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The architecture of the chess player's brain

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ABSTRACT

The game of chess can be seen as a typical example for an expertise task requiring domain-specific training and experience. Despite intensive behavioural studies the neural underpinnings of chess performance and expertise are not entirely understood. A few functional neuroimaging studies have shown that expert chess players recruit different psychological functions and activate different brain areas while they are engaged in chess-related activities. Based on this functional literature, we predicted to find morphological differences in a network comprised by parietal and frontal areas and especially the occipito-temporal junction (OTJ), fusiform gyrus, and caudate nucleus. Twenty expert chess players and 20 control subjects were investigated using voxel-based and surface-based morphometry as well as diffusion tensor imaging. Grey matter volume and cortical thickness were reduced in chess players compared with those of control men in the OTJ and precunei. The volumes of both caudate nuclei were not different between groups, but correlated inversely with the years of chess playing experience. Mean diffusivity was increased in chess players compared with that of controls in the left superior longitudinal fasciculus and the Elo score (a chess tournament ranking) was inversely related to mean diffusivity within the right superior longitudinal fasciculus. To the best of our knowledge we showed for the first time that there are specific differences in grey and white matter morphology between chess players and control subjects in brain regions associated with cognitive functions important for playing chess. Whether these anatomical alterations are the cause or consequence of the intensive and long-term chess training and practice remains to be shown in future studies.

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1. Introduction

To perform chess requires the orchestration of several psychological functions among them attention, perceptual grouping, and various memory functions (Bilalić, McLeod, & Gobet, 2009; Gobet, 1998; Gobet & Waters, 2003). Currently there is consensus among cognitive psychologists that chess performance needs substantial practice. Thus, chess is seen as a typical example for an expertise task requiring domain-specific experience. In this context Simon and Chase (1973) formulated the 10-year rule of expertise, stating that to reach grandmaster level in chess at least 10 years of intense practice is required. Several recent studies support this notion by showing a monotonic relationship between deliberate chess practice and chess performance using longitudinal (De Bruin, Smits, Rikers, & Schmidt, 2008) and retrospective study designs (Charness, Tuffiash, Krampe, Reingold, & Vasyukova, 2005). Thus, the positive relation between accumulated amount of chess practice and performance resembles the practice–performance relation in other fields such as music, sports, and teaching (Ericsson, 2004). However, although practice is important in determining chess performance, general intelligence, visuospatial intelligence, and talent are also discussed as factors contributing to chess performance. Thus, some authors favour a kind of interaction between practice and talent explaining chess performance (Howard, 2013).

Despite intensive behavioural studies the neural underpinnings of chess performance and expertise are not entirely understood. A few neuroimaging studies have been conducted in the last 20

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years examining brain activations in the context of chess using different methods and experimental paradigms. Some studies featured only novices (Atherton, Zhuang, Bart, Hu, & He, 2003; Nichelli et al., 1994; Onofrj et al., 1995), examined experts during chess-related-visual search tasks (Campitelli, Gobet, Head, Buckley, & Parker, 2007), compared experts with novices during chess-related and chess-unrelated visual perception tasks (Bilalić, Langner, Erb, & Grodd, 2010; Bilalić, Langner, Ulrich, & Grodd, 2011), or measured brain activations in chess experts or novices during chess moves or at rest (Amidzic, Riehle, Fehr, Wienbruch, & Elbert, 2001; Duan et al., 2012a, 2012b).

Taken together, these studies have shown that expert chess players recruit different psychological functions and activate different brain areas while they are engaged in chess-related activities. For example, in chess-related visual search tasks only chess-experts demonstrate bilateral activation in brain areas involved in object perception (bilateral posterior temporal areas, fusiform gyrus, left inferior parietal lobe, and especially in the occipito-temporal junction, OTJ) or expertise-related pattern recognition (bilateral retrosplenial cortex and bilateral collateral sulcus) (Bilalić et al., 2010, 2011). In addition, during chess games only experts recruit brain areas involved in memory chunking, knowledge storage, and retrieval (frontal and parietal lobes) while novices recruit more strongly the medial temporal cortex (e.g. the hippocampus) that is more strongly involved in learning and retrieving of new information (Amidzic et al., 2001). In a more recent study by Duan et al. the authors examined brain activations during the performance of a Chinese chess-based problem-solving task and identified that chess masters and grandmasters demonstrated increased activation in neural networks involved in the control of cognitive functions such as attention, executive functions, and problem-solving (Duan et al., 2012b). The new finding of this study was that the grandmasters and masters also showed a much stronger suppression of the default mode network (DMN) during chess-related problem-solving than the novices. In addition, when examining the resting-state functional connectivity in the DMN they uncovered that, compared to novices, the DMN in grandmasters and masters showed an increased functional connectivity between the caudate nucleus and the DMN network hubs, suggesting an important role of the DMN-caudate nucleus loop in chess expertise.

Taken together, there are substantial differences between chess experts in terms of the involved psychological functions as well as substantial differences in terms of the underlying neurophysiological systems. Most likely these differences have been established as a consequence of intensive chess practice. Since intensive practice of cognitive and motor tasks is associated with substantial anatomical changes (Jancke, 2009; May, 2011; Zatorre, Fields, & Johansen-Berg, 2012) it is most likely that those brain regions, which are most strongly involved in controlling chess tasks, have been changed by neuroplastic mechanisms. However, little is known so far with respect to the anatomical plasticity in chess players. To the best of our knowledge there is only one study, which has examined structural differences in chess experts compared to chess novices (Duan et al., 2012b). In this study chess experts compared with novices showed reduced grey matter (GM) volume bilaterally in the caudate nucleus. The authors associate this GM volume reduction with the idea of synaptic pruning and the beneficial elimination of redundant and unused synapses within the caudate nucleus allowing more efficient local computations and more efficient integration of information from adjacent brain regions.

In the present study, we conducted a comprehensive neuroanatomical analysis in order to identify characteristic neuroanatomical differences between expert and novice chess players. For this purpose we applied diffusion tensor imaging (DTI) as well as voxel-based (VBM) and surface-based morphometry (SBM) in the context of structural MRI to delineate specific anatomical features of the white matter (WM) and GM architecture. With the above-mentioned functional findings in mind, we aimed at investigating whether brain regions differentially activated as a function of chess expertise are also morphologically altered as a result of structural neuroplasticity induced by intensive, long-term chess training and extensive chess playing experience that included international chess tournaments.

Our hypotheses can be divided into three broad classes: (1) predictions with respect to brain regions involved in chess-related "higher cognitive functions" such as probed in the contrasts reported above by the following studies (Amidzic et al., 2001; Atherton et al., 2003; Duan et al., 2012a, 2012b; Nichelli et al., 1994; Wan et al., 2011). (2) Predictions with respect to those brain areas associated with chess-related "lower cognitive mechanisms" such as the recognition of objects and their relations (Bilalić et al., 2011, 2010). (3) A third prediction is related to the putative specific role of the caudate nucleus in chess playing (Duan et al., 2012a).

According to these three prediction classes we hypothesise that the chess player's brain will demonstrate specific anatomical features in (1) brain areas associated with higher cognitive functions (e.g. memory and executive functions) in a distributed cortical network including parietal, frontal, and temporal regions. (2) With respect to the second class of predictions we anticipate specific anatomical features in brain areas that have been shown to be involved in the recognition of objects and their relations (e.g. the OTJ and fusiform gyrus). (3) Finally, we predict anatomical alterations in the caudate nucleus as suggested by Duan et al. (2012a).

Besides DTI that investigates differences in WM architecture, we used VBM and SBM techniques in order to measure morphological GM differences in the hypothesised brain areas. Although both techniques are based on the same T1-weighted MR images, they measure different morphological features. With VBM we examine probabilistic GM volume differences while the SBM technique provides us cortical thickness measures. We used both techniques in order to track down whether between-group differences potentially found in the VBM analysis are driven by differences in cortical thickness.

2. Materials and methods

2.1. Subjects

Twenty expert male chess players with a mean age of 28.9 years (standard deviation, SD $\pm$ 6.03 years) and 20 control male subjects matched for age, handedness, and education participated in the study (mean age $\pm$ SD; 27.2 $\pm$ 6.32 years). The Elo score (Elo, 1978), an international chess tournament classification system, was used to evaluate chess playing proficiency (Table 1). The sample of chess players included three grandmasters, seven international masters, and six FIDE (Fédération Internationale des Échecs) masters. The rest of the chess players did not have any international chess title. Handedness was evaluated according to the procedure proposed by Annett (1970). The participants had no history of neurological, neuropsychological, or psychiatric disease, and denied taking illegal drugs or medication. The research reported in the present study was conducted according to the principles expressed in the Declaration of Helsinki. The local ethics committee of the canton Zurich approved the study and written informed consent was obtained from all participants.

2.2. Neuropsychological assessment

Several cognitive domains were assessed in the expert chess players and control men. Fluid intelligence was measured with Raven's advanced progressive matrices (Raven, 1998). Visuospatial abilities, especially mental rotation performance, were assessed with the mental rotation test version A (Peters et al., 1995). The immediate visuospatial block span was evaluated with the block-tapping test (similar to the block of Corsi) (Schellig, 1997). Due to logistical restrictions and time

Table 1
Demographic, behavioural, and global brain measures of the chess players and control men.

	Chess players (n=20)				Control men (n=20)				Significance
Measure	**Mean**	**SD**	**Min.**	**Max.**	**Mean**	**SD**	**Min.**	**Max.**	***p*-value**
Age (years)	28.9	6.02	19.7	41.2	27.2	6.32	17.4	42.8	0.38
Education (years)	16.6	2.09	13.0	21.0	17.6	4.29	12.0	28.0	0.33
Elo score	2366	107	2187	2560	–	–	–	–	–
Age at chess playing commencement (years)	7.9	3.08	4.0	14.0	–	–	–	–	–
Experience of chess playing (years)	19.7	6.58	8.0	31.0	–	–	–	–	–
Total chess playing (hours)	13231	14416	2496	52000	–	–	–	–	–
Raven's advanced progressive matrices	28.3	5.08	20.0	35.0	28.5	3.25	23.0	36.0	0.85
Mental rotation task – version A	12.8	5.07	5.0	23.0	13.1	3.23	9.0	21.0	0.83
Block tapping test (immediate block span)	6.3	0.97	5.0	8.0	6.1	0.95	5.0	8.0	0.37
Intracranial volume (cm^3)	1271.1	100.5	1076.0	1473.6	1223.9	136.9	991.1	1517.6	0.22
Total left cortical grey matter volume (cm^3)	262.3	20.0	238.0	312.7	255.4	19.8	228.5	301.8	0.28
Total right cortical grey matter volume (cm^3)	265.8	21.0	239.8	316.5	257.9	20.7	228.1	310.1	0.24
Total left cortical surface area (cm^2)	1105.7	57.97	1015.3	1249.3	1063.4	74.06	922.7	1226.5	0.052
Total right cortical surface area (cm^2)	1110.6	60.05	1028.1	1240.0	1070.0	74.47	924.7	1235.2	0.065
Average left cortical thickness (mm)	2.578	0.103	2.427	2.732	2.607	0.111	2.367	2.847	0.40
Average right cortical thickness (mm)	2.591	0.109	2.423	2.775	2.617	0.118	2.376	2.830	0.47
Total left cortical white matter volume (cm^3)	272.2	22.7	232.3	325.0	261.0	26.8	221.7	304.3	0.16
Total right cortical white matter volume (cm^3)	273.4	23.5	234.1	330.2	262.1	26.2	225.0	307.2	0.16
Total left cortical white matter area (cm^2)	925.9	46.9	835.9	1028.6	895.0	67.3	751.2	1003.4	0.10
Total right cortical white matter area (cm^2)	932.4	51.7	841.0	1032.9	902.3	65.5	759.7	1023.8	0.11

Abbreviations: Max., maximum; Min., minimum; n, number of subjects; p-value, error probability; and SD, standard deviation.

constraints, it was not possible to test the expert chess players cognitively in more detail and therefore we also did not assess long-term memory performance.

2.3. MRI data acquisition

Magnetic resonance imaging (MRI) scans were acquired on a 3.0 T Philips Achieva whole body scanner (Philips Medical Systems, Best, The Netherlands) equipped with a transmit-receive body coil and a commercial eight-element head coil array capable for sensitivity encoding (SENSE). Three volumetric 3D T1-weighted gradient echo sequence (fast field echo) scans were obtained from all 40 participants. Slices were acquired in the sagittal plane with a measured and reconstructed spatial resolution of $0.94 \times 0.94 \times 1.00\ mm^3$ (matrix 256×256 pixels, 160 slices). Further imaging parameters were: field of view FOV=$240 \times 240\ mm^2$, echo-time TE=3.7 ms, repetition-time TR=8.06 ms, flip-angle α=8°, and SENSE factor SF=2.1. Scan time was about 8 min/scan. The three T1-weighted MRI scans were realigned and averaged to obtain a single image with an increased signal-to-noise and contrast-to-noise ratio.

Two identical diffusion-weighted spin-echo echo-planar imaging sequences were applied to all 40 participants' brain. Slices were acquired in the transversal plane with a measured and reconstructed spatial resolution of $2.0 \times 2.0 \times 2.0\ mm^3$ (matrix 112×112 pixels, 75 slices). Further imaging parameters were: field of view FOV=$224 \times 224\ mm^2$, echo-time TE=55 ms, repetition-time TR=13,472 ms, flip-angle α=90°, and SENSE factor SF=2.1. Diffusion was measured in 32 non-collinear directions with a b-value of b=1000 s/mm^2 preceded by a non-diffusion-weighted volume (reference volume). Scan time was about 10 min/sequence. The scans from the two DTI sequences were realigned and averaged to obtain diffusion-weighted data with an increased signal-to-noise ratio.

2.4. Voxel-based morphometry – analysis of probabilistic grey matter volume

Between-group differences in GM volume were evaluated by using voxel-based morphometry (VBM) (Ashburner & Friston, 2000; Good et al., 2001a). T1-weighted MRI scans were analysed with the FSL-VBM tool (Douaud et al., 2007) (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSLVBM), an optimised VBM protocol (Good et al., 2001b) that was carried out with FMRIB Software Library (FSL) version 5.0.1 (Smith et al., 2004) (www.fmrib.ox.ac.uk/fsl). First, structural images were brain-extracted and segmented into different tissue classes before being registered to the MNI 152 standard space using non-linear registration. The resulting images were averaged and flipped along the x-axis to create a left–right symmetric, study-specific GM template. Second, all native GM images were non-linearly registered to this study-specific template and "modulated" to correct for local expansion (or contraction) due to the non-linear component of the spatial transformation. The modulated GM images were then smoothed with an isotropic Gaussian kernel with a sigma of 5.0 mm (corresponding to a kernel with a full width at half-maximum of about 11.5 mm). These GM maps were then subjected to statistical analyses (see below).

We restricted the statistical analysis to cortical and subcortical structures, which turned out to be specific, or at least, differentially involved in chess playing. Structures included the caudate nucleus (Duan et al., 2012a, 2012b; Wan et al., 2011), superior parietal lobule (Atherton et al., 2003), inferior parietal lobule comprised by the angular gyrus, supramarginal gyrus (anterior and posterior part), and the parietal operculum (Amidzic et al., 2001; Atherton et al., 2003; Bilalić et al., 2010, 2011; Nichelli et al., 1994), occipito-temporal junction (Bilalić et al., 2010, 2011) parieto-occipital junction (Nichelli et al., 1994), precuneus (Wan et al., 2011), occipital pole and intracalcarine cortex (Nichelli et al., 1994), fusiform gyrus (temporal and occipital parts) (Bilalić et al., 2010, 2011), and the premotor cortex (Atherton et al., 2003; Nichelli et al., 1994). The anterior cingulate cortex was investigated in addition due to its prominent role in error detection, a cognitive function also important for the game of chess. The masks of these regions of interest were derived from the Juelich histological atlas (premotor cortex) (https://www.jubrain.fz-juelich.de/apps/cytoviewer/cytoviewer-main.php), the Harvard-Oxford subcortical (caudate nucleus) and cortical (all other ROIs) structural atlas (http://www.cma.mgh.harvard.edu/fsl_atlas.html) as implemented in FSL.

Although the caudate nucleus is included in the VBM analysis, which operates at the voxel level, we also investigated the caudate nucleus as a whole using the fully automated subcortical segmentation procedure implemented in the FreeSurfer software suite (http://surfer.nmr.mgh.harvard.edu/fswiki) that provides the total volume of the caudate nucleus. To rule out that local brain differences are confounded by global brain differences, we also computed global brain measures such as intracranial volume, hemispheric GM and WM volumes and surface area as well as cortical thickness using the standard procedure of FreeSurfer.

2.5. Analysis of fractional anisotropy and mean, axial and radial diffusivity

Here we applied tract-based spatial statistics (TBSS) (Smith et al., 2006) using FSL (FMRIB Software Library; http://www.fmrib.ox.ac.uk/fsl/) (Smith et al., 2004) tools such as the FDT (FMRIB Diffusion Toolbox) (Behrens et al., 2003) to create fractional anisotropy (FA), mean, axial and radial diffusivity maps. FA, a marker for the integrity of WM, is a measure of the degree of directional preference of water diffusion (Basser, Mattiello, & LeBihan, 1994). Mean diffusivity is the average of the diffusion tensor's three eigenvalues ($\lambda1+\lambda2+\lambda3$)/3 and represents the amount of diffusion independent of the diffusion direction. Axial diffusivity, a parameter reflecting the principal direction of diffusion in WM (Song et al., 2002), was estimated using the first eigenvalue ($\lambda1$) of the diffusion tensor. Axial diffusivity reflects rather the properties of the axonal membrane than the properties of myelin. The second and third eigenvalues were averaged and referred to as radial diffusivity ($\lambda2+\lambda3$)/2 (Basser et al., 1994; Song et al., 2002), rather a marker for the properties of the myelin sheets than the properties of the axonal membrane. The following steps were realised: Eddy current and head movement corrections were applied using the EDDY_CORRECT tool of FDT. An individual binary brain mask was created on the non-diffusion weighted images using BET (Brain Extraction Tool). Tensors were fitted to the data using the DTIFIT tool of FDT after the b-vectors were adjusted for the rotations introduced by head movement correction. Linear and non-linear spatial registrations of the FA map into a standard stereo-tactic space (MNI space represented by the FMRIB58-FA template) were applied using FSL's registration tools FLIRT and FNIRT, respectively. These transformations were then applied to the mean, axial and radial diffusivity maps using the TBSS_NON_FA tool. Next, the mean of all subjects' aligned FA images is created, and then 'thinned'

using standard image processing techniques to create a mean FA skeleton that represents the centres of major tracts common to the group of subjects. Each subject's aligned FA data is then projected (perpendicular to the local tract direction) onto this skeleton so that the projected FA values are taken from the centres of the tracts in the original FA image (Smith et al., 2007). These maps were then subjected to statistical analyses (see below).

To restrict the statistical analysis to the fibre tracts, which interconnect the GM regions associated with chess playing (see above), we used probability maps of the superior longitudinal fasciculus (arcuate and temporal part) and the cingulum (cingulate and hippocampal part) derived from the JHU (Johns Hopkins University) WM tractography atlas (Hua et al., 2008) implemented in FSL. The probability maps were neither thresholded nor combined into a single mask.

2.6. Surface-based morphometry – analysis of cortical thickness

Cortical surface reconstruction, cortical parcellation, and subcortical volumetric segmentation were performed with the FreeSurfer software (version 5.3.0), which is documented and available online (http://surfer.nmr.mgh.harvard.edu/). The technical details of these procedures are described in prior publications (Dale, Fischl, & Sereno, 1999; Fischl & Dale, 2000; Fischl et al., 2001, 2004). The 3D structural T1-weighted MRI scans were used to construct models of each subject's cortical surface in order to measure cortical thickness and cortical surface area. This fully automated procedure comprised segmentation of the cortical WM (Dale et al., 1999), tessellation of the GM/WM junction, inflation of the folded surface tessellation patterns (Fischl, Sereno & Dale, 1999) and automatic correction of topological defects in the resulting manifold (Fischl et al., 2001). This surface was then used as starting point for a deformable surface algorithm designed to find the GM/WM and pial (GM/cerebrospinal fluid (CSF)) surfaces with sub-millimetre precision (Fischl & Dale, 2000). The procedures for measuring cortical thickness have been validated against histological analysis (Rosas-Cholula et al., 2013) and manual measurements (Kuperberg et al., 2003; Salat et al., 2004). This method uses both intensity and continuity information from the surfaces in the deformation procedure in order to interpolate surface locations for regions in which the MR image is ambiguous (Fischl & Dale, 2000). For each subject, cortical thickness of the cortical ribbon was computed on a uniform grid (comprised by vertices) with 1 mm spacing across both cortical hemispheres, with the thickness being defined by the shortest distance between the GM/WM and pial surface models. The thickness maps produced are not limited to the voxel resolution of the image and thus sensitive for sub-millimetre differences between groups (Fischl & Dale, 2000). The way in which the resolution of the cortical thickness maps goes beyond the resolution of the original acquisition is conceptually similar to a (conventional) partial volume correction procedure. The cortex is smooth at the spatial scale of several millimetres, which is imposed as constraint by FreeSurfer to estimate the location of the surface with subvoxel accuracy. For instance, if a given voxel is darker than its neighbouring GM it probably contains more CSF and so the surface model is at a slightly different position than if the neighbouring voxels were brighter and therefore contain probably more WM. Cortical thickness, surface area, and volume measures were mapped to the inflated surface of each participant's brain reconstruction; thus allowing visualisation of data across the entire cortical surface (gyri and sulci) without the data being obscured by cortical folding. Data were resampled for all subjects and rendered onto a common spherical coordinate system (Fischl, Sereno, Tootell & Dale, 1999). Then surface-based vertex-wise cortical thickness maps were computed for each hemisphere and participant. For the whole-brain vertex-wise analysis, the data were smoothed on the surface tessellation using an iterative nearest-neighbour averaging procedure with 139 iterations on the left hemisphere and 138 iterations on the right hemisphere, corresponding to a 2D surface-based diffusion smoothing kernel with a FWHM of about 15 mm. These maps were subjected to statistical whole brain analyses (see below).

2.7. Statistical analyses

2.7.1. Voxel-based morphometry and diffusion tensor imaging

For the VBM and DTI data, voxel-wise general linear models (GLM) were applied using permutation-based non-parametric statistical procedures (Hayasaka & Nichols, 2003; Nichols & Holmes, 2002) that also correct for multiple comparisons across space (FSL's randomise tool). The threshold free cluster enhancement (TFCE) technique was used in addition (Smith & Nichols, 2009). The TFCE technique addresses problems of smoothing, threshold dependence and localisation in cluster inference. Many image enhancement and thresholding techniques make use of spatial neighbourhood information to boost the validity in extended areas of signal (Smith & Nichols, 2009). The most common such approach in neuroimaging is cluster-based thresholding, which is often more sensitive than voxel-wise thresholding. However, a limitation is the need to define the initial cluster-forming threshold (Smith & Nichols, 2009). The TFCE technique avoids this problem and it is recommended to use this technique when analysing VBM and DTI data with FSL's randomise tool.

Error probability was set at $p < 0.05$ corrected for multiple comparisons using 5000 permutations in all analyses. This permutation-based non-parametric procedure that also corrects for multiple comparisons across space derives the null distribution by permuting the subject's group membership randomly. Chess players and controls were contrasted with respect to local probabilistic GM volume (VBM) and local FA, mean, axial, and radial diffusivity (DTI). Within the chess players, the Elo score, age of chess playing commencement, years of chess playing experience, and lifetime hours of chess training have been correlated with the local brain measures (derived from the VBM and DTI analyses). As described above, we restricted the statistical analyses to a priori defined regions of interest. The peak coordinates of the clusters reported are in Montreal Neurological Institute (MNI) stereotactic space.

2.7.2. Surface-based morphometry

For the exploratory and confirmatory whole brain analysis of the SBM data, a GLM based on parametric statistics was applied within FreeSurfer (MRI_GLMFIT tool) without applying the TFCE technique that has been used in the VBM and DTI analyses. Although the SBM data reported in the present study are not corrected for multiple comparisons, we indicated the clusters that survive a Monte Carlo simulation based on the cluster extent and 5000 permutations using FreeSurfer's MRI_GLMFIT-SIM tool. Here, synthetic random z-fields were generated, smoothed, and then statistically tested to assess how many times the resulting randomly produced clusters reach or exceed the size of the true clusters. Error probability was set at $p < 0.05$ in both the uncorrected and corrected analyses. In the uncorrected analysis, we additionally applied a cluster extent threshold that only considers clusters larger than 200 mm^2 in size. The size of this cluster threshold was determined arbitrarily. Combining a height threshold with a cluster extent threshold helps guarding against spurious findings because false positives do not cluster in space.

2.7.3. Demographic, behavioural, and global brain characteristics

For the comparison of demographic, behavioural, and global brain measures between groups (independent t-tests) as well as for the correlation between the Elo score and total hours of training (Spearman's correlation) within chess players IBM SPSS statistics version 20 was used (SPSS, an IBM company, Armonk, New York). Error probabilities for the comparisons of the demographic, behavioural, and global brain measures were corrected for multiple comparisons using Bonferroni correction. Error probability is indicated two-tailed if not otherwise stated. Instead of Pearson's correlation, Spearman's correlation was used where parametric assumptions were not given (see below).

3. Results

3.1. Demographic, behavioural, and global brain characteristics

Demographic, behavioural and global brain characteristics are summarised in Table 1. There were no significant differences between expert chess players and controls with respect to age, education, and performance in the Raven's advanced progressive matrices test (Raven, 1998), mental rotation test version A (Peters et al., 1995), and block-tapping test (Schellig, 1997) as well as with respect to intracranial volume, left and right total cortical GM and WM volume and surface area, and average cortical thickness as revealed by t-tests for independent samples.

With respect to the weekly and lifetime hours of chess training, four expert chess players showed extreme values. Therefore, a procedure for rank ordered data (Spearman's correlation) was applied for correlations involving theses two variables because outliers do not bias nonparametric tests. The Elo score was weakly but positively correlated with the amount of time spent for chess training per week (Spearman's correlation $r = 0.36$, $p = 0.061$, one-tailed) as well as correlated with lifetime hours of chess training (Spearman's correlation $r = 0.29$, $p = 0.108$, one-tailed), but these correlations did not reach statistical significance (see Section 4). The Elo score of the chess players neither significantly correlated with age at chess playing commencement (Pearson's correlation $r = 0.05$, $p = 0.42$, one-tailed) nor with the years of chess playing experience (Pearson's correlation $r = 0.23$, $p = 0.16$, one-tailed).

3.2. Group differences in probabilistic grey matter volume (VBM) and white matter diffusivity (DTI)

GM volume was reduced in chess players compared with that of control men in a cluster located in the left OTJ (Fig. 1B, Table 2).

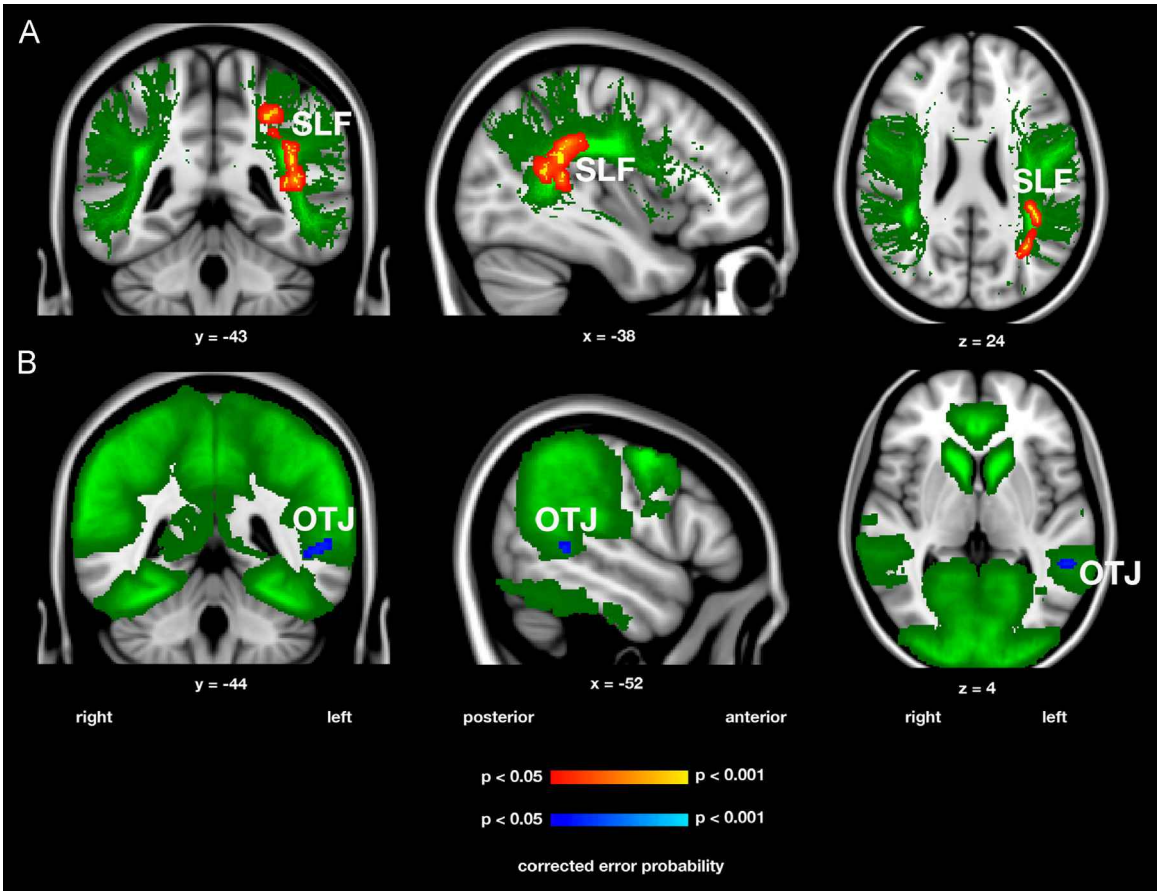

Fig. 1. Regions with altered grey and white matter architecture in chess players. Shown are clusters with increased mean diffusivity (red–yellow) in the left superior longitudinal fasciculus (SLF, A) and decreased probabilistic grey matter volume (blue–lightblue) in the left occipito-temporal junction (OTJ, B) in chess players compared with control men. The regions of interest subjected to the statistical analysis are shown in green–lightgreen. Colour bars indicate alpha error probability that is corrected for multiple comparisons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Regions with increased mean diffusivity and decreased probabilistic grey matter volume in chess players compared with control men.

Name	Letter in Fig. 1	Number of voxels	Error probability	MNI coordinates		
				x	*y*	*z*
Increased mean diffusivity						
Left superior longitudinal fasciculus (below supramarginal gyrus)	A	729	0.035	−38	−43	24
Decreased grey matter volume						
Left occipito-temporal junction (posterior middle temporal gyrus)	B	44	0.041	−52	−44	4

p-values are corrected for multiple comparisons using permutation-based non-parametric testing across space (FSL's randomise tool with 5000 permutations). Abbreviations: Fig., figure; MNI, Montreal Neurological Institute.

There was no cluster with increased GM volume in chess players compared with that of controls. A whole-brain analysis did not reveal any additional statistically significant cluster with GM volume changes (when applying correction for multiple comparisons) and the cluster in the left OTJ (see above) showed only a slightly increased error probability of $p=0.072$ in the whole-brain compared with $p=0.041$ in the ROI approach. It should be noted that when applying a whole-brain analysis, a lot of brain regions, for which we did not have any a priori hypothesis, would be subjected to the statistical analysis, which would reduce the statistical power.

Mean diffusivity was increased in chess players compared with that of controls in a cluster located in the left superior longitudinal fasciculus (Fig. 1A, Table 2). There was no cluster with reduced mean diffusivity in chess players compared with that of controls. There were also no significant differences between the groups with respect to FA and axial and radial diffusivities. Whole brain analyses did not reveal any additional statistically significant (when applying correction for multiple comparisons) cluster with changed diffusivity values.

3.3. Correlations between chess-related parameters and probabilistic grey matter volume (VBM) and white matter diffusivity (DTI)

Within the regions of interest, there was no cluster with significant (either positive or negative) correlations between probabilistic local GM volume on one hand and the Elo score,

age of chess playing commencement, years of chess training, and lifetime hours of chess training and gaming on the other hand.

However, when regressing these behavioural measures against the DTI-derived parameters (FA, mean, axial, and radial diffusivity) several clusters with negative correlations were found. The Elo score was inversely related to mean diffusivity in two clusters within the right superior longitudinal fasciculus (Fig. 2A, Table 3), both clusters located in the WM underlying the right supramarginal gyrus. Within the same region, axial diffusivity was also inversely related to the Elo score (Fig. 2B, Table 3), suggesting that differences in mean diffusivity are rather driven by differences in axial than radial diffusivity. The same cluster that revealed an inverse relationship between the Elo score and mean diffusivity within the right superior longitudinal fasciculus (Fig. 2A, Table 3) showed also an inverse relation among lifetime hours of chess training and gaming and mean diffusivity (Fig. 2C, Table 3), although the Elo score and lifetime hours of chess training and playing are only moderately correlated.

There were no positive correlations between mean or axial diffusivity on one hand and the Elo score, age of chess playing commencement, years of chess training, and lifetime hours of chess training and gaming on the other hand. No significant (neither positive nor negative) correlations were found between these behavioural measures on one hand and FA and radial diffusivity on the other hand. No whole brain analyses were conducted for the correlations.

3.4. Group differences in cortical thickness (SBM)

The exploratory and confirmatory whole brain analysis of cortical thickness differences revealed only clusters with reduced cortical thickness in chess players compared with that of control men mainly in occipito-temporal and parietal regions including the OTJ. Most interesting clusters are those found in the right and left OTJ, in the left and right precunei (PrCun) as well as the one in the left supramarginal gyrus (SMG) (Fig. 3). The cluster in the right OTJ is the only cluster of all clusters presented in Fig. 3 that survives cluster extent error correction for multiple comparisons.

Further clusters with reduced cortical thickness in chess players compared with control men were located within the middle temporal gyrus, superior and inferior temporal sulci, temporal pole, superior frontal gyrus, cuneus, middle occipital gyrus, subcentral gyrus, and posterior segment of the Sylvian fissure of the left hemisphere. In the right hemisphere, clusters were located within the superior and inferior temporal sulci, superior temporal gyrus, pars opercularis, occipital areas, and the marginal part of cingulate sulcus (Fig. 3). Because we applied a whole brain analysis uncorrected for multiple comparisons in our SBM approach and did not had any a priori hypothesis with respect to brain areas outside the regions of interest (see above), we do not discuss these regions further. Future analyses are clearly necessary to confirm the significance of these regions before any sound conclusions can be drawn.

3.5. Volume of the caudate nucleus

The mean volumes of the left caudate nucleus (mean/standard deviation: chess players 4082.5/415.9 mm^3, control men 4074.6/578.6 mm^3) and that of the right caudate nucleus (chess players 4181.3/432.7 mm^3, control men 4136.6/597.2 mm^3) were not significantly different between groups (left caudate: $p=0.33$, right caudate: $p=0.48$, analysis of covariance corrected for total GM volume). There was no significant correlation between the Elo score of the chess players and their left (Pearson's correlation $r=-0.06$, $p=0.80$) or right caudate nucleus volume ($r=-0.05$, $p=0.83$) and the left and right caudate nucleus volumes were also not related to the age of chess playing commencement ($r=-0.07$, $p=0.76$ and $r=-0.06$, $p=0.80$, respectively). However, the left and right caudate nucleus volumes were inversely related to the years of chess playing experience ($r=-0.67$, $p=0.001$ and $r=-0.62$, $p=0.003$, respectively), revealing that more years of experience goes with smaller caudate nucleus volumes.

Because age and years of chess training and playing experience are heavily confounded ($r=0.868$, $p=7.15E\text{-}7$) it remains unclear whether the effect reported is driven by chess experience or rather by age. However, we were able to show that there is an effect related to chess experience that goes beyond the age effect. To illustrate this, we first computed the association between age and caudate volume for each group separately. For chess players, age was strongly negatively related to the left caudate volume ($r=-0.787$, $p=0.000038$) and also to the right caudate volume ($r=-0.774$, $p=0.000061$), whereas in control subjects, age was not significantly related to caudate volumes (left caudate: $r=-0.263$, $p=0.262$; right caudate: $r=-0.325$, $p=0.162$).

Therefore, we computed whether the differences in the correlation coefficients between chess players and control men were statistically significantly different using Fisher's r-to-z-transformation. Both differences in the correlation coefficients are significant (left caudate volume: $z=-2.32$, $p=0.02$, two-tailed; right caudate volume: $z=-2.02$, $p=0.043$, two-tailed) revealing that there is an effect of the years of chess experience on the caudate volume that goes beyond the effect of age.

4. Discussion and conclusion

The aim of this study is to identify specific anatomical features of the chess player's brain. Our analysis was guided by three specific hypotheses based on previous neuroimaging studies conducted with chess experts and chess novices. We hypothesised that the chess player's brain will demonstrate specific anatomical features in (1) brain areas associated with higher cognitive functions in a distributed cortical network including parietal, frontal, and temporal regions, (2) in brain regions known to be involved in the recognition of objects and their relations (e.g. the OTJ and the fusiform gyrus), and (3) finally in the caudate nucleus. In order to identify these specific features we applied three different neuroimaging techniques: 1.) VBM to delineate probabilistic GM volume differences, 2.) SBM to identify differences in terms of cortical thickness, and 3.) DTI to investigate differences in the WM architecture.

4.1. Structurally altered brain regions in chess players

In our group analysis we only identified a very few differences between chess players and control subjects. In chess players compared to control subjects there were reduced GM volume and cortical thickness bilaterally in the OTJ. In addition, chess players compared to controls demonstrated increased mean diffusivity within two clusters of the left superior longitudinal fasciculus. Beside these differences there were no further anatomical features that were different between chess players and control subjects even when the statistical threshold was lowered. Thus, we did not identify substantial anatomical differences in the distributed cognitive network including several brain areas in the frontal and parietal regions. We also did not identify differences between chess players and controls in the caudate nucleus. Thus we could not replicate the findings of Duan et al. (2012a) who identified reduced caudate volumes in chess players compared with control subjects. However, the volumes of the left and right caudate nucleus were inversely related to the years of chess playing experience revealing that more years of experience goes

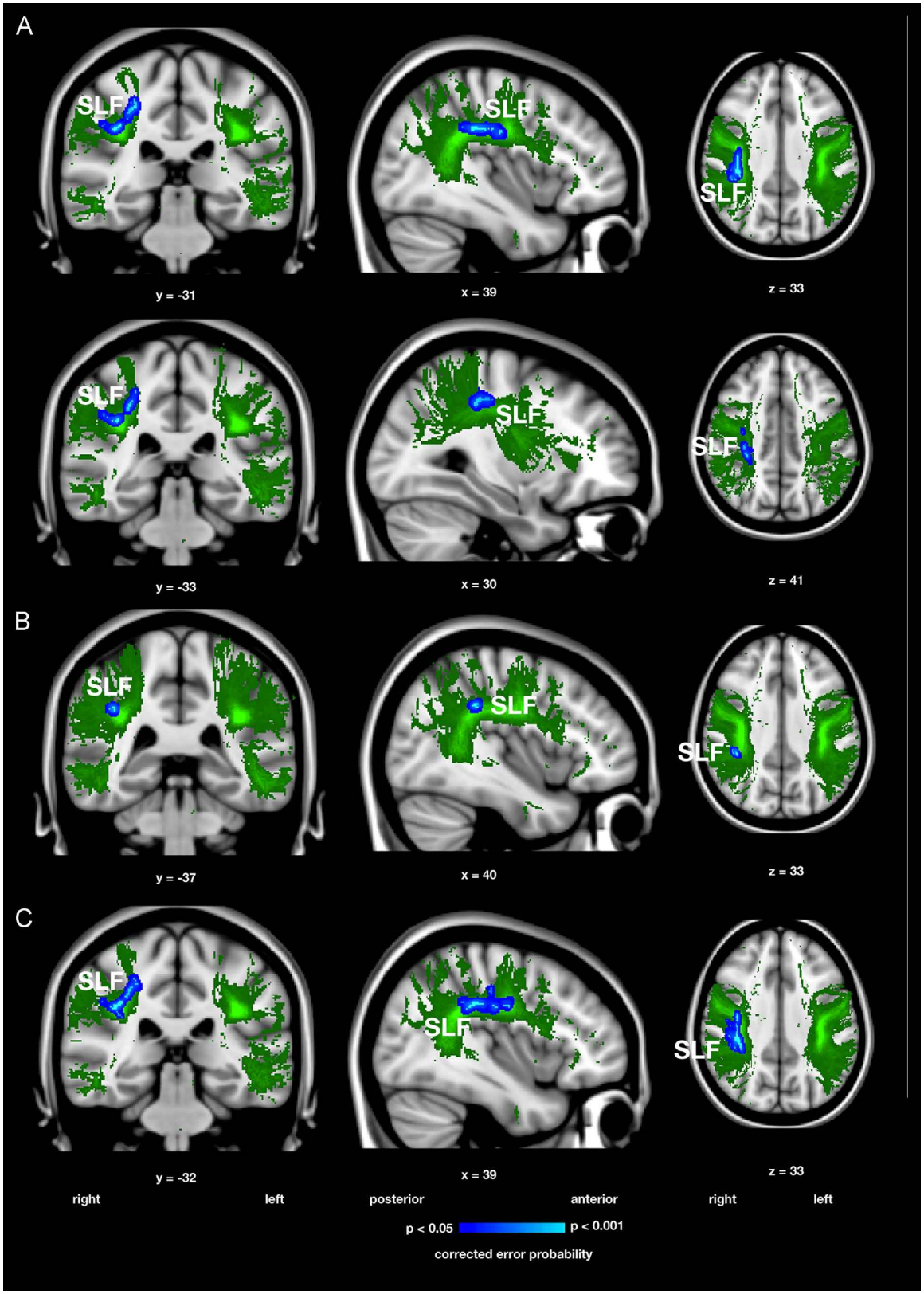

Fig. 2. Associations between mean/axial diffusivity and the Elo score as well as lifetime hours of chess training. Shown are clusters with negative correlations (blue–lightblue) between the Elo score and mean diffusivity in the right superior longitudinal fasciculus (SLF, A) and between the Elo score and axial diffusivity in the right SLF (B), in the same region as the cluster in A. Lifetime hours of chess training correlated negatively with mean diffusivity in the right SLF (C), in the same region as the clusters in A and B. The regions of interest (left and right SLF) subjected to the statistical analysis are shown in green–lightgreen. The colour bar indicates alpha error probability that is corrected for multiple comparisons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Regions with negative correlations between mean/axial diffusivity and the Elo score as well as lifetime hours of chess training.

Correlations between	Letter in Fig. 2	Number of voxels	Error probability	MNI coordinates		
				x	*y*	*z*
Elo score and mean diffusivity						
Right superior longitudinal fasciculus (below supramarginal gyrus)	A	298	0.027	39	−31	33
Right superior longitudinal fasciculus (below supramarginal gyrus)	A	170	0.033	30	−33	41
Elo score and axial diffusivity						
Right superior longitudinal fasciculus (below supramarginal gyrus)	B	26	0.031	40	−37	33
Lifetime hours of chess training and mean diffusivity						
Right superior longitudinal fasciculus (below supramarginal gyrus)	C	793	0.015	39	−32	33

p-values are corrected for multiple comparisons using permutation-based non-parametric testing across space (FSL's randomise tool with 5000 permutations). Abbreviations: Fig., figure; MNI, Montreal Neurological Institute.

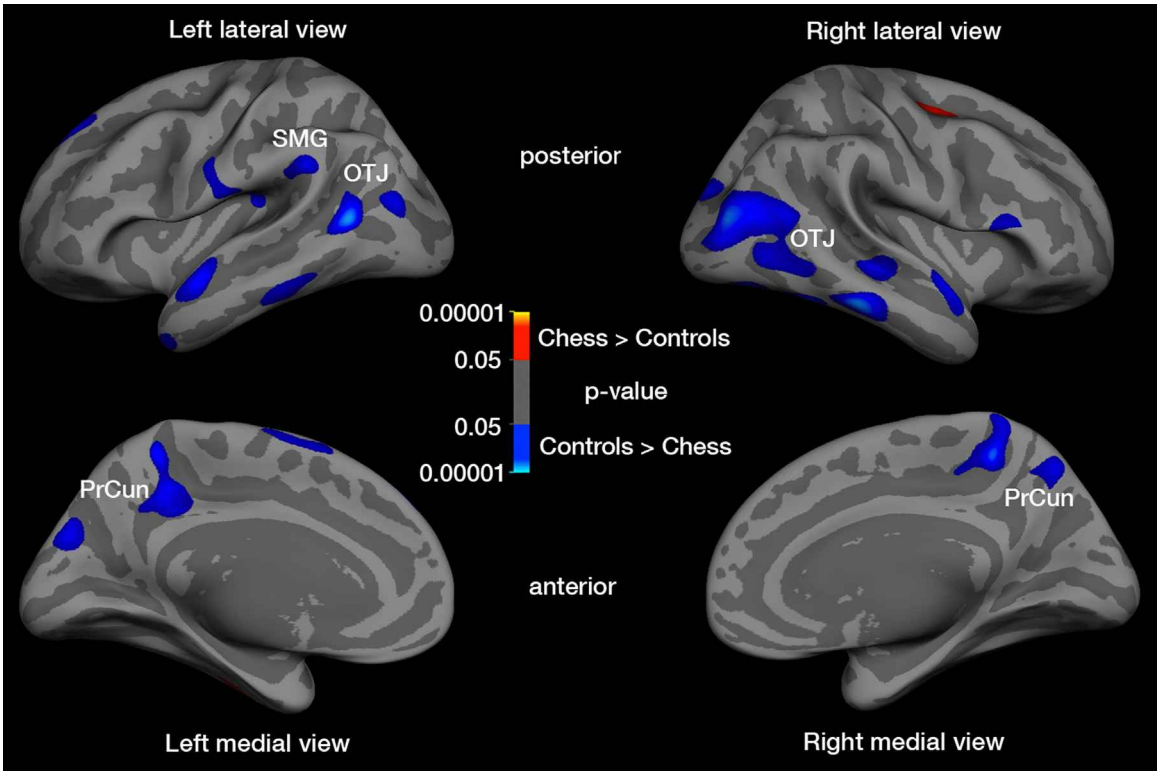

Fig. 3. Regions with reduced cortical thickness in chess players revealed in an exploratory whole brain analysis. Shown are clusters with reduced cortical (blue–lightblue) in the left and right occipito-temporal junction (OTJ), precuneus (PrCun), and supramarginal gyrus (SMG) besides other regions in chess players compared with control men. Note there is only one cluster with increased cortical thickness (red–yellow) in chess players. Colour bars indicate alpha error probability uncorrected for multiple comparisons. The right OTJ cluster is the only cluster that survives cluster extent error corrections for multiple comparisons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with smaller caudate nucleus volumes. These negative correlations are in line with findings reported by Duan et al. (2012a).

The OTJ for which we identified the only substantial anatomical difference between chess players and novices in terms of GM and cortical thickness is known to be involved in the recognition of objects and their relations. This region has repeatedly been shown to be activated when chess players process visually presented chess game positions (Bilalić et al., 2010, 2011). Bilalic et al. relate these activations to the advantage of chess experts in object perception utilised during the perception of chess-specific stimuli (e.g. chess configurations). The OTJ is a brain area, which is not only involved in the perception of chess-related stimuli, but is rather a brain area that is involved in many different perceptional processes, which are not directly related to chess-specific object perception, e.g. watching at signed narratives (Courtin et al., 2011) and during shape perception (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2007). However, the common denominator of these perceptual processes is the association of visual information with higher cognitive stimulus properties. The OTJ is partly overlapping with the posterior superior temporal sulcus (STS) region, which has also been recognised as a brain area devoted to integrate information from different modalities (Hein and Knight, 2008).

The precuneus (medial parietal lobe) seems to play an important role in chess playing (Wan et al., 2011). Although we did not find any difference in the precuneus in our VBM analysis when correcting for multiple comparisons, we found evidence for structural differences in the precuneus in our uncorrected SBM analysis where cortical thickness was reduced in the left and right precunei in chess players compared with that of control men (Fig. 3). The importance of the precuneus for playing chess on a

high level has further been elaborated by Duan et al. who showed a broader task-induced deactivation of the DMN in a chess problem-solving task in chess experts compared with novices (Duan et al., 2012b) as well as enhanced integration (functional connectivity) between the caudate nucleus and the regions of the DMN including the precuneus in the resting-state in chess experts compared with novices (Duan et al., 2012a). The deactivation of the DMN has been previously explained as the reallocation of cognitive resources in order to focus more on the task and suppress unrelated and irrelevant thoughts (Fox et al., 2005). There is no doubt that chess playing benefits from such a neural mechanism. Furthermore, it has also been shown that individual differences in resting-state functional connectivity predict task-induced BOLD activity (Mennes et al., 2010).

Taken together, chess experts demonstrate specific anatomical features in at least three brain areas (OTJ, caudate nucleus, and precuneus) that are obviously important nodes in the neural network activated during chess playing.

4.2. Is bigger better or is less smarter?

But why are these regions, which are obviously that strongly involved in identifying chess positions, smaller in terms of GM volume and demonstrate reduced cortical thickness in chess players? Actually, this is difficult to explain on the basis of the current knowledge since it is not that clear how cortical thickness and GM volume are related to the performance in psychological tasks.

Mostly, it is argued that measures of cortical morphology (GM volume or cortical thickness) are positively related to cognitive performance. This "bigger-is-better" or "thicker-is-better" assumption is reflected for example in findings of training-related enhancement of performance and associated increases in GM volume or cortical thickness (Jancke, 2009; May, 2011). There are also studies demonstrating a reduction in GM volume or cortical thickness as a consequence of non-use (Langer, Hänggi, Muller, Simmen, & Jäncke, 2012). Other studies identified a positive correlation between cortical thickness as well as GM volume and psychological performance measures (Karama et al., 2011; Engvig et al., 2010). On the other hand, cortical thickness generally declines with ageing and this goes hand in hand with a decline of cognitive functions (Rathi et al., 2013). Thus, it seems to be quite straightforward to argue that increased cortical thickness and GM volume would be associated with better performance in psychological tasks.

In fact, the picture is a bit more complicated since some studies have shown that deficits in psychological functions can also be associated with increased cortical thickness. For example, individuals with congenital amusia compared to that of healthy control subjects show enhanced cortical thickness and reduced GM volume in the auditory cortex (Hyde et al., 2007). Other studies have shown that it is the rate of increase in cortical thickness rather than thickness itself that correlates with better cognitive performance (here with psychometric intelligence) (Shaw et al., 2006). Studies combining morphometric with neurophysiological measures also revealed partly inconclusive results. For example, studying normally developing children revealed a negative correlation between blood oxygenation level dependent (BOLD) responses and cortical thickness in fronto-parietal regions in an orthographic task (Lu et al., 2009). A more recent study from our own lab identified that a thinner auditory cortex was associated with larger N1 amplitudes to acoustic stimuli (measured with electroencephalography) reflecting a more efficient neurophysiological processing in the auditory cortex that is associated with a thinner auditory cortex (Liem, Zaehle, Burkhard, Jancke, & Meyer, 2012).

The reason for this, at a first glance, heterogeneous picture depends on the fact that GM volume and cortical thickness are influenced by several microscopic features that can be influenced at different stages during ontogeny. Meanwhile it is known that GM volume and cortical thickness as measured by MRI methods are influenced by early sensory influences, maturation processes, age-dependent influences, as well as use-dependent influences. Each of these factors most probably influences GM volume and cortical thickness differently. For example, it has been suggested that sensory deprivation during early childhood may cause a substantial reduction of pruning of the exuberant cortico-cortical and/or cortico-thalamo-cortical connections that exist during early infancy. This reduced pruning due to sensory deprivation will result in a greater survival of these exuberant connections and a thicker visual cortex. This has been suggested for early or congenitally blind subjects who demonstrate a thicker visual cortex than sighted control subjects (Anurova, Renier, De Volder, Carlson, & Rauschecker, 2014). Changes in GM volume or cortical thickness in adulthood due to training or practice are mostly likely caused by axonal sprouting and/or an increase in spine density in brain structures critical for a certain task or performance. But which of these microscopic aspects are different in the chess players will be examined in our study? Our chess experts have commenced playing chess between 4 and 14 years with a mean age of 8 years. Thus, it is possible that most of our chess players have received substantial chess-related stimulation during early childhood. From neurophysiological studies we know that the rapid phase of synaptogenesis in early childhood is followed by subsequent longer period of pruning during which synapses are eliminated by about 40% to reach near-mature levels at 11 years of age (Huttenlocher, de Courten, Garey, & Van der Loos, 1982; Huttenlocher & de Courten, 1987; Huttenlocher, 1984, 1990). Thus, it could be possible that the chess-specific stimulation of the OTJ might have caused a stronger pruning of cortico-cortical and/or thalamo-cortical connections in chess experts than in control subjects since the chess experts might have used the OTJ to cope with the chess tasks. We are aware of the fact that our interpretation is partly speculative, but we believe that it is highly plausible in the context of the sensory-deprivation studies. An interesting strategy to directly test our hypothesis would be to compare chess-experts commenced playing chess very early life with chess experts who have started substantially later (e.g. older than 18 years).

We also identified increased mean diffusivity in the left superior longitudinal fasciculus in chess players compared with that of control men. In addition, the Elo score and lifetime hours of chess training were inversely related to mean diffusivity in the right superior longitudinal fasciculus. The superior longitudinal fasciculus connects parieto-temporal brain regions with frontal brain areas and is a major fibre tract of the dorsal visual stream and also the dorsal attentional control system (Capotosto, Babiloni, Romani, & Corbetta, 2009). Thus, this fibre tract is necessary for attentional control and the transformation of visual information to the frontal executive system. Thus, it is plausible to assume that this fibre tract is involved in the control of psychological operations used during chess playing.

Increased MD (and decreased FA) reflects more radial diffusion (perpendicular to the fibres) than axial diffusion (along the fibres) or both. In clinical populations, increased MD and/or decreased FA are commonly interpreted as reduced WM integrity and reduced fibre coherence (Assaf & Pasternak, 2008; Sexton, Mackay, & Ebmeier, 2009). Increased FA and/or decreased MD in diseases are rarely reported in the DTI literature, although the loss of fibres that turn, cross, and/or twist within a single voxel should be accompanied by an increase in FA and a decrease in MD. Denser connected components within a network, a potential structural

marker of increased network efficiency, might consist of an increased number of fibres turning, crossing, and/or twisting that would be reflected by increased MD and decreased FA. Although, there is consensus that the axonal membranes are the most important hindrance for water diffusion in fibre tracts (Beaulieu, 2002) and that myelin is not needed for anisotropic diffusion and only modulates the diffusion tensor by about 20% (Gulani, Webb, Duncan, & Lauterbur, 2001), the actual and individual contributions of the axonal membrane, myelin, neurofilaments, and microtubuli are still a matter of dispute (Beaulieu, 2002). DTI neuroplasticity studies suggested that better motor or cognitive functioning is associated with increased FA/decreased MD as well as associated with decreased FA/increased MD (Bengtsson et al., 2005; Hänggi, Koeneke, Bezzola, & Jäncke, 2010; Schmithorst & Wilke, 2002).

4.3. Limitations

Several limitations of the present study are worth mentioning. First, chess involves an abstract skill-set, which unquestionably draws upon a multitude of cognitive functions and their interactions. Using a univariate localizationalist approach in looking at the complex skills involved in chess is an inherent shortcoming of the study. A topological approach of both structural and functional whole-brain connectivity networks as opposed to a topographical approach should be applied in future studies that aim at investigating the neural correlates of chess expertise. Second, although differences in diffusion parameters were found between the groups, these results should not be considered as direct evidence for enhanced or reduced structural connectivity. Diffusion parameters derived from DTI data cannot provide such information. Third, due to logistical restrictions and time constraints it was not possible to assess the cognitive profile of the chess players in greater detail. Forth, although the sample size of the present study was of moderate size ($n=40$), further morphological differences that would survive corrections for multiple comparisons might be revealed if using larger samples. Last, due to the fact that we investigated a cross-sectional sample, we cannot infer the direction of causality. Longitudinal studies are needed to track down whether the morphological alterations revealed in the chess player's brain are the cause (nature, genetic disposition for a particular trait) or the consequence (nurture, structural neuroplastic adaptations) of the intensive and long-term chess training and experience. A longitudinal study design also permits to investigate the dynamics of the morphological alterations, i.e. whether they mainly occur early in chess training course or whether these changes are continuously established across the entire course of chess training.

4.4. Conclusions

We showed to the best of our knowledge for the first time that the grey and white matter architecture is altered in the brain of expert chess players compared with that of control subjects. Our structural findings complement and extent the results of the functional imaging studies investigating brain activity associated with chess-relevant cognition. Structural and functional investigations on chess expertise in particular might help to shed light on the neural substrate underlying human problem-solving mechanisms in general.

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