

Similar prefrontal cortical activities between general fluid intelligence and visuospatial working memory tasks in preschool children as revealed by optical topography

Mariko Kuwajima · Toshiyuki Sawaguchi

Received: 28 December 2009 / Accepted: 3 September 2010 / Published online: 19 September 2010
© Springer-Verlag 2010

Abstract General fluid intelligence (gF) is a major component of intellect in both adults and children. Whereas its neural substrates have been studied relatively thoroughly in adults, those are poorly understood in children, particularly preschoolers. Here, we hypothesized that gF and visuospatial working memory share a common neural system within the lateral prefrontal cortex (LPFC) during the preschool years (4–6 years). At the behavioral level, we found that gF positively and significantly correlated with abilities (especially accuracy) in visuospatial working memory. Optical topography revealed that the LPFC of preschoolers was activated and deactivated during the visuospatial working memory task and the gF task. We found that the spatio-temporal features of neural activity in the LPFC were similar for both the visuospatial working memory task and the gF task. Further, 2 months of training for the visuospatial working memory task significantly increased gF in the preschoolers. These findings suggest that a common neural system in the LPFC is recruited to improve the visuospatial working memory and gF in preschoolers. Efficient recruitment of this neural system may be important for good performance in these functions in

preschoolers, and behavioral training using this system would help to increase gF at these ages.

Keywords PFC · gF · Executive function · Spatial matching-to-sample · Preschoolers · fNIRS

Introduction

General fluid intelligence (gF) is related to reasoning ability, novel problem-solving, and adaptation to new situations. It is a major intellectual component of individual differences among both adults and children (Cattell 1973; Engle et al. 1999), and it is closely related to social risk success (Gottfredson 1998, 2004) and scholastic achievement (e.g., Luo et al. 2003; Frey and Detterman 2004). Therefore, it is important to improve gF in children to enhance their educational activities, and identification of the neural substrates of gF in children would promote such improvement. However, the neural substrate of gF in children, particularly preschoolers (4–6 years old), is poorly understood. In adults, gF is associated with neural activity in the lateral prefrontal cortex (LPFC) and other related areas (e.g., the posterior parietal cortex) (Duncan et al. 2000; Gray et al. 2003). Therefore, gF is likely to be associated with LPFC activity also in preschoolers, although neuroimaging evidence for this hypothesis is lacking.

It is well known that gF in adults is related to working memory, particularly to its capacity (Engle et al. 1999; Conway et al. 2002, 2003; Ackerman et al. 2005; Kane and Engle 2002; Kane et al. 2004, 2005; Oberauer et al. 2005). Working memory is responsible for the temporary storage and manipulation of information, and is a critical foundation for various cognitive functions (Baddeley 1986, 1992).

M. Kuwajima · T. Sawaguchi
Laboratory of Cognitive Neurobiology,
Hokkaido University Graduate School of Medicine,
N15W7, Kita-ku, Sapporo 060-8638, Japan

M. Kuwajima · T. Sawaguchi
Research Institute of Science and Technology for Society,
Japan Science and Technology Agency, Otemachi 1-1-2,
Chiyoda-ku, Tokyo 100-0004, Japan

T. Sawaguchi (✉)
Humanity Neuroscience Institute,
Yamanote 1-6-5, Nishi-ku, Sapporo 063-0001, Japan
e-mail: hq.toshi.sawaguchi@main.nifty.jp

The LPFC plays a major role in working memory (e.g., Freedman and Oscar-Berman 1986; Funahashi et al. 1993; Jonides et al. 1993; McCarthy et al. 1994; Sawaguchi and Iba 2001). Thus, not surprisingly, a brain-imaging study revealed a positive correlation between gF and neural activity related to working memory ability in the LPFC (Gray et al. 2003). In preschoolers, we previously demonstrated that the LPFC is activated during a visuospatial working memory task, similar to the case with adult subjects (Tsujimoto et al. 2004).

Based on these findings, we hypothesized that gF is associated with LPFC activity and that gF and visuospatial working memory share a common neural system within the LPFC during the preschool years. To address these hypotheses, we examined neural activity in the LPFC of preschool children (4–6 years old) while they performed a spatial matching-to-sample (SMS) task and a gF task, using a functional near-infrared spectroscopy (fNIRS) brain-imaging technique and optical topography (OT). The SMS paradigm is adequate for assessing working memory for visuospatial information in preschoolers (Tsujimoto et al. 2004). Further, OT takes advantage of the principle that near-infrared light is absorbed by oxygenated and deoxygenated hemoglobin (e.g., Kono et al. 2007). Because OT is noninvasive and does not require a head constraint, it is useful for imaging neural activity in the cerebral cortex in preschoolers (Tsujimoto et al. 2004). We also performed a behavioral study in a larger sample of preschoolers to examine the possible correlation between gF and visuospatial working memory abilities during the preschool

years. In the same sample, we performed a pilot study on the effect of working memory training with the SMS task on gF.

Methods

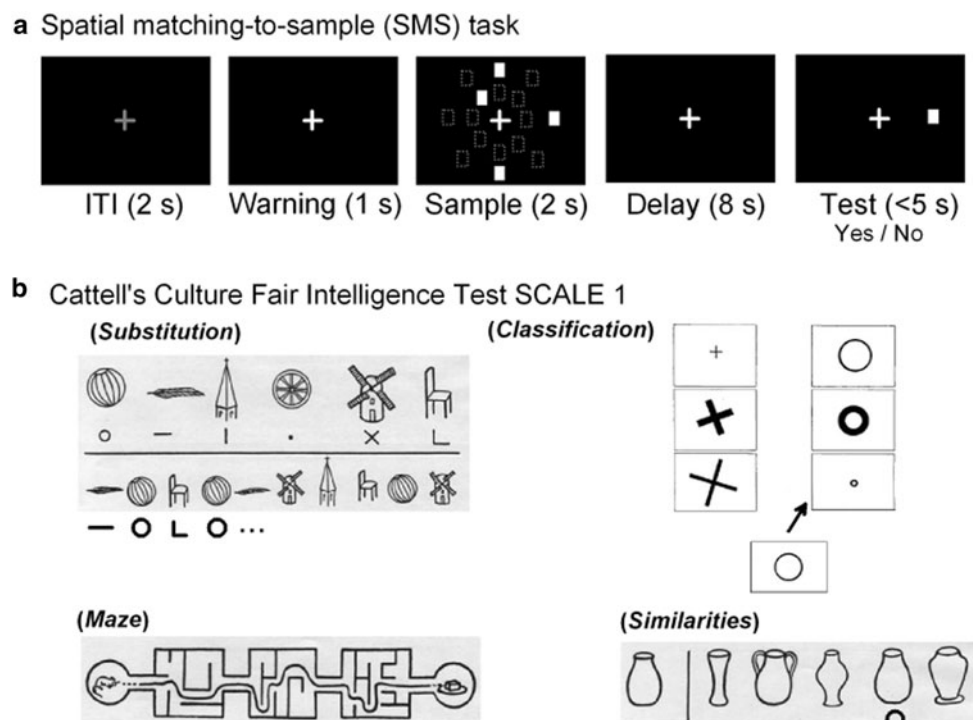
Subjects for the behavioral-level study

Ninety healthy preschool children [ages 4–6 years, 70.3 ± 8.21 (mean \pm SD) months, 46 males and 44 females] participated in the behavioral-level study. The children were currently attending Kannami-Sakura Nursery School, Shizuoka, Japan, or Sapporo International School, Hokkaido, Japan. The parents of all participants provided written informed consent prior to the start of the study, and the experiment was approved by the guidelines of our institutes and the Code of Ethics of the World Medical Association (Declaration of Helsinki) (Rickham 1964).

Behavioral tasks

We employed a spatial matching-to-sample (SMS) task as a visuospatial working memory task (c.f., Sawaguchi and Yamane 1999) (Fig. 1a) and Cattell's Culture Fair Intelligence Test (CFIT) SCALE 1 (Cattell and Briston 1933; Cattell 1940; Cattell et al. 1941) (Fig. 1b). In the SMS task, after a warning period of 1 s, a sample cue array consisting of several squares (approximately $1.5^\circ \times 1.5^\circ$) was presented on a computer monitor for 2 s. This was followed by a delay period of 8 s, after which a white square

Fig. 1 Behavioral tasks.
a Spatial matching-to-sample (SMS) task (with memory load = 4). In the SMS task, the subjects remembered the locations of sample cues. They were then required to report whether or not the location of the test cue was identical to that of one of the sample cues.
b Cattell's Culture Fair Intelligence Test (CFIT) SCALE 1. This test consists of four separate and timed subtests (Substitution, Classification, Maze, and Similarities)



(approximately $1.5^\circ \times 1.5^\circ$) was presented as a test cue. (The average spatial separation between no probes and the nearest point in the sample array is 2° .) The subjects were required to decide whether or not the test cue location was identical to any of the sample cue locations. The subjects reported their response by pressing a button on a computer keyboard within 5 s; “yes” was indicated by the right index finger and “no” by the left index finger. When a subject responded, the test cue was turned off, and the trial ended. Each trial was followed by an intertrial interval (ITI) of 2 s with a gray cross (approximately $1^\circ \times 1^\circ$) appearing in the center of the display. One block consisted of ten trials, with the same number of sample cue stimuli being presented in each. All subjects started with four samples because the four-sample cue condition appeared to be suitable for examining a subject’s abilities during the practice tests they performed before the experiments in the group condition. (That is, during practice it seemed too easy when fewer than four memory items were used, and too difficult when more than four memory items were used.) After the practice, we started the experimental session. In this session, the task difficulty was adjusted to each subject’s performance by changing the number of sample cue stimuli. The criterion for changing this number was a correct score rate over 80%, in which case we increased the number of sample cue stimuli in the next block. When the subject had a correct rate of less than 80%, we decreased the number of sample cue stimuli in the next block. All subjects performed at least three blocks of trials in total, and three blocks seem to be the most that most of the subjects could complete before losing their concentration. The CFIT SCALE 1 was composed of four separate and timed subtests (Substitution, Classification, Maze, Similarities).

Data analysis for the behavioral-level study

We examined capacity, accuracy, and reaction time as measures of visuospatial working memory ability. The capacity was defined as a value of x when $y = 0.75$ in a fitted regression line ($y = mx + b$, where x is the number of sample cue stimuli, and y is the correct rate under each sample cue condition). The accuracy and reaction time were defined as the rate of correct responses and the reaction time under the four-sample cue condition, respectively. We used four-sample cue conditions to analyze accuracy and reaction time because we examined the abilities of all subjects in this memory load. In another memory load, these abilities were examined in only a subset of the subjects. Each measure of visuospatial working memory ability was significantly correlated with age in months ($r = 0.27$, $t = 2.61$, $df = 88$, $P < 0.05$ for capacity; $r = 0.25$, $t = 2.38$, $df = 88$, $P < 0.05$ for

accuracy; $r = -0.32$, $t = 3.25$, $df = 88$, $P < 0.01$ for reaction time). Therefore, the working memory ability must be corrected by age in months. We therefore introduced the “working memory quotient” (WQ) to factor out age-dependent differences in visuospatial working memory abilities. We prefer this method over multiple regression analysis in which working memory capacity, accuracy, reaction time, and age are the dependent variables while gF is an independent variable. Because gF was corrected by age in months, we think that it is also appropriate to correct working memory abilities by age in months. Of course, we understand that multiple regression analysis is useful for examining the correlations among several components. Further, the methods used by Cowan et al. (2005), in which the capacity was measured by the original accuracy and reaction time by using varying memory loads, are also useful in case the accuracy and reaction time were measurable with varying memory loads in all subjects.

To use the WQ in the present work, we first used the least-squares method to calculate the best-fit regression between each visuospatial working memory ability (W) and each age in months (M), as follows:

$$W(\text{capacity}) = 0.0585 \times M - 1.5926$$

$$W(\text{accuracy}) = 0.0058 \times M + 0.1824$$

$$W(\text{reaction time}) = -22.749 \times M + 3735.3.$$

Since the reaction time was negatively correlated with M and we wished to use the same method for calculating WQ for each ability, “mental age” (MA) for each ability was calculated with the following equations:

$$MA(\text{capacity}) = \{W(\text{capacity}) + 1.5926\}/0.0585$$

$$MA(\text{accuracy}) = \{W(\text{accuracy}) - 0.1824\}/0.0058$$

$$MA(\text{reaction time})$$

$$= \{-W(\text{reaction time})/22.749 - 3735.3\}/22.749.$$

WQ(capacity, accuracy, reaction time) was calculated using these equations for each subject, as follows:

$$WQ(\text{capacity, accuracy, or reaction time})$$

$$= MA(\text{capacity, accuracy or reaction time})/M \times 100.$$

For example, when the age of a subject is 74 months and his or her working memory capacity is 4.4, MA is 102.4 months $\{=(4.4 + 1.5926)/0.0585\}$ and WQ(capacity) is 138 $(= 102.4/74 \times 100)$.

Subjects for the neural-level study

Five healthy preschool children [aged 4–6 years, 62.8 ± 3.49 months (mean \pm SD), 3 males and 2 females: AK, HT, KS, RS, MW] participated in the neural-level study. The children were attending Sapporo International School,

Hokkaido, Japan. The parents of each child provided written informed consent and were informed of the purpose of the study; they were also made aware of the safety of OT. The experiment was approved by the guidelines of our institutes and the Code of Ethics of the World Medical Association (Declaration of Helsinki) (Rickham 1964).

Behavioral task for the neural-level study

We employed the same tasks as used in the behavioral-level study, although we made some modifications to make them suitable for this study (Fig. 2a, b). The SMS task was exactly the same as that used for the behavioral-level study except that the warning period was random (1–3 s) and the ITI was longer (25 s). The subjects performed the four-sample cue condition in eight trials. The number of trials was restricted to eight because that seemed to be the limit of the subjects' ability to concentrate. For the same reason, we used only one memory load value, i.e., four memory loads. The CFIT SCALE 1 was restricted to the Classification subtest because this subtest was easy to control, and performance on it significantly predicted the raw score for gF in our behavioral-level study (standardized partial correlation coefficient, $r = 0.24$, $df = 88$, $P < 0.001$; multiple regression analysis was used with the raw score of gF as the dependent variable, and the performance in subtests one to four as the predictor variables). In the CC (Cattell's Classification) task, after a warning period of 1 s, six sample pictures (approximately $7^\circ \times 6^\circ$; three in one group and three in another) and one test picture (approximately

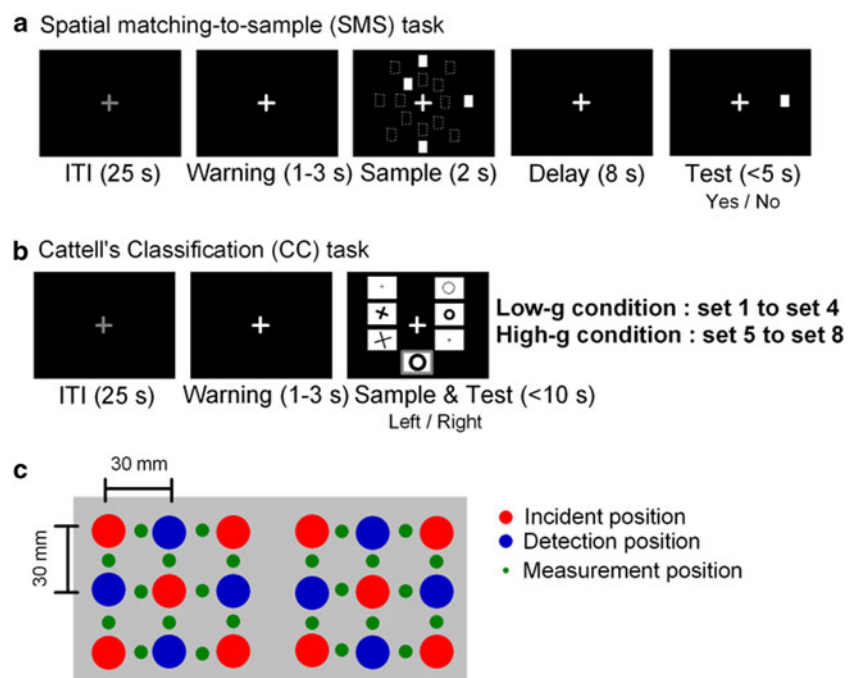
$7^\circ \times 6^\circ$) were presented simultaneously. The subject was required to decide which group the test cue belonged in. The subject reported his or her response by pressing a button within 10 s; the "right side" was indicated by the right index finger, and the "left side" by the left index finger. When the subject responded, the sample pictures and test pictures were turned off, and the trial ended. Each trial was followed by an ITI of 25 s, during which a gray cross was presented at the center of the display.

All subjects were instructed in the task rules before commencing the experimental session. After receiving the instruction, they practiced samples of the SMS and CC tasks. Once they understood the task rules and were able to perform adequately (approximately 80% correct responses), the experimental session began. In the experimental session, the subjects each performed two blocks of eight trials, each trial consisting of four "Low-g" trials and four "High-g" trials, randomly selected. The Low-g trials were defined as set 1 to set 4 of the Classification subtest, and the High-g trials were defined as set 5 to set 8 of that subtest. The order of tasks and conditions was counterbalanced among the subjects.

OT measurements

During task performance, we measured hemoglobin oxygenation in the subjects' LPFC using a 24-channel event-related OT system (OMM-3000; Shimadzu Corp., Kyoto, Japan). The area measured covered the $60 \times 60 \text{ mm}^2$ area of each frontal cortex, including the LPFC.

Fig. 2 Behavioral tasks for the neural-level study (a, b) and positions of the OT measurements (c). **a** Spatial matching-to-sample (SMS) task (with memory load = 4). **b** Cattell's Classification Test (CC task). In the CC task, the subject was required to decide to which group the test cue belonged (in this example, the test cue belonged to the "circle" group). **c** Configuration of incident position, detection position, and measurement position for the two hemispheres



The methods of recording were similar to those used in our previous studies on the prefrontal cortex in preschool children (Tsujiimoto et al. 2004), except that we used the OT system from Shimadzu Corp. (Khoa and Nakagawa 2008). This system contains three laser diodes 780, 805, and 830 nm as light sources. The system used a cutoff filter whose threshold was 50 Hz wavelength. In the LPFC of each hemisphere, five emitters and four detectors were placed at alternate square intersection points on a 3×3 grid (Fig. 2c). This configuration enabled us to detect signals from 12 channels in each hemisphere (a total of 24 channels). Near-infrared rays leave each illuminator, pass through the skull and the brain tissue of the cortex, and are received by the detector optodes (Khoa and Nakagawa 2008). The system detected cortical changes in oxy-hemoglobin concentration ($C_{\text{oxy-Hb}}$), deoxy-hemoglobin concentration ($C_{\text{deoxy-Hb}}$), and total hemoglobin concentration ($C_{\text{total-Hb}}$). We adjusted the sensitivity of each measurement point after the phantom experiment every time. Therefore, the sensitivity of each measurement point was not varied by more than 5% of the original value during the resting period. The spatial resolution was a few centimeters. We used 10–20 standard positions, which were usually used for the electroencephalographic landmarks (c.f., Okamoto et al. 2004) to posit a similar optical probe for all subjects. Briefly, in this method, we measured the length between nasion andinion. Then, we divided the length between the nasion andinion among the rates of 10, 20, 20, 20, and 10% (Fpz, Fz, Cz, Pz, Oz). Next, we measured the length between the nasion andinion through the auditory canal. By referring to this length and points above (Fpz, Fz, Cz, Pz, Oz), we were able to determine certain points in the frontal cortex. So, we placed the probe carefully by referring to these points. Raw optical data were recorded every 85 ms. The timing of each task event, such as the onset of the sample cue, was also transmitted to the data-collection computer from the task-control computer via parallel I/O connections. These digitized data were stored on a hard disk drive and were eventually transferred to magneto-optical diskettes for further off-line analysis.

Data analysis for the neural-level study

To analyze the transmittance data adequately, we excluded the data from the error trials and inappropriate data obtained when the subject moved too much. The mean numbers of error trials were 3 for the SMS task, 2.4 for the High-g task, and 2.2 for the Low-g task. The methods used to extract the features with wavelet analysis were described in detail in a previous study (Khoa and Nakagawa 2008). Briefly, in this system, reflected near-infrared rays were changed according to the change in the hemoglobin concentration. Therefore, we were able to measure changes in

hemoglobin concentration as changes in brain activity. First, we defined the “insensitive” measurement points by visual inspection after the phantom examination. Then, we defined the criterion to determine insensitive measurement points as a hemoglobin concentration above 0.2 mM, which was based on the average of all correct trials. Inadequate signals were recorded because some of the sensors were placed poorly or placed too far from the brain. Data were then smoothed using a Savitzky–Golay filter, which is a roll-off filter. The smoothing point was 39, and the one smoothing was performed. The cardiac pulse was removed by this method. The baseline was then corrected for the subsequent analyses. The baseline was defined as the average of the parameters obtained from 10 s before the cue presentation until the start of the cue presentation. After these processes, we defined the “activation period” and “control period” for each task with the time delay of the blood flow following brain activation, as follows: (1) the control period was the period from 5 s before cue presentation until the start of cue presentation for each task; (2) the activation period in the SMS task was the period from the start of the cue presentation until 15 s after cue presentation; and (3) the activation period in the CC task was the period from the start of the sample cue presentation until 8 s after cue presentation.

To investigate whether or not the activation levels differed significantly among tasks at each recording site, we compared the concentration of oxy-hemoglobin ($C_{\text{oxy-Hb}}$) during the control period with that during the activation period using Student’s *t* test ($P < 0.05$) for each task for each channel separately for each subject. In this procedure, we compared the $C_{\text{oxy-Hb}}$ serving every 85 ms during the control period with that during the activation period. For this comparison, we used the average data from each trial. To compare the activation levels between the High-g and Low-g conditions for the CC task, we applied a paired *t* test during the activation period. Only when this comparison showed a significant difference ($P < 0.05$), the change in $C_{\text{oxy-Hb}}$ was considered significant for the CC task. In addition, to clarify the gF-associated changes in $C_{\text{oxy-Hb}}$, we usually examined $C_{\text{oxy-Hb}}$ in the CC task by subtracting the concentration seen in the Low-g condition from that in the High-g condition, because the activation period in the CC task involved components other than gF, such as hand and eye movements. This method was considered useful for detecting the gF component.

Procedures of working memory training

Sixty of the children [aged 4–6 years, 63.0 ± 6.93 months (mean \pm SD), 30 males and 30 females] in the behavioral-level study also participated in the examination of the training effect on gF. The subjects were divided into three

groups ($n = 20$ in each; the number of males was approximately equal to the number of females in each group): (1) the working memory training group [60.9 ± 6.87 months (mean \pm SD), 10 males and 10 females], (2) the placebo-training group [63.2 ± 6.93 months, 9 males and 11 females], and (3) the no-training group [64.9 ± 6.74 months, 11 males and 9 females]. The average number of training days was 6 per week for about 2 months. On each training day, the subjects trained for about 10 min. During each training session, the experimenter directed the subject to perform the SMS task (working memory training group) or placebo task (placebo-training group) at a similar rate and for a similar number of trials (a total of ~ 40 trials) for ~ 10 min at the same time each day. The working memory training and placebo training were conducted in two separate rooms. In the working memory training group, the subject performed an SMS task. This task was exactly the same as that used in the behavioral-level study except that it was somewhat modified for the training: there were always four sample cues and the delay period was 8 s. The training was performed under a group condition. The instructor presented a visual cue printed on a sheet of paper for about 2 s, then hid the paper. This was followed by a “delay period” of 8 s. The instructor then presented a sheet of paper with the test cue printed on it. Children were required to make an oral response of “yes” or “no”. The placebo-training group performed a conditional response task. In this task, the children made oral responses (i.e., “yes” or “no”) to visual cues, as in the SMS task. These cues were the same as the matching cues in the SMS task and were allocated to “yes” or “no” cues. The “yes” and “no” cues were switched in different daily sessions. Thus, the placebo task consisted of responses and response cues similar to those in the SMS task, but it did not require working memory. The procedure in the “placebo” task was similar to that in the SMS task, even though this task did not include the short-term delay period.

The gF scores were compared before and after the training period for each subject by using the same test as used in that study (i.e., CFIT SCALE 1). For the comparison of gF, a modified version of the original CFIT was made, matching the CFIT instruction. Each subject performed the original CFIT before the training and the modified CFIT after the training. A paired t test was used for the comparison of pre- and post-training gF.

Results

Correlation between working memory accuracy and gF

The mean gF of our subjects (aged 52–83 months) in the behavioral study was 134.1 ± 23.7 (mean \pm SD, $n = 90$), as assessed by the CFIT SCALE 1 test. We examined these

preschoolers’ capacity, accuracy, and reaction time in the SMS task. Table 1 shows the relationships between three types of memory loads (i.e., two, four, and six spatial cues) and working memory abilities (accuracy, reaction time). As shown, accuracy decreased as memory load increased, and the difference in accuracy by different memory-load conditions was statistically significant ($P < 0.01$, one-way ANOVA, $df = 2, 267$, $F = 4.696$), although accuracy in the two memory load was not significantly different from that in the four memory load ($P > 0.05$, paired t test). Accuracy in the six memory load was significantly different from that in the four memory load ($P < 0.05$, paired t test). On the other hand, reaction time did not differ across different memory loads (two vs. four memory load, $P > 0.05$, four vs. six memory load, $P > 0.05$, paired t test). Next, we calculated the working memory quotient (WQ). Each WQ(capacity, accuracy, and reaction time) was positively and significantly correlated with gF (Fig. 3a, b, c; Table 2). We also examined the relationship between WQ and gF subscores (i.e., Substitutions, Classification, Maze, and Similarities). In this procedure, gF subscores were corrected by age in months because the value of WQ was also corrected by age in months. In the gF subsets, Classification was positively and significantly correlated with all of the WQs (capacity, accuracy, reaction time) (Table 3). In contrast, the other gF subscores were significantly correlated with only a subset of the WQ or not significantly correlated with all WQs.

Because WQ(capacity) was highly correlated with WQ(accuracy) ($r = 0.76$, $df = 88$, $P < 0.001$; Table 1), we used stepwise multiple regression analysis to determine which components of the WQ more accurately predicted gF. The best-fit multiple regression equation, using standard partial regression coefficients, was formulated as follows (Fig. 3d):

$$\text{gF} = 0.33 \times \text{WQ}(\text{accuracy}) + 0.18 \times \text{WQ}(\text{reaction time}).$$

The gF values measured using this equation were significant even at the 0.05% level ($F = 8.47$, $df = 2, 87$,

Table 1 Relationship between memory load and working memory abilities

	Mean	SD
Accuracy (rate)		
2 memory load	0.64	0.22
4 memory load	0.59	0.19
6 memory load	0.55	0.18
Reaction time (ms)		
2 memory load	2003.88	650.23
4 memory load	2135.60	571.11
6 memory load	1942.46	50.77

SD standard deviation

Fig. 3 Correlation between gF and working memory ability
a WQ(capacity),
b WQ(accuracy),
c WQ(reaction time).
r correlation coefficient;
P probability. **d** Standard partial regression coefficients for the best-fit multiple regression equation for gF with WQ.
r multiple correlation coefficient; *r*² proportion of shared variance

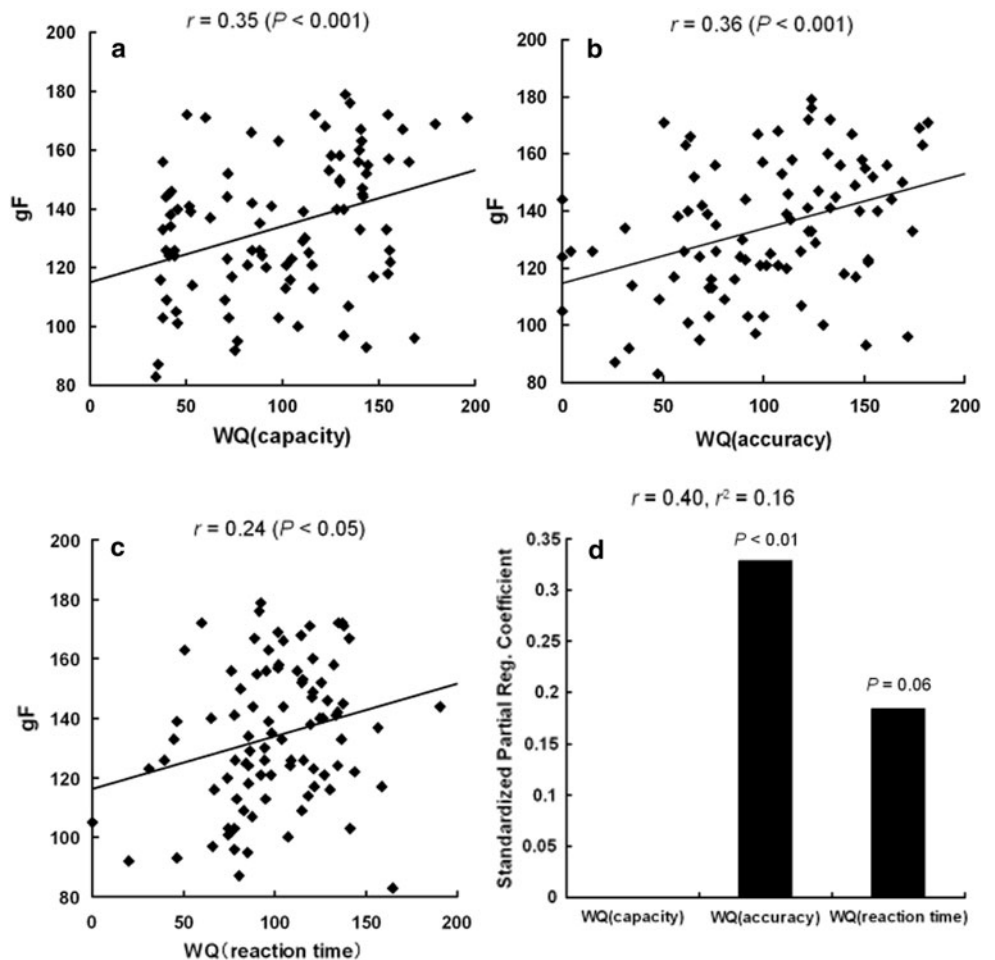


Table 2 Correlation matrix of gF and WQ

	Correlation coefficient			gF
	WQ (capacity)	WQ (accuracy)	WQ (reaction time)	
WQ(capacity)	–			
WQ(accuracy)	0.76***	–		
WQ(reaction time)	0.06	0.17	–	
gF	0.35***	0.36***	0.24*	–

* $P < 0.05$; *** $P < 0.001$

Table 3 Correlation matrix of gF subtests and WQ

	Correlation coefficient				gF
	Substitution	Classification	Maze	Similarities	
WQ(capacity)	0.09	0.36***	0.28**	0.16	0.35***
WQ(accuracy)	0.12	0.32**	0.21*	0.25*	0.36***
WQ(reaction time)	–0.12	0.23*	0.17	0.29**	0.24*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

$P = 0.00044$, $P < 0.001$). The multiple correlation coefficient (*r*) was 0.40, and the proportion of shared variance (*r*²) was 16.3%. WQ(capacity) was excluded from

this best-fit multiple regression equation. WQ(accuracy) was statistically significant ($t = 3.30$, $P = 0.0014$, $df = 89$, $P < 0.01$), and WQ(reaction time) tended to be as well ($t = 1.85$, $P = 0.067$, $df = 89$, $P < 0.1$). Thus, the correlation between gF and WQs was highly significant, and the gF was predicted most closely by WQ(accuracy).

Behavioral performance at the neural-level study

During the measurement of neural activity, we examined the correct rate and reaction times of the behavioral performance of the 5 subjects used in this brain-imaging study. The success rate in the SMS task was $62 \pm 22.8\%$ (mean \pm SD), and the reaction time was 1870.2 ± 551.0 ms (mean \pm SD).

The CC (Cattell’s Classification) task was used as the gF task in the brain activity study. The rate of correct responses under the Low-g condition of the CC task was not significantly different from that under the High-g condition ($72.5 \pm 24.0\%$ for the Low-g condition; $77.5 \pm 25.6\%$ for the High-g condition; $df = 4$, $P = 0.65$, NS, paired *t* test). However, the reaction time was significantly shorter for the Low-g condition of the CC task than for the High-g condition

(3265.2 ± 893.6 ms for the Low-g condition; 4180.0 ± 1157.0 ms for the High-g condition; $df = 4$, $P < 0.05$, paired t test). This indicates that the task load was significantly different between the Low-g and High-g conditions of the CC task. We therefore usually examined neural data for the High-g condition minus the Low-g condition in the CC task to identify neural activity associated with gF.

Neural activity in the LPFC and its spatial similarity between the SMS and CC tasks

While the subjects were performing the SMS and CC tasks, we measured spatiotemporal changes in C_{oxy}-Hb using a 24-channel event-related OT system. We found that C_{oxy}-Hb increased in the LPFC of all subjects during the SMS task, confirming our previous finding that the LPFC of preschoolers is activated (i.e., there is an increase in C_{oxy}-Hb) during SMS task performance (Tsujiimoto et al. 2004). The number of regions (channels) associated with significant increases in C_{oxy}-Hb varied from subject to subject, and we found that this number was significantly correlated with the difference in accuracy and reaction time in the SMS task across the subjects (Spearman rank correlation test, rank correlation coefficient = 0.76, $P < 0.01$, for accuracy; rank correlation coefficient = 0.82, $P < 0.01$, for reaction time; also see Fig. 6). These findings suggest that the increase in brain activity during the SMS task is related to working memory, including its accuracy. The LPFC also showed an increase in C_{oxy}-Hb during the

CC task in all subjects, although the number of regions with significant increases in C_{oxy}-Hb varied from subject to subject, as was the case in the SMS task.

An example is shown in Fig. 4, where the spatiotemporal pattern of the change in C_{oxy}-Hb during the CC task (High-g minus Low-g) is illustrated before and after the onset of the sample/test stimulus. As shown in Fig. 4 (RS, a 5-year-old subject), C_{oxy}-Hb increased after the onset of the sample/test stimulus in wide regions of the recorded area of the LPFC of both hemispheres. The increase in C_{oxy}-Hb was sustained for some seconds after the sample/test stimulus onset, and the areas showing an increase seemed to change after the stimulus onset. Further, C_{oxy}-Hb decreased in some areas of the LPFC bilaterally. Thus, the LPFC showed hemodynamic changes during the CC task, which were characterized by a major increase and a minor decrease in C_{oxy}-Hb.

In the comparison of C_{oxy}-Hb in the activation period between the SMS task and CC task (the High-g condition minus the Low-g condition) in each subject, some similar regions of the LPFC showed clear increases in C_{oxy}-Hb during both tasks. Figure 5 shows a typical example. In this subject (RS, a 5-year-old subject), similar regions of the left LPFC showed clear increases during the SMS and CC tasks at ~ 10 and ~ 7 s after the onset of the sample cue for the SMS task and the sample/test stimulus for the CC task, respectively.

To confirm the spatial similarity of the C_{oxy}-Hb increase between the tasks, we examined the spatial distribution of the overall change in C_{oxy}-Hb during the

Fig. 4 The spatiotemporal pattern of the change in concentration of oxy-hemoglobin (C_{oxy}-Hb) during the CC task performance (High-g minus Low-g) for the right and left LPFC of RS in a 5-year-old subject. The onset of the sample/test stimulus is 0 s. Data were smoothed using a Savitzky–Golay filter. *Inset* the approximate recording area. *Sup* superior, *Inf* inferior, *Ant* anterior, *Pos* posterior

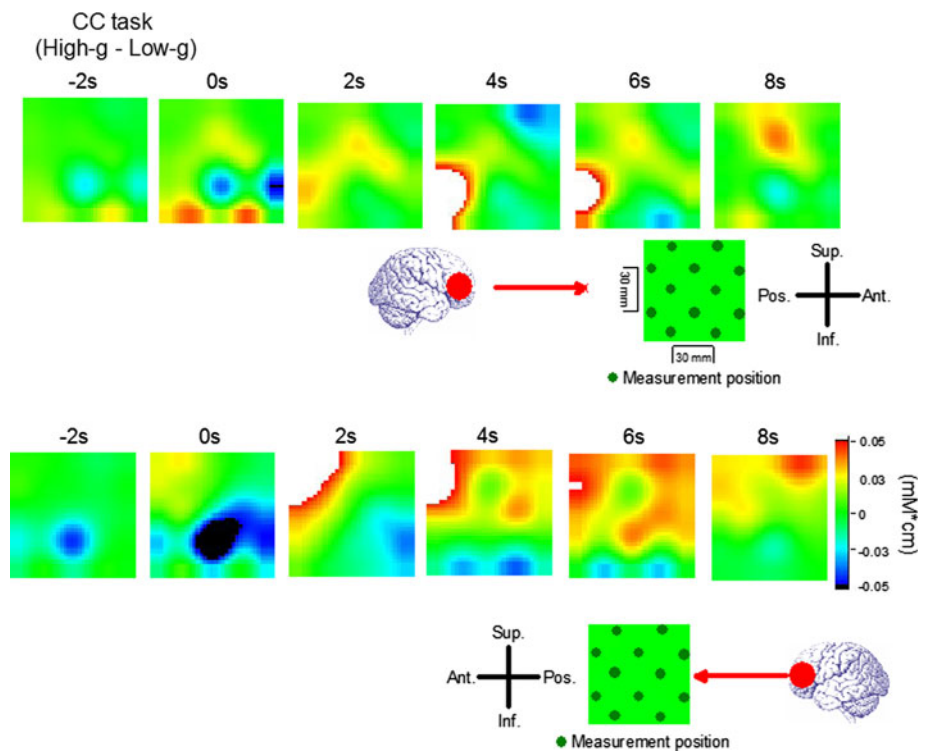


Fig. 5 Spatial pattern of changes in C_{oxy}-Hb in the left LPFC in RS in a 5-year-old subject. The image during the SMS task performance was captured for approximately 10 s following the onset of the sample cue. The image for the CC task (contrast for High-g minus Low-g) was captured approximately 7 s following the onset of the sample/test cue. Data were smoothed using a Savitzky–Golay filter. The *cross* indicates the location where a clear increase in C_{oxy}-Hb was evident during the performance of both the SMS and CC tasks. The *inset* and abbreviation are the same as those in Fig. 4

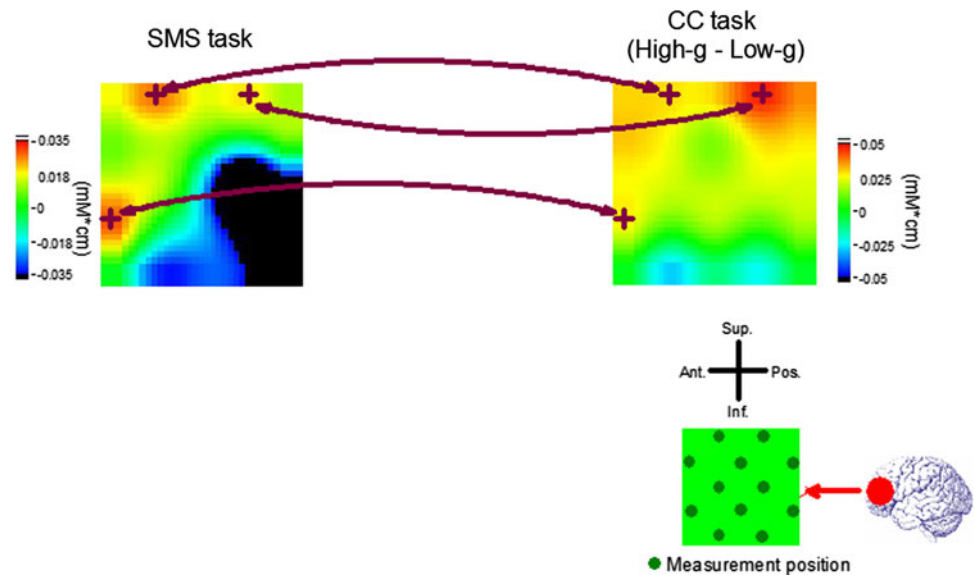
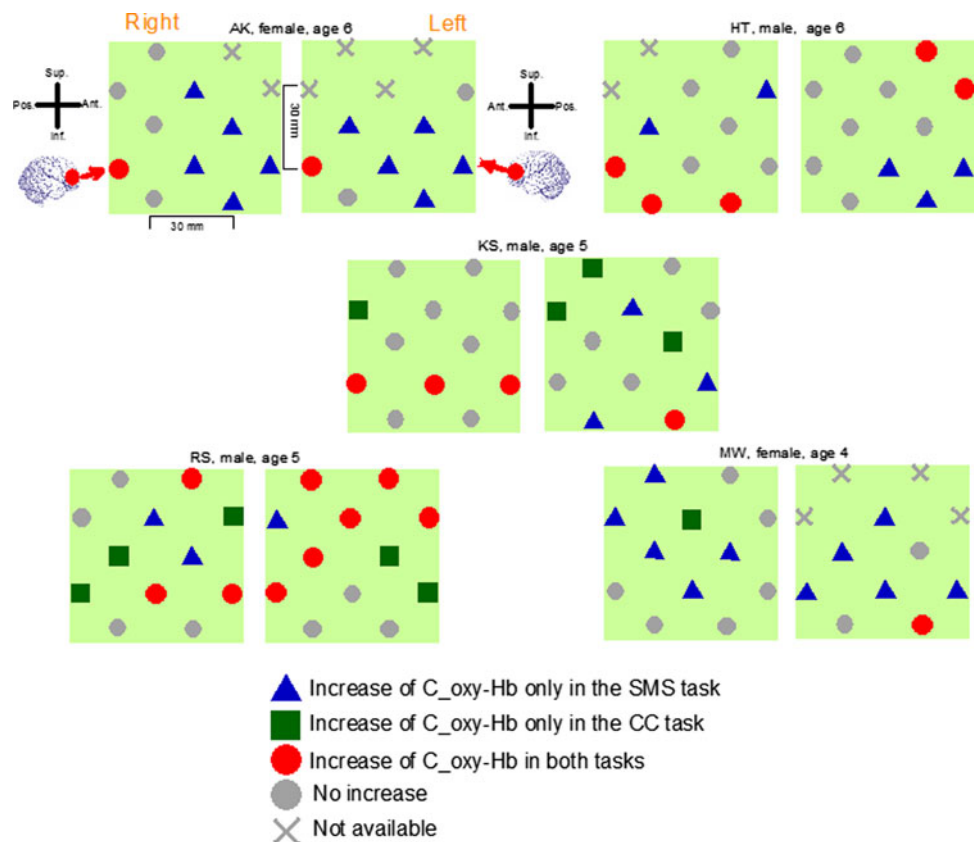


Fig. 6 Schematic diagram showing the spatial distribution of changes in C_{oxy}-Hb in the left and right hemispheres in 5 subjects. The *colored symbols* excluding the *gray symbols* indicate the position (channel) showing a significant increase ($P < 0.05$) in C_{oxy}-Hb during the activation period. The *inset* and abbreviation are the same as those in Fig. 4

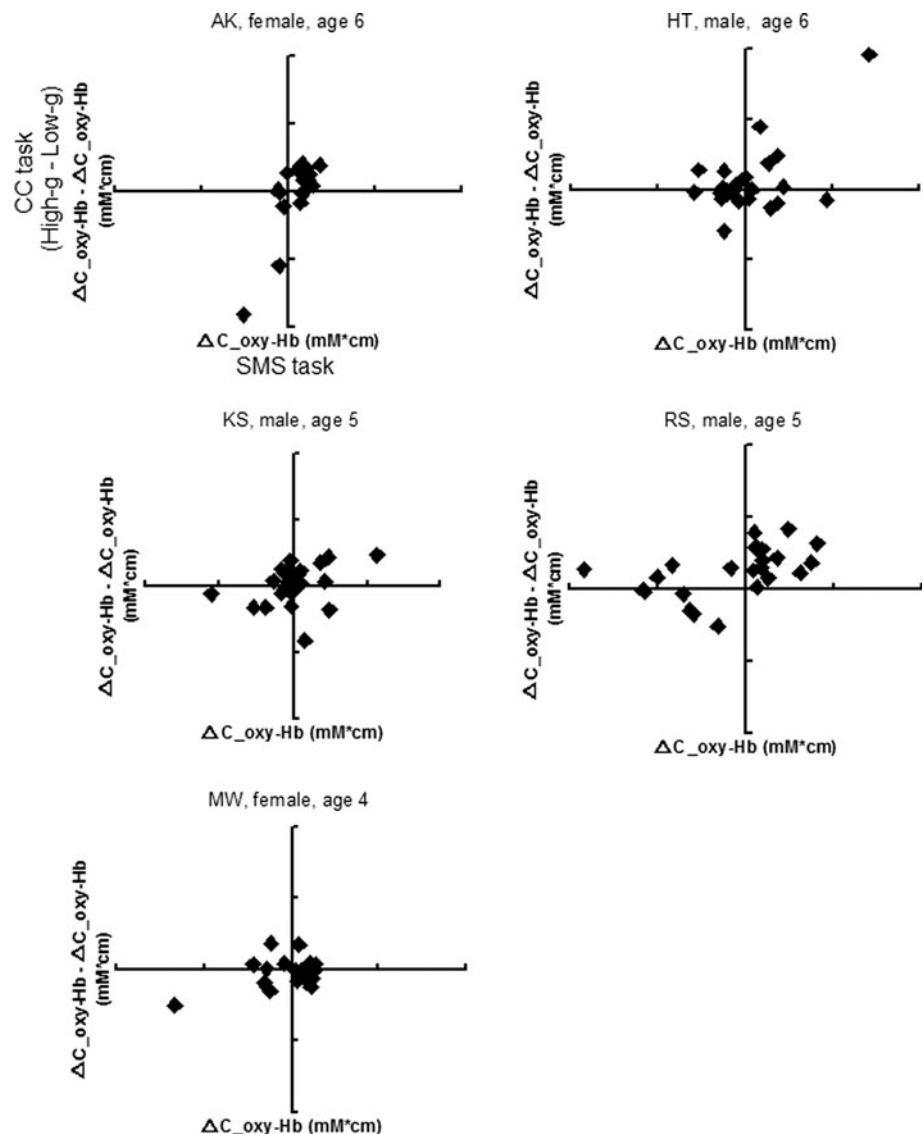


activation period of the SMS and CC tasks in each hemisphere of each subject. The results are shown in Fig. 6, which illustrates the measurement points with significant increases in C_{oxy}-Hb for only the SMS task, only the CC task, or both. As shown in Fig. 6, some regions showed significant increases in both tasks for all subjects, although there were individual differences in the number and position of these regions. We examined the difference in

hemoglobin oxygenation between the two hemispheres and within each hemisphere. However, the hemisphere bias for the increase in C_{oxy}-Hb was not clearly observed at either the individual or population level (χ^2 or Fisher's test, $df = 1$, $P > 0.05$, NS).

To further confirm the spatial similarity of the LPFC activity between the SMS and CC tasks, we compared changes in C_{oxy}-Hb between these tasks among different

Fig. 7 Change in C_{oxy}-Hb during the performance of the SMS task (*x* axis) and the change seen during the CC task (High-g minus Low-g) (*y* axis) in subjects. Data from the insensitive measurement positions were excluded from the analysis



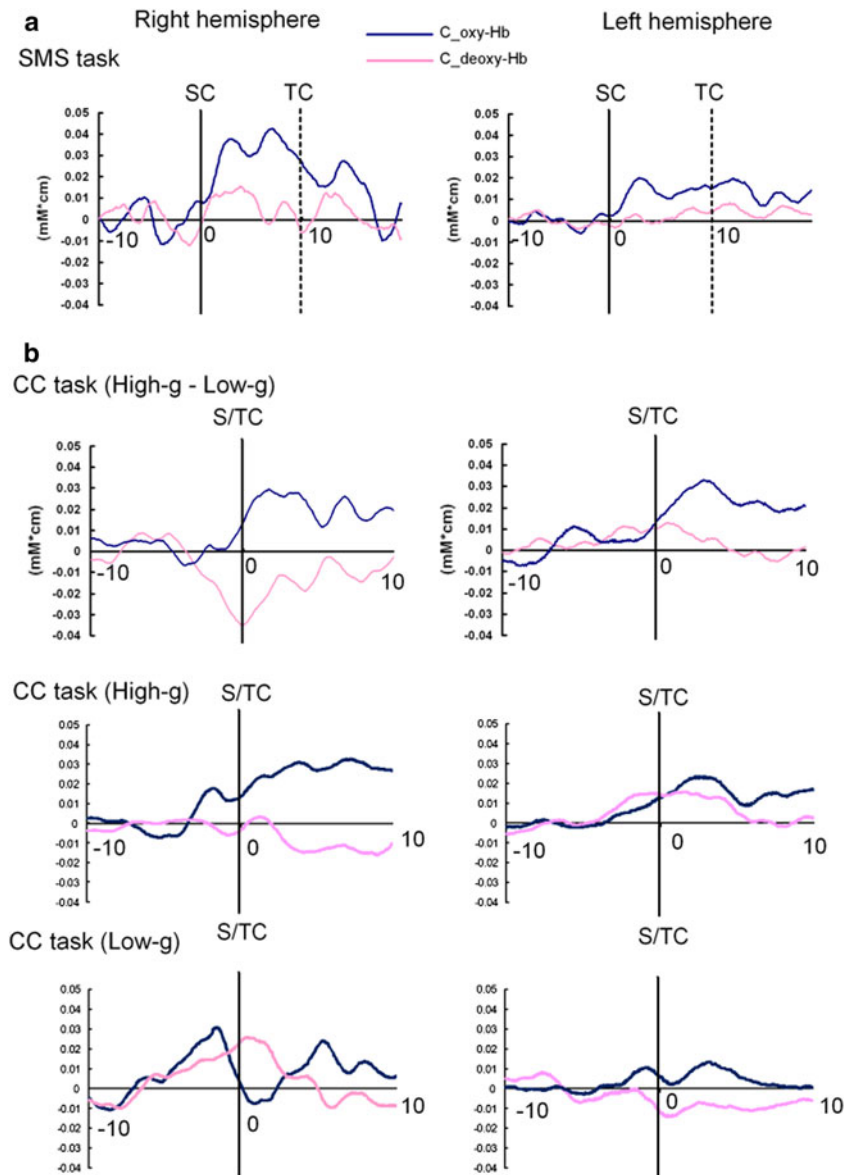
measuring points for each subject. In Fig. 7, the change in C_{oxy}-Hb during the CC task performance (High-g minus Low-g) is plotted against that during the SMS task performance for all measuring points excluding the insensitive measurement points of each subject. Obviously, the sample did not show normal distribution, and we employed non-parametric tests for the spatial distribution analysis. Even when the C_{oxy}-Hb changes at all available measuring points were compared (i.e., including insignificant and/or decreased points) between the SMS and CC tasks, a non-parametric correlation test (Spearman's rank correlation test) revealed positive correlations between them for all subjects (rank correlation coefficient, 0.23–0.57), which were statistically significant for all but one subject (rank correlation coefficients, 0.50, $P < 0.01$ for AK; 0.40, $P < 0.01$, for HT; 0.39, $P < 0.01$, for KS; 0.57, $P < 0.01$, for RS; 0.23, $P > 0.05$, NS, for MW). Furthermore, the

paired comparison by a nonparametric test (Wilcoxon signed rank test) revealed no significant differences ($P > 0.05$, NS) in C_{oxy}-Hb change between these tasks in all available measurement points for all subjects. Thus, the spatial profile in C_{oxy}-Hb was similar between the tasks for all subjects.

Temporal profiles of activity in the LPFC

To examine whether or not temporal profiles of neural activity in the LPFC are similar between the SMS and CC tasks, we measured the temporal changes in C_{oxy}-Hb as well as in the deoxy-Hb concentration (C_{deoxy}-Hb) at the population level ($n = 5$) at points where a significant increase in C_{oxy}-Hb had been observed during both tasks ($n = 10$ for right hemispheres, $n = 11$ for left hemispheres; these points are indicated by red

Fig. 8 The time courses of C_{oxy-Hb} and $C_{deoxy-Hb}$ changes in the LPFC in subjects for the points showing a significant increase in C_{oxy-Hb} during performance of both the SMS task and the CC task. **a** The time courses of C_{oxy-Hb} and $C_{deoxy-Hb}$ changes in the SMS task. The data are the mean concentration changes. **b** The time courses of C_{oxy-Hb} and $C_{deoxy-Hb}$ changes in the CC task. C_{oxy-Hb} and $C_{deoxy-Hb}$ changes are shown separately for conditions (High-g—Low-g, High-g, Low-g). *SC* sample cue onset, *TC* test cue onset; *S/TC* sample/test cue onset



dots in Fig. 6). The temporal profiles of these changes appeared to be similar between the tasks (the CC task, High-g—Low-g, High-g, and the SMS task) (Fig. 8a, b). C_{oxy-Hb} during SMS was clearly increased and sustained during the delay period in both hemispheres. In the CC task, C_{oxy-Hb} was also increased and sustained for more than 10 s after the sample/cue onset in both hemispheres in the High-g—Low-g and High-g conditions. In contrast, the increase in C_{oxy-Hb} in the Low-g condition was smaller than that in the High-g condition. Further, the increase in the Low-g condition was not sustained for more than 10 s. This finding suggests that the activity in the High-g—Low-g conditions represented gF-related activity. The onset latency of the significant increase in C_{oxy-Hb} during the SMS task was similar to that during the CC task. In contrast to C_{oxy-Hb} ,

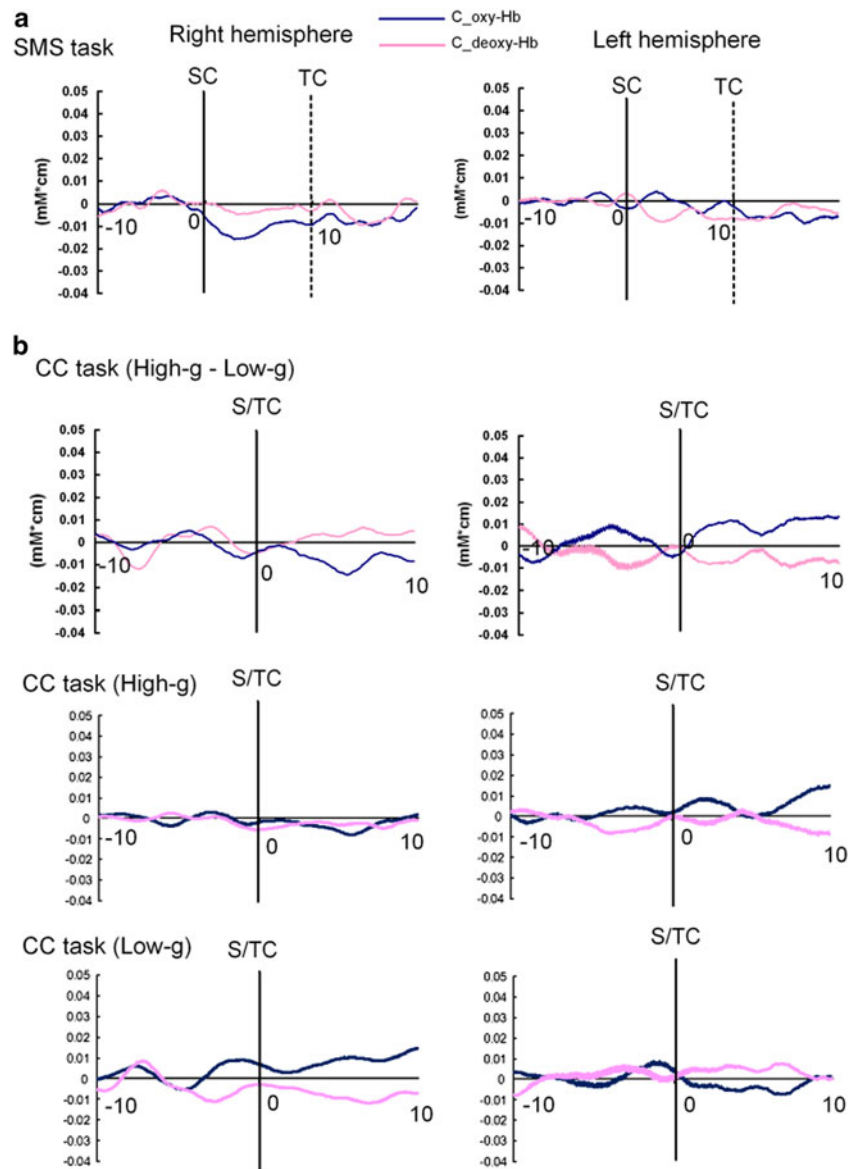
$C_{deoxy-Hb}$ did not show any clear increase during the delay period in the SMS task or after the sample onset in the CC task (Fig. 8a, b). These findings for the SMS task are similar to those described in our previous study using fNIRS and a working memory (SMS) task in preschool children (Tsujiimoto et al. 2004), in which the change in C_{oxy-Hb} , but not in $C_{deoxy-Hb}$, was shown to represent task-related neural activities.

Because the spatial change in C_{oxy-Hb} was similar in both tasks (see above), we also examined the temporal population change in C_{oxy-Hb} in all available regions ($n = 46$ for the right hemisphere, $n = 41$ for the left hemisphere; these points are indicated by dots that were excluded from the red dots in Fig. 6), excluding the points showing a significant increase in C_{oxy-Hb} during both tasks. Although the temporal change was relatively small,

Fig. 9 The time courses of C_{oxy-Hb} and C_{deoxy-Hb} changes in the LPFC in subjects in all available points excluding the points showing a significant increase in C_{oxy-Hb} during both the SMS and CC tasks.

a The time courses of C_{oxy-Hb} and C_{deoxy-Hb} changes in the SMS task. The data are the mean concentration changes.

b The time courses of C_{oxy-Hb} and C_{deoxy-Hb} changes in the CC task. C_{oxy-Hb} and C_{deoxy-Hb} changes are shown separately for conditions (High-g—Low-g, High-g, Low-g). The abbreviations are the same as those in Fig. 8



it also appeared to be similar during both tasks, with a few sustained decreases in the right hemisphere appearing after the cue or cue/target onset for either task (SMS and High-g—Low-g, High-g, Fig. 9a, b).

The effect of working memory training on gF

The effect of working memory training with the SMS task was examined for a total of 20 preschoolers. gF was significantly higher after 2 months of training (~10 min daily, 6 days per week; mean \pm SD, 135.1 ± 14.0 for pre-training, 147.6 ± 7.5 for post-training; $P < 0.001$, $df = 19$, paired t test) (Fig. 10). In contrast, gF was not significantly different between pre- and post-training for either the placebo-training (135.2 ± 11.1 for pre-training, 136.1 ± 11.8 for post-training; $P = 0.72$, $df = 19$, NS) or

no-training group (135.2 ± 14.6 for pre-training, 135.5 ± 13.9 for post-training; $P = 0.93$, $df = 19$, NS) (Fig. 10). We confirmed that there was significant interaction between the training type and both pre- and post-training (two-way ANOVA, $F = 3.115$, $P < 0.05$). In the working memory training group, there were no significant correlations/differences in percent increase of gF with respect to either age in months (correlation coefficient $r = 0.24$, $P = 0.31$, $df = 18$, NS) or gender (males vs. females, 10.5 ± 14.3 vs. $10.2 \pm 10.6\%$, $P > 0.05$, U- test). In addition, among the four CFIT subsets, the Classification score was the most significantly increased by working memory training (8.9 ± 3.8 for pre-training, 10.8 ± 3.0 for post-training; $P < 0.001$, $df = 19$, paired t test), followed by Substitution (14.1 ± 5.7 for pre-training, 17.5 ± 4.7 for post-training; $P < 0.01$). The scores for the

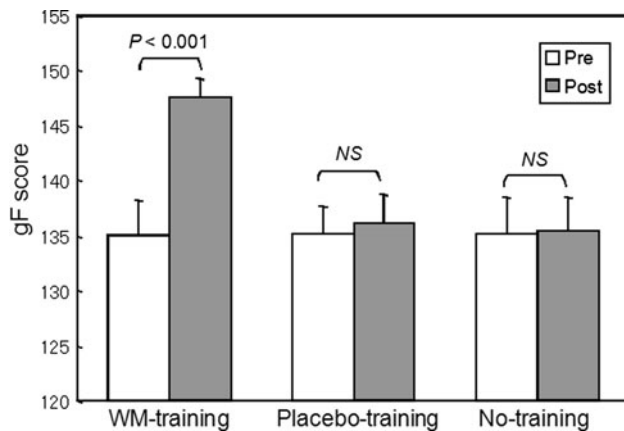


Fig. 10 The effect of working memory (WM) training (~10 min daily, 6 days a week, 2 months) on gF in the preschoolers. gF was significantly higher after training than before in the WM training group (paired *t* test) but not in the placebo-training or no-training group. Means \pm SEM are shown for the pre- and post-training scores

other subtests (Maze and Similarities) did not change after working memory training (Maze, 20.6 ± 5.0 for pre-training, 21.7 ± 5.1 for post-training; $P = 0.24$, NS; Similarities, 18.4 ± 4.7 for pre-training, 18.2 ± 4.1 for post-training; $P = 0.78$, NS).

Discussion

To our knowledge, this is the first study in which the LPFC showed similar neural activities between a gF task and a visuospatial working memory task in preschoolers (4–6 years old). Together with the behavioral-level finding that gF was significantly correlated with visuospatial working memory ability (particularly accuracy) during the preschool years, our findings suggest that a common neural system in the LPFC is recruited for these functions in preschoolers.

Correlation between gF and working memory accuracy

In several studies, gF has been correlated with working memory in adults (Conway et al. 2002, 2003; Engle et al. 1999; Gray et al. 2003; Ackerman et al. 2005; Kane and Engle 2002; Kane et al. 2004, 2005; Oberauer et al. 2005). Of the various components of visuospatial working memory in the SMS task, gF was most significantly correlated with its accuracy. Several studies in adults have demonstrated that gF correlates with working memory capacity (Engle et al. 1999; Conway et al. 2002, 2003; Ackerman et al. 2005; Kane and Engle 2002; Kane et al. 2004, 2005; Oberauer et al. 2005). In contrast to these studies, working memory capacity did not significantly predict gF in our study. Since WQ(capacity) was highly correlated with

WQ(accuracy), the present findings are not inconsistent with these previous results. However, using stepwise multiple regression analysis, we found that WQ(accuracy), not WQ(capacity), was the major variable in predicting gF in children. This seems consistent with a study by Gray et al. (2003) that showed a significant correlation between gF and working memory accuracy in adults performing an n-back task. In their study, the correlation between gF and working memory ability in “lure” trials was 0.36, comparable to that ($r = 0.36$) in the present study.

It has been proposed that working memory capacity and gF constructs share ~50% of their variance (Kane et al. 2005) and that working memory capacity is a strong predictor of gF (Oberauer et al. 2005). However, only 16% of the gF variability in the present study could be explained by variances in WQ(accuracy) and WQ(reaction time). This discrepancy might have been due to differences in subject ages and/or the task used, although further studies will be needed to clarify the primary reason for these discrepancies. Nevertheless, our findings should be useful for developing a methodology to improve gF in children (also see below).

Methodological comments on event-related OT

We examined brain activity in the LPFC of preschoolers using an event-related OT technique. The technique adopted here is a type of near-infrared spectroscopy (NIRS) (Jöbsis 1977). OT can measure temporal changes in hemoglobin oxygenation from multiple regions simultaneously, via multiple pairs of light emitters and detectors (Koizumi et al. 1999, 2003). Indeed, OT has been used to examine hemodynamic changes associated with various cortical functions using a block-design paradigm (Maki et al. 1995, 1996; Watanabe et al. 1998; Sato et al. 1999; Miyai et al. 2001; Kennan et al. 2002), as previously used in some fMRI studies.

More recently, Tsujimoto et al. (2004) developed an event-related design in OT, similar to the event-related fMRI. They demonstrated this methodology’s usefulness in studying cognitive functions of the LPFC in both adults and children. However, brain imaging even with event-related OT has some disadvantages compared to brain imaging with fMRI or PET, such as (1) its relatively low spatial resolution; (2) its inability to measure the absolute value of oxy- or deoxy-hemoglobin in the brain; (3) its inability to examine the activity of medial/ventral cortices or subcortical structures; and (4) its inability to examine the activity of the whole brain simultaneously. However, fMRI and PET are difficult to employ in children, particularly preschoolers, because of the possible invasiveness of these modalities in developing brains and because of the requirement for a rigid head constraint. In contrast, because OT is noninvasive in nature and does not require a rigid

head constraint, it is useful for examining the cortical neural activity of children, particularly preschoolers (see Tsujimoto et al. 2004). We therefore used an event-related OT paradigm in preschoolers and succeeded in showing spatiotemporal changes in hemodynamics in the LPFC during SMS and CC tasks.

However, the present OT method has some critical limitations. First, aside from the LPFC, the present OT cannot examine cortical areas that are important for gF, such as the parietal lobe, anterior cingulate cortex, some specific regions in the temporal lobe and occipital lobe, and limbic areas such as the hippocampus (Deary et al. 2010). Furthermore, it is difficult to use OT to examine preschoolers for a prolonged period because of their inability to concentrate for extended periods. Hence, we tested the SMS task in only one memory load condition during the OT examination. Therefore, it should be noted that our findings and discussions about the neural activity for working memory and gF have some limitations and are only related to the LPFC.

Neural system for visuospatial working memory and gF in the LPFC

We focused on LPFC because it is involved in gF in adults (Prabhakaran et al. 1997; Duncan et al. 2000; Gray et al. 2003) and adolescents (Lee et al. 2006), but this might not always be the case in children. gF is thought to provide the ability to govern performance in all cognitive tasks (c.f., Tsujimoto 2008). The keys to understanding gF are the relationship between gF and working memory and the neural systems underlying them (Jensen 1998; Deary et al. 2010). We focused here on the LPFC activity of preschoolers who performed the SMS and CC tasks. As a result, some of the same regions in this cortical area showed clear increases in oxy-Hb concentrations (C_{oxy}-Hb) during both tasks (SMS task and CC task; High-g condition minus Low-g condition). The major component of the SMS task should be visuospatial working memory, because the accuracy and reaction time on SMS task significantly correlated with the number of significant activation points, and C_{oxy}-Hb showed a sustained increase during the delay period, as found in our previous study (Tsujimoto et al. 2004). In the CC task, C_{oxy}-Hb increased after the onset of the sample/test cue associated with the problem-solving of each gF test in High-g—Low-g and in High-g conditions. Since the increase in C_{oxy}-Hb in the cortex is associated with neural activation, these findings suggest that some of the same parts of the LPFC are activated in relation to visuospatial working memory and gF in preschool children.

Although the regions that were significantly activated during both tasks were limited in each subject and varied

both between subjects and within individual subjects, the spatial patterns of the changes including the decrease in C_{oxy}-Hb were similar during both tasks for all subjects. A decrease in C_{oxy}-Hb is associated with neural deactivation, and it has been demonstrated that not only activation but also deactivation in the frontal cortex is important for cognitive functions (e.g., Coull et al. 1998; Gilbert and Fiez 2004; Sakatani et al. 2006; Weissman et al. 2006). Further, the temporal profiles of the change in C_{oxy}-Hb were similar for the performance of both tasks. These findings suggest that a common neural system within the LPFC is one of the systems underlying the performance of both tasks during the preschool years.

However, as described earlier, our study also includes several limitations: the number of subjects was small ($n = 5$), the activation patterns observed were varied, and only limited regions were examined. Further studies will be needed to clarify these points. Nevertheless, we consider that the present findings allow us to conclude that a common neural system at least in the LPFC may be recruited for the performance of visuospatial working memory and gF in preschoolers. In a neuron-level study with an SMS paradigm in nonhuman primates, the LPFC was shown to contain a subset of neurons that exhibited sustained activity during the delay period (Sawaguchi and Yamane 1999); this finding is in line with our present observation of a sustained increase in C_{oxy}-Hb in the LPFC during the delay period of the SMS task. These neurons appear to play a role in increasing the accuracy of visuospatial working memory (Sawaguchi and Yamane 1999). Further, a previous study has suggested that strong links between gF and working memory occur in common neural systems (Prabhakaran et al. 1997), and a brain-imaging study in adults found a positive correlation in the LPFC between gF and activity related to working memory accuracy (Gray et al. 2003). Therefore, this common neural system is likely related to the accuracy of working memory. In addition, the C_{oxy}-Hb change included not only an increase but also a decrease (deactivation) (see above), and at least some of the neural deactivation has been demonstrated to be associated with neural efficiency for frontal cortical functions (Pochon et al. 2002; Neubauer et al. 2004; Hall et al. 2005; Koch et al. 2006). Taken together, the previous and present findings suggest that the efficient recruitment and usage of a common neural system in the LPFC may be important for good performance of visuospatial working memory and gF in preschoolers.

Many studies have suggested that the fronto-parietal network is crucial for gF (Prabhakaran et al. 1997; Duncan et al. 2000; Gray et al. 2003; Lee et al. 2006). Lee et al. (2006) suggested that the parietal region is more important than the frontal cortex for gF (“superior-g”) in adolescents. However, as we did not examine here the activity of the

parietal cortex, it is unknown how the activity of this cortex or the fronto-parietal network is associated with gF or its level during the preschool years. Further, other areas, such as the anterior cingulate cortex, specific regions in the temporal and occipital lobe, and limbic areas including the hippocampus, which plays an important role in gF (Deary et al. 2010), were not assigned in this study. These problems remain to be addressed by further studies on children in this age range.

Implications for education and therapeutic methods

Given the nature of gF and the significance of education in early childhood, we believe that our findings are important for education and related activities for preschool children. Our results suggest that appropriate activity in the neural system of the LPFC for visuospatial working memory may form one of the critical bases for gF during the preschool years.

Although gF is known to be substantially heritable (Plomin et al. 1994; Finkel et al. 1995, Finkel and McGue 1997), it is possible that gF may be improved even by training in a simple visuospatial working memory task associated with LPFC activity during these years. Indeed, the SMS task is quite simple and easy even for preschoolers, whose daily performance in the SMS task during a period of 2 months significantly increased gF, by ~10% on average in the present study. The gF score did not increase in either the placebo-training group or the no-training group, and two-way ANOVA demonstrated a significant interaction between pre- and post-training for each training type. Further, as indicated earlier, the same sample of children showed a significant correlation between gF and performance on the SMS task, which required visuospatial working memory. Thus, we conclude that visuospatial working memory training could increase gF in the preschoolers.

Among four subtests for gF examination, the Classification score was most significantly increased by working memory training. This appears consistent with the finding that the score of Classification, but not those of other subtests, was positively and significantly correlated with all of the WQs (see Table 3). This suggests that, among gF subtests, Classification is most strongly associated with visuospatial working memory, and that working memory training affects the neural system for Classification most strongly among the neural systems for gF subtests.

In adults, working memory training for 5 weeks is known to modulate neural activity related to working memory (Olesen et al. 2004). Further, a positive correlation between gF and working memory-related activity has been found in the adult LPFC (Gray et al. 2003). Therefore, our SMS training is likely to modulate the neural system for

visuospatial working memory, which is probably one of the common neural systems for visuospatial working memory and gF, thereby increasing gF in preschoolers. This notion is further supported by the present findings that the Classification score was significantly correlated with all WQs, being the most significantly increased by SMS training, and that neural activity for Classification (i.e., CC task) was similar to that for the SMS task in the LPFC. Recently, Jaeggi et al. (2008) demonstrated that it is possible to improve gF in adults by working memory training. Our findings are consistent with theirs, suggesting that working memory training is applicable to gF improvement in a wide range of ages, from preschool children to adults.

In the working memory training examination, we did not compare LPFC activity before and after the training. Further, there was no follow-up study performed. Therefore, it remains unknown how long the gF level would be maintained without further training. Moreover, the training significantly improved the subscore on only some gF tests. Thus, the present examination of the effect of working memory training on gF has some critical limitations, and further studies are needed. Nevertheless, the results of this examination should be useful for improving gF in the preschool years. We believe that the methodology used here that is, daily training with a simple visuospatial working memory task would be useful for developing educational activities in normal children, and may also be as an effective therapy for children with gF or working memory malfunctions such as ADHD (Klingberg et al. 2005). In this way, daily working memory training could make a significant contribution to the social well-being of children.

Acknowledgments This work was supported by the Research Institute of Science and Technology for Society (RISTEX), part of the Japan Science and Technology Agency (JST), Japan. The authors thank J. Tsunada, S. Tsujimoto, and K. Wajima for their valuable comments on this study. We are grateful to G. Hirano, T. Tanase, K. Kaneko, and H. Yanaka for their technical assistance and encouragement throughout this study. We thank Y. Endo and other Kannami-Sakura Nursery School teachers, as well as M. Shigematsu, T. Uchiyama, and other Sapporo International School teachers. We also thank M. Watanabe for his helpful discussion.

References

- Ackerman PL, Beier ME, Boyle MO (2005) Working memory and intelligence: the same or different constructs? *Psychol Bull* 131:30–60. doi:10.1037/0033-2909.131.1.30
- Baddeley A (1986) Working memory. Oxford University Press, Oxford
- Baddeley A (1992) Working memory. *Science* 255:556–559. doi:10.1126/science.1736359
- Cattell RB (1940) A culture free intelligence test: I. *J Educ Psychol* 31:161–180. doi:10.1037/h0059043
- Cattell RB (1973) Measuring intelligence with the culture fair tests. Institute for Personality and Ability Testing, Champaign

- Cattell RB, Briston H (1933) Intelligence tests for mental ages of four to eight years. *Brit J Educ Psychol* 3:142–169
- Cattell RB, Feingold SN, Sarason SB (1941) A culture free intelligence test: II. Evaluation of culture intelligences on test performance. *J Educ Psychol* 32:81–100. doi:10.1037/h0058456
- Conway ARA, Cowan N, Bunting MF, Theriault DJ, Minkoff SRB (2002) A latent variable analysis of working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence. *Intelligence* 30:163–183. doi:10.1016/S0160-2896(01)00096-4
- Conway ARA, Kane MJ, Engle RW (2003) Working memory capacity and its relation to general intelligence. *Trends Cogn Sci* 7:547–552. doi:10.1016/j.tics.2003.10.005
- Coull JT, Frackowiak RS, Frith CD (1998) Monitoring for target objects: activation of right frontal and parietal cortices with increasing time on task. *Neuropsychologia* 36:1325–1334. doi:10.1016/S0028-3932(98)00035-9
- Cowan N, Elliott EM, Saults JS, Morey CC, Mattox S, Hismjatullina A, Conway ARA (2005) On the capacity of attention: its estimation and its role in working memory and cognitive aptitudes. *Cogn Psychol* 51:42–100. doi:10.1016/j.cogpsych.2004.12.001
- Deary IJ, Penke L, Johnson W (2010) The neuroscience of human intelligence differences. *Nat Rev Neurosci* 11:201–211. doi:10.1038/nrn2793
- Duncan J, Seitz RJ, Kolodny J, Bor D, Herzog H, Ahmed A, Newell FN, Emslie HA (2000) Neural basis for general intelligence. *Science* 289:457–460. doi:10.1126/science.289.5478.457
- Engle RW, Tuholski AW, Laughlin JE, Conway ARA (1999) Working memory, short-term memory, and general fluid intelligence: a latent-variable approach. *J Exp Psychol* 128:309–331. doi:10.1037/0096-3445.128.3.309
- Finkel D, McGue M (1997) Sex differences and nonadditivity in heritability of the multidimensional personality questionnaire scales. *J Pers Soc Psychol* 72:929–938. doi:10.1037/0022-3514.72.4.929
- Finkel D, Pedersen NL, McGue M, McClearn GE (1995) Heritability of cognitive abilities in adult twins: comparison of Minnesota and Swedish data. *Behav Genet* 25:421–431. doi:10.1007/BF02253371
- Freedman M, Oscar-Berman M (1986) Bilateral frontal lobe disease and selective delayed response deficits in humans. *Behav Neurosci* 100:337–342. doi:10.1037/0735-7044.100.3.337
- Frey MC, Detterman DK (2004) Scholastic assessment or g? The relationship between the scholastic assessment test and general cognitive ability. *Psychol Sci* 15:373–378. doi:10.1111/j.0956-7976.2004.00687.x
- Funahashi S, Bruce CJ, Goldman-Rakic PS (1993) Dorsolateral prefrontal lesions and oculomotor delayed-response performance: evidence for mnemonic scotomas. *J Neurosci* 13:1479–1497
- Gilbert AM, Fiez JA (2004) Integrating rewards and cognition in the frontal cortex. *Cogn Affect Behav Neurosci* 4:540–552. doi:10.3758/CABN.4.4.540
- Gottfredson LS (1998) The general intelligence factor. *Sci Am Presents* 9:24–29
- Gottfredson LS (2004) Intelligence: is it the epidemiologists' elusive "fundamental cause" of social class inequalities in health? *J Pers Soc Psychol* 86:174–199. doi:10.1037/0022-3514.86.1.174
- Gray JR, Chabris CF, Braver TS (2003) Neural mechanisms of general fluid intelligence. *Nat Neurosci* 6:316–322. doi:10.1038/nn1014
- Hall DA, Fussell C, Summerfield AQ (2005) Reading fluent speech from talking faces: typical brain networks and individual differences. *J Cogn Neurosci* 17:939–953. doi:10.1162/0898929054021175
- Jaeggi SM, Buschkuhl M, Jonides J, Perrig WJ (2008) Improving fluid intelligence with training on working memory. *Proc Natl Acad Sci USA* 105:6829–6833. doi:10.1073/pnas.0801268105
- Jensen AR (1998) The g factor. The science of mental ability (human evolution, behavior, and intelligence). Praeger Pub, London, pp 85–88
- Jöbsis FF (1977) Noninvasive infrared monitoring of cerebral and myocardial oxygen sufficiency and circulatory parameters. *Science* 198:1264–1267. doi:10.1126/science.929199
- Jonides J, Smith EE, Koeppe RA, Awh E, Minoshima S, Mintun MA (1993) Spatial working memory in humans as revealed by PET. *Nature* 363:623–625. doi:10.1038/363623a0
- Kane MJ, Engle RW (2002) The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: an individual-differences perspective. *Psychonomic Bull Rev* 9:637–671
- Kane MJ, Hambrick DZ, Tuholski SW, Wilhelm O, Payne TW, Engle RW (2004) The generality of working memory capacity: a latent-variable approach to verbal and visuospatial memory span and reasoning. *J Exp Psychol Gen* 133:189–217. doi:10.1037/0096-3445.133.2.189
- Kane MJ, Hambrick DZ, Conway AR (2005) Working memory capacity and fluid intelligence are strongly related constructs: comment on Ackerman, Beier, and Boyle. *Psychol Bull* 131:66–71. doi:10.1037/0033-2909.131.1.66
- Kennan RP, Kim D, Maki A, Koizumi H, Constable RT (2002) Non-invasive assessment of language lateralization by transcranial near infrared optical topography and functional MRI. *Hum Brain Mapp* 16:183–189. doi:10.1002/hbm.10039
- Khoa TQD, Nakagawa M (2008) Functional near infrared spectroscopy for cognition brain tasks by wavelets analysis and neural networks. *Int J Biol Med Sci* 1:28–33
- Klingberg T, Fernell E, Olesen PJ, Johnson M, Gustafsson P, Dahlstrom K, Gllberg CG, Forssberg H, Westerberg H (2005) Computerized training of working memory in children with ADHD—a randomized, controlled trial. *J Am Acad Child Adolesc Psychiat* 44:177–186. doi:10.1097/00004583-200502000-00010
- Koch K, Wagner G, von Consbruch K, Nenadic I, Schultz C, Ehle C, Reichenbach J, Sauer H, Schlosser R (2006) Temporal changes in neural activation during practice of information retrieval from short-term memory: an fMRI study. *Brain Res* 1107:140–150. doi:10.1016/j.brainres.2006.06.003
- Koizumi H, Yamashita A, Maki A, Yamamoto T, Ito Y, Itagaki H, Kennan R (1999) Higher-order brain function analysis by transcranial dynamic near-infrared spectroscopy imaging. *J Biomed Opt* 4:403–413. doi:10.1117/1.429959
- Koizumi H, Yamamoto T, Maki A, Yamashita Y, Sato H, Kawaguchi H, Ichikawa N (2003) Optical topography: practical problems and new application. *Appl Phys* 42:3054–3062. doi:10.1364/AO.42.003054
- Kono T, Matsuo K, Tsunashima K, Kasai K, Takizawa R, Rogers MA, Yamasue H, Yano T, Taketani Y, Kato N (2007) Multiple-time replicability of near-infrared spectroscopy recording during prefrontal activation task in healthy men. *Neurosci Res* 57:504–512. doi:10.1016/j.neures.2006.12.007
- Lee KH, Choi YY, Gray JR, Cho SH, Chae JH, Lee S, Kim K (2006) Neural correlates of superior intelligence: stronger recruitment of posterior parietal cortex. *NeuroImage* 29:578–586. doi:10.1016/j.neuroimage.2005.07.036
- Luo D, Thompson LA, Detterman DK (2003) Phenotypic and behavioral genetic covariation between elemental cognitive components and scholastic measures. *Behav Genet* 33:221–246. doi:10.1023/A:1023438323100
- Maki A, Yamashita Y, Ito Y, Watanabe E, Mayanagi Y, Koizumi H (1995) Spatial and temporal analysis of human motor activity

- using non-invasive NIR topography. *Med Phys* 22:1997–2005. doi:[10.1118/1.597496](https://doi.org/10.1118/1.597496)
- Maki A, Yamashita Y, Watanabe E, Koizumi H (1996) Visualizing human motor activity by using non-invasive optical topography. *Front Med Biol Eng* 7:285–297
- McCarthy G, Blamire AM, Puce A, Nobre AC, Bloch G, Hyder F, Goldman-Rakic P, Shulman RG (1994) Functional magnetic resonance imaging of human prefrontal cortex during a spatial working memory task. *Proc Natl Acad Sci USA* 91:8690–8694
- Miyai I, Tanabe HC, Sase I, Eda H, Oda I, Konishi I, Tsunazawa Y, Suzuki T, Yanagida T, Kubota K (2001) Cortical mapping of gait in humans: a near-infrared spectroscopic topography study. *NeuroImage* 14:1186–1192. doi:[10.1006/nimg.2001.0905](https://doi.org/10.1006/nimg.2001.0905)
- Neubauer AC, Grabner RH, Freudenthaler HH, Beckmann JF, Guthke J (2004) Intelligence and individual differences in becoming neurally efficient. *Acta Psychol (Amst)* 116:55–74. doi:[10.1016/j.actpsy.2003.11.005](https://doi.org/10.1016/j.actpsy.2003.11.005)
- Oberauer K, Schulze R, Wilhelm O, Suss HM (2005) Working memory and intelligence—their correlation and their relation: comment on Ackerman, Beier, and Boyle. *Psychol Bull* 131:61–65. doi:[10.1037/0033-2909.131.1.61](https://doi.org/10.1037/0033-2909.131.1.61)
- Okamoto M, Dan H, Sakamoto K, Takeo K, Shimizu K, Kohno S, Oda I, Isobe S, Suzuki T, Kohyama K, Dan I (2004) Three-dimensional probabilistic anatomical crano-cerebral correlation via the international 10–20 system oriented for transcranial functional brain mapping. *NeuroImage* 21:99–111. doi:[10.1016/j.neuroimage.2003.08.026](https://doi.org/10.1016/j.neuroimage.2003.08.026)
- Olesen PJ, Westerberg H, Klingberg T (2004) Increased prefrontal and parietal activity after training of working memory. *Nat Neurosci* 7:75–79. doi:[10.1038/nn1165](https://doi.org/10.1038/nn1165)
- Plomin R, Pedersen NL, Lichtenstein P, McClearn GE (1994) Variability and stability in cognitive abilities are largely genetic later in life. *Behav Genet* 24:207–215. doi:[10.1007/BF01067188](https://doi.org/10.1007/BF01067188)
- Pochon JB, Levy R, Fossati P, Lehericy S, Poline JB, Pillon B, Le Bihan D, Dubois B (2002) The neural system that bridges reward and cognition in humans: an fMRI study. *Proc Natl Acad Sci USA* 99:5669–5674. doi:[10.1073/pnas.082111099](https://doi.org/10.1073/pnas.082111099)
- Prabhakaran V, Smith JAL, Desmond JE, Glover GH, Gabrieli DE (1997) Neural substrates of fluid reasoning: an fMRI study of neocortical activation during performance of the Raven's progressive matrices test. *Cognit Psychol* 33:43–63. doi:[10.1006/cogp.1997.0659](https://doi.org/10.1006/cogp.1997.0659)
- Rickham PP (1964) Human experimentation. Code of Ethics of the World Medical Association. Declaration of Helsinki. *Br Med J* 2:177
- Sakatani K, Yamashita D, Yamanaka T, Oda M, Yamashita Y, Hoshino T, Fujiwara N, Murata Y, Katayama Y (2006) Changes of cerebral blood oxygenation and optical pathlength during activation and deactivation in the prefrontal cortex measured by time-resolved near infrared spectroscopy. *Life Sci* 78:2734–2741. doi:[10.1016/j.lfs.2005.10.045](https://doi.org/10.1016/j.lfs.2005.10.045)
- Sato H, Takeuchi T, Sakai KL (1999) Temporal cortex activation during speech recognition: an optical topography study. *Cognition* 73:B55–B66. doi:[10.1016/S0010-0277\(99\)00060-8](https://doi.org/10.1016/S0010-0277(99)00060-8)
- Sawaguchi T, Iba M (2001) Prefrontal cortical representation of visuospatial working memory in monkeys examined by local inactivation with muscimol. *J Neurophysiol* 86:2041–2053
- Sawaguchi T, Yamane I (1999) Properties of delay-period neuronal activity in the monkey dorsolateral prefrontal cortex during a spatial delayed matching-to-sample task. *J Neurophysiol* 82:2070–2080
- Tsujimoto (2008) The prefrontal cortex: functional neural development during early childhood. *Neuroscientist* 14:345–358. doi:[10.1177/1073858408316002](https://doi.org/10.1177/1073858408316002)
- Tsujimoto S, Yamamoto T, Kawaguchi H, Koizumi H, Sawaguchi T (2004) Prefrontal cortical activation associated with working memory in adults and preschool children: an event-related optical topography study. *Cereb Cortex* 14:703–712. doi:[10.1093/cercor/bhh030](https://doi.org/10.1093/cercor/bhh030)
- Watanabe E, Maki A, Kawaguchi K, Takashiro Y, Yamashita H, Koizumi H (1998) Non-invasive assessment of language dominance with near-infrared spectroscopic mapping. *Neurosci Lett* 256:49–52. doi:[10.1016/S0304-3940\(98\)00754-X](https://doi.org/10.1016/S0304-3940(98)00754-X)
- Weissman DH, Roberts KC, Visscher KM, Woldorff MG (2006) The neural bases of momentary lapses in attention. *Nat Neurosci* 9:971–978. doi:[10.1038/nm1727](https://doi.org/10.1038/nm1727)