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Neural correlates underlying mental calculation in abacus experts: a functional magnetic resonance imaging study

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Abstract

Experts of abacus operation demonstrate extraordinary ability in mental calculation. There is psychological evidence that abacus experts utilize a mental image of an abacus to remember and manipulate large numbers in solving problems; however, the neural correlates underlying this expertise are unknown. Using functional magnetic resonance imaging, we compared the neural correlates associated with three mental-operation tasks (numeral, spatial, verbal) among six experts in abacus operations and eight nonexperts. In general, there was more involvement of neural correlates for visuospatial processing (e.g., right premotor and parietal areas) for abacus experts during the numeral mental-operation task. Activity of these areas and the fusiform cortex was correlated with the size of numerals used in the numeral mental-operation task. Particularly, the posterior superior parietal cortex revealed significantly enhanced activity for experts compared with controls during the numeral mental-operation task. Comparison with the other mental-operation tasks indicated that activity in the posterior superior parietal cortex was relatively specific to computation in 2-dimensional space. In conclusion, mental calculation of abacus experts is likely associated with enhanced involvement of the neural resources for visuospatial information processing in 2-dimensional space.

Introduction

To perform complex calculations, most people have relied on physical devices such as pencils and papers, mechanical calculators, slide rules, and more recently digital computers. One such device, gradually downplayed in the computer age, is an abacus, or "soroban" in Japanese. Interestingly, however, abacus experts not only manipulate the tool skillfully in its physical form but also gain the ability to mentally calculate extraordinarily large numbers—often more than 10 digits—with unusual speed and accuracy (Stigler, 1984). To achieve this level of skill, abacus players initially practice to simulate abacus operations in mind with actual finger movements, as if they could push imagined abacus beads (Fig. 1A). However, they eventually cease to use overt finger movements because it is believed that finger movements rather slow down calculation speed at higher levels of skill.

Mental arithmetic requires integration of multiple cognitive functions including number recognition, retrieval of arithmetic facts, temporary storage of intermediate results, and manipulation of mental representations. Much effort has been devoted to clarify cognitive mechanisms and underlying neural correlates of number recognition and arithmetic operations. Linguistic processing is suggested to play an essential role in exact mental calculation in adults on one hand (Dehaene et al., 1999); it is likely that visuospatial processing is also important, especially in the developmental stage, for acquiring mathematical concepts on the other

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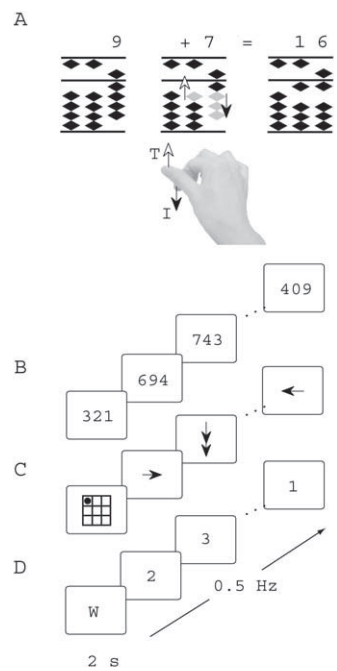

Fig. 1. Abacus operation and behavioral tasks. (A) The basic operation of a Japanese abacus or "soroban." It has columns of beads, and each of them has a place value, corresponding to the ones, tens, hundreds, and so on (i.e., base-10 system of numeration). Once a specific column of beads is arbitrarily defined as the "ones," the other columns are valued relative to it. Each column of beads has an upper and a lower section. The bead in the upper section is equal to 5 times the unit value of the columns when it is pushed down toward the horizontal dividing bar, and each of the 4 lower beads is equal to 1 unit value of the columns when pushed up. For example, for the addition of 9 and 7, 4 lower beads up and 1 upper bead down in a column represent the number 9. To execute the addition requiring a carrying, one first subtracts the complement of the addend to 10 (3 here) and then adds 1 to the tens column. One can accomplish this calculation using a single finger movement, twisting the thumb (T) and the index finger (I) to push up 1 bead in the tens column (white arrow) and to push down 3 beads in the ones column (black arrow), respectively. (B) In the numeral mental-operation task, subjects were asked to add a series of numbers presented visually. (C) In the spatial mental-operation task, subjects were required to mentally move the marker location according to an arrow or a pair of arrows. For example, one should move the marker 1 square to the right, as indicated by the single arrow pointing to the right, and then down 2 squares, as indicated by the double arrows pointing down, and so forth. (D) In the verbal mental-operation task, subjects first remembered the day of the week specified by a *kanji* character and advanced the date as instructed by the numbers. For example, one first advanced the day from Wednesday to Friday by the number 2, from Friday to Monday by the number 3, and so forth.

(Simon, 1999). Recently, a neuroimaging study on a non-abacus calculation prodigy has indicated that expertise uses different brain regions from those for nonexperts (Pesenti et al., 2001).

The neural correlates of the calculation strategy employed by abacus experts remain unknown, although psychological studies have shown that visual strategy underlies this unusual calculation ability (Hatano et al., 1977; Hatano and Osawa, 1983; Stigler, 1984; Hatta and Ikeda, 1988). In the present study, we investigated brain activity during mental calculation in six top-level Japanese abacus experts, using functional magnetic resonance imaging (fMRI). Based on previous psychological evidence (Hatano et al., 1977; Hatano and Osawa, 1983; Stigler, 1984; Hatta and Ikeda, 1988), we hypothesized that the mental calculation of abacus experts might primarily depend on brain areas involved in visual, visuospatial, and visuomotor imagination rather than those involved in linguistic information processing.

To test this hypothesis, we used mental-operation tasks in which subjects serially and mentally updated mental representations according to external stimuli (Hanakawa et al., 2002; Sawamoto et al., 2002). The mental-operation tasks had advantages for the study of mental calculation in abacus experts. First, no motor response was required during task periods. We considered this important because motor responses for behavioral reports would affect the activity of brain areas underlying visuomotor imagery. Previous neuroimaging studies on visuomotor imagery showed that the underlying neural correlates substantially overlapped with brain areas for high-order motor control (Grezes and Decety, 2001; Hanakawa et al., 2003). Second, the mental-operation tasks can investigate different mental representations (e.g., numeral, spatial, or verbal representations) by changing a rule associating a given stimulus with a requisite mental operation. Third, accuracy of task performance was appraisable after each task period. This process provided a behavioral observation, which was necessary for assessing experimental confounders such as task difficulty.

Materials and methods

Subjects

The abacus-expert group consisted of one man and five women, ranging between 24–30 (mean $\pm$ SD = 28 $\pm$ 2.8) years old. All had been qualified as Japanese abacus masters with the highest degree (10th level) for both mental calculation and actual abacus operations. All had experienced greater than 17 years of almost daily abacus training for the purpose of competition. They were all right-handed with a laterality index (LI) of 0.8–1, except for one ambidextrous woman (LI = −0.2) (Oldfield, 1971). The nonexpert control group included one man and seven women, ranging between 22–33 (24 $\pm$ 3.6) years old. Nonexperts had negligible experience in abacus operations. All nonexperts were right-handed (LI = 0.8–1), except for one ambidextrous woman (LI = 2.5). All subjects gave written informed consent according to the study protocol approved by the institutional ethics committee.

Task

We used three versions (numeral, spatial, and verbal) of mental-operation tasks (Hanakawa et al., 2002). All mental-operation tasks began with the presentation of a prime stimulus (PS) for 2 s, followed by a task period of 30 s. During each task period, 15 instruction stimuli (IS) were presented with fixed interstimulus intervals of 2 s (stimulus frequency, 0.5 Hz). Throughout the task periods, subjects were asked to fixate on the visual stimuli without any accompanying movement. Each version of the mental-operation tasks was termed according to the most natural strategy, although all mental-operation tasks involve a type of computation, either vector or scalar operation, necessary for updating mental representations.

In the numeral mental-operation task, each PS and IS was an Arabic number (Fig. 1B). Subjects were asked to add up all presented numbers and report the final sum after each task period. In a preliminary experiment outside of the scanner, subjects practiced the numeral mental-operation task with different levels of difficulty (problems with single-, three-, or six-digit numbers as addends). All abacus experts considered the task with three-digit numbers most essential since they were the most frequently used number unit or abacus "width" for practice. On the other hand, all control subjects considered the numeral task with more than single-digit numbers impossible. Obviously, subjective difficulty of the numeral mental-operation task was different between the two groups, if the same problems were used for both. Therefore, we asked abacus experts to perform the task with three different levels of difficulty and then planned to use accuracy of the performance to match the task difficulty between the two groups. For the abacus experts, single-digit numbers were presented as PS and IS to three subjects of six, three-digit numbers were presented to all subjects, and six-digit numbers were presented to all but one who thought the task too difficult. These three conditions within the numeral mental-operation task also allowed us to explore brain areas in which activity change was correlated with the size of numbers within the task (i.e., number-size effect). For the control group, only single-digit numbers were used for PS and IS.

In the spatial mental-operation task, PS was a marker presented in one square of a grid subdivided into nine squares, and each IS was either an arrow or a pair of tandem arrows pointing in one of four directions (up, down, right, or left) (Fig. 1C). During the task periods after the PS disappeared, subjects mentally moved the marker on the imagined grid according to the ISs and reported the final location of the marker. Visuospatial imagery was expected as a natural strategy for the spatial mental-operation task.

In the verbal mental-operation task, PS was a *kanji* character indicating one of the days of the week, and each IS was a single-digit number (1, 2, or 3) (Fig. 1D). Starting from the day indicated by the PS, subjects serially advanced the day of the week according to the ISs (e.g., the number 2 meant 2 days later) and reported the day they finally reached. The days of the week constitute one of the most familiar string of words to Japanese people, regardless of abacus expertise. Therefore, the natural strategy was sequentially advancing the days in mind based on verbal–phonological rehearsal.

Subjects reported the final image of the task after the last IS for behavioral assessment. After each task period, the response stimulus comprising two visual stimuli side-by-side was displayed for 2 s. The response stimuli were a pair of numbers, grids with a marker, and *kanji* characters for the numeral, spatial, and verbal mental-operation tasks, respectively. The task solution was reported via a wrist extension movement: a left wrist extension indicated that the left figure was correct; a right wrist extension indicated that the right figure was correct; and a bilateral wrist extension indicated that neither was correct. Thus, the probability of a randomly occuring correct answer was 33%. Accuracy of the responses served as behavioral observations to assess task performance.

A visual fixation task, in which subjects kept fixating on a cross flashing on and off at the same rate as ISs, served as a common baseline. In each experimental run (4 min), task periods were repeated four times for the same mental-operation task version, alternated with baseline periods for the visual fixation task, in 30-s blocks. A scanning run for each task condition was repeated two times.

Functional MRI

FMRI experiments were conducted on a 1.5-T scanner with a standard head-coil (GE, Milwaukee, WI, USA). T2*-sensitive, gradient-echo echo planar images were obtained (interscan intervals = 6 s, echo time = 43 ms, flip angle = 90°, field of view = 22 cm, matrix size = 64 × 64, 38 contiguous axial slices, and voxel size = 3.5 mm^3). High-resolution, T1-weighted, 3-dimensional structural images were acquired before the fMRI acquisition for anatomic registration (fast spoiled gradient-recalled at steady-state image, data matrix = 256 × 256 × 124, voxel size = 0.86 × 0.86 × 1.5 mm). Subjects lay supine on a scanner bed. Foam cushions and elastic tape were used to minimize head motion. subjects viewed visual stimuli back-projected onto a screen, through a mirror built into a standard head coil. Each visual stimulus, subtending a 2.5° (vertical) × 2.5–5° (horizontal) visual angle, was presented in the center of view; the subjects were able to see the stimuli without moving their eyes. The absence of overt movements was confirmed in a preliminary training session outside of the scanner as well as during the actual fMRI acquisition, via constant visual inspection. Monitoring for eye movement was not available.

Image analysis was performed using statistical parametric mapping (SPM99, http://www.fil.ion.ucl.ac.uk/spm) implemented on MATLAB (MathWorks, Inc., Natick, MA, USA). After the first two images from each run were discarded, the remaining functional images were spatially aligned and resliced using sinc interpolation. The anatomical images were individually coregistered onto the mean functional images from each subject and spatially normalized to fit a Montreal Neurological Institute template (Evans et al., 1993) based on the standard stereotaxic coordinate system (Talairach and Tournoux, 1988). The functional images were spatially normalized using the same transformation matrix and smoothed with a 3-dimensional Gaussian kernel of 10-mm full width at half maximum.

A first-level multiregression analysis was performed to test the correlation between MRI signal changes and a boxcar function convolved with the canonical hemodynamic response function. In this process, a global difference in signal intensity was removed, using proportional scaling. Planned linear contrasts were applied to the parameter estimates from the multiregression analysis, which yielded t statistic maps (Friston et al., 1995). The effects of interest within each group were tested in terms of the conjoint effects across subjects (Friston et al., 1999). A statistical threshold was set at the height threshold of $P < 0.05$ (corrected for multiple comparisons).

For the between-group comparisons of activity during the numeral task, the task involving six-digit numbers for experts was compared with the task for nonexperts because the task performance was comparable only between these two conditions across the groups (see Results). Mean effect images reflecting a slope of a particular regressor were computed from the first-level multiregression analysis and were used in a second-level two-sample t test based on a random effects model. This analysis allowed population level inference between abacus experts and nonexperts. For the between-group comparisons, an explicit mask image was used for each contrast in the two-sample t test (experts minus controls or controls minus experts) to limit the search volume to brain areas showing task-related activity in each group (from second-level one-sample t test, $P < 0.005$, uncorrected). This was to avoid detecting between-group differences due to "deactivations" greater in a control group than a group of interest since there are still many unsolved issues in interpreting deactivations in neuroimaging studies (Gusnard and Raichle, 2001). Again, a statistical threshold was set at the height threshold of $P < 0.05$ (corrected for multiple comparisons). Similarly, the between-group difference in activity was tested for the other two mental-operation tasks.

Results

Task performance

For the numeral mental-operation task, accuracy was statistically not different between the experts during six-digit number addition (87% correct) and the nonexperts during single-digit number addition (77% correct, $P = 0.36$ by U test). However, the abacus experts during the numeral task for the other number sizes (100% correct for both single- and three-digit numbers) demonstrated significantly superior performance in task accuracy over the nonexperts ($P = 0.01$). Accuracy was comparable between the two groups both for the spatial mental-operation task (experts, 97% correct; controls, 90% correct, $P = 0.44$) and for the verbal mental-operation task (experts, 94% correct; controls, 91% correct, $P = 0.61$). Constant visual inspection during scanning did not detect any movement during the task periods, except for that necessary for the behavioral report.

Brain activity: general patterns

Brain activity associated with each mental-operation task, relative to the visual fixation task, was examined as a conjunction analysis across subjects for each group (Table 1,Fig. 2A). For the abacus experts, the numeral mental-operation task induced activity in the frontal operculum, superior precentral sulcus (SPcS), posterior parietal cortex including intraparietal sulcus areas (IPS), and posterior superior parietal cortex/precuneus, fusiform gyrus, and cerebellar hemisphere. This activity was bilaterally symmetrical. For the controls, the numeral mental-operation task activated the prefrontal cortex, Broca's area, medial frontal areas including the anterior cingulate cortex and presupplementary motor area (pre-SMA), and lateral parietal area. Nonexperts also showed activity in the areas observed during the numeral task for experts (i.e., frontal operculum, SPcS, IPS, posterior parietal cortex, fusiform gyrus, and cerebellar hemisphere); however, this calculation-related activity for controls was strongly lateralized to the left hemisphere. This pattern of activity during mental calculation was consistent with previous neuroimaging studies (de Jong et al., 1996; Dehaene et al., 1996; Rueckert et al., 1996; Burbaud et al., 1999; Rickard et al., 2000; Gruber et al., 2001; Pesenti et al., 2001; Zago et al., 2001).

The spatial mental-operation task induced symmetrical bilateral activity of the frontal operculum, SPcS, IPS, posterior superior parietal cortex, precuneus, and visual association areas. This activity was very similar between the two groups; moreover, the activity in the premotor and parietal cortices during the spatial task for both groups was almost identical to that observed during mental calculation for experts. During the verbal mental-operation task, experts and nonexperts both exhibited activity primarily in the medial frontal areas (anterior cingulate cortex and pre-SMA), SPcS, lateral parietal areas, and IPS. This activity was predominantly in the left hemisphere in the two groups, although the experts tended to exhibit more activity of the right hemisphere.

It appeared that abacus experts activated both hemispheres regardless of the versions of mental-operation tasks (see Fig. 2A). For a more quantitative analysis, laterality index was calculated for task-related activity changes in the SPcS and IPS regions, using parameter estimates from the first-level multiregression analysis in each individual (see legend to Fig. 2B). Nonparametric statistics revealed that the laterality of activity was different between the two groups only during the numeral mental-operation task (U test, $P = 0.039$ for SPcS and $P = 0.029$ for IPS) (Fig. 2B).

Brain activity during mental calculation: effect of number size for abacus experts

We investigated the effect of number size on mental abacus operations (Fig. 3). Left IPS and posterior superior parietal cortex demonstrated significant activity during the

Table 1
Activity during mental operation tasks as revealed by conjoint analysis across subjects in each group

Regions (Brodmann area)	Cluster size	Coordinates			Z value	P corrected
		x	y	z		
A. Numeral mental-operation task						
Abacus experts						
1. L precuneus (7)	1311	−18	−66	60	Infinite	0.000
L intraparietal sulcus (40/7)		−34	−48	54	Infinite	0.000
2. R intraparietal sulcus (40/7)	363	42	−52	56	Infinite	0.000
3. R precuneus (7)	60	14	−66	64	Infinite	0.000
4. R superior precentral sulcus (6)	103	24	−6	54	Infinite	0.000
5. L frontal operculum (6)	73	−48	6	28	6.89	0.000
6. L superior precentral sulcus (6)	34	−32	−6	52	6.55	0.000
7. L cerebellar hemisphere	14	−36	−74	−28	6.28	0.000
8. Cerebellar vermis	11	6	−76	−30	6.00	0.000
9. R frontal operculum (6)	13	50	10	36	5.99	0.000
10. L fusiform gyrus (37)	8	−52	−62	−16	5.88	0.000
11. R cerebellar hemisphere	10	40	−74	−24	5.83	0.000
Nonexperts						
1. L precuneus (7)	810	−24	−62	56	Infinite	0.000
L lateral parietal area (40)		−46	−40	54	Infinite	0.000
L intraparietal sulcus (40/7)		−40	−48	58	Infinite	0.000
2. R cerebellar hemisphere	677	30	−63	−32	Infinite	0.000
3. L superior precentral sulcus (6)	704	−32	0	54	Infinite	0.000
L Broca's area (44)		−50	10	26	Infinite	0.000
4. L cerebellar hemisphere	211	−38	−62	−30	Infinite	0.000
5. R anterior cingulate cortex (24)	191	4	14	45	Infinite	0.000
L medial frontal gyrus (6)		−2	1	61	7.31	0.000
6. R superior precentral sulcus (6)	86	34	0	54	Infinite	0.000
7. L prefrontal cortex (46)	97	−52	34	16	Infinite	0.000
8. L fusiform gyrus (37/19)	19	−48	−58	−12	6.91	0.000
B. Spatial mental-operation task						
Abacus experts						
1. R intraparietal sulcus (40/7)	933	40	−46	44	Infinite	0.000
2. R precuneus (7)	470	14	−64	62	Infinite	0.000
3. L precuneus (7)	1668	−12	−70	58	Infinite	0.000
L intraparietal sulcus (40/7)		−38	−48	56	Infinite	0.000
4. L superior precentral sulcus (6)	223	−32	−8	52	Infinite	0.000
5. R superior precentral sulcus (6)	89	28	−4	62	Infinite	0.000
6. R frontal operculum (6)	21	56	8	32	6.68	0.000
7. L middle temporal gyrus (39)	43	38	−76	28	6.50	0.000
8. R middle temporal gyrus (37)	5	−46	−62	4	6.05	0.000
9. R middle occipital gyrus (19)	6	52	−66	−8	5.90	0.000
Nonexperts						
1. L precuneus (7)	639	−16	−70	60	Infinite	0.000
L intraparietal sulcus (40/7)		−42	−46	60	Infinite	0.000
2. R superior precentral sulcus (6)	334	32	0	52	Infinite	0.000
3. L superior precentral sulcus (6)	701	−28	−6	50	Infinite	0.000
4. R intraparietal sulcus (40/7)	527	42	−42	56	Infinite	0.000
R precuneus (7)		20	−64	56	Infinite	0.000
5. L middle occipital gyrus (19)	113	−52	−72	−10	Infinite	0.000
6. R cerebellar hemisphere	55	40	−48	−38	Infinite	0.000
7. R supramarginal gyrus (40)	15	56	−24	36	6.69	0.000
8. L frontal operculum (6)	48	−56	8	32	6.51	0.000
9. L supramarginal gyrus (40)	10	−60	−26	34	6.47	0.000
10. Anterior cingulate cortex (24)	17	0	10	50	5.89	0.000

numeral mental-operation task with every number size tested. The task on larger number size gradually induced increased activity in additional brain areas, in which activity was otherwise subthreshold, especially in the right hemisphere. There was a number-size-dependent, monotonous increase in activity in IPS (*x, y, z* = −34, −52, 56 on the left; *x, y, z* = 40, −58, 56 on the right), posterior superior parietal cortex/precuneus (*x, y, z* = −18, −66, 60 on the

Table 1 *(continued)*

Regions (Brodmann area)	Cluster size	Coordinates			Z value	P corrected
		x	y	z		
C. Verbal mental-operation task						
Abacus experts						
1. L lateral parietal area (40)	806	−52	−46	48	Infinite	0.000
L intraparietal sulcus (40/7)		−38	−52	50	Infinite	0.000
2. R lateral parietal area (40)	367	54	−40	50	7.80	0.000
R intraparietal sulcus (40/7)		42	−46	48	7.13	0.000
3. L frontal operculum (6)	87	−48	−2	36	7.50	0.000
4. R superior precentral sulcus (6)	38	24	2	58	6.73	0.000
5. R anterior cingulate cortex (6)	61	4	10	54	6.55	0.000
6. L Broca's area (44)	29	−48	10	38	6.36	0.000
7. R intraparietal sulcus (40/7)	28	34	−62	46	6.27	0.000
8. L superior precentral sulcus (6)	15	−30	−12	48	6.19	0.000
9. L medial frontal gyrus (6)	6	−2	2	62	6.04	0.001
10. L precuneus (7)	16	−18	−64	50	6.02	0.001
Nonexperts						
1. L medial frontal cortex (6)	191	−2	0	66	Infinite	0.000
2. L lateral parietal area (40)	207	−50	−42	50	7.74	0.000
3. L superior precentral sulcus (6)	86	−44	0	54	7.53	0.000
4. L intraparietal sulcus (40/7)	117	−28	−62	56	7.43	0.000
5. R cerebellar hemisphere	67	32	−64	−30	7.27	0.000

left; *x, y, z* = 14, −66, 64 on the right), left frontal operculum (*x, y, z* = −48, 6, 28), SPcS (*x, y, z* = −28, −4, 46 on the left; *x, y, z* = 24, −4, 50 on the right), and left fusiform gyrus (*x, y, z* = −46, −62, −18).

Brain activity during mental-operation tasks: between-group comparisons

When calculation-related activity was compared between the two groups, only the left posterior superior parietal cortex/precuneus showed significantly greater activity for abacus experts than controls (Fig. 4A, Table 2). On the other hand, no hyperactive area was detected for the controls during the numeral mental-operation task.

When activity during the spatial mental-operation task was compared, the expert group revealed hyperactivity in the right IPS while the control group did not show any hyperactivity over the expert group (Table 2). For the verbal mental-operation task, there was no significant between-group difference.

In the left posterior superior parietal cortex/precuneus, brain activity exhibited significant group-by-task interaction ($P = 0.007$, repeated-measures ANOVA with Greenhouse–Geisser correction), reflecting overactivity for experts during the numeral mental-operation task. A confirmatory Student *t* test showed that the posterior superior parietal activity was different only during the numeral mental-operation task between the two groups (Fig. 4B). A within-group ANOVA followed by a posterior test (Student–Newman–Keuls, $P < 0.05$) showed significantly greater activity during the numeral task over the verbal task for abacus experts and greater activity during the numeral and spatial tasks over the verbal task for nonexperts.

Discussion

General discussion

The present study, for the first time to our knowledge, reported the neural correlates during mental calculation in abacus experts. The most significant finding was that the left posterior superior parietal cortex/precuneus, where controls also revealed some calculation-related activity, showed much enhanced activity during mental arithmetic of abacus experts. Additionally, there was no significant between-group difference in activity of this area for the two control tasks. We tested between-group differences using a statistical method that allowed population-level inference; this analysis gave a significant result despite a relatively small number of subjects for this type of analysis, probably because of the prominent difference in this area. We also found more involvement of right SPcS and IPS during mental calculation in abacus experts, although the between-group difference was significant only in the laterality index analysis. These areas, the posterior superior parietal cortex and right frontoparietal areas, have been often indicated as neural substrates subserving visuospatial/visuomotor processing. Hence, our main conclusion is that mental abacus operation is associated with enhanced activity in the areas relevant for visuospatial/visuomotor information processing, which is consistent with our a priori hypothesis. One, however, needs caution to conclude that this visuospatial processing during mental calculation is truly exclusive for abacus experts because activity in those visuospatial areas has also been observed for nonexperts during mental calculation. We therefore consider that the difference in brain

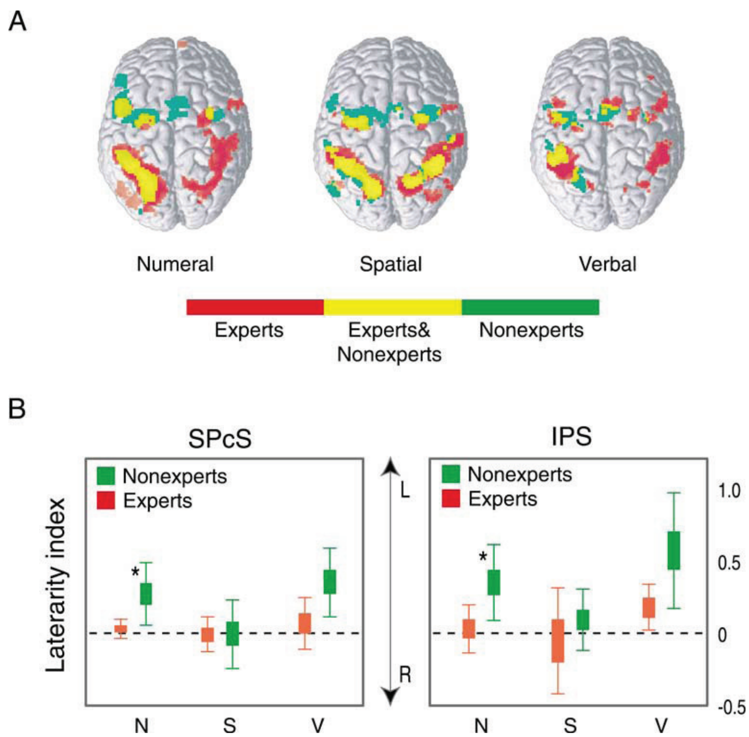

Fig. 2. General pattern of activity during each mental-operation task. (A) Activity during the three mental-operation tasks relative to a visual fixation task for abacus experts and nonexperts (within-group conjunction analysis, $P < 0.05$ corrected for multiple comparisons), rendered onto a standard brain. Significant activity only for abacus experts is shown in red, activity only for nonexperts in green, and the spatial overlap of activity in yellow. (B) Laterality of activity for the superior precentral sulcus (SPcS) and intraparietal sulcus (IPS), where the three mental-operation tasks commonly induced activity. A liberal threshold of $P < 0.001$ (uncorrected) was used only to locate these activities in each individual; all subjects showed suprathreshold activity in all four regions at this threshold. Estimated mean signal increase (SI, arbitrary unit) at the most significantly activated single voxel was computed in each area in each individual and then was used to calculate a laterality index (LI), that is SI for left minus SI for right, divided by the sum of SI for both sides. The more involvement of the right hemisphere was evident for experts compared with nonexperts only during the numeral mental-operation task (*$P = 0.039$ for SPcS and *$P = 0.029$ for IPS by U test).

activity between the two groups primarily reflects different weight on calculation strategy employed in each group: more involvement of visuospatial strategy for abacus experts and more involvement of linguistic strategy for nonexperts.

The areas in which we found enhanced activity for abacus experts are different from the areas where Pesenti et al. found increased activity for a prodigy of nonabacus calculation (Pesenti et al., 2001). There are several possible sources that can explain this discrepancy. First, we examined six experts who had gone through similar training processes for years, as opposed to one prodigy. Second, it is possible that the discrepancy truly reflects a difference in calculation strategy, since the well-trained subject studied by Pesenti et al. had developed an original calculation strategy, which strongly relied on episodic memory. Third, there are differences in the behavioral tasks between the two studies. We used mental-operation tasks that did not require any motor response during the task periods (Hanakawa et al., 2002; Sawamoto et al., 2002). Cognitive tasks usually require multiple responses for behavioral reports. However, it is not entirely reasonable to assume that motor components of cognitive tasks (i.e., preparation for and execution of motor responses such as verbalization) can be removed from the tasks, by subtracting out activity evoked by a control sensorimotor task. For example, more complex arithmetic problems usually result in more complex solutions to verbalize or retrieve from working memory; therefore, the complex vs simple arithmetic contrast reflects neural activity not only for complex computation but also for complex responses, especially when a task includes multiple responses. On the other hand, one must be cautious about how to interpret the present results, because the all mental-operation tasks involve some computation, either in 1 dimension (numeral and verbal) or 2 dimensions (spatial).

Another issue in the experimental design is how to control task difficulty between experts and nonexperts; an appropriate calculation task for experts would be too difficult for nonexperts. The present task design forced subjects to solve problems at the same speed between the two groups. A single variable for the numeral task (i.e., number size) was modulated for the expert group to experience the same difficulty as for the nonexperts group. A comparison was then made for the conditions in which accuracy was similar between the two groups, assuming that accuracy would reflect subjective difficulty of the tasks. The present exper-

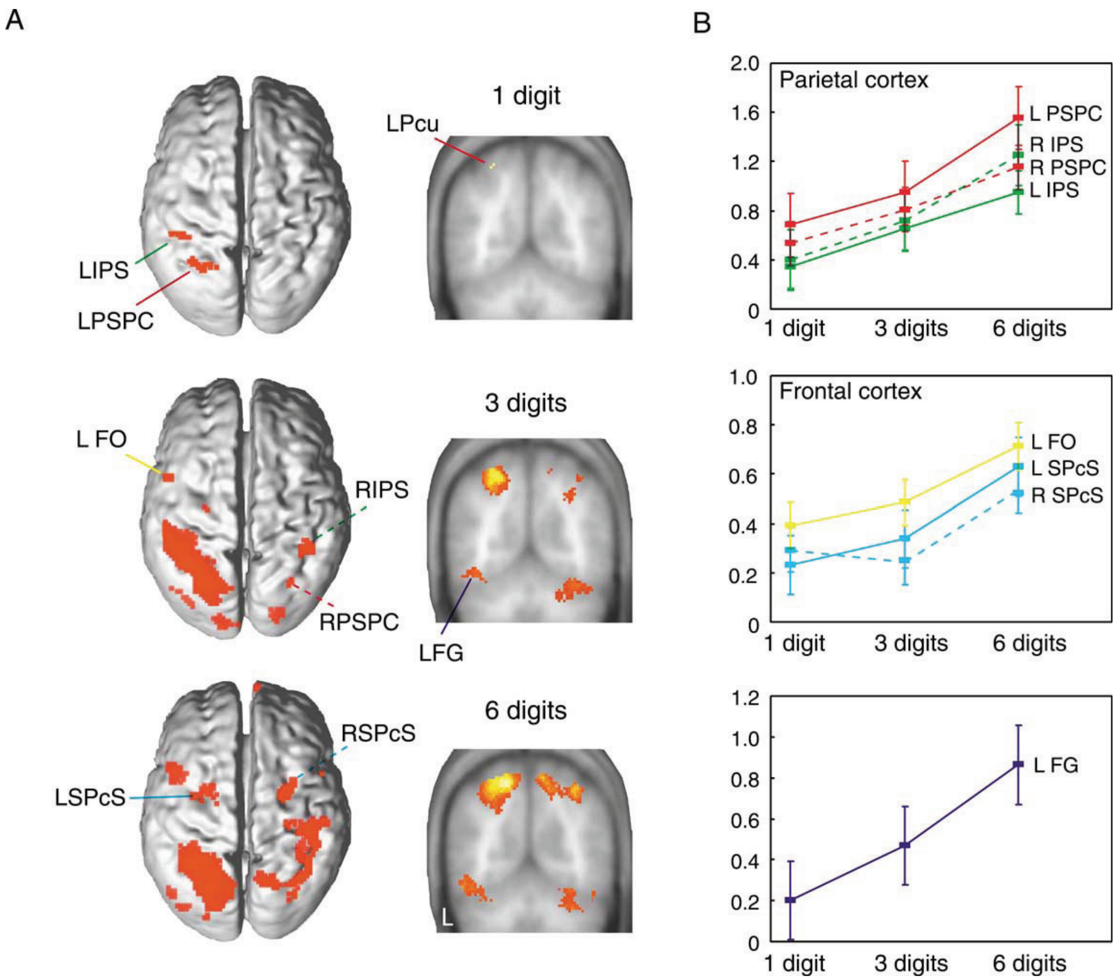

Fig. 3. Number size effect during mental calculation of abacus experts. (A) Activity during the numeral mental-operation task of abacus experts shown for each number size (within-group conjunction analysis, $P < 0.05$ corrected for multiple comparisons). Abacus experts exhibited activity that increased monotonously in association with number size of the calculation problems. This type of activity was present in the bilateral superior precentral sulcus (SPcS), left frontal operculum (FO), bilateral intraparietal sulcus (IPS), bilateral posterior superior parietal cortex (PSPC), and left fusiform gyrus (FG). Activity is shown on a surface-rendered image (left) and a coronal section (right) of the anatomic MRI averaged over six abacus experts. (B) The mean effect size in arbitrary unit (vertical axis) is plotted against the number of digits in problems (horizontal axis). Error bars show standard error of the mean.

imental design also provided an opportunity to examine the effect of number size on mental abacus operation. The results revealed the brain areas in which activity was increased monotonously as number size in arithmetic problems was increased. To our knowledge, only one has reported number size effect in mental calculation, although the comparison was very limited (problems with operands ranged from 1 to 5 versus operands ranged from 5 to 9) (Stanescu-Cosson et al., 2000), which revealed number size effect in the frontal operculum and the middle potion of IPS. In addition to these areas shown in calculation nonexperts, abacus experts in the present study revealed remarkable number size effect in the SPcS region and posterior superior parietal cortex/precuneus. This finding underscores significance of these two areas in mental abacus operation.

The semiquantitative, laterality index analysis for the three mental-operation tasks suggested more involvement of the right frontoparietal areas (SPcS and IPS areas) in mental abacus operation, yet the direct comparisons of the task-related activity between the two groups did not yield significant differences in these areas. This discrepancy reflected the fact that nonexperts also showed brain activity in the right frontoparietal areas during the numeral mental-operation task (see legend to Fig. 2). Nevertheless, the observation of right frontoparietal overactivity is consistent with a study claiming the relative significance of right hemisphere for mental abacus operation (Hatta and Ikeda, 1988). The participation of the right hemisphere supports a role of visuospatial processing in mental abacus operation since there is evidence that spatial information is predominately processed in the right hemisphere (Kohler et al., 1998). Very recently, Formisano and colleagues (Formisano et al., 2002) reported neuroimaging findings that indicate functional segregation between the left and right parietal cortices. They suggested that the left parietal cortex would be involved in the generation of spatial mental images while

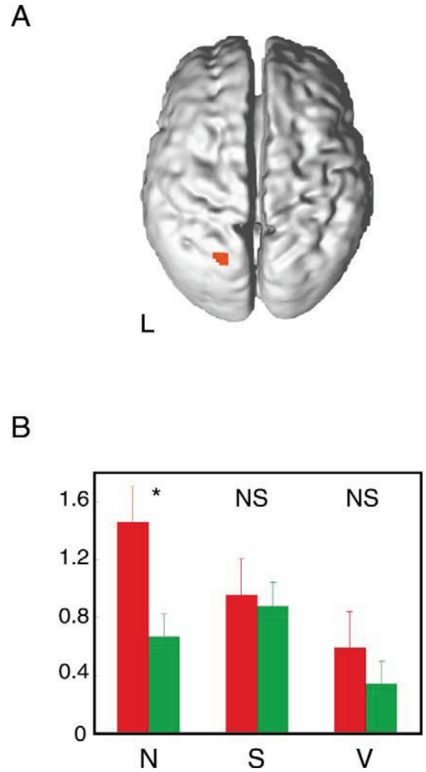

Fig. 4. Between-group comparisons. (A) Left posterior superior parietal cortex showing calculation-related overactivity for the abacus experts is projected onto a surface-rendered MRI. (B) Estimated mean effect size (arbitrary unit) for each mental-operation task in the left posterior superior parietal cortex. Only the numeral mental-operation task induced a significantly different brain activity in this area between the two groups.

the right parietal cortex would be engaged in the manipulation and comparison of such images. This proposed role of the right parietal cortex is consistent with the prominent right parietal activity during mental abacus operation as well as the spatial mental-operation task for both groups. Also, there is abundant evidence indicating that the posterior superior parietal cortex/precuneus, the most emphasized neural substrate for mental abacus here, is important for visuospatial processing as discussed below. Therefore, the results from the present study generally confirmed our hypothesis that neural substrates for visuospatial information processing including spatial working memory (Tanaka et al., 2002) underlie mental calculation ability of abacus experts. The results also suggested that these visuospatial areas might play some roles in standard mental calculation strategy (Simon, 1999), which could explain the mild activity in the right frontoparietal areas observed for nonexperts.

Parietal cortex

The parietal cortex has been the primary focus of attention as neural substrates underlying calculation because impairment of the parietal cortex, especially on the left, can cause dyscalculia or anarithmetia (Kahn and Whitaker, 1991). More recently, growing evidence has suggested that the parietal cortex is composed of multiple anatomofunctional subdivisions, and impairment of each subdivision may relate to dysfunction of a specific component of calculation ability. For example, a lesion in the left perisylvian part of the inferior parietal cortex can impair the ability to manipulate numbers in a verbal format but spare the ability to manipulate nonverbal number representations, possibly representing "verbal anarithmetia" (Cohen et al., 2000a). The lateral parietal area shown for the verbal task for both experts and nonexperts is consistent with this perisylvian parietal area. This is reasonable because the verbal mental-operation task supposedly involves more verbal aspects of mathematic operation than nonverbal aspects.

Lesions in more dorsal and caudal parts of the parietal cortex, including the posterior angular gyrus and IPS, can cause a more general deficit in number processing or semantic aspects of quantity processing (Takayama et al., 1994), possibly representing "semantic anarithmetia" (Cohen et al., 2000a). Neuroimaging experiments have supported the significance of this area for number quantity manipulation (Dehaene et al., 1999; Stanescu-Cosson et al., 2000; Pinel et al., 2001). In the present study, both experts and nonexperts revealed marked activity in areas surrounding the left IPS, supporting the general importance of this area in quantity manipulation regardless of arithmetic expertise (Pesenti et al., 2001). By contrast, the right IPS is

Table 2
Between-group comparisons

Regions (Brodmann area)	Cluster size	Coordinates			Z value	P corrected
		x	y	z		
Numeral mental-operation task						
Experts-nonexperts						
L posterior superior parietal cortex (7)	12	−22	−62	58	5.19	0.041
Spatial mental-operation task						
Experts-nonexperts						
R intraparietal sulcus (40)	12	40	−48	44	5.38	0.036

Note. Other pairs of comparisons did not show any significant difference in activity between the two groups with a threshold of $P < 0.05$ corrected for multiple comparisons.

important in the operation of visual images (Formisano et al., 2002), which is very likely essential for mental abacus operation.

The posterior superior parietal cortex/precuneus was more active during the numeral task for abacus experts than nonexperts. This zone also exhibited marked number size effect for abacus experts, which has not been reported for nonexperts (Stanescu-Cosson et al., 2000). Although activity in the posterior superior parietal cortex/precuneus can be observed for mental calculation in nonexperts, this area has seldom been a focus of attention as the underlying neural resources for mental calculation. Given that all mental-operation tasks involve mathematical operations, the differential involvement of this area may give us a hint to clarify a functional role of this area. This area was also highly active during the spatial mental-operation task for both of the groups but not during the verbal mental-operation task.

One hypothesis is that the posterior superior parietal cortex plays a significant part in computational operation in 2- and higher-dimensional space (i.e., vector-type operation). It is very likely that one needs a vector- or matrix-type of computational operations to work on a putative visual form of mental abacus that must be represented in 2-dimensional space. This idea can explain high activity during the spatial mental-operation task that also requires computational operations in 2-dimensional space as opposed to the verbal task that primarily requires a scalar- or sequence-type of operations in 1-dimensional space. This hypothesis is consistent with evidence that the posterior superior parietal cortex is dedicated to visuospatial information processing, which primarily deals with 2- or higher-dimensional space (Mellet et al., 1996, 1998; Simon et al., 2002). Judging from this property and anatomic location, this parietal subdivision might correspond to the parietal area V6a in nonhuman primates (Rosa and Tweedale, 2001). It is suggested that, as opposed to object-motion detected by V5, V6a functions to detect self-motion. This is consistent with an a priori hypothesis that enhanced motor imagery subserves mental arithmetic for abacus experts. Area V6a also has a putative role in directing skeletomotor activity to extrapersonal space, which again requires vector-type computation.

We propose a hypothesis that multiple parietal cortical modules for mental calculation are organized in such a way that the anterolateral parietal areas primarily concern verbal aspects of numerals with emphasis on sequence-type of operations, the middle parietal areas concern general conceptual aspects of calculation, and the posteromedial parietal areas concern vector-type operation in 2- and higher-dimensional space.

Frontal cortex

It is less likely that only the parietal cortex plays a role in mental calculation of abacus experts. We rather think that the posterior superior parietal cortex functions in concert with other brain areas dedicated to visuospatial information processing. The numeral mental-operation task for abacus experts and spatial task for both groups induced symmetrical bilateral activation of the SPcS region. The SPcS region also revealed number size effect for mental abacus operations. Importantly, the parietal area V6a has an anatomic connection with the dorsal premotor cortex (F2 and F7) (Matelli et al., 1998). The SPcS region probably corresponds to F7, the rostral part of the dorsal premotor cortex (PMdr) (Geyer et al., 2000), or "pre-PMd" (Picard and Strick, 2001). This area is distinct from the frontal eye fields occupying the ventrolateral part of the SPcS (Courtney et al., 1998; Hanakawa et al., 2002); hence, it is less likely that the whole SPcS activity for abacus arithmetic entirely resulted from eye movements. The dorsal premotor cortex is important in motor imagery (Gerardin et al., 2000; Hanakawa et al., 2003) as well as visuomotor association (Wise et al., 1997). Furthermore, along with the posterior superior parietal cortex, PMdr has been implicated in spatial information processing, spatial working memory, or visuospatial imagery not necessarily associated with movement (Mellet et al., 1996; Courtney et al., 1998; Richter et al., 2000). To summarize, the SPcS and posterior superior parietal regions seem to conjointly function in both nonmotor mental operations and visuomotor control. This may explain the fact that simultaneous performance of motor tasks interferes with mental abacus operations (Stigler, 1984), which may most vividly characterize the difference between abacus and nonabacus calculation strategies.

The left prefrontal cortex, frontal operculum including Broca's area, and pre-SMA appeared to be more active during the numeral task for nonexperts than for experts; yet, there was no significant population-level difference there possibly because of low statistical power. The part of the lateral frontal area is suggested to play a role in nonabacus mental arithmetic (Burbaud et al., 1995; Rickard et al., 2000). Also, there is a patient report of acalculia after a lesion involving lateral frontal cortex (Tohgi et al., 1995). Medial frontal areas including the pre-SMA and anterior cingulate cortex are also suggested to have a role for mental calculation (Lucchelli and De Renzi, 1993; Hanakawa et al., 2001).

Other areas

Although there was no overactivity in this area for abacus experts over nonexperts, we found number size effect in the left fusiform cortex. The parietal cortex functionally interconnects with the fusiform gyrus, part of the ventral visual pathway (Buchel et al., 1999). The fusiform gyrus is shown to represent visual word form (Cohen et al., 2000b). One interesting question regards whether this area also represents visual form of an abacus, which will need future testing using nonvisual stimuli for behavioral tasks.

Conclusions

In summary, the present results indicate that abacus experts primarily share the underlying neural correlates for mental calculation with nonexperts: visual form areas in the fusiform gyrus, multiple parietal areas, frontal operculum, and parts of the premotor areas. However, activity during mental calculation of abacus experts was characterized by overactivity in the posterior superior parietal cortex/precuneus and more involvement of frontoparietal areas in the right hemisphere. These differences were interpreted as reflecting more visuospatial/visuomotor imagery processing for mental calculation of abacus experts in comparison with nonexperts. Among these areas, the posterior superior parietal overactivity likely reflected spatial information processing in 2-dimensional space, which would be a characteristic of mental abacus operations. To date there is no lesion study on anarithmetia in abacus experts to support these hypotheses. To further the understanding of the functional neuroamatomy of abacus expertise, a future study modulating brain activity during mental abacus operation with transcranial magnetic stimulation will be warranted.

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