity (ERPs) was recorded in 3-month-old infants while they were habituated to a set of objects sharing the same numerosity and identity (Izard, Dehaene-Lambertz, & Dehaene, 2008). A deviant stimulus that could differ in numerosity or object identity was occasionally introduced. ERPs related to these deviant stimuli were recorded and averaged separately for standard versus deviant numerosity trials, and for standard versus deviant object trials. While object change activated a stream of left ventral temporal regions, numerosity change led to the activation of a right network along the dorsal pathway including the right inferior parietal and frontal regions. However, the timing of numerosity change effect did not vary with the numerical distance. There was no difference between the response to numerosity that deviated of one from the standard (two versus three objects), and the response to numerosity that deviated of four or eight from the standard (four versus eight or twelve objects). These findings suggest a sensitivity to numerosity change in infants as young as 3 months. However, it has been previously shown that even older infants were not able to discriminate numerosities when images were presented at the rate used in the present study (Wood & Spelke, 2005). Therefore, it was not clear whether these changes in brain activity really reflected numerosity processing.

A similar paradigm was used to compare brain activation between 4-year-old children and adults (Cantlon et al., 2006). They passively viewed successive displays containing the same number of elements and element shape. Occasionally, a stimulus was presented that deviated from the reference display in either the number of elements (number deviants) or the shape of elements (shape deviants). In both groups, regions in and around the left and right IPS showed significantly greater activity to number deviants than to shape deviants. Number-related activity was strikingly identical in adults and 4-year-old children, with only a greater extent of activation in the right IPS for adults. There was also a trend of hemispheric differences across the two groups. Indeed, adults had significantly more activity bilaterally in the IPS regions and children had less activity, on average, in the left IPS region.

Other experiments compared the cerebral activity of older children and adults during active tasks like number comparison. In a pioneer study (Temple & Posner, 1998), ERPs were recorded while 5-year-old children and adults compared numbers presented as canonical dot patterns or Arabic numerals to the fixed standard 5. Although children were slower than adults, a numerical distance effect was found in both groups. Furthermore, the ERP components, the localisation and the timing at which this effect appeared, were similar in children and adults, with only slightly delayed peaks in the former. This suggests that adults and children as young as 5 years recruit the same cerebral network when comparing numerals.

The fMRI data offer a more balanced view and suggest age-related changes during number comparison. Brain activation of 10-year-old children and adults were analysed when they compared pairs of Arabic numerals separated by a small or a large numerical distance (Ansari, Garcia, Lucas, Hamon, & Dhital, 2005). On the one hand, several frontal and parietal regions including the IPS were modulated by numerical distance (i.e., more activated for the small distance relative to the large distance) in both groups, but more strongly for adults than for children. On the other hand, the modulation of the right precentral and inferior frontal gyri by the numerical distance was larger in children than in adults. This was interpreted as a shift from a strong involvement of right frontal areas to increasing engagement of IPS and posterior parietal regions with age. However, these results were only partially replicated with non-symbolic comparison. When children of 10 years and adults had to select the larger of two displays of squares (controlled for the total area and the surface arrangement), greater modulation of the left IPS by the numerical distance was found in adults relative to children (Ansari & Dhital, 2006). Moreover, the IPS activation related to the numerical distance was left-lateralised in children and bilateral in adults. Yet, contrary to the symbolic processing, no frontal areas showed more modulation by numerical distance for children as compared to adults.

Another experiment cast more doubt on the possible developmental changes in IPS activation during number processing (Kaufmann et al., 2008). To investigate the number-related role of fingers, brain activation of 8-year-old children and adults was compared during three classification tasks. Participants were asked to classify two horizontally presented hands according to numbers of fingers raised (non-symbolic numerical task), orientation of the palms (spatial task), or orientation of thumb colours (colour task). Conjunction analysis for each group separately indicated common parietal activation for numerical and spatial processing in the right superior parietal lobe surrounding the IPS for adults, but not for children. Compared with adults, children showed greater activation for the numerical task relative to the spatial task in the supramarginal gyrus bilaterally, in the right postcentral and precentral gyri. However, these differences were mainly due to deactivations of these areas in adults. These findings thus indicate a negative correlation between brain activation in some parietal regions and age during finger-based number processing.

Finally, two fMRI studies have compared brain activation between children and adults during simple calculation. In a first experiment (Kawashima et al., 2004), adults and children had to mentally solve single-digit addition, subtraction, and multiplication problems. Both groups showed similar activation in the frontal and parietal cortices. Only a few areas including the right IPS were more activated in adults than in children during subtraction and multiplication. Another experiment investigated more closely possible developmental changes during calculation. Brain activation was recorded while children and adolescents aged between 8 and 19 years performed simple addition and subtraction problems (Rivera, Reiss, Eckert, & Menon, 2005). Significant positive correlations between activation and age were observed in the left supramarginal gyrus and IPS (a trend was also observed in the angular gyrus), coupled with negative correlations in several prefrontal brain regions (see Fig. 2-5). These results suggest that older children engage less strongly auxiliary cognitive functions such as executive processes and working memory while solving arithmetical problems, and rely more strongly on task-specific parietal areas. Furthermore, these functional age-related changes were not associated with a reduction of grey matter within each of these regions.

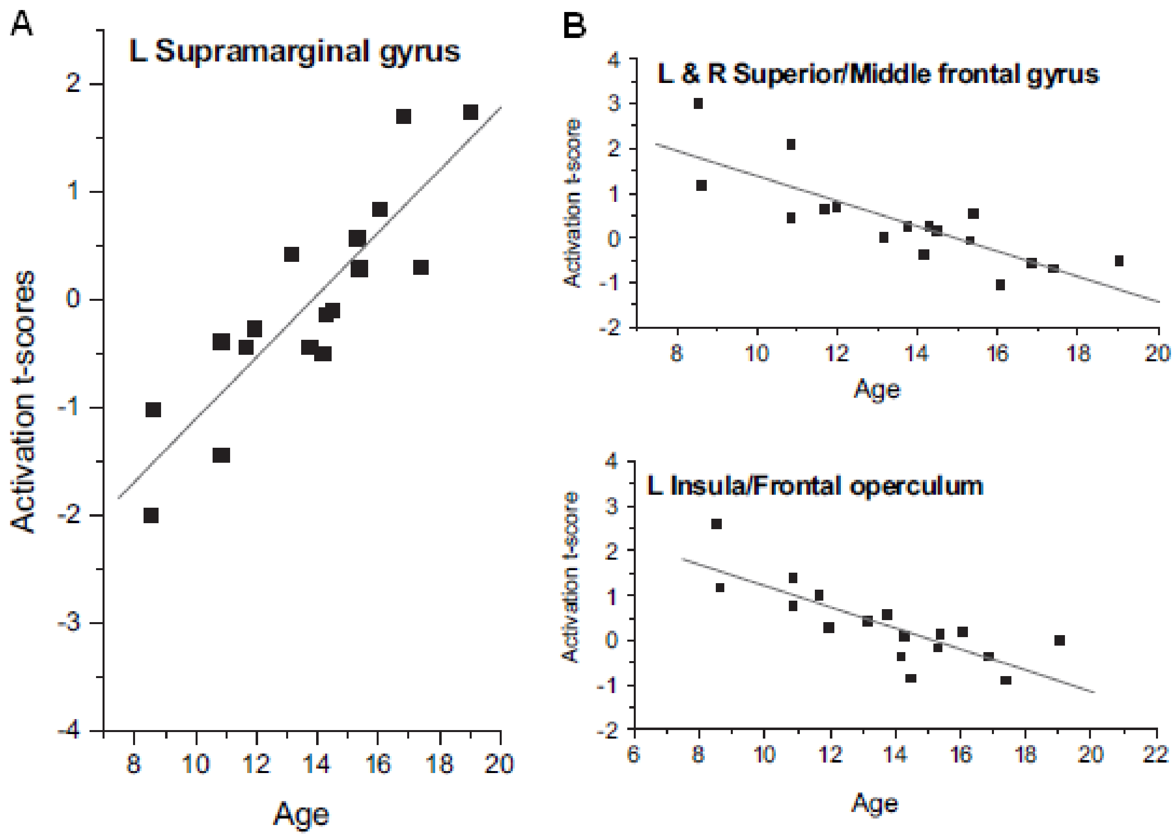

Figure 2-5. Correlations between age and brain activation during mental arithmetic (based on *t*-scores representing experimental trials minus control trials) showed (A) age-related increases in brain responses in the left supramarginal gyrus, and (B) age-related decreases in brain responses in the left superior frontal gyrus and insula/frontal operculum (adapted from Rivera et al., 2005).

In summary, the short-term training based on calculation yielded changes in brain activation of two main parietal regions. On the one hand, more activation for trained relative to untrained problems was observed in the regions close to the left angular gyrus. This change was found after training on multiplication but not on subtraction, and is supposed to reflect a role of this area in the acquisition of skilled fact retrieval. However, the angular gyrus was found to be often deactivated not only during arithmetical training (Ischebeck et al., 2007; Ischebeck et al., 2006), but also in other numerical (Grabner et al., 2007) and non-numerical (for a review, see Gusnard & Raichle, 2001) tasks compared to low-level control conditions. This makes training-related changes of brain activation in the angular gyrus difficult to interpret. On the other hand, the level of activity in areas around the IPS was found to decrease during training in children (Qin et al., 2004) and adults (Ischebeck et al., 2007). These changes were interpreted as reflecting greater demands on number magnitude processing for novel problems. Yet, compared to trained problems, solving untrained problems also implied strong requirements on executive control and working memory. Moreover, repeated problems were always solved significantly faster and more accurately than novel problems. Therefore, the less involvement of the IPS for trained relative to untrained problems could be due to a general improvement in performances rather than lower demands on number magnitude. Further investigation is required to compare training on numerical and non-numerical materials of the same difficulty to be sure that the IPS modulation is related to number processing.

Concerning studies on age-related differences, the majority of data converge to report an increasing implication of the regions in and around the IPS during the development of numerical abilities. This has been observed in various numerical task, such as number comparison on symbolic (Ansari et al., 2005) and non-symbolic quantities (Ansari & Dhital, 2006), calculation (Kawashima et al., 2004), and even in the absence of explicit number processing (Cantlon et al., 2006). Compared to children, the activation of the IPS in adults was found to be higher (Ansari et al., 2005; Kawashima et al., 2004), more extended (Cantlon et al., 2006), and more bilateral (Ansari & Dhital, 2006; Cantlon et al., 2006). A positive correlation was also observed between age and IPS activity (Rivera et al., 2005). However, none of the previous experiments requiring an explicit number processing used non-numerical control tasks. The only study which contrasted numerical with spatial or perceptual tasks failed to find differences in IPS activity between children and adults (Kaufmann et al., 2008). The lack of greater activation in the IPS for number relative to non-numerical judgments could be due to the involvement of common spatial processes. These issues will be further investigated in Chapter 6 through an original experiment that aims at determining changes in frontal and parietal regions during number comparison. Brain activation of children and adults was recorded while they compared the magnitude of two Arabic numerals, or the colour of two non-numerical symbols. If the IPS is specifically involved in the development of numerical abilities, then this area should show an increasing number-related activation with age.

Yet, the IPS seems to be more sensitive to number changes than to object identity changes in preschool children (Cantlon et al., 2006) and infants (Izard et al., 2008). Considering recent data that reported an homolog cerebral network in non-human primates to process numerosities (e.g., Diester & Nieder, 2007), these findings suggest that neural response to numbers could be biologically determined. It remains to know whether both parietal cortices are similarly involved in number processing during human development. The right IPS was found to be preferentially activated when children had to compare non-symbolic quantities as dots patterns (Cantlon et al., 2006), or arrays of squares (Ansari et al., 2006). Further support for this right lateralisation comes from a recent ERPs study investigating brain areas dedicated to numerosity processing in infancy (Izard et al., 2008). By contrast, the left IPS could play a crucial role in the processing of symbolic quantities during childhood (Rivera et al., 2005). Together, this suggests that non-symbolic number processing, supported by the right IPS early in development, could serve as a basis for more sophisticated symbolic abilities of adults which would develop in the left IPS. Nevertheless, this hypothesis is not confirmed by data collected on adults. While some findings indicate that the right IPS is activated in Arabic numbers but not in number words processing (Kadosh, Kadosh, Kaas et al., 2007), others report an involvement of this area in both symbolic and non-symbolic number quantities (Piazza et al., 2007).