



White matter neuroplastic changes in long-term trained players of the game of “Baduk”¹ (GO): A voxel-based diffusion-tensor imaging study

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ABSTRACT

Currently, one of the most challenging issues in modern neuroscience is learning-induced neural plasticity. Many researchers have identified activation-dependent structural brain plasticity in gray and white matter. The game of Baduk is known to require many cognitive processes, and long-term training in such processes would be expected to cause structural changes in related brain areas. We conducted voxel-based analyses of diffusion-tensor imaging (DTI) data and found that, compared to inexperienced controls, long-term trained Baduk players developed larger regions of white matter with increased fractional anisotropy (FA) values in the frontal, cingulum, and striato-thalamic areas that are related to attentional control, working memory, executive regulation, and problem-solving. In addition, inferior temporal regions with increased FA indicate that Baduk experts tend to develop a task-specific template for the game, as compared to controls. In contrast, decreased FA found in dorsolateral premotor and parietal areas indicate that Baduk experts were less likely than were controls to use structures related to load-dependent memory capacity. Right-side dominance in Baduk experts suggests that the tasks involved are mainly spatial processes. Altogether, long-term Baduk training appears to cause structural brain changes associated with many of the cognitive aspects necessary for game play, and investigation of the mechanism underpinning such changes might be helpful for improving higher-order cognitive capacities, such as learning, abstract reasoning, and self-control, which can facilitate education and cognitive therapies.

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Introduction

Recent researches have suggested that, in adult brains, structural neuroplasticity plays a crucial role relative to functional plasticity in adaptation to the external environment and pathological conditions (Driemeyer et al., 2008). Many studies have investigated structural plasticity in human and animal brains. Animal studies have revealed experience-dependent and lesion-induced structural plasticity in both developing and adult brains (Butz et al., 2009; Keck et al., 2008). Studies of neuroplasticity in humans have reported that activation-dependent structural brain plasticity was associated with a transient and highly

selective increase in brain gray matter in elderly subjects who learned three-ball cascade juggling (Driemeyer et al., 2008). Long-term musical training such as keyboard or piano practice, also caused regionally specific structural plasticity in gray or white matter (Bengtsson et al., 2005; Hyde et al., 2009), and several studies have reported associations between meditation training and neuroplasticity, indicating that meditation can improve attention and self-regulation (Lazar et al., 2005; Luders et al., 2009; Tang et al., 2007). In addition, studies have reported structural brain changes under many pathological conditions, such as repetitive painful stimulation (Teutsch et al., 2008), amnesia/multiple sclerosis (Manning, 2008), occipital lobectomy (Govindan et al., 2008), chronic schizophrenia (Oh et al., 2009), and cognitive behavioral therapy for chronic fatigue syndrome (de Lange et al., 2008).

Baduk is a traditional Far Eastern board game. It probably originated in China or the Himalayas and is believed to be about 3000 years old; it has also been played in Korea for a long time (<http://english.baduk.or.kr>). It is a game of skill and, thus, probably involves many cognitive capabilities, just like chess, its Western counterpart (Barrett, 2002; Yoshikawa et al., 1999). Baduk is basically

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¹ “Baduk” is the Korean name which replaces the Japanese name “GO,” designating a traditional Far Eastern board game with two kinds of pieces (black and white stones) manipulated by two opponents. For game-play details, see Introduction.

a game of territory: the board, marked with a grid of 19 lines, may be thought of as an area of land to be shared between the two players. One player uses black pieces (called ‘stones’) and the other uses white ones. A simple rule govern where and how the stones are moved onto the intersections on the board by the two players, and each player’s objective is to occupy more territory than the other player and to prevent the opposite player from gaining territory by surrounding and capturing the opponent’s stones. In contrast, chess pieces have specific identities and roles and are moved according to specific individual rules. The two games share common executive actions with respect to spatial positioning, but the former is believed to require more complex strategies than the latter (Atherton et al., 2003; Chen et al., 2003). Two recent studies used functional magnetic resonance imaging (fMRI) to investigate the effects of Baduk and chess (Atherton et al., 2003; Chen et al., 2003). They found that both games activated similar areas associated with the “game” condition, such as bilateral activation in the pre-motor area of the frontal lobe as well as several regions of the parietal and occipital lobes. These areas are engaged during attention, spatial perception, imagery, mental rotation, and mnemonic processes. The authors had initially hypothesized that both games would involve a high degree of frontal lobe function, especially in the so-called general intelligence domain, corresponding to the lateral prefrontal cortex (Duncan et al., 2000; Sternberg, 2000). However, the results indicated that neither game activated the g-intelligence area; the games primarily activated spatial mechanisms rather than logical and computational skills. The fMRI results showed that Baduk’s main effect was to facilitate right hemispheric dominance, suggesting that it requires more human-specific skills than does chess, which was associated with left-side dominance; this also makes it more difficult to create computer programs for Baduk than for chess (Barrett, 2002; Chen et al., 2003; Yoshikawa et al., 1999). Nevertheless, it is necessary to consider structural changes in addition to studies of functional development to clarify how Baduk affects brain organization (Guye et al., 2008). Therefore, this study used diffusion-tensor imaging to investigate how long-term Baduk training affects white matter structural plasticity (Izhikevich and Edelman, 2008).

The objective of the study was to elucidate structural brain development related to the cognitive components needed to play Baduk, based on white matter neuroplastic changes. Because fractional anisotropy (FA) values reveal the structural integrity and coherence of white matter tracts, we conducted voxel-based group analyses on the FA maps of diffusion-tensor imaging (DTI) between Baduk experts and unskilled controls. This process helped us to clarify the developmental course of the brain with regard to the underlying cognitions associated with long-term Baduk training in order to more fully understand human cognitive mechanisms in terms of structural neuroplasticity, and to assess the possibility of using mental training activities such as Baduk for brain development (Bengtsson et al., 2005; Tang et al., 2007).

Materials and methods

Participants

A total of 17 experienced Baduk players (14 men, three women) were recruited from the Korea Baduk Association. One woman’s diffusion-weighted volume was corrupted and therefore excluded from analyses (see [Image preprocessing and template preparation](#) for the detailed procedures used to exclude corrupted volume). All of the remaining 16 players had trained for about 12 years (12 ± 1.55); eight were professional players and eight were still training. Professional qualification for Baduk differs by country; in Korea, talented amateur players may enroll as trainees in the Korea Baduk Association. Through intense competition, six of these trainees attain professional status each year. Professional rankings are classified into nine grades (from 1 *dan* to 9 *dan*) based on achievement. These rankings are

Table 1
Demographic characteristics of Baduk expert and control groups.

	Experts (n = 16)	Controls (n = 19)	Statistical analysis ^a		
			T- or χ^2 -value	df	p-value
Sex (M/F)	14/2	13/6	1.793	1	0.181
Handedness (right/left)	16/0	19/0			
Age (years), mean (SD)	17.25 (1.125)	17.95 (1.682)	-1.460	31.530	0.154
Education (years), mean (SD)	10.44 (1.209)	11.74 (1.851)	-2.492	31.239	0.018*
Estimated IQ, mean (SD)	93.19 (10.42)	101.21 (13.11)	-2.016	32.910	0.052

Note. * $p < 0.05$, ^a Independent t-test if the two groups had heterogeneous variances and chi-square analysis for categorical data. df = degrees of freedom, M = male, F = female, SD = standard deviation, IQ = intelligence quotient.

distinct from amateur ratings and have analogous systems across countries, which are generally recognized as equivalent levels. Most professional players begin studying Baduk seriously as very young children. A total of 19 normal controls (13 men, six women), who were sex- and age-matched with those in the Baduk expert group using *chi*-square testing, also participated for purposes of comparison. However, we included more female controls than female experts while remaining within the statistical limit (see [Table 1](#)); we followed this procedure to minimize the effect of sex on the voxel-based statistical analysis, using age and sex as covariates, because only two female experts were included in this study (actually, most Baduk experts are men). Only those subjects without special training in Baduk, chess, or other similar board games, and without sufficient interest in these games to play them frequently, were included in the control group. All participants were right-handed. None of the subjects had a history of neurological or psychiatric problems. The study procedures were approved by the local institutional review board, and written informed consent was obtained from all subjects after the procedures had been fully explained.

MRI acquisition

Whole-brain diffusion-weighted magnetic resonance images were obtained in 12 non-collinear gradient orientations using a single-shot echo-planar imaging sequence on a 1.5-T Siemens MAGNETOM scanner (Erlangen, Germany) with the following parameters: 112×128 acquisition matrix, $2 \times 2 \times 2$ -mm³ voxels, 75 axial slices, slice thickness 2 mm, and slice gap 0 mm. The FOV (field of view) = 224×256 mm², TE (echo time) = 83 ms, and TR (repetition time) = 9200 ms. The b-factor was 1000 s/mm². Non-weighted baseline images (B0) were acquired 10 times and averaged to improve the signal-to-noise ratio.

Image preprocessing and template preparation

The acquired DICOM images were converted to NIfTI format using MRIConvert 2.0 (<http://lcn.uoregon.edu/~jolinda/MRIConvert>), and the next preprocessing steps were performed using FDT v2.0 (FMRIB’s Diffusion Toolbox, <http://www.fmrib.ox.ac.uk/fsl/fdt/index.html>) and SPM5 (<http://www.fil.ion.ucl.ac.uk/spm>). Spatial distortions in the diffusion-weighted images induced by eddy currents and simple head motion were corrected using affine registration to the individual B0 images. The eddy current corrected images were masked using the binarized volume obtained by skull-stripping the B0 image using the brain extraction tool of the FMRIB Software Library (BET, <http://www.fmrib.ox.ac.uk/fsl/bet2/index.html>) for application to the next tensor calculating step. Diffusion tensor matrices were generated at each voxel from the set of 12 diffusion-weighted images and one non-diffusion weighted image, from which the three eigenvalues and corresponding eigenvectors were computed. Next, FA maps were

produced based on the three diffusivities indicated by the eigenvalues and their mean (Basser and Jones, 2002; Jiang et al., 2006). Additionally, gray matter (GM), white matter (WM), cerebro-spinal fluid (CSF), and non-brain tissue were segmented for each participant's B0 volume in their native space using FMRIB's automated segmentation tool (FAST, <http://www.fmrib.ox.ac.uk/fsl/fast4/index.html>), and the extracted GM and WM were utilized for the subsequent template preparation. To prevent the inclusion of bad DTI volumes in the subsequent procedures, we closely monitored all steps of the preprocessing procedures, determined the appropriateness of the orientation of local vectors in the V1 maps (e.g., vector maps corresponding to the highest eigenvalue), and finally extracted 11 major fiber tracks (including the superior longitudinal fasciculus, inferior longitudinal fasciculus, genu and splenium of the corpus callosum, uncinate fasciculus, inferior fronto-occipital fasciculus, etc.) according to previously proposed protocols (Wakana et al., 2007) using the classical tracking algorithm implemented in MEDINRIA software (<http://www-sop.inria.fr/asclepios/software/MEDINRIA/>). After such scrutiny, only one volume, obtained from a female expert, was excluded; this volume was excluded due to unacceptable aspects of the orientations of the V1 map and the reconstructed fiber tracks. This may have been attributable to an unexpected and previously unrecognized problem that arose during the acquisition of that volume.

To ensure that our data were matched accurately, we developed a customized template using SPM5, based on previously described optimized protocols (Càmara et al., 2007; Good et al., 2001). The procedure for developing the optimized template consisted of three steps. First, B0 images were normalized to the EPI-derived ICBM-152 (International Consortium for Brain Mapping) template and the normalized images were smoothed with 8-mm full-width at half-maximum (FWHM) and averaged for use as the initial template. Second, B0 images were normalized again to the initial template, and then the normalized images were segmented into GM, WM, and CSF/non-brain tissues. Gray and white matters were extracted and merged after thresholding their probability maps above 0.8, and then the extracted gray and white matter were smoothed with 12-mm FWHM and thereafter averaged to become the G+W template. We applied the values (8 and 12 mm, respectively) proposed by Good et al. (2001) for the sizes of smoothing kernel during the aforementioned two steps without loss of generality. Finally, individual gray and white matter previously extracted in their native-space using FAST were spatially normalized to the G+W template, and FA and B0 volumes were normalized using the resulting deformation field. The final normalized FA images were resliced to match the voxel size to $1 \times 1 \times 1\text{-mm}^3$ and then smoothed using 4-mm and 8-mm FWHM, respectively, before statistical analysis (Jones et al., 2005). The two results using 4-mm and 8-mm FWHM isotropic Gaussian kernels revealed very similar spatial distributions, but we selected the results from the 4-mm FWHM due to its superior spatial resolution (Càmara et al., 2007). The WM mask was prepared for voxel-wise statistical analyses by smoothing extracted WMs from this final normalized B0 and then averaging the voxel intensities. Throughout the complex procedure involved in preparing for the optimized template, we utilized anatomical information confined to the white and gray matter, and the additional application of the WM mask in voxel-wise tests was used to restrict the voxels to primarily WM areas, which is consistent with the focus of this study. Therefore, the use of the WM mask reduced the number of statistical comparisons and thereby lowered the rate of false positives.

Statistical analysis

We assessed continuously distributed demographic variables including age, education level, and IQ using independent *t*-tests, and we used *chi*-square tests to compare categorical demographic data

such as gender and handedness between the expert and control groups. Significance was set at $p < 0.05$ (see Table 1).

Three-dimensional voxel-wise statistical tests were conducted between the expert and control groups based on smoothed and spatially normalized FA images using voxel-based procedures similar to those used in our previously published study (Yoo et al., 2007). However, to profoundly reduce the high risk of Type I error caused by the large numbers of comparisons executed in three-dimensional spaces, we performed this analysis in two steps. First, we conducted a voxel-wise ANOVA in which the two groups served as the between-subjects variable, and age and sex were covariates to reduce the well-known age- and sex-related effects on white matter development (Càmara et al., 2007; Choi et al., 2010). We performed separate additional statistical analyses with IQ and education as covariates because significant differences between expert and control groups emerged with respect to these variables (see Table 1). We thresholded the statistical map produced from this ANOVA using a method modified from that developed by Baudewig et al. (Baudewig et al., 2003) that has been used elsewhere for DTI voxel-based analyses (Alexopoulos et al., 2008; Hoptman et al., 2008). We selected clusters above 100 contiguous voxels ($>100\text{ mm}^3$) with significant group differences ($p < 0.05$), combined with the additional constraint that at least one voxel in the cluster must be significant at $p < 0.005$ or better. This combination of *alpha*-level and cluster size selection along with the additional constraint of maximal voxel significance can greatly eliminate Type I errors. Second, we conducted successive voxel-wise *t*-tests with the same covariates for the "effects of interest" clusters identified in the initial ANOVA. At this step, we raised the threshold for significant group differences to $p < 0.01$ with an increased cluster size constraint of more than 200 voxels ($>200\text{ mm}^3$), and we tightened the maximum voxel significance to $p < 0.001$ to enhance specificity beyond that possible in the previous step. This step can provide additional protection against Type I errors (Hoptman et al., 2008). The voxel-based statistical procedures were performed using SPM5 and additional operations were performed in the MATLAB (Mathworks, USA) environment.

We identified and labeled all specific anatomical structures that survived the statistical thresholding using the coordinate system of the stereotaxic atlas for the human brain (Talairach and Tournoux, 1988) and the human white matter atlas (Mori et al., 2005). The final statistical mapping images were overlaid over the canonical T1 template of a single subject with two cross-sectional (e.g., coronal and sagittal sections) (Figs. 1 and 2) and volume-rendered images (Fig. 3). In the figures, cross-sectional images are displayed according to radiological convention, meaning that the right side of the image corresponds to the left side of the brain. Tables 2 and 3 identify the labels of regions corresponding to relatively definite white matter tracts in parentheses next to the anatomical nomenclature of the cortical structures.

Results

Demographic characteristics

Table 1 lists the differences in the demographic characteristics of Baduk experts and controls. No significant group differences appeared for gender ($\chi^2 = 1.793$, $df = 1$, $p = 0.181$). No significant group difference appeared for age (mean \pm SD, 17.25 ± 1.125 for Baduk experts, 17.95 ± 1.682 for controls; $t = -1.460$, $df = 31.530$, $p = 0.154$). However, Baduk experts demonstrated slightly lower IQs than did controls (mean \pm SD, 93.19 ± 10.42 for Baduk experts, 101.21 ± 13.11 for controls; $t = -2.016$, $df = 32.910$, $p = 0.052$) as estimated by the Korean version of the Wechsler Adult Intelligence Scale (K-WAIS) (Kim and Lee, 1995), and a significant difference appeared between the two groups for level of education (mean \pm SD, 10.44 ± 1.209 for

Baduk experts, 11.74 ± 1.851 for controls; $t = -2.492$, $df = 31.239$, $p = 0.018$).

Voxel-wise group difference maps

In the first voxel-wise analysis, using age and sex as covariates, the expert group exhibited increased FA, as compared to controls, in many regions of white matter (Fig. 1 and Table 2). In the frontal lobe, the expert group exhibited FA increases in the right medial frontal gyrus (or anterior cingulate), right superior frontal gyrus, right middle frontal gyri, right inferior frontal gyri, and right insula, as compared with the control group, indicating right-sided predominance. In contrast, in the temporal lobe, increased FA values were observed in white matter regions, including the left superior temporal gyrus and left inferior temporal (or fusiform) gyrus, corresponding to posterior thalamic radiation (PTR) and inferior longitudinal fasciculus (ILF), suggesting left-sided predominance. When we observed the limbic and subcortical structures, Baduk experts exhibited increased FA values, as compared to controls, in the right midcingulate/paracingulate gyri, the WM region

near the right lenticular nucleus such as the globus pallidus, and WM regions close to right claustrum/putamen and caudate body, corresponding to superior thalamic radiation (STR) and anterior thalamic radiation (ATR). The expert group also exhibited right-sided predominance in these areas, similar to that in the frontal lobe. No areas of the parietal and occipital lobes revealed any significant FA increases in the Baduk experts, as compared to the controls. The expert group exhibited decreased FA values, as compared to the control group, in some smaller regions (Fig. 1 and Table 2): in the frontal areas, the right orbito-frontal and right/left precentral gyri (premotor areas), and in the parietal lobe, the right precuneus (or superior parietal lobule, BA7).

The second voxel-wise analysis, using IQ and education as covariates, revealed distributions that were very similar to those discussed above (Fig. 2 and Table 3). Compared to the control group, the expert group showed increased FA in right frontal areas, including the superior frontal gyrus (or anterior cingulate), medial frontal gyrus, middle frontal gyrus, and inferior frontal gyrus (or insula) as well as in the left medial and middle frontal WM areas. As in the previous analysis, the expert group also demonstrated frontal right-hemispheric dominance. Similar to the

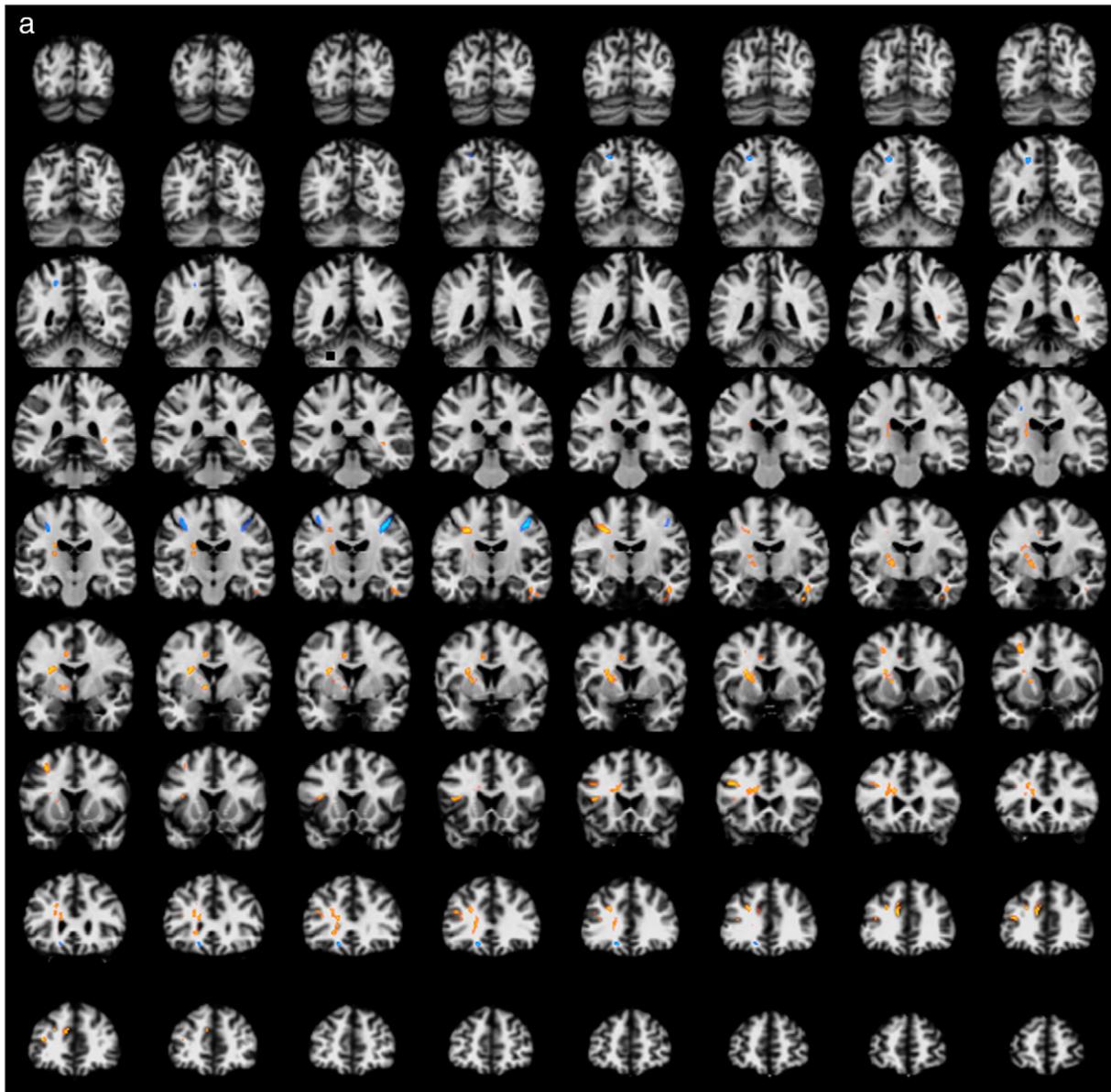


Fig. 1. The statistical images obtained by the two-step voxel-wise analysis, using age and sex as covariates, are overlaid over the canonical T1 template of a single subject (see the text for detail). The cross-sectional representations are displayed by radiological convention meaning that the right side of image corresponds to left side of brain and vice versa. Red color displays the regions of increased FA and blue color indicates the regions of decreased FA for the Baduk expert group, as compared to the control group. (a) Coronal section and (b) axial section.

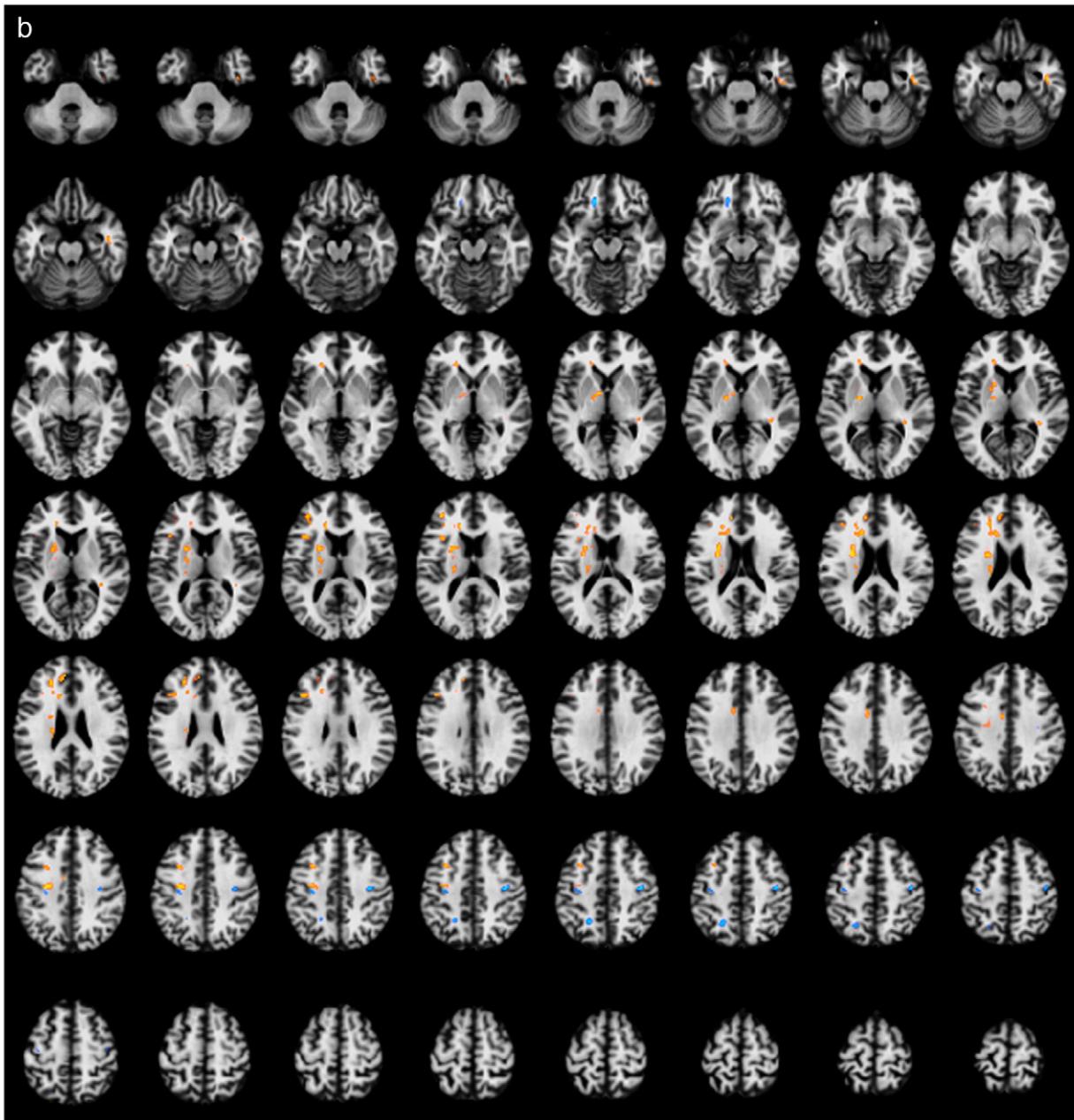


Fig. 1 (continued).

first voxel-based analysis, the Baduk experts showed higher FA than controls in left inferior temporal areas (including the fusiform gyrus). In subcortical areas, experts showed higher FA than controls in the right peri-lenticular WM regions near the globus pallidus, putamen and thalamus. Unlike the aforementioned analysis using age and sex as covariates, the present analysis showed that Baduk experts had increased FA, compared with controls, in several parietal areas, including the precuneus and postcentral gyrus of both hemispheres. On the other hand, the expert group exhibited lower FA than did the control group in frontal areas, including the right/left inferior frontal gyri and the bilateral premotor areas as well as in parietal areas, including the right precuneus and left inferior parietal lobule. In this second analysis, additional decreased FA was found in the WM region close to the right hippocampus (corresponding to the fornix and stria terminalis) in Baduk experts, as compared to controls.

In the context of both voxel-based analyses, the right frontal/subcortical areas and left temporal gyri that showed higher FA in Baduk experts than controls, and the bilateral premotor areas and right

precuneus that showed lower FA in experts than controls, emerged as the areas most affected by long-term Baduk training, after eliminating age- and sex-related effects and neuropsychological influences (reflected by IQ and education level), respectively. Comparing the results of Tables 2 and 3, as well as those of Figs. 1 and 2, will help to more definitely identify the common robust structures.

Discussion

To the best of our knowledge, this is the first DTI study to investigate the structural brain development of WM tracts involved during Baduk training. First, considering the robust areas common to the results of two aforementioned voxel-based analyses, skilled players exhibited increased FA in several regions, as compared to controls, revealing multiple significant structures (Tables 2, 3 and Figs. 1, 2): in the frontal lobe, the right medial frontal (or anterior cingulate) WM, right middle frontal WM, right superior frontal WM regions, and right peri-insula (or inferior frontal gyri) WM site; in the

temporal lobe, the left inferior temporal or fusiform WM regions; in subcortical regions, WM regions near the right lenticular nucleus (including the putamen and globus pallidus) and other right WM sites near the caudate body/caudate, corresponding to the anterior/posterior limbs of the internal capsule. Compared with the control group, Baduk experts exhibited decreased FA values in the following regions: bilateral premotor WM regions and right precuneus WM (Tables 2, 3 and Figs. 1, 2). Second, several specific areas emerged as noteworthy from each voxel-wise analysis. In the first analysis, using sex/age as covariates, the Baduk expert group demonstrated higher FA in the cingulum in the right limbic lobe and lower FA in a right orbito-frontal WM site than did the control group (Table 2 and Fig. 1). In the second analysis, with IQ and education as covariates, the experts showed increased FA in several areas belonging to the left frontal and right/left parietal lobes, and decreased FA in the right/left inferior frontal gyri and the peri-hippocampal WM in the limbic lobe (Table 3 and Fig. 2). Generally, regions of increased FA suggested right-sided predominance, especially in frontal and limbic/subcortical

areas; these results differ from previous fMRI data related to Baduk (Chen et al., 2003) that showed prominent right lateralization in parietal areas. However, temporal regions were characterized by increased FA in left-side areas compared with right-side areas.

The DTI results showing prominent frontal regions of increased FA indicate that, compared with the control group, the Baduk experts have highly developed cognitive functions associated with the frontal brain such as attentional control, encoding/maintenance/retrieval of memory processes, problem solving, and other executive functions. Many studies have shown that prefrontal areas are closely linked with anterior cingulate (Bundesen et al., 2002; Kondo et al., 2004; Schlösser et al., 2006) or subcortical areas (Bundesen et al., 2002; McNab and Klingberg, 2008; Monchi et al., 2006) or both (Anderson et al., 2008; Parris et al., 2007) in service of the attentional modulations or executive control related to many cognitive processes including working memory tasks. Our DTI results revealed increased FA in several frontal sites, including pericallosal WMs extending to the frontal lobe and connecting both hemispheres, areas in the right cingulum bundle that carry connections

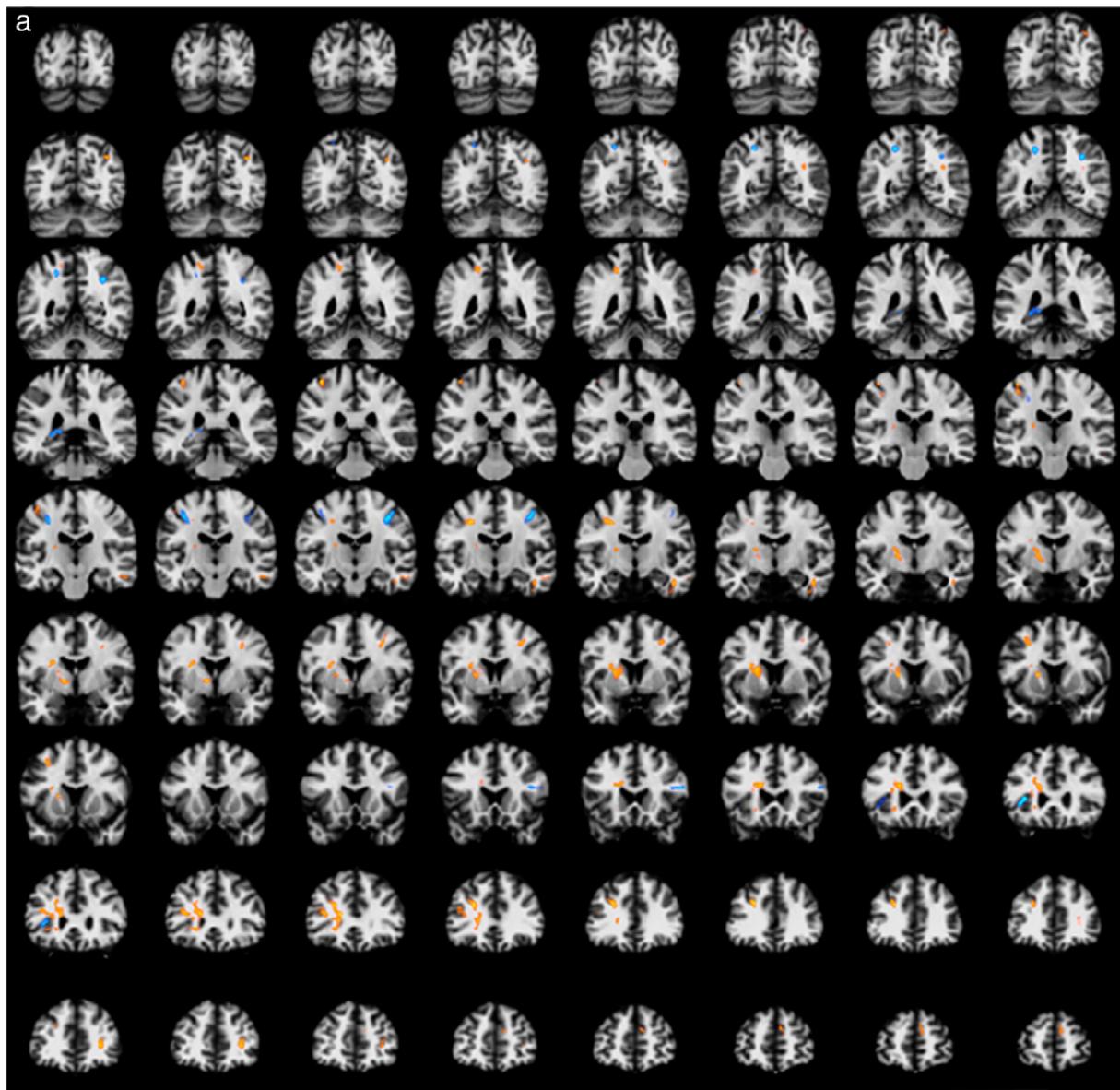


Fig. 2. The statistical images obtained by the two-step voxel-wise analysis, using IQ and education as covariates, are overlaid over the canonical T1 template of a single subject (see the text for detail). The cross-sectional representations are displayed by radiological convention meaning that the right side of image corresponds to left side of brain and vice versa. Red color displays the regions of increased FA and blue color indicates the regions of decreased FA for the Baduk expert group, as compared to the control group. (a) Coronal section and (b) axial section.

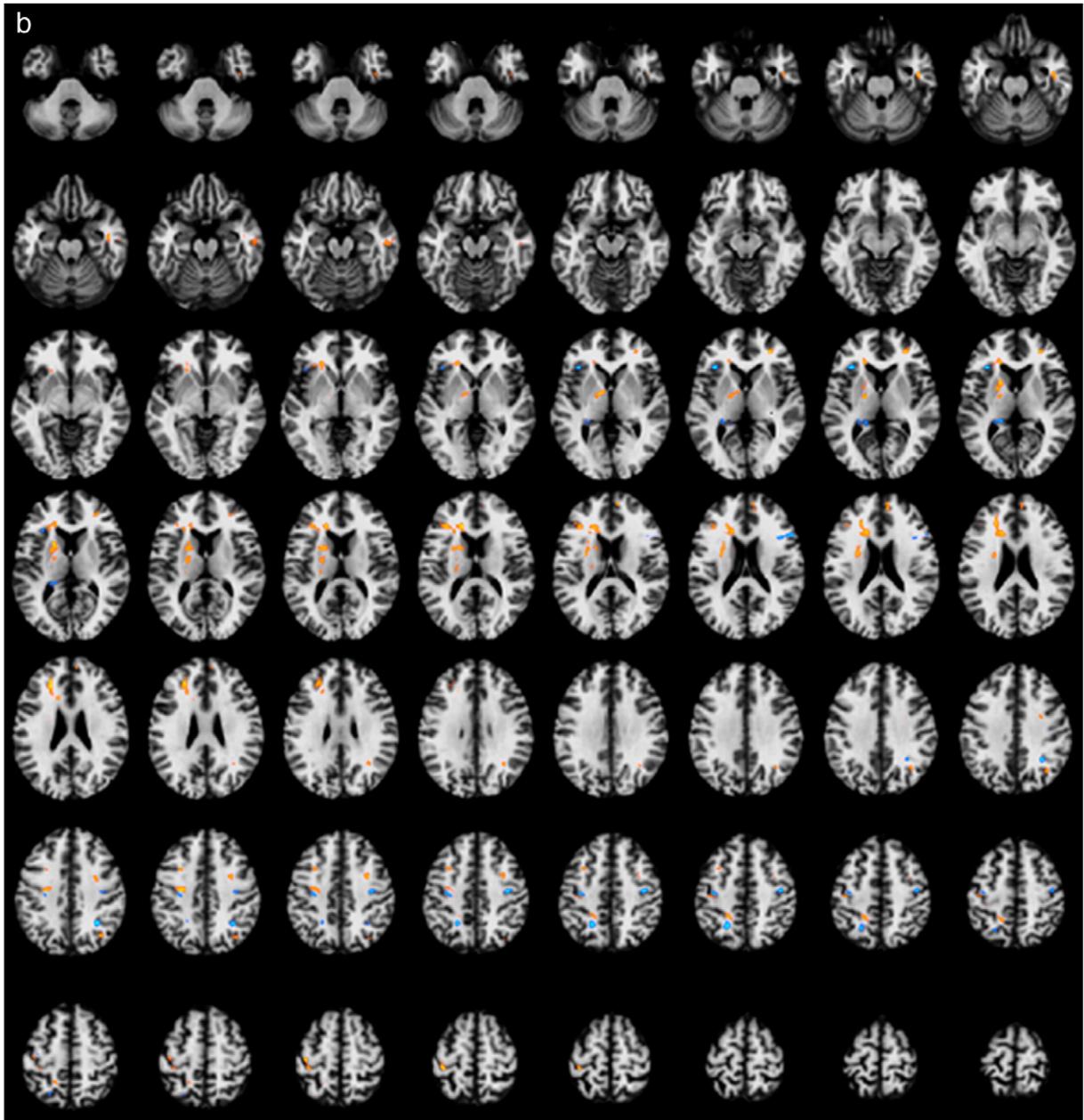


Fig. 2 (continued).

spreading from the cingulate gyri (Mori et al., 2005), and several right subcortical WM regions near the globus pallidum, putamen, and caudate body, suggesting that fronto-cingulo-striatal regulatory structures are better developed in expert Baduk players than in controls.

Our results also revealed that Baduk players exhibited increased FA values in inferior temporal or fusiform regions (including the ILF), which are associated with perceiving/manipulating visuo-spatial information (Cabeza and Nyberg, 2000) and shifting attentional focus in spatial attention tasks (Gitelman et al., 1999; Weidner et al., 2009) (Fig. 3a). De Rover et al. (2008) conducted an fMRI study and found that during spatial-associative memory retrieval, activation was enhanced in higher-order visual regions such as the fusiform gyrus, the lingual gyrus, and the cuneus, whereas temporal-associative retrieval strategies tended to elevate activity in the globus pallidus and the thalamus. Several other studies have reported fronto-striato-thalamic involvement in time-related processes (Ferrandez et al., 2003; Hintón and Meck, 2004). Within the context of these results, our finding that Baduk experts had

increased FAs in temporal areas (including left inferior temporal regions or left fusiform gyri), as well as in fronto-striato-perithalamic regions, supports the hypothesis that Baduk experts utilize temporal strategies in addition to spatial strategies, such as object identification, during Baduk game play. A previous fMRI study of recognition memory in chess players reported a similar spatial distribution to that found in our DTI study; it found that activity in the temporal lobe including the fusiform gyrus, parahippocampal gyrus, and inferior temporal gyrus, executed the role of long-term memory chunks (or templates) of domain-specific information related to chess, thereby improving the expertise of chess players (Campitelli et al., 2007).

Our findings of a consistent decrease of FA in the bilateral dorsolateral premotor areas as well as in the right parietal lobes of the Baduk expert group suggest that Baduk experts are less dependent on working memory load than are controls (Owen et al., 2005) (Fig. 3b). In terms of the less important, but nonetheless interesting areas, the results of the first statistical analysis showed that Baduk experts exhibited an isolated

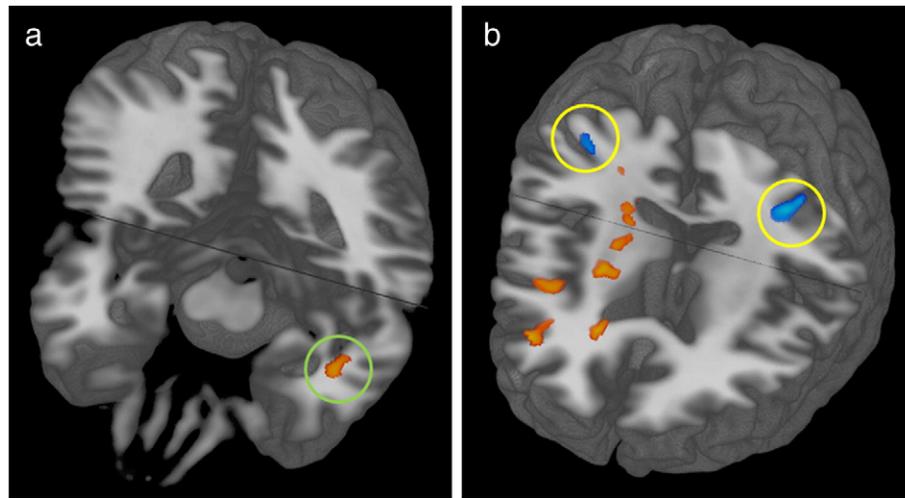


Fig. 3. Two characteristic areas regarding long-term Baduk training, that were common to the separate results from two statistical analyses using different covariates, are volume-rendered on the canonical T1 template. Left inferior temporal gyrus with increase FA in Baduk experts compared to controls (a) and bilateral premotor WM areas with lower FA in Baduk experts than controls (b).

decrease of FA in the right orbito-frontal area, which, together with other frontal sites, is related to self-monitoring and emotional processing (Beer et al., 2006). Decreased FA in this area may reflect a diminished need for self-regulatory effort with regard to behavioral and emotional controls as a result of long-term mental training (Banks et al., 2007; Coccaro et al., 2007). In addition, the specific results of the second analysis showed decreased FA in the WM region close to the hippocampus. According to a magnetoencephalic study about chess game (Amidzic et al., 2001), amateur players utilized the hippocampus/medial temporal lobe, which suggests the processing of elementary information, whereas chess

experts demonstrated the activation in the frontal lobe, intimating higher-order reasoning and the utilization of expert memory chunks drawn from well-organized memory stores of chess knowledge. Similarly, our finding indicates that Baduk experts develop frontal areas primarily, and that non-experts use hippocampal structures for information processing during Baduk play.

Taken together, the results of our DTI study of Baduk experts revealed many interesting findings from the standpoint of structural neurodevelopment. First, Baduk experts appear to have developed right-side dominant fronto-striatal mechanisms with increased WM connections,

Table 2

Regions of FA differences between Baduk expert and control groups obtained by voxel-wise statistical procedures with age and sex as covariates.

Hemisphere	Anatomical structure	Cluster size (mm ³)	Talairach coordinate ^a		
			x	y	z
<i>Experts > Controls</i>					
Frontal lobe					
Right	Medial frontal gyrus/anterior cingulate (lateral to genu of CC)	295	11	41	19
Right	Superior frontal gyrus/anterior cingulate (anterior part of CC)	1424	24	43	25
Right	Middle frontal gyrus, BA6	323	33	12	45
Right	Middle frontal gyrus	243	38	44	14
Right	Middle frontal sub-gyral (SCR)	409	28	-12	40
Right	Middle frontal gyrus/inferior frontal gyrus, triangular part	222	41	22	28
Right	Insula/inferior frontal gyrus, opercular part	230	37	19	13
Temporal lobe					
Left	Superior temporal sub-gyral (RLIC, PTR)	208	-34	-37	6
Left	Inferior temporal gyrus/fusiform gyrus, BA20 (SS, ILF)	420	-43	-10	-26
Limbic lobe					
Right	Midcingulate/paracingulate gyrus (CG)	263	11	-2	37
Subcortical regions					
Right	Globus pallidus (PLIC, STR)	382	11	-2	1
Right	Extra-nuclear/caudate body (PLIC, STR)	496	23	-19	24
Right	Putamen/caudate (ALIC, CPT/ATR)	1118	27	7	19
<i>Experts < Controls</i>					
Frontal lobe					
Right	Orbitofrontal sub-gyral (UNC)	200	15	34	-15
Right	Precentral gyrus	266	30	-20	40
Left	Precentral gyrus	480	-37	-15	46
Parietal lobe					
Right	Precuneus/superior parietal lobule, BA7 (PCR, CC/PTR)	341	22	-56	49

Note. ^aTalairach coordinate represents peak of cluster (+x = right, +y = anterior, +z = superior). CC = corpus callosum, SCR = superior corona radiata, PCR = posterior corona radiata, ATR = anterior thalamic radiation, STR = superior thalamic radiation, PTR = posterior thalamic radiation, ALIC = anterior limb of internal capsule, PLIC = posterior limb of internal capsule, RLIC = retrolenticular limb of internal capsule, CPT = cerebro-pontine tract, SS = sagittal stratum, ILF = inferior longitudinal fasciculus, CG = cingulum, UNC = uncinata fasciculus. *Experts > Controls*: the regions of higher FA in Baduk expert group as compared to control group, *Experts < Controls*: the regions of lower FA in Baduk expert group as compared to control group.

Table 3

Regions of FA differences between Baduk expert and control groups obtained by voxel-wise statistical procedures with IQ and education period as covariates.

Hemisphere	Anatomical structure	Cluster size (mm ³)	Talairach coordinate ^a		
			x	y	z
<i>Experts > Controls</i>					
Frontal lobe					
Right	Superior frontal gyrus/anterior cingulate (anterior part of CC) (including broad areas of medial frontal gyrus/anterior cingulate (CC), middle frontal gyrus and inferior frontal gyrus/insula)	2674	24	44	25
Right	Middle frontal gyrus, BA6	203	32	12	45
Right	Middle frontal sub-gyral (SCR)	285	27	-13	41
Left	Medial frontal gyrus (CC/CG)	210	-7	58	20
Left	Middle frontal gyrus (ACR, CC/ATR)	284	-28	45	2
Left	Middle frontal sub-gyral (SCR)	320	-29	-1	39
Temporal lobe					
Left	Inferior temporal gyrus/fusiform gyrus, BA20 (SS, ILF)	317	-43	-10	-26
Left	Inferior temporal gyrus (SS,ILF)	201	-57	-19	-21
Parietal lobe					
Right	Precuneus (SCR, CC)	316	19	-45	49
Right	Postcentral gyrus	403	38	-32	62
Left	Precuneus (SLF)	341	-35	-67	39
Subcortical regions					
Right	Globus pallidus (PLIC, STR) (including areas near putamen/thalamus)	689	11	-2	1
Right	Putamen/claustrum (ALIC, CPT/ATR)	1120	27	7	19
<i>Experts < Controls</i>					
Frontal lobe					
Right	Inferior frontal gyrus, triangular part (ACR, UNC)	274	37	26	2
Right	Precentral gyrus	284	33	-18	45
Left	Inferior frontal gyrus (SLF)	201	-53	20	18
Left	Precentral gyrus	421	-37	-15	46
Parietal lobe					
Right	Precuneus/superior parietal lobule, BA7 (PCR, CC/PTR)	417	22	-56	49
Left	Inferior parietal lobule/supramarginal or angular gyrus	259	-31	-52	40
Limbic lobe					
Right	Hippocampus/arahippocampal gyrus (Fx/St)	281	18	-36	5

Note. ^aTalairach coordinate represents peak of cluster (+x = right, +y = anterior, +z = superior). CC = corpus callosum, ACR = anterior corona radiata, SCR = superior corona radiata, PCR = posterior corona radiata, ATR = anterior thalamic radiation, STR = superior thalamic radiation, PTR = posterior thalamic radiation, ALIC = anterior limb of internal capsule, PLIC = posterior limb of internal capsule, CPT = cerebro-pontine tract, SS = sagittal stratum, SLF = superior longitudinal fasciculus, ILF = inferior longitudinal fasciculus, CG = cingulum, UNC = uncinata fasciculus, Fx = fornix, St = stria terminalis. *Experts > Controls*: the regions of higher FA in Baduk expert group as compared to control group, *Experts < Controls*: the regions of lower FA in Baduk expert group as compared to control group.

as reflected by increased FA. In addition, Baduk experts exhibited increased FA in inferior temporal regions compared to controls (Fig. 3a), whereas controls exhibited increased FA in bilateral premotor areas and parietal sites, compared to experts (Figs. 1, 2, and 3b). These findings suggest that Baduk experts tend to develop memory chunks (Campitelli et al., 2007), and that controls tend to develop load-dependent memory capacity (Owen et al., 2005). Therefore, inexperienced controls tend to utilize premotor and parietal areas to execute their tasks, and Baduk training appears to shift core structures to the right-side dominant fronto-striatal circuit and temporal areas for information processing.

Historically, many debates have been hotly undertaken regarding the basis of exceptional talents in numerous fields, such as music, sports, mathematics, chess, and so on (Ericsson et al., 2009). In common parlance, talent has typically implied innateness, which was supported by genetic studies using large numbers of twin pairs about high-level cognitive abilities and exceptional performances in other areas (Coon and Carey, 1989; Haworth et al., 2009). On the other hand, many recent studies have asserted that adaptation to continuous and extensive practice, along with well-organized teaching and a supportive environment, is more critical to the achievement of expert performances than is activation of special genes (Ericsson et al., 2009). However, talented individuals in many fields, including music and sports, tend to be identified early and nurtured from childhood, which makes the effects of genes and extensive practice indistinguishable from each other (Bengtsson et al., 2005). Because all the Baduk experts recruited for this study also started training very young, it is possible that innate factors influenced our selection of the Baduk experts. Along these lines, a report

on the navigating talents of London taxi drivers attributed these skills to extensive training during adulthood (Woollett et al., 2009). Using voxel-based measures on structural brain MRI data, the authors revealed that the expertise acquired in adulthood can cause significant changes in gray matter volume as well as in neuropsychological profiles. Likewise, additional investigations of long-term Baduk players whose training began after adolescence period will be necessary to more precisely control for the genetic influences on Baduk expertise.

Some aspects of our findings remain subject to careful consideration. First, our subject population was small, which might reduce its statistical power. However, it is difficult to collect DTI data for Baduk experts, so our findings may still be valuable as a survey on the effects of Baduk training on structural changes in the brain. Second, structural information such as that provided by DTI scanning can be coupled with functional analysis such as fMRI to clarify the anatomo-functional network for neural functions (Casey et al., 2000; Guye et al., 2008). To this end, we are currently preparing to analyze fMRI data about working memory obtained from the same expert participants. In addition, the combined analysis of the two modalities should yield comprehensive results. Third, with regard to the demographic features of our subjects (Table 1), we found significant group differences in level of education (approximately 1 year, $t = -2.492$, $df = 31.239$, $p = 0.018$) and in estimated IQ scores ($t = -2.016$, $df = 32.910$, $p = 0.052$). Baduk players might tend to concentrate on their training rather than on formal education, even as early as childhood. The relatively shorter period of formal education might be partially responsible for the fact that Baduk players tended to score somewhat lower on IQ scores than did the control group (Pearson's

correlation coefficient between IQ and education was 0.285, with $p = 0.097$). However, more importantly, several studies have investigated the association between superior expertise and neuropsychological factors. Many studies have reported on the relationship between autistic traits (including impairments in social cognition and executive functions) and savant skills (Happé and Vital, 2009). In addition, one interesting study investigated the cognitive costs associated with the expertise which was acquired in adulthood. According to Woollett et al. (2009) London taxi drivers with navigational expertise obtained from extensive training during adulthood performed more poorly in spatial memory and anterograde associative memory tests, in spite of increased posterior hippocampal volumes. They also asserted that cognitive factors improved and posterior hippocampal volumes decreased in the retired taxi drivers. Nonetheless, it seems that their study was not able to completely exclude genetic effects. Taken together, the lower levels of IQ among Baduk experts than among controls may have been influenced by the assumptive innate neuropsychological traits of the selected group or may be related to the neurocognitive deficits caused during extensive training in this area of expertise. However, additional comprehensive and multi-dimensional analyses, including neuropsychological tests and longitudinal studies, must be performed to completely understand the complex neuro-developmental course and cognitive evolution involved in long-term Baduk training. Despite these considerations, our findings revealed that Baduk training appears to have a significant effect on the brain over long periods of training given that significant WM consistency emerged from the results of the voxel-based statistical analyses after eliminating such potentially confounding effects.

Conclusions

The results of our study revealed that Baduk experts develop structural fronto-cingulo-striato-thalamic connectivity, as evidenced by increased FA of WM tracts, as compared with those of non-experts. These structures are associated with cognitive processes that include spatial perception, attention, working memory, executive control, and problem solving (Chen et al., 2003). In addition, the experts' increased FA in inferior temporal areas indicates that, unlike the situation in controls, task-specific templates had developed in experts' neural mechanisms, enabling the efficient operation of tasks related to playing Baduk (de Rover et al., 2008). Right hemispheric dominance in Baduk experts also suggests that the involved tasks are mainly spatial processes (Thomason et al., 2009). Therefore, this study demonstrated that brain training, such as that required to become an expert Baduk player, might cause structural changes in the brain that are particularly helpful with regard to engaging in such foundational tasks as learning, abstract reasoning, problem-solving, and self-control.

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References

- Alexopoulos, G.S., Murphy, C.F., Gunning-Dixon, F.M., Latoussakis, V., Kanellopoulos, D., Klimstra, S., Lim, K.O., Hoptman, M.J., 2008. Microstructural white matter abnormalities and remission of geriatric depression. *Am. J. Psychiatry* 165, 238–244.
- Amidzic, O., Riehle, H.J., Fehr, T., Wienbruch, C., Elbert, T., 2001. Pattern of focal γ -bursts in chess players. *Nature* 412, 603.
- Anderson, J.R., Fincham, J.M., Qin, Y., Stocco, A., 2008. A central circuit of the mind. *Trends Cogn. Sci.* 12, 136–143.
- Atherton, M., Zhuang, J., Bart, W.M., Hu, X., He, S., 2003. A functional MRI study of high-level cognition. I. The game of chess. *Cogn. Brain Res.* 16, 26–31.
- Banks, S.J., Eddy, K.T., Angstadt, M., Nathan, P.J., Phan, K.L., 2007. Amygdala–frontal connectivity during emotion regulation. *Soc. Cogn. Affect. Neurosci.* 2, 303–312.
- Barrett, L., 2002. Do chess and GO need 'g'? *Trends Cogn. Sci.* 6, 499.
- Basser, P.J., Jones, D.K., 2002. Diffusion-tensor MRI: theory, experimental design and data analysis—a technical review. *NMR Biomed.* 15, 456–467.
- Baudevig, J., Dechent, P., Merboldt, K.D., Frahm, J., 2003. Thresholding in correlation analyses of magnetic resonance functional neuroimaging. *Magn. Reson. Imaging* 21, 1121–1130.
- Beer, J.S., John, O.P., Scabini, D., Knight, R.T., 2006. Orbitofrontal cortex and social behavior: integrating self-monitoring and emotion-cognition interactions. *J. Cogn. Neurosci.* 18, 871–879.
- Bengtsson, S.L., Nagy, Z., Skare, S., Forsman, L., Forssberg, H., Ullén, F., 2005. Extensive piano practicing has regionally specific effects on white matter development. *Nat. Neurosci.* 8, 1148–1150.
- Bundesden, C., Larsen, A., Kyllingsbæk, S., Paulson, O.B., Law, I., 2002. Attentional effects in the visual pathways: a whole-brain PET study. *Exp. Brain Res.* 147, 394–406.
- Butz, M., Wörgötter, F., van Ooyen, A., 2009. Activity-dependent structural plasticity. *Brain Res. Rev.* 60, 287–305.
- Cabeza, R., Nyberg, L., 2000. Imaging cognition II: an empirical review of 275 PET and fMRI studies. *J. Cogn. Neurosci.* 12, 1–47.
- Cámara, E., Bodammer, N., Rodríguez-Fornells, A., Tempelmann, C., 2007. Age-related water diffusion changes in human brain: a voxel-based approach. *Neuroimage* 34, 1588–1599.
- Campitelli, G., Gobet, F., Head, K., Buckley, M., Parker, A., 2007. Brain localization of memory chunks in chessplayers. *Int. J. Neurosci.* 117, 1641–1659.
- Casey, B.J., Giedd, J.N., Thomas, K.M., 2000. Structural and functional brain development and its relation to cognitive development. *Biol. Psychol.* 54, 241–257.
- Chen, X., Zhang, D., Zhang, X., Li, Z., Meng, X., He, S., Hu, X., 2003. A functional MRI study of high-level cognition II. The game of Go. *Cogn. Brain Res.* 16, 32–37.
- Choi, C.-H., Lee, J.-M., Koo, B.-B., Park, J.S., Kim, D.-S., Kwon, J.S., Kim, I.Y., 2010. Sex differences in the temporal lobe white matter and the corpus callosum: a diffusion tensor tractography study. *NeuroReport* 21, 73–77.
- Coccaro, E.F., McCloskey, M.S., Fitzgerald, D.A., Phan, K.L., 2007. Amygdala and orbitofrontal reactivity to social threat in individuals with impulsive aggression. *Biol. Psychiatry* 62, 168–178.
- Coon, H., Carey, G., 1989. Genetic and environmental determinants of musical ability in twins. *Behav. Genet.* 19, 183–193.
- de Lange, F.P., Koers, A., Kalkman, J.S., Bleijenberg, G., Hagoort, P., van der Meer, J.W.M., Toni, I., 2008. Increase in prefrontal cortical volume following cognitive behavioral therapy in patients with chronic fatigue syndrome. *Brain* 131, 2172–2180.
- de Rover, M., Petersson, K.M., van der Werf, S.P., Cools, A.R., Berger, H.J., Fernández, G., 2008. Neural correlates of strategic memory retrieval: differentiating between spatial-associative and temporal-associative strategies. *Hum. Brain Mapp.* 29, 1068–1079.
- Driemeyer, J., Boyke, J., Gaser, C., Büchel, C., May, A., 2008. Changes in gray matter induced by learning—revisited. *PLoS ONE* 3, e2669.
- Duncan, J., Seitz, R.J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., Newell, F.N., Emslie, H., 2000. A neural basis for general intelligence. *Science* 289, 457–460.
- Ericsson, K.A., Nandagopal, K., Roring, R.W., 2009. Toward a science of exceptional achievement: attaining superior performance through deliberate practice. *Ann. N. Y. Acad. Sci.* 1172, 199–217.
- Ferrandez, A.M., Hugueville, L., Lehericy, S., Poline, J.B., Marsault, C., Pouthas, V., 2003. Basal ganglia and supplementary motor area sub-tend duration perception: an fMRI study. *Neuroimage* 19, 1532–1544.
- Gitelman, D.R., Nobre, A.C., Parrish, T.B., LaBar, K.S., Kim, Y.-H., Meyer, J.R., Mesulam, M.-M., 1999. A large-scale distributed network for covert spatial attention: further anatomical delineation based on stringent behavioral and cognitive controls. *Brain* 122, 1093–1106.
- Good, C.D., Johnsrude, I.S., Ashburner, J., Henson, R.N.A., Friston, K.J., Frackowiak, R.S.J., 2001. A voxel-based morphometric study of ageing in 465 normal adult human brains. *Neuroimage* 14, 21–36.
- Govindan, R.M., Chugani, H.T., Makki, M.I., Behen, M.E., Dornbush, J., Sood, S., 2008. Diffusion tensor imaging of brain plasticity after occipital lobectomy. *Pediatr. Neurol.* 38, 27–33.
- Guye, M., Bartolomei, F., Ranjeva, J.-P., 2008. Imaging structural and functional connectivity: towards a unified definition of human brain organization? *Curr. Opin. Neurol.* 21, 393–403.
- Happé, F., Vital, P., 2009. What aspects of autism predispose to talent? *Philos. Trans. R. Soc. B-Biol. Sci.* 364, 1369–1375.
- Haworth, C.M.A., Dale, P.S., Plomin, R., 2009. Generalist genes and high cognitive abilities. *Behav. Genet.* 39, 437–445.
- Hinton, S.C., Meck, W.H., 2004. Frontal-striatal circuitry activated by human peak-interval timing in the supra-second range. *Cogn. Brain Res.* 21, 171–182.
- Hoptman, M.J., Nierenberg, J., Bertisch, H.C., Catalano, D., Ardekani, B.A., Branch, C.A., DeLisi, L.E., 2008. A DTI study of white matter microstructure in individuals at high genetic risk for schizophrenia. *Schizophr. Res.* 106, 115–124.
- Hyde, K.L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A.C., Schlaug, G., 2009. Musical training shapes structural brain development. *J. Neurosci.* 29, 3019–3025.
- Izhikevich, E.M., Edelman, G.M., 2008. Large-scale model of mammalian thalamocortical systems. *Proc. Natl. Acad. Sci. U. S. A.* 105, 3593–3598.
- Jiang, H., van Zijl, P.C.M., Kim, J., Pearlson, G.D., Mori, S., 2006. DtiStudio: resource program for diffusion tensor computation and fiber bundle tracking. *Comput. Methods Programs Biomed.* 81, 106–116.
- Jones, D.K., Symms, M.R., Cercignani, M., Howard, R.J., 2005. The effect of filter size on VBM analyses of DT-MRI data. *Neuroimage* 26, 546–554.
- Keck, T., Mrcsic-Flogel, T.D., Afonso, M.V., Eysel, U.T., Bonhoeffer, T., Hübener, M., 2008. Massive restructuring of neuronal circuits during functional reorganization of adult visual cortex. *Nat. Neurosci.* 11, 1162–1167.
- Kim, Z.S., Lee, Y.S., 1995. Validity of short forms of the Korean-Wechsler Adult Intelligence Scale. *Korean J. Clin. Psychol.* 14, 111–116.

- Kondo, H., Morishita, M., Osaka, N., Osaka, M., Fukuyama, H., Shibasaki, H., 2004. Functional roles of the cingulo-frontal network in performance on working memory. *Neuroimage* 21, 2–14.
- Lazar, S.W., Kerr, C.E., Wasserman, R.H., Gray, J.R., Greve, D.N., Treadway, M.T., McFarvey, M., Quinn, B.T., Dusek, J.A., Benson, H., Rauch, S.L., Moore, C.I., Fischl, B., 2005. Meditation experience is associated with increased cortical thickness. *NeuroReport* 16, 1893–1897.
- Luders, E., Toga, A.W., Lepore, N., Gaser, C., 2009. The underlying anatomical correlates of long-term meditation: larger hippocampal and frontal volumes of gray matter. *Neuroimage* 45, 672–678.
- Manning, L., 2008. Do some neurological conditions induce brain plasticity processes? *Behav. Brain Res.* 192, 143–148.
- McNab, F., Klingberg, T., 2008. Prefrontal cortex and basal ganglia control access to working memory. *Nat. Neurosci.* 11, 103–107.
- Monchi, O., Petrides, M., Strafella, A.P., Worsley, K.J., Doyon, J., 2006. Functional role of the basal ganglia in the planning and execution of actions. *Ann. Neurol.* 59, 257–264.
- Mori, S., Wakana, S., Nague-Poetscher, L.M., van Zijl, P.C.M., 2005. MRI atlas of human white matter. Elsevier.
- Oh, J.S., Kubicki, M., Rosenberger, G., Bouix, S., Levitt, J.J., McCarley, R.W., Westin, C.-F., Shenton, M.E., 2009. Thalamo-frontal white matter alterations in chronic schizophrenia: a quantitative diffusion tractography study. *Hum. Brain Mapp.* 30, 3812–3825.
- Owen, A.M., McMillan, K.M., Laird, A.R., Bullmore, E., 2005. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Hum. Brain Mapp.* 25, 46–59.
- Parris, B.A., Thai, N.J., Benattayallah, A., Summers, I.R., Hodgson, T.L., 2007. The role of the lateral prefrontal cortex and anterior cingulate in stimulus–response association reversals. *J. Cogn. Neurosci.* 19, 13–24.
- Schlösser, R.G.M., Wagner, G., Sauer, H., 2006. Assessing the working memory network: studies with functional magnetic resonance imaging and structural equation modeling. *Neuroscience* 139, 91–103.
- Sternberg, R.J., 2000. The holy grail of general intelligence. *Science* 289, 399–401.
- Talairach, J., Tournoux, P., 1988. Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: an approach to cerebral imaging. Thieme Medical Publishers, Inc., New York.
- Tang, Y.-Y., Ma, Y., Wang, J., Fan, Y., Feng, S., Lu, Q., Yu, Q., Sui, D., Rothbart, M.K., Fan, M., Posner, M.I., 2007. Short-term meditation training improves attention and self-regulation. *Proc. Natl. Acad. Sci. U. S. A.* 104, 17152–17156.
- Teutsch, S., Herken, W., Bingel, U., Schoell, E., May, A., 2008. Changes in brain gray matter due to repetitive painful stimulation. *Neuroimage* 42, 845–849.
- Thomason, M.E., Race, E., Burrows, B., Whitfield-Gabrieli, S., Glover, G.H., Gabrieli, J.D.E., 2009. Development of spatial and verbal working memory capacity in the human brain. *J. Cogn. Neurosci.* 21, 316–332.
- Wakana, S., Caprihan, A., Panzenboeck, M.M., Fallon, J.H., Perry, M., Gollub, R.L., Hua, K., Zhang, J., Jiang, H., Dubey, P., Blitz, A., van Zijl, P., Mori, S., 2007. Reproducibility of quantitative tractography methods applied to cerebral white matter. *Neuroimage* 36, 630–644.
- Weidner, R., Krummenacher, J., Reimann, B., Müller, H.J., Fink, G.R., 2009. Sources of top-down control in visual search. *J. Cogn. Neurosci.* 21, 2100–2113.
- Woollett, K., Spiers, H.J., Maguire, E.A., 2009. Talent in the taxi: a model system for exploring expertise. *Philos. Trans. R. Soc. B-Biol. Sci.* 364, 1407–1416.
- Yoo, S.Y., Jang, J.H., Shin, Y.-W., Kim, D.J., Park, H.-J., Moon, W.-J., Chung, E.C., Lee, J.-M., Kim, I.Y., Kim, S.I., Kwon, J.S., 2007. White matter abnormalities in drug-naïve patients with obsessive-compulsive disorder: a diffusion tensor study before and after citalopram treatment. *Acta Psychiat. Scand.* 116, 211–219.
- Yoshikawa, A., Kojima, T., Saito, Y., 1999. Relations between skill and the use of terms—an analysis of protocols of the game of Go. *Lect. Notes Comput. Sci.* 1588, 282–299.