Mental calculation in a prodigy is sustained by right prefrontal and medial temporal areas

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Calculating prodigies are individuals who are exceptional at quickly and accurately solving complex mental calculations. With positron emission tomography (PET), we investigated the neural bases of the cognitive abilities of an expert calculator and a group of non-experts, contrasting complex mental calculation to memory retrieval of arithmetic facts. We demonstrated that calculation expertise was not due to increased activity of processes that exist in non-experts; rather, the expert and the non-experts used different brain areas for calculation. We found that the expert could switch between short-term effort-requiring storage strategies and highly efficient episodic memory encoding and retrieval, a process that was sustained by right prefrontal and medial temporal areas.

Much psychological research has been devoted to studying the modifications of cognitive processes resulting from domain-specific expertise[1,2]. To date, the investigation of extensive learning-related cerebral changes has largely focused on motor[3,4] or visuo-perceptive skill acquisition[5], rather than higher-level cognition. Mental calculation, which requires the coordination of various basic and complex cognitive processes, is a good example of high-level cognitive skill for which some individuals, called calculating prodigies[6], reach a high level of expertise. Current models of arithmetical cognition assume that adults solve simple arithmetic problems (such as 3×6) without actual computation, by retrieving the answer from a network of stored declarative associations[7,8]. In contrast, more complex problems (such as 37×62) are not stored in memory but require application of actual computational procedures. From a functional point of view, solving computation-based problems is a complex cognitive skill requiring numbers to be held and manipulated on a short-term representational medium while the dedicated resolution algorithm is applied. Applying the algorithm involves sequential control of the various steps, decomposition of the stimuli according to their semantic meaning (for example, whether digits correspond to units or tens), memory retrieval of intermediate results, short-term storage of those results, and application of basic arithmetical rules. Intermediate results must be kept in mind until used, but then must be forgotten to keep the memory load at a minimum. The whole process thus involves various working memory mechanisms, such as updating, in charge of the central executive, and the attentional control system, responsible for strategy selection and for control and coordination of the mechanisms involved in short-term storage and processing tasks[9].

Because computation-based problems have a high short-term memory demand, educated adults need much time and effort to solve them. In contrast, calculating prodigies solve complex mental calculations quickly and accurately. It has been proposed that expert calculators, through practice, have acquired knowledge structures and procedures for efficiently encoding and retrieving specific information in long-term memory. This would enable them to circumvent the limited capacity of short-term memory and the slowness of long-term encoding when applying complex algorithms. Instead of keeping intermediate results in short-term memory, these results would be rapidly encoded in long-term working memory with cues facilitating efficient retrieval, hence improving performances by decreasing short-term demand[1]. Using efficient episodic encoding–retrieval cues would decrease the storage retrieval times in long-term memory, and would prevent proactive interference caused by previous storage of similar information; moreover, in contrast to general long-term memory processes, such skilled memory mechanisms would apply specifically to each domain of expertise. However, the nature of the representational medium underlying calculation expertise is not yet known. Here we contrasted computation with retrieval-based problems to isolate the calculation processes, while equalizing, in an expert calculator, the complexity of the visual processing of the stimuli, the verbal production of the answer, and the fact retrieval component. Such a comparison is indeed hard to realize in non-expert subjects alone because strict equalization of problem complexity is intrinsically impossible. The expert calculator was R. Gamm, a young healthy man who exhibits exceptional calculation abilities and has trained his memory for arithmetic facts and calculation algorithms several hours each day for years (**Table 1**). Our recent experimental investigation[10] showed how, at a behavioral level, his highly efficient long-term memory storage and retrieval processes, his knowledge of calculation algorithms, and his good short-term memory capacity all contribute to his calculation expertise. Episodic memory critically contributes to R. Gamm's expertise, as demonstrated by his ease in storing novel numerical information. For instance, he was able to correctly rec-

Table 1. Examples of calculations done by R. Gamm.

Types of problems	Examples	R Gamm's answer	Correct answer
Raising numbers to powers	99^5	9,509,900,499	(correct)
	53^9	3,299,763,591,802,133	(correct)
Roots	$^{2}\sqrt{}(973487)$	984	986.65*
	$^{5}\sqrt{}(8547799037)$	96	96.61*
Sines	sin 287	–0.956304756	(correct)
Division of prime numbers	31/61	(answer with 60 decimals)	(all correct)

*answers rounded off

ognize multi-digit numbers corresponding to products that he had computed several hours before, in tests involving long series of problems.

RESULTS

Our protocol capitalized on the possibility of unambiguously separating two types of problems that R. Gamm could solve either by computation (multiplication of two 2-digit numbers; for example, 76 × 82) or by direct memory retrieval (knowing the square of a 2-digit number; for example, 76 × 76; **Fig. 1** and Methods). Using the squaring task as the memory-based condition for R. Gamm not only allowed us to ensure that both types of problems were kept equivalent, but also allowed us to disentangle general effects of expertise (such as faster response times and higher motivation for domain-specific problems) from the specific effect of expertise on computation processes and their neural substrates. The most critical question of this PET investigation was what, in the expert calculator's pattern of activations, would reflect standard calculation processes shared with non-expert calculators, and what would be specific to his exceptional abilities. Control subjects matched with R. Gamm for age and educational level, but who had no exceptional calculation abilities, were thus asked to solve computation- and memory-based problems (see Methods).

Similarities in expert and non-expert calculators' pattern of activations were assessed by a conjunction analysis of computation- versus retrieval-based calculation in R. Gamm and the control subjects. This analysis showed that in both R. Gamm and control subjects, calculation processes activated the brain bilaterally, but with a clear left-sided predominance (the supramarginal gyrus, the intraparietal sulcus, and the ventral visual route composed of the inferior occipital and middle occipital gyri, as well as the occipito–temporal junction in the left hemisphere only; **Table 2**; **Fig. 2**). We found other activation foci at the junction between the left precentral and inferior frontal sulci, in the inferior frontal sulcus bilaterally and in the left middle frontal gyrus.

Besides these similarities, several areas were significantly more activated in R. Gamm than in non-experts, when contrasting computation-based with retrieval-based calculation (**Table 2**; **Fig. 2**). These activations were in five brain regions, the medial frontal and the parahippocampal gyri, the upper part of the anterior cingulate gyrus, the occipito–temporal junction in the right hemisphere, and the left paracentral lobule ($p \leq 0.001$, not corrected for multiple comparisons).

To demonstrate that the activations in these five areas were because of R. Gamm's calculation expertise, and not simply because of the greater number of calculations he did in comparison to non-experts, we did two kinds of control experiments (see Methods). First, we compared the blood flow variation maps from the computation and retrieval-based calculation conditions obtained in each subject. We found that, for all the non-expert calculators, no t-values in the five activated regions were significant (**Fig. 2**, histograms). Second, we contrasted the complex calculation task with a lower-order cognitive baseline task in non-expert calculators (reading numerals, see Methods), and found that these five regions were actually deactivated in non-experts during the computation-based condition (Z-scores for this contrast in the five regions ranged from –1.69 to –4.01). This finding demonstrates that there was no activity we could have missed in these five regions during complex calculation, due to the lower number of calculations actually done by the non-expert calculators. Indeed, it demonstrates that these five regions have no role in complex calculation in non-expert calculators.

DISCUSSION

The massive involvement of the visuospatial working memory and visual imagery networks[11–13] strongly suggests that, during complex calculation, numbers are held and manipulated onto a visual type of short-term representational medium. Although fewer stimuli were seen in the computation-based condition, the

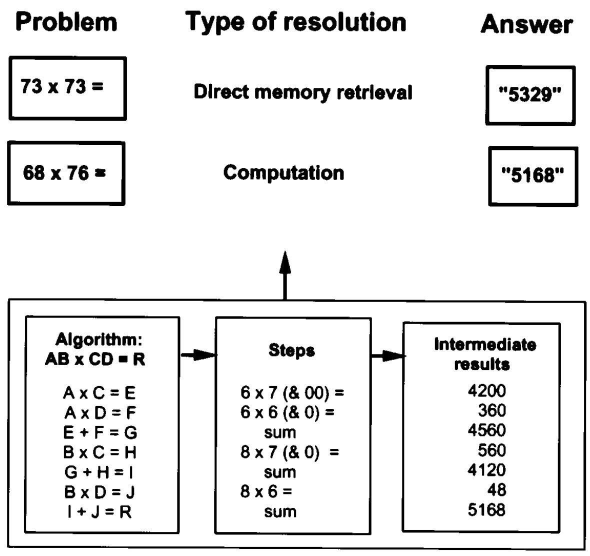

Fig. 1. Example of the two kinds of mental calculation tasks done during PET, and the type of resolution used by R. Gamm. Bottom, dedicated algorithm used by R. Gamm to solve complex mental calculation problems.

occipital areas were more activated, suggesting that visual imagery strategies were applied to visually perceived stimuli. This held for both the expert and the non-expert calculators. Hence, these areas likely participate in mental calculation networks shared by most educated adults when problems are presented visually. The left intraparietal sulcus and precentral gyrus were found, in previous studies, to be jointly activated when Arabic digits were compared (leading to the processing of their magnitude meaning), multiplied or added[14,15]. The present results support the critical involvement of this left parietal area in number processing and calculation, most likely in the semantic aspects of magnitude processing[16]. The results again suggest a contribution of the precentral gyrus, possibly when some form of computation is required. The exact involvement of this network is currently under debate. We propose that the joint activation of the parietal and precentral areas may reflect the involvement of a finger movement representation network. Such a network would underlie finger counting and numerosity quantification during childhood[17,18], and, by extension, would become the substrate of some numerical knowledge and processes[15] in adults. Developmental[19,20], cross-cultural[21], neuropsychological[22] and neuroimaging[23] findings support this interpretation.

Most of the areas activated only in the expert are associated with episodic memory processes, and may correspond to episodic encoding and retrieval of intermediate results. This is consistent with our finding that R. Gamm's long-term episodic memory storage and retrieval processes are exceptionally efficient, which allows him to easily store and retrieve arithmetical information from memory during calculation. During episodic retrieval using an event-related fMRI design, a network composed of the right medial frontal gyrus, right anterior cingulate gyrus and bilateral parietal visual association cortices has been observed[24], confirming and extending other findings[25,26]. The anterior cingulate cortex (ACC) is implicated in episodic memory retrieval processes such as the selection of items or responses from episodic memory[24,27]. Most importantly, the ACC participates in executive processes, which include evaluating cognitive states for detecting response competition conflicts and representing the knowledge that strategic processes need to be engaged[28], monitoring performance for detecting errors[29], and interacting with the lateral prefrontal cortex before compensatory mechanisms are implemented[30]. This role of cognitive processing regulation in the upper part of the ACC[31] again reflects expertise in adapting behavior to complex situations and errors, and is consistent with the expert's consciousness of his actual level of performance and with his ability to detect and immediately self-correct his occasional calculation errors. Medial temporal structures (the hippocampal, parahippocampal and nearby regions) are involved in episodic and visuospatial memory. Their activations are increasingly often observed during episodic encoding and retrieval (sometimes bilaterally), regardless of the verbal or nonverbal nature of the materials tested. More specifically, the parahippocampal region in the right hemisphere controls the storing and maintenance of stimuli representations across long delays[32], and seems predominantly dedicated to the visuospatial aspects of these processes. This finding is consistent both with the visuospatial nature of the working-memory processes observed in the present study, and R. Gamm's previous introspective reports describing long-term memory encoding and retrieval of numerical information via visual images[10].

Taken together, these results fit the assumed functional components of computation-based calculation and show the neural network for complex calculation out of problem encoding, fact retrieval and response production processes in an expert calcu-

Table 2. Brain areas activated during calculation (as compared to memory retrieval) either in both the calculating prodigy and non-expert calculators, or only in the calculating prodigy.

Anatomical localization of maximum voxel	Coordinates (mm)			Z-score
	x	*y*	*z*	
Conjunction analysis				
Left inferior/middle occipital gyrus	–50	–60	–14	5.6
Left inferior occipito–temporal junction	–52	–52	–24	5.2
Right inferior/middle occipital gyrus	54	–60	–10	4.7
Left supramarginal gyrus	–52	–40	46	6.2
Left intraparietal sulcus	–22	–68	48	5.9
Left intraparietal sulcus/intra-occipital sulcus	–28	–84	22	4.2
Right supramarginal gyrus	42	–40	50	5.5
Right intraparietal sulcus	22	–70	54	4.6
Left precentral sulcus/inferior frontal sulcus	–38	2	26	5.0
Right inferior frontal sulcus	42	36	26	4.1
Left middle frontal gyrus	–32	8	54	3.9
Left inferior frontal sulcus	–46	30	22	3.6
Calculating-prodigy-specific areas				
Left paracentral lobule	–12	–34	68	3.7
Right middle occipito–temporal junction	60	–52	–4	3.6
Right medial frontal gyrus	14	26	56	3.6
Right anterior cingulate gyrus	4	46	30	3.1
Right parahippocampal gyrus	18	8	–44	3.1

Top, conjunction analysis between calculating prodigy and the group of non-experts. Bottom, calculating-prodigy-specific areas. Coordinates correspond to the location of the extremum of the cluster of activation within the stereotactic space. All activations are significant; $p \leq 0.001$ (not corrected for multiple comparisons).

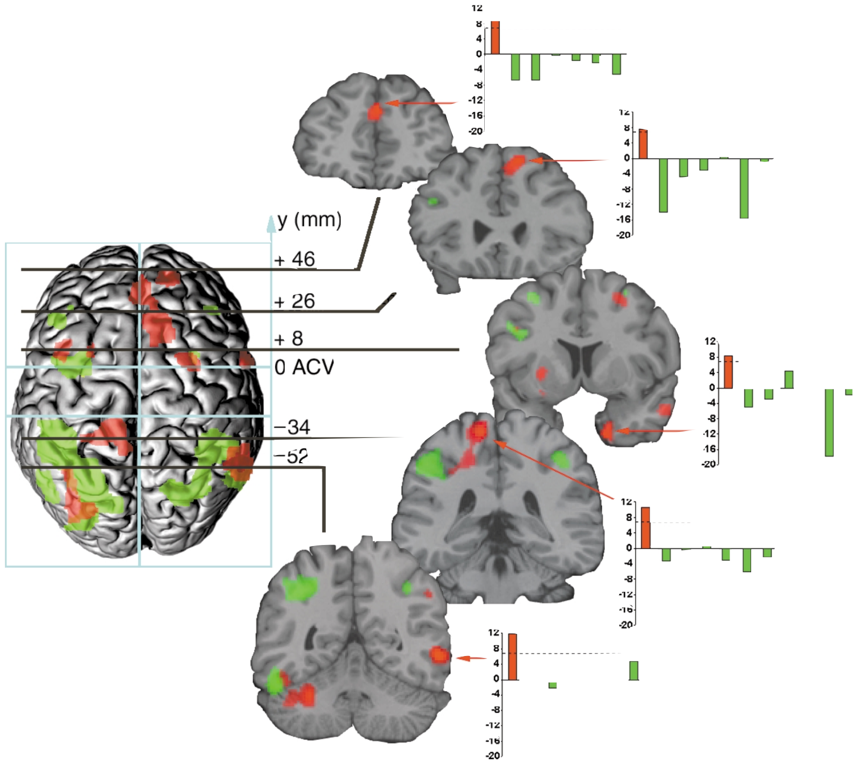

Fig. 2. Brain areas activated during complex mental calculation either by both R. Gamm and the group of six non-expert calculators (green) or specifically by R. Gamm (red). Left, top view of the brain template with stereotactic frame of reference (ACV, anterior commissure verticalization). Right, selected coronal slices showing anterior cingulate, right medial frontal, basal ganglia and right medial temporal specific activations during complex mental calculation in R. Gamm. For each region, the histogram shows the average (across three trials) normalized rCBF variations in each individual (red, R. Gamm; green, nonexpert calculator) expressed as *t*-values. The dotted line indicates the *t*-value threshold for activation significance at 0.05 (corrected for multiple comparisons). From top to bottom, the areas are the right anterior cingulate gyrus, the right medial frontal gyrus, the right parahippocampal gyrus, the left paracentral lobule and the right occipito-temporal junction (**Table 2**).

lator. Most importantly, the results neuroanatomically support the idea that acceleration of existing processes and local modulation of activations do not account for high-level cognitive expertise. Rather, such expertise involves new processes relying on different brain areas. In the case of calculation expertise, these new processes include the following: switching from strictly short-term, effort-requiring storage strategies to highly efficient episodic memory encoding and retrieval strategies, application of automated resolution algorithms, andcareful monitoring and control of such algorithmic resolution. Along with our behavioral investigation of R. Gamm's performance, the present neuroanatomical results thus strongly support the theoretical framework of the long-term working memory[1]. We show that high-level expertise—here, calculation expertise—results in processes and brain activations not present in non-expert calculators. In addition, the use of long-term episodic mechanisms to expand the limitation of the short-term working memory partly accounts for high-level expertise.

METHODS

Subjects. The expert calculator was R. Gamm, a 26-year-old healthy German right-handed calculating prodigy, who presents exceptional abilities in raising two-digit numbers to powers, extracting roots, calculating sines, dividing two prime numbers, and multiplying multi-digit numbers (example problems in **Table 1**). To raise two-digit numbers to the second up to the fifth power, R. Gamm retrieves the answers directly from memory (response latencies ranging respectively from 710 to 1120 ms). R. Gamm can, among distractor numbers, recognize and identify multi-digit numbers that correspond to powers of two- and three-digit numbers. He also correctly recognizes multi-digit numbers corresponding to products that he computed several hours before, demonstrating the importance of episodic memory processes in his exceptional abilities. He is an expert in calendar calculation; using a dedicated algorithm, for any date, he can give the day of the week on which it falls. (For example, "Which day of the week was 6 May 1951?" "A Sunday.") He has extensive knowledge about mathematical properties of numbers. For example, he knows many periodic prime numbers, that is, prime numbers whose inverses have as many recurrent decimal positions as the prime number itself minus 1, and he knows their corresponding period. (For example, dividing 1 by 113 results in a number with 112 decimals, constituting a period that is repeated *ad infinitum*.) Since he began to develop his calculation abilities at the age of 20, he has trained 1 to 4 hours every day. Further details on his calculation abilities, as well as on his long- and short-term memory capacities have been presented elsewhere[10]. The non-expert subjects were 6 right-handed healthy male French students (21 ± 1 years old). All were free from nervous disease or injury and had no abnormality on their T1-weighted high-resolution magnetic resonance images. To ensure their comparability with R. Gamm, they were selected as free from mathematical anxiety, on the basis of their good performance in simple and complex multiplication tasks; their scores were within normal range in visual and auditory digit-span, and in visuospatial span tasks. Details of non-experts' selection procedure as well as PET activation results for other experimental tasks not reported here are presented elsewhere[33]. The local ethics committee (CCPPRB of Basse-Normandie) gave approval for this experiment; informed written consent was obtained from each subject.

Tasks. Two calculation tasks were contrasted, each involving either computation- or retrieval-based problems. Our behavioral investigation showed that R. Gamm can directly retrieve the squares of two-digit numbers from memory, whereas he computes the products of two two-digit numbers using a dedicated algorithm (**Fig. 1**). His response latencies (averaging 709 ms and 4 s, respectively) reflect these two types of resolution. The numerical magnitude as well as the visual and verbal complexity of the operands and answers were equivalent in both types of problems. During PET imaging, problems appeared on a computer screen and remained visible until the answer was given aloud. In both conditions, the rate of stimulus presentation was determined by the response speed, to equalize difficulty. This resulted in an averaged presentation rate of one item every 6 s for computation-based problems, and every 2.5 s for retrieval-based problems. Because complex problems also involved retrieving from memory the arithmetic facts composing intermediate results, memory retrieval processes were similarly involved in both conditions.

For non-expert subjects, retrieval-based problems comprised the simplest multiplication facts (answers ranging from 4 to 45) for which the probability of direct retrieval was highest[34]; computation-based problems comprised multiplications of two 2-digit numbers with answers less than 1000. Hence, the two types of problems differed in the following respects: their numerical magnitude and complexity, their solving time (about 1 s and about 20 s, respectively), their error rate, and the level of math anxiety they caused[35]. Problems were displayed on a computer screen and remained present until the answer was given aloud. The average rate of presentation was one item every 20 s for computation-based problems and every 2.5 s for retrieval-based problems. Again, memory-retrieval processes of arithmetic facts were similarly involved in both conditions.

Data acquisition and analysis. Regional cerebral blood flow (rCBF) was measured 12 times in R. Gamm and 6 times in non-experts, while they replicated the two tasks in a fixed, random order. For each rCBF measurement, sixty-three 2.425-mm-thick contiguous brain slices were acquired simultaneously on the ECAT HR+ PET camera in 3-dimensional mode (Siemens, Erlangen, Germany). A single 90-s scan was acquired and reconstructed, including a correction for head attenuation using a measured transmission scan, with a Hanning filter of 0.5/mm cut off frequency and a pixel size of 2×2 mm^2. Tasks started 30 s before the intravenous bolus injection of 8 mCi of ^{15}O-labeled water. Automatic realignment of PET images was realized with automated image registration[36]. The images were smoothed using a Gaussian filter of 12 mm full width at half maximum (FWHM), leading to a final smoothness of 15 mm FWHM. Condition comparisons were done with SPM99 (Wellcome Department of Cognitive Neurology, London, UK, http://www.fil.ion.ucl.ac.uk/spm/spm99.html) with statistical threshold at 0.001 not corrected for multiple comparisons. The conjunction analysis[37] used orthogonalized conditions (computation-based versus memory-based calculation in R. Gamm and the control subjects) with a statistical threshold set at 0.001 not corrected for multiple comparisons. The specific activations of R. Gamm during computation were revealed by contrasting computation- versus retrieval-based conditions in R. Gamm with computation- versus retrieval-based conditions in controls. The conditions were masked by R. Gamm's computation- versus retrieval-based conditions with a threshold at 0.05, to cancel out deactivations during the retrieval condition.

Specificity of R. Gamm's activations were checked in two ways. First, to show that R. Gamm's individual activations were unique to him and not present in any of the non-expert subjects, we conducted an individual analysis, computing normalized rCBF variations in the computation- versus retrieval-based condition in each of the five specific regions (those that reached the 3.09 Z threshold; **Table 2**) for R. Gamm and each non-expert calculator. We then computed t-values (using 3 trials for R. Gamm to balance his and the non-expert calculators' number of measurements) and tested them to 0 (paired t-test) at a 0.01 significance level (Bonferroni correction for 5 regions). Second, to verify that the absence of activation in these regions in the non-expert calculators was not related to the presence of similar activations during both computation and retrieval-based conditions (baseline effect), we obtained PET data (three trials) from the non-expert calculators during a baseline condition consisting of number reading. We generated a map of the contrast between the computation-based conditions and this baseline condition, and verified in this contrast that no activation focus specific to R. Gamm was activated in the non-expert calculators group.

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