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Abstract
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Common substrate for mental arithmetic and finger representation in the parietal cortex

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A B S T R A C T

The history of mathematics provides several examples of the use of fingers to count or calculate. These observations converge with developmental data showing that fingers play a critical role in the acquisition of arithmetic knowledge. Further studies evidenced specific interference of finger movements with arithmetic problem solving in adults, raising the question of whether or not finger and number manipulations rely on common brain areas. In the present study, functional magnetic resonance imaging (fMRI) was used to investigate the possible overlap between the brain areas involved in mental arithmetic and those involved in finger discrimination. Solving subtraction and multiplication problems was found to increase cerebral activation bilaterally in the horizontal part of the intraparietal sulcus (hIPS) and in the posterior part of the superior parietal lobule (PSPL). Finger discrimination was associated with increased activity in a bilateral occipito-parieto-precentral network extending from the extrastriate body area to the primary somatosensory and motor cortices. A conjunction analysis showed common areas for mental arithmetic and finger representation in the hIPS and PSPL bilaterally. Voxelwise correlations further showed that finger discrimination and mental arithmetic induced a similar pattern of activity within the parietal areas only. Pattern similarity was more important for the left than for the right hIPS and for subtraction than for multiplication. These findings provide the first evidence that the brain circuits involved in finger representation also underlie arithmetic operations in adults.

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Introduction

The use of fingers to count objects or calculate goes back to the Ancient Times (e.g., Cicero, Epistle ad Atticum, V, 21, 13, 106–43 BCN) and is further illustrated in famous counting systems (e.g., Beda Venerabilis, De tempore ratione, 672–735 ACN) commonly used across Europe in the Middle Ages (Butterworth, 1999; Williams and Williams, 1995). The success of these counting systems across times and cultures is likely to result from their capacity to pass the bottleneck of pre-existing representations in the brain of each individual (De Cruz, 2006). In this view, fingers constitute a useful means for acquiring and communicating arithmetic knowledge because they provide a physical counterpart for mental operations and they rely on pre-existing representations in the sensorimotor system. Several developmental studies have confirmed the intimate relationship between numbers and fingers. Children’s score in finger discrimination tests is the best predictor of their later arithmetical skills (Noël, 2005) and finger proved to be very important while learning to add or subtract numbers (Costa et al., 2011; Domahs et al., 2008). In adults, behavioural studies reported faster numerical judgements when target numbers were primed by finger configurations congruent with the finger-counting habits of the participants (Badets et al., 2010; Di Luca & Pesenti, 2008; Di Luca et al., 2006, 2010). A trace of finger-counting habits was also found in electrophysiological studies showing increased corticospinal excitability (CSE) in hand muscles during various numerical tasks (Andres et al., 2007; Sato et al., 2007).

There is now a large agreement that the parietal cortex plays an important role in mental calculation, as shown by numerous neuropsychological (e.g., Takayama et al., 1994) and brain imaging studies (for a recent meta-analysis, see Arsalidou and Taylor, 2011). Several studies showed that arithmetic factors, such as problem size (De Smedt et al., 2011; Stanescu-Cosson et al., 2000), number of operands (Menon et al., 2000) and strategy (Delazer et al., 2003, 2005; Grabner et al., 2009), influence the blood-oxygen level-dependent (BOLD) signal in the horizontal part of the intraparietal sulcus (hIPS) and in the posterior part of superior parietal lobule (PSPL), a region extending from the posterior segment of the IPS to the precuneus. In contrast to subtraction and addition that may require calculation procedures, the multiplication of single digits generally leads to direct retrieval of the problem and its answer from long-term memory (Campbell,
predict that the involvement of representational aspects do not necessarily imply a different implementation as a function of the level of practice with counted items and any ordered series (Andres et al., 2007). Whereas 2008; Di Luca et al., 2006, 2010). Procedural aspects refer to the role numbers or results of arithmetic operations implicitly activate a mental representation of the body in order to specify the somatic nature of their interactions. In line with this, previous fMRI studies showed that activations in the primary motor (M1) and somatosensory cortex (S1) were sensitive to the hand used to perform finger movements, whereas activations of the hIPS and PSPL occurred irrespective of hand laterality (Haaland et al., 2004; Harrington et al., 2000; Pelgrims et al., 2009, 2011). However, so far, this apparent anatomical similarity only stems from indirect comparisons of results coming from different studies using different methods.

Moreover, the functional mechanism that accounts for the potential overlap between mental arithmetic and finger representation in the human brain remains to be specified. First, it is unclear whether the processes and/or representations related to finger discrimination form an intrinsic component of number processing, or whether they complement the core number system by providing helpful tools to manipulate numbers, such as other slave systems involved in visuospatial or linguistic aspects of number processing (Dehaene et al., 2003). Second, it is essential to determine how much the potential overlap between mental arithmetic and finger representation is related to the somatic representation of the body in order to specify the embodied nature of their interactions. In line with this, previous fMRI studies showed that activations in the primary motor (M1) and somatosensory cortex (S1) were sensitive to the hand used to perform finger movements, whereas activations of the hIPS and PSPL occurred irrespective of hand laterality (Haaland et al., 2004; Harrington et al., 2000). A third question concerns the influence of representational and procedural aspects of finger counting on the implementation of arithmetic operations in finger circuits. Representational aspects were evidenced in behavioural studies showing that numbers or results of arithmetic operations implicitly activate a mental configuration of fingers (Badets et al., 2010; Di Luca & Pesenti, 2008; Di Luca et al., 2006, 2010). Procedural aspects refer to the role of fingers in instantiating the one-to-one correspondence between counted items and any ordered series (Andres et al., 2007). Whereas representational aspects do not necessarily imply a different implementation of each operation in finger circuits, procedural aspects predict that the involvement of finger circuits will differ across operations as a function of the level of practice with finger counting. In children, single-digit multiplication problems are mostly solved by memory retrieval from the fourth grade (Cooney et al., 1988), whereas subtraction often involves computational strategies with a great emphasis on finger-based calculation procedures in the early stages of acquisition (Fuson, 1988; pp. 278–279). Adults report almost exclusive reliance on retrieval for multiplication (i.e., 98% and 95% for small and large problems respectively), whereas this strategy is much less used for subtraction (i.e., 73% and 42% for small and large problems respectively; Campbell and Xue, 2001). The status of addition is less clear where memory retrieval in-between multiplication and subtraction (i.e., 88% and 64% for small and large addition problems respectively; Campbell and Xue, 2001). A dual-task experiment showed that concurrent finger movements slow down addition and subtraction, whereas multiplication remains unaffected, even after matching problems for response speed and accuracy (Michaux et al., submitted for publication). This difference was attributed to the fact that multiplication is less sensitive to finger interference because answers can be retrieved from long-term memory without computation. It is unclear, however, whether the predicted overlap between the brain circuits underlying finger discrimination and those involved in mental arithmetic will differ between operations. If the influence of finger use on arithmetic operations is strictly related to procedural aspects of counting in childhood, then finger circuits should overlap exclusively with those involved in subtraction. The finding of a similar overlap for subtraction and multiplication would mean that the influence of finger use on arithmetic operations is not limited to the procedural aspects of counting but entails a representation of the numbers and/or intermediary results on the fingers regardless of arithmetic operation.

In order to address these issues, we used fMRI to measure the BOLD signal in the brain of healthy adults who had to solve subtraction and multiplication problems or to discriminate the position of the fingers on the left and right hand. The similarity between the pattern of activity observed during finger discrimination and that observed during each arithmetic operation was further explored by computing voxelwise correlations between tasks.

Material and methods

Participants

Eighteen French-speaking males (mean ± S.D.: 21.3 ± 2.5 years) gave their informed consent to participate to this study. All participants were right-handed according to the Edinburgh Handness Inventory (mean EHI score ((right − left)/(right + left)) ± S.D.: 0.81 ± 0.16; Oldfield, 1971). They had no history of neurological or psychiatric disorders, had normal or corrected-to-normal vision, and they were unaware of the purpose of the study. The experiment was non-invasive and was performed in accordance with the ethical standards laid down in the 1964 Helsinki Declaration. The experimental protocol was approved by the Biomedical Ethical Committee of the Université catholique de Louvain.

Tasks and stimuli

The three experimental tasks were matched with specific control tasks in terms of visual display and response requirements (see Fig. 1). In the finger discrimination task (adapted from Kinsbourne and Warrington, 1962), the participants held a wooden block of irregular shape in each hand, with half of the fingers flexed in the holes and the other half extended over the bumps of the blocks; the thumb was positioned on the lateral face of the block to allow a stable grip (Fig. 1A). In each trial, the palm view of a left or right hand was displayed on the screen in black on a white background. During the experimental blocks, one finger was red and the participants were instructed to answer aloud “yes” if their corresponding finger was flexed into a hole of the wooden block and “no” if it was extended over a bump, without moving or looking at their fingers (Fig. 1B). All fingers but the thumb were tested in each experimental block, using a pseudo-random order, so that the same finger was not coloured in red in two consecutive trials. In the control task, all fingers on the drawing had the same colour, either black or red, and the participants had to decide whether it was red by answering aloud “yes” or “no” (Fig. 1C). Different wooden blocks were placed in the left and right hands at the beginning of each run in order to prevent the participants from relying on learned associations between finger names and expected answers. The left and right hands were tested in separate series of trials to avoid confusion between finger discrimination and left–right orientation during the task. During the arithmetic tasks, one Arabic digit ranging from 3 to 9 was displayed on the screen and the participants had to subtract it from 11 or 13, or to multiply it by 3 or 4, depending on the run (Fig. 1C); the control task required reading single uppercase letters (C, D, F, G, H, J). The wooden blocks were removed from the hands of the participants during the arithmetic tasks. In total, the
participants performed 15 trials for each finger of the two hands, 12 trials for each digit (or letter) in each arithmetic (or reading) task, except for 3 and 4 (or C and D) that were presented 6 times in each arithmetic (or reading) task.

Procedure

The participants practiced all tasks outside the magnet room in order to get familiar with the instructions and response requirements. In particular, they were trained to produce audible responses while keeping bucco-laryngo-facial movements to a minimum. In the magnet room, the participants were lying in the scanner with both arms resting along the body, palms up, and viewed the stimuli projected on a screen, in the rear of the scanner, via a tilted mirror mounted on the head coil. Each experimental task and its control were tested twice in 6 runs counterbalanced across participants. We used a block-design paradigm with short series of 17,500 ms, interleaved with 10,000 ms fixation periods, to optimize the signal-to-noise ratio while controlling for speech-related head motion artefacts (Birn et al., 2004). Each run consisted of 132 volumes and was preceded by 4 dummy scans to allow for magnetic saturation effects. Acquisition parameters were: TE = 50 ms, TR = 2500 ms, flip angle = 90°, FOV = 220×220 mm, 36 slices acquired in an ascending interleaved sequence, slice thickness = 3.5 mm with no interslice gap, SENSE factor (parallel imaging) = 2.5.

Data analysis

A first analysis of variance (ANOVA) was performed on error rates and median response latencies (RLs) of correct trials with task (subtraction, multiplication vs. finger) as a within-subject factor. A second ANOVA was performed on the median RLs in the finger discrimination task with hand side (left vs. right) and fingers (index, middle, ring vs. pinkie) as within-subject factors. This ANOVA was not conducted on error rates due to empty cells. Paired-sample t-tests were used for post-hoc comparisons (p<.05, Bonferroni adjustment for multiple comparisons). Average RLs are reported with standard errors (S.E.) corrected for within-subject designs (Loftus and Masson, 1994).

The functional data were processed and analyzed using Statistical Parametric Mapping (SPM5, Welcome Department of Cognitive Neurology, London, UK, http://www.fil.ion.ucl.ac.uk/spm). The functional images were (1) corrected for slice acquisition delays, (2) re-aligned to the first scan of the first run (closest to the anatomical scan) to correct for within- and between-run motion, (3) coregistered with the anatomical image, (4) normalized to the MNI template using an affine fourth degree 8-spline interpolation transformation and a voxel size of 2×2×2 mm³ after the skull and bones had been removed with a mask based on the individual anatomical images, and (5) spatially smoothed using an 8-mm FWHM Gaussian kernel. Condition-related BOLD signal changes were estimated for each participant by a general
linear model in which the responses evoked by each condition were modelled by a standard hemodynamic response function. The contrasts of interest were computed at the individual level to identify the cerebral areas significantly activated by subtraction or multiplication. The significant cerebral activations for the critical contrasts (finger discrimination minus colour judgement; subtraction minus letter reading; multiplication minus letter reading; multiplication minus subtraction; subtraction minus multiplication) were examined at the group level in random-effect analyses with the statistical threshold set at $p<0.05$ corrected for the false discovery rate ($q_{FDR}$). In order to reveal the brain areas commonly activated in finger and arithmetic tasks, the contrasts computed at the group level were entered in a conjunction analysis using the minimum statistic (MS) compared to the conjunction null (CN; Nichols et al., 2005).

Voxelwise correlations were then computed between task-related changes of the BOLD signal in the areas revealed by the conjunction analysis. If two tasks recruit the same neuronal populations, a positive correlation is expected because the pattern of voxels showing low and high activity increases should be similar for both tasks; dissimilar patterns of peak voxels between tasks should be reflected by a null or negative correlation (Dormal et al., 2010; Downing et al., 2007; Peelen et al., 2006, 2007). The clusters revealed by the conjunction analysis were intersected with a 5-mm-radius sphere centred on peak voxels, using the MarsBar toolbox (http://marsbar.sourceforge.net; Brett et al., 2002), and $t$-values were extracted for each contrast and each participant from a set of normalized but unsmoothed data. First, we measured (1) the correlation between the $t$-values of the contrast [finger discrimination–colour judgement] and the $t$-values of the contrast [subtraction–letter reading] and (2) the correlation between the $t$-values of the contrast [finger discrimination–colour judgement] and the $t$-values of the contrast [multiplication–letter reading] across the voxels of each cluster. Pearson coefficients were computed at the individual level and the mean coefficient of each correlation was tested against 0 using a one-sample $t$-test with $ SUBJECT$ as a random factor (for statistical procedures, see Lorch and Myers, 1990). Because the finger task was correlated both with the subtraction task and with the multiplication task, $p$-values were adjusted to control for Type 1 error with $\alpha=0.05/2$. Second, as a control, we measured voxelwise correlations between tasks in 5-mm spheres centred on the peak voxel in the left and right extrastriate body areas (EBA), which were activated during finger discrimination but not during mental arithmetic. The between-task correlations measured for each area revealed by the conjunction analysis were directly compared to the between-task correlations measured for the EBA of the same hemisphere using paired-sample $t$-tests with $ SUBJECT$ as a random factor. A Bonferroni correction was applied to take into account that each EBA was compared to multiple areas (2 in the left hemisphere, i.e. the hIPS and PSPL, and 3 in the right hemisphere, i.e. the hIPS, PSPL and IFG). Third, the coefficients obtained for homologue parietal areas were entered in a repeated-measure ANOVA with CORRELATION (finger-subtraction vs. finger-multiplication), SITE (hIPS vs. PSPL) and HEMISPHERE (left vs. right) as within-subject factors, and $ SUBJECT$ as a random factor, in order to investigate the effect of these factors on the size of the coefficients. A Bonferroni correction was applied where needed in post-hoc comparisons.

Results

Behavioural results

The error rates did not differ between subtraction (mean $\pm$ S.E.: $3.5 \pm 1.1\%$), multiplication ($3.9 \pm 0.5\%$) and finger discrimination ($3.3 \pm 0.6\%$; $F<1$). A significant effect of TASK was found on RLs ($F(2.34)=14.84$, $p<.001$), showing that performance was slower in the subtraction task ($305 \pm 23$ ms) than in the multiplication ($792 \pm 24$ ms, $t(17)=3.20$, $p<.016$) and finger discrimination tasks ($695 \pm 20$ ms, $t(17)=5.02$, $p<.001$; Fig. 2A). In the finger discrimination task, a main effect of FINGER ($F(3,51)=7.55$, $p<.001$) was found, with slower responses for the middle finger ($746 \pm 13$ ms) when compared to the index ($683 \pm 11$ ms, $t(17)=3.77$, $p<.01$) and the pinkie ($661 \pm 9$ ms, $t(17)=4.29$, $p<.01$), and for the ring finger ($721 \pm 14$ ms) when compared to the pinkie ($t(17)=3.69$, $p<.01$). Performance was as fast and accurate for the left ($701 \pm 8.3$ ms and $2.1 \pm 0.6\%$) and right hands ($705 \pm 8.3$ ms and $4.6 \pm 1.2\%$; $F<1$).

fMRI results

The contrast between mental arithmetic and letter reading showed bilateral activations in the hIPS, in the PSPL, and right-sided activations in the orbital part of the inferior frontal gyrus (IFG; Fig. 2B and Table 1). The direct contrast between multiplication and subtraction revealed further activations in the left and right superior temporal gyri (STG). No area was significantly more activated during subtraction than multiplication. The contrast between finger discrimination and colour judgement showed a bilateral occipito-parieto-precentral network (Fig. 2C and Table 1). Increased activity was observed bilaterally in the EBA, the hIPS, the PSPL and the frontal eye fields (FEF). Clusters of activation were also found in the left inferior precentral sulcus (PrCS), the right IFG and the right middle frontal gyrus (MFG). The direct contrasts between the left and right hands, and vice-versa, revealed additional activations in the contralateral M1 and S1.

The conjunction analysis showed common activations for finger discrimination, subtraction and multiplication in the hIPS and PSPL, bilaterally, and in the right IFG (Fig. 2D). In order to investigate further the functional overlap between finger discrimination and each arithmetic task, we measured voxelwise correlations in each area identified in the conjunction analysis. Table 2 provides the Pearson coefficients for the correlation between the $t$-values of the [finger discrimination–colour judgement] contrast and the $t$-values of the subtraction–letter reading contrast, and for the correlation between the $t$-values of the [finger discrimination–colour judgement] contrast and the $t$-values of the [multiplication–letter reading] contrast for the four parietal clusters. In the hIPS and PSPL, positive correlations were found between the activation patterns elicited by finger discrimination and each arithmetic task (all $r$ ranging between .3 and .6; all $p<.004$). Voxelwise correlations between task-related patterns in the EBA, chosen as a control site because of its specific contribution to finger discrimination, showed only weak and nonsignificant correlations (all $r$ between $-.08$ and $-2$, all $p>.1$, corrected for multiple comparisons). In the left hemisphere, correlations between finger- and arithmetic-related patterns were significantly larger in the hIPS and PSPL than in the EBA (all $p<.004$, corrected for multiple comparisons; Table 2). In the right hemisphere, a significant difference was observed between the PSPL and the EBA (all $p<.021$, corrected for multiple comparisons) but not between the hIPS and the EBA (all $p>.1$). The ANOVA with HEMISPHERE (left vs. right), AREA (hIPS vs. PSPL) and CORRELATION (finger-subtraction vs. finger-multiplication) as within-subject factors revealed a main effect of AREA ($F(1,17)=8.34$, $p<.01$), with larger correlations in the PSPL than in the hIPS, and an interaction between AREA and HEMISPHERE ($F(1,17)=5.49$, $p<.032$), indicating that the difference between the two areas mainly concerned the right hemisphere (right PSPL vs. right hIPS: $t(17)=3.3$, $p<.05$). No significant difference was found between activation patterns in the PSPL and the hIPS of the left hemisphere ($t(17)=1.56$, $p>.1$). Results also showed a main effect of CORRELATION ($F(1,17)=8.23$, $p<.001$), indicating that the activation pattern observed during finger discrimination was more similar to the one observed during subtraction than during multiplication across all parietal areas. Finally, correlations between activation patterns in the right IFG (finger-subtraction: $r=2.1 \pm .07$; finger-multiplication: $r=2.2 \pm .08$) failed to be significant and did not differ from the correlations measured for the right EBA, chosen as a control site (all $p>.1$).
Discussion

The present study tested the hypothesis that the cerebral network involved in mental arithmetic overlaps with the one involved in finger discrimination. To do so, whole brain activity was measured while participants solved subtraction and multiplication problems or performed a finger discrimination task. The behavioural results showed that subtraction was performed more slowly than multiplication or finger discrimination, whereas the error rate was equal in the three tasks. Discriminating the position of the middle and ring fingers took longer than discriminating the position of the index and pinkie, which is reminiscent of the greater difficulties of brain-damaged patients...
with finger agnosia to recognize central than lateral fingers (Benton, 1959; Kinsbourne and Warrington, 1962). The ability to discriminate fingers do not just provide a common representation of numbers (Dehaene et al., 2003). This neural overlap should therefore be considered as reflecting an intrinsic component of number processing (for a similar proposal, see Di Luca and Pesenti, 2008; Zago et al., 2011). Second, because neural overlap was found in parietal areas whose contribution to finger discrimination was not specific to the left or the right hand, it is reasonable to assume that this overlap is not related to somatic representations. Third, the higher pattern similarity between finger discrimination and subtraction, when compared to multiplication, suggests that the neural overlap is partially determined by the strategy used to solve arithmetic problems. The multiplication and subtraction problems used in the present study typically lead to a rate of memory retrieval of respectively 95% and 42% in occidental cultures (Campbell and Xue, 2001). Our behavioural data confirms that multiplication problems were solved through fast and automatic processes, such as memory retrieval, whereas subtraction problems required more time-consuming computational strategies. In line with this, dual-task experiments showed that finger movements slowed down arithmetic operations solved by counting whereas operations solved by memory retrieval remained unaffected (Imbo et al., 2011; Michaux et al., submitted for publication). Another dual-task experiment showed that multiplication but not subtraction was delayed by concurrent phonological rehearsal, corroborating the idea that these two operations rely on partially distinct processes and/or representations (Lee and Kang, 2002). Our brain imaging results therefore suggest that the role of fingers in arithmetic operations depends on procedural aspects of finger counting. However, procedural aspects are not sufficient to account for the implementation of arithmetic operations in finger circuits. Indeed, although the pattern similarity was less important, multiplication also led to overlapping activations with finger discrimination in the hIPS and PSPL because finger-counting strategies do not directly contribute to solving multiplication problems, such overlap is best explained by the implicit activation of finger configurations representing the manipulated numbers and/or the intermediate results.

Below, we propose an explanation that emphasizes procedural aspects of finger counting, while suggesting that the use of a stable counting sequence could contribute to derive digital representations of numbers.

### Table 1

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Brain area x</th>
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<th>z</th>
<th>T-value</th>
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<td>Multiplication–subtraction</td>
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<td>−20</td>
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### Table 2

<table>
<thead>
<tr>
<th>Finger and subtraction</th>
<th>Left hemisphere</th>
<th>Right hemisphere</th>
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<tbody>
<tr>
<td>PSPL</td>
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<td>0.61 ± 0.06*</td>
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<tr>
<td>hIPS</td>
<td>0.59 ± 0.08*</td>
<td>0.41 ± 0.06</td>
</tr>
<tr>
<td>EBA</td>
<td>0.11 ± 0.10</td>
<td>0.22 ± 0.10</td>
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</table>

<table>
<thead>
<tr>
<th>Finger and multiplication</th>
<th>Left hemisphere</th>
<th>Right hemisphere</th>
</tr>
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<tbody>
<tr>
<td>PSPL</td>
<td>0.44 ± 0.09*</td>
<td>0.56 ± 0.07*</td>
</tr>
<tr>
<td>hIPS</td>
<td>0.54 ± 0.01*</td>
<td>0.41 ± 0.09</td>
</tr>
<tr>
<td>EBA</td>
<td>−0.08 ± 0.11</td>
<td>0.08 ± 0.10</td>
</tr>
</tbody>
</table>

x, y, z = MNI stereotaxic coordinates of the peak voxels; k = cluster size (number of voxels); EBA = extrastriate body area, FEF = frontal eye fields, hIPS = intraparietal sulcus (horizontal part), IFG = inferior frontal gyrus (orbital part), M1 = primary motor cortex, MFG = middle frontal gyrus, PCCS = pre-central sulcus (inferior part), PSPL = posterior superior parietal lobe, S1 = primary somatosensory cortex, STG = superior temporal gyrus.

* p < .05; minimum cluster size k = 100 voxels.

### Table 2

<table>
<thead>
<tr>
<th>Finger and subtraction</th>
<th>Left hemisphere</th>
<th>Right hemisphere</th>
</tr>
</thead>
<tbody>
<tr>
<td>PSPL</td>
<td>0.59 ± 0.07*</td>
<td>0.61 ± 0.06*</td>
</tr>
<tr>
<td>hIPS</td>
<td>0.59 ± 0.08*</td>
<td>0.41 ± 0.06</td>
</tr>
<tr>
<td>EBA</td>
<td>0.11 ± 0.10</td>
<td>0.22 ± 0.10</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Finger and multiplication</th>
<th>Left hemisphere</th>
<th>Right hemisphere</th>
</tr>
</thead>
<tbody>
<tr>
<td>PSPL</td>
<td>0.44 ± 0.09*</td>
<td>0.56 ± 0.07*</td>
</tr>
<tr>
<td>hIPS</td>
<td>0.54 ± 0.01*</td>
<td>0.41 ± 0.09</td>
</tr>
<tr>
<td>EBA</td>
<td>−0.08 ± 0.11</td>
<td>0.08 ± 0.10</td>
</tr>
</tbody>
</table>
In the finger discrimination task, the absence of visual feedback put strong demands on the ability to represent the relative position of the fingers, as evidenced by increased RLs for the middle fingers that have more neighbours than the others. The pattern of activation in this task was analogue to the one observed in the contrast between complex and simple finger movements in other fMRI studies (Haaland et al., 2004; Harrington et al., 2000). These studies showed that activity along the IPS increased each time a new finger was moved, irrespective of hand laterality, whereas M1 and S1 were activated in response to contralateral movements regardless of finger changes. The parietal cortex was found to react to finger transitions, whatever the total number of fingers involved in the sequence, indicating that its contribution was mainly determined by the need to individuate fingers. Cell recordings in the monkey homologue of the hIPS showed that neuronal activity in this area predicts a transition between two different movements, with incremental increases reflecting the number of times a movement is repeated before a transition (Sawamura et al., 2002). Altogether, these results suggest that the parietal network underlying finger discrimination is endowed with suitable properties for keeping track of incremental changes during arithmetic operations. We therefore propose that, during development, the wiring of number and finger circuits in the parietal cortex enables the implementation of a successor function that improves the representation of the number sequence and helps keeping track of incremental changes during arithmetic operations. This interpretation fits with electrophysiological results showing an increase of CSE in hand muscles whenever items have to be put in correspondence with the elements of an ordered series, being the number sequence or the alphabet (Andres et al., 2007). Importantly, the implementation of a successor function in the parietal cortex would not only contribute to keep track of incremental changes but it also provides a medium to represent numbers on fingers. Because finger counting relies on a stable sequence (i.e. from the thumb to the pinkie in most occidental cultures; Lindemann et al., 2011), the relative position of each finger can be used to infer the cardinality of a number. The digital representations derived from the mapping of the number sequence onto fingers can in turn support other functions in mental arithmetic, such as the creation/consolidation of arithmetic facts or the decomposition of a problem in intermediate steps (Domahs et al., 2008). The latter functions could explain the overlap between finger discrimination and multiplication in the parietal cortex. Along the same lines, the finger individualisation process underlying one-to-one correspondence is likely to support exact arithmetic operations with small and large numbers, but we do not exclude a more specific contribution to small arithmetic problems whose answer can be readily represented through configurational representations (Kauffman et al., 2008; Thompson et al., 2004). In order to address this issue, future fMRI studies should investigate whether the BOLD signal in finger-related areas correlates with problem size in arithmetic tasks.

The hIPS activation extends in areas whose role in visuomotor functions, such as pointing or grasping, is well established both in human and non-human primates (Binkofskii et al., 1999; Simon et al., 2002). The same areas have also been related to movement preparation and motor intention (Göbel et al., 2004; Rushworth et al., 2003; Thoenissen et al., 2002). In contrast, the PSPL is known to interact with the FEF to support eye movements and attention shifts (for a meta-analysis, see Grosbras et al., 2005). The correlation between the pattern of activation observed in the PSPL during finger discrimination and arithmetic could therefore indicate that the two tasks share common resources for attention allocation over the mental representation of fingers and numbers (Hubbard et al., 2005). It has been shown that computing the result of an arithmetic problem is analogue to shifting attention to the left or right side of a mental number line (Knops et al., 2009b; McCrink et al., 2007; Pinhas and Fischer, 2008). Indeed, a common neural code was found for leftward saccades and subtraction and for rightward saccades and addition in the PSPL (Knops et al., 2009a). The involvement of the PSPL in multiplication problems solved by memory retrieval is more difficult to reconcile with its role in attention orientation. Several brain imaging studies corroborated the finding of increased activity in the hIPS and PSPL during basic multiplication (Andres et al., 2011; Chochon et al., 1999; Dehaene et al., 1996; Kiefer and Dehaene, 1997; Rickard et al., 2000), sometimes with an extension to the parieto-occipital junction (POJ) known for its role in eye-hand coordination (Prado et al., 2005; Zago et al., 2001). The companion role of the PSPL and POJ in solving basic multiplication problems was also evidenced with fMRI in a patient whose lesions in the left perisylvian areas prevented her to solve this operation normally (Cohen et al., 2000). A first explanation could be that the PSPL contributes to narrow down the range of potential answers to multiplication problems by shifting attention along a mental number line, as for addition and multiplication (Dehaene and Cohen, 1991). A recent developmental study showed that 5- to 7-year-old children are indeed able to approximate the answer of non-symbolic multiplication problems above chance level, before they receive formal schooling in this operation (McCrink and Spellke, 2010). Alternatively, it has been proposed that the robust parietal activations observed during basic multiplication problems reflects magnitude-based strategies that can facilitate their solving (Chochon et al., 1999), for example to reverse the order of the operands or to decompose a multiplication into a series of additions (Campbell, 1994; LeFevre et al., 1996). In this view, the PSPL would contribute to shifting attention between operands or zooming in and out the different parts of a decomposed problem. The FEF were not activated during arithmetic tasks in our study but previous studies suggest that these areas also contribute to represent numbers on a visuospatial medium (Knops et al., 2009a; Rusconi et al., 2011). Further research is required, however, to determine the exact nature of the processes shared by finger discrimination and mental arithmetic in the hIPS and PSPL.

Finally, a cluster of activation was found in the inferior part of the left PrCS during finger discrimination but not during mental arithmetic, in contrast with several previous results (Arsalidou and Taylor, 2011). Further studies are required to explain this discrepancy, for example, by using a larger set of arithmetic problems. It is worth noting that activation in the left PrCS might have been underestimated in the finger discrimination task as well, because the colour judgement task, used as a reference, also involved finger drawings. A recent study tested the involvement of the left and right premotor/motor cortex as a function of the preferred counting direction of the participants (Tschentscher et al., 2012). Viewing numbers between 1 and 5, with both hands at rest, led to higher activation in the right premotor/motor cortex of left-starters when compared to right-starters, showing that the preferred starting hand influenced the activations induced by small numbers in the contralateral hemisphere. No difference was observed for numbers ranging from 6 to 10. These results suggest that future studies should take into account the relationship between hand preference for finger-based calculation and hemispheric lateralization of motor activity in order to decipher the role of the premotor/motor cortex in mental arithmetic. In the present study, the only common focus of activation in the frontal lobe was located in the right IFG. It has been argued that this area controls the search within working memory contents (Lepsiens et al., 2005). A previous study showed that this area was equally activated when numbers, syllables or locations were manipulated vs. rehearsed in working memory (Zago et al., 2008). Our multi-voxel pattern analysis suggests that numbers and fingers do not activate the same parts of the IFG, meaning that the recruitment of this area is not completely independent of the contents stored in working memory.

Conclusion

The present study adds further evidence to the view that the brain areas involved in finger representation might offer a support for arithmetic operations. Results showed that finger discrimination and mental arithmetic share common parietal and frontal areas in the adult brain. In contrast with the EBA and S1/M1, these areas do not
contribute to somatic representations, as evidenced by a similar increase of activity while representing the left or right hand. Voxelwise correlations were used to explore further the neural overlap between finger discrimination and arithmetic tasks, and similar patterns of activity were found in the hIPS and PSPL but not in the IFG. Correlations were higher in the left than in the right hIPS and they were also influenced by arithmetic operation. The parietal areas involved in finger discrimination seem more important to index numerical changes during subtraction than during multiplication, presumably because multiplication problems are mostly solved by memory retrieval with the support of additional areas in the temporal cortex. Future research should clarify the nature of the neural mechanisms shared by finger discrimination and mental arithmetic in the hIPS and PSPL with a special emphasis on the respective contribution of motor and spatial processes.

Acknowledgments

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