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Original Article

Lenticular nucleus volume predicts performance in real-time strategy game: cross-sectional and training approach using voxel-based morphometry

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It is unclear why some people learn faster than others. We performed two independent studies in which we investigated the neural basis of real-time strategy (RTS) gaming and neural predictors of RTS game skill acquisition. In the first (cross-sectional) study, we found that experts in the RTS game StarCraft[®] II (SC2) had a larger lenticular nucleus volume (LNV) than non-RTS players. We followed a cross-validation procedure where we used the volume of regions identified in the first study to predict the quality of learning a new, complex skill (SC2) in a sample of individuals who were naive to RTS games (a second (training) study). Our findings provide new insights into how the LNV, which is associated with motor as well as cognitive functions, can be utilized to predict successful skill learning and be applied to a much broader context than just video games, such as contributing to optimizing cognitive training interventions.

Keywords: real-time strategy games; game performance; training; neuroimaging

Introduction

Some people learn faster than others. Skill learning—the process that makes people more accurate, efficient, and faster in a given task—depends on several personal characteristics. From the psychological perspective, there have been theories and data regarding the prediction of learning based on individual differences in noncognitive and cognitive determinants since the 1950s. Specifically, skill learning was well predicted by age;¹ general ability measures, such as verbal, spatial, and numerical reasoning; as well as working memory capacity^{2–4} and fluid intelligence.⁵ Additionally, Yesavage *et al.*⁶ showed that individuals with higher

mental status in terms of their scores in the Mini-Mental State Examination⁷ were characterized by better outcomes after memory training. There were also attempts to verify more basic cognitive abilities like perceptual–speed and psychomotor characteristics as predictors of skill development in complex paradigms (i.e., air traffic control simulation task).⁸ It needs to be pointed out that because the process of skill acquisition is dynamic, cognitive and noncognitive constructs may differentially determine individual differences in task performance, depending on, for example, the type and stage of the task's practice.⁹ For example, one of the most well-documented associations between individual differences in the noncognitive domain and skill

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acquisition was from the personality domain (e.g., Big Five Inventory).¹⁰

The picture is even more complicated when it comes to the relationship between the ability to master new skills and its neuroanatomical predictors. Plenty of cross-sectional imaging studies have demonstrated structural brain differences between experts in music, sport, and video games and nonexperts and showed that experts had more gray matter volume (GMV) in certain brain regions.¹¹⁻¹⁷ However, deliberate practice is necessary but not sufficient to account for individual differences in experts and novices.¹⁸⁻²⁰ One of the criticisms of cross-sectional studies as providing the evidence for practice-dependent brain changes is that preexisting differences in brain organization could explain some of the differences we observe between experts and nonexperts. For example, the GMV in the hippocampus of London taxi drivers may be larger because they have regular experience with navigation, or because they have some brain structure characteristics that predisposed them to become taxi drivers.²¹ Another study showed complementary evidence in the domain of specific predispositions and experience-dependent brain plasticity.²² There are separate groups of studies that assessed regional brain morphometry characteristics of subjects who underwent longitudinal assessments using magnetic resonance imaging (MRI).²³ They showed changes in gray matter (GM) during skill acquisition of, for example, juggling,²⁴ playing video games,^{25,26} learning languages,²⁷ playing music,^{28,29} and aerobics,^{30,31} and established a theory of brain volume (BV) expansion in task-relevant areas as an indicator of neural plasticity,³² especially during the initial stage of learning.³³ Given the above-described examples, the debate about the predictive neural markers of learning has thus far been inconclusive and still is one of the most challenging areas in cognitive neuroscience. Currently, we can observe a growing interest in how individual differences in the structure of the human brain can influence the ability to learn and master complex skills.^{34,35} Particularly, since the brain's GM characteristics are one of the most adequate biological structures that could determine cognitive abilities, it is essential to look at it as a variable predicting training efficacy.

Scientists reported that preexisting neuroanatomical profiles, including both cortical

thickness and white matter (WM) microstructure, predict the outcomes of individuals following multistrategic memory training.³⁶ There is also evidence suggesting that variance in WM structure correlates with the ability to learn musical skills in nonmusicians, offering an alternative explanation for the structural differences observed between musicians and nonmusicians.³⁷ Only a few studies have explored preexisting neural characteristics in the case of learning how to play video games, as an example of complex skill acquisition. In 2018, Momi et al.³⁸ identified that the lingual gyrus is involved in the ability to predict the trajectories of moving objects in action video games. Other researchers have mostly investigated the volumetric characteristics of the basal ganglia (BG), a group of subcortical nuclei involved in motor and procedural learning, as well as in reward learning and memory.^{39–41}

In the study reported here, we examined brain GMV-related differences in the acquisition of skill in a novel and complex cognitive-motor task, the real-time strategy (RTS) game. We chose the game StarCraft[®] II (SC2) on the basis of evidence suggesting that playing this cognitively demanding strategic video game requires a host of specialized skills, including translating mental plans into motor movements, performing actions with precise timing, bimanual hand coordination, and processing rapid visual information.⁴² These skills are trained and become increasingly automatic with the amount of practice.43 What is more, we can use telemetry data from the game (e.g., perceptionaction cycle (PAC) latency, actions per minute (APM), or hotkey select (HS) usage) to have more detailed measures of skill learning during the course of the game and use it for further investigations. Moreover, a player's current skill level can be determined by their position in one of the six tiers in the game (a detailed description is provided in the Methods section), and what is also important, it classifies players on the basis of the Elo score-like rating systems that allow for the objective assessment of changes in player's expertise over time. One additional benefit of SC2 is that it belongs to a group of games that comprise professional electronic sports (eSports). Because competitive and professional players of eSports titles dedicate a great deal of time to playing individual games, they are a sample with a more stable source



Figure 1. Overview of the study design. First, the GMV ROIs were identified in the cross-sectional study (A), and then they were used to predict RTS game skill acquisition in an independent training study (B). As a next step, a longitudinal study was conducted with the same RTS game as in the first study (SC2) on a new group of NVGPs. GMV, gray matter volume; MRI, magnetic resonance imaging; NVGPs, non-video game players; ROIs, regions of interest; SC2, StarCraft II.

of video game experience. This makes the analysis of connections between in-game actions and brain structures more feasible.

In the current study, we wanted to test whether it is possible to predict the level of skills acquired during RTS game training on the basis of specific brain GMVs. Our main hypothesis tested the possibility of predicting the quality of skill acquisition (SC2) on the basis of the volume of brain regions identified in a group of expert players. In our attempt to understand the neural predictors of learning success in the SC2 environment, we took a two-step approach. First, we analyzed a cross-sectional sample of expert RTS players (those placed in the top five SC2 leagues) and non-video game players (NVGPs) to investigate whether RTS video game experience is associated with volumetric differences in GM. In the second step, we used information gathered during the first study to inform the analyses of data gathered during the second training study, where naive volunteers were trained with SC2.

With those steps, we followed a cross-validation procedure⁴⁴ in which one sample of subjects is used to identify brain regions (ROIs) that differ

two groups (in our case, RTS experts and NVGPs), and another sample (NVGPs) to predict skill acquisition (in our case, complex skill learning during SC2 training) from the ROIs identified in the first step. Details of this procedure are depicted in Figure 1A and B. To our knowledge, this is the first study where individual neuroanatomical differences between healthy adults were used as a predictor of learning outcomes in an RTS action video game.

Materials and methods

The cross-sectional study

Participants. Sixty-four (n = 64) right-handed, male subjects with a mean age of 24.55 years (SD = 3.66) participated in this study. Two subjects (n = 2) were excluded from the analysis because of bad quality MRI data (image artifacts), so the final sample consisted of 62 (n = 62) participants. All subjects were male because of difficulties in recruiting female participants with adequate video game experience. All subjects completed an online questionnaire about demographics, education status, and video game playing experience. In our self-designed questionnaire (online questionnaire on

the GEX platform),⁴⁵ we asked additional questions to assess how often individuals engage in various game genres. We broke the game genres down into the following categories: first-person shooter (FPS), RTS, role playing, sports, a multiplayer online battle arena, racing, puzzles, fighting, turn-based strategy, adventure, and platform games. Inclusion criteria for the RTS experts in our study were as follows: (1) experience with SC2 play, (2) played RTS games at least 6 h/week for the previous 6 months, (3) declared playing SC2 for more than 60% of the total game play time, and (4) is an active player (played matches in the last two seasons) and has been placed in one of the five SC2 leagues (Gold, Platinum, Diamond, Master, and Grandmaster). Inclusion criteria for NVGPs were as follows: little or no previous experience with RTS video game play, and experience with other types of video games, totaling no more than 8 h/week (most played less than 6 h) over the past 6 months. The mean age of the RTS expert group (n = 31) was 24.71 years (SD = 4.27) and 24.39 years (SD = 3.00) in the NVGP group (n = 31).

The education level was matched between groups (all participants were at an undergraduate level). The mean of years of education of the RTS expert group was 15.55 years (SD = 2.77) and 16.10 years for the NVGP group (SD = 2.95). We controlled for working memory capacity using the Operation Span Task (OSPAN);⁴⁶ the mean score was 51.77 (SD = 12.74) for RTS experts and 51.71(SD = 13.19) for NVGPs. The average hours per week of video games played in different genres from the last six months in RTS experts was 22.74 h (11.79) and 2.39 h (2.28) for NVGPs. The minimum for RTS experts was 10 h/week for the previous 6 months (experience with game genres presented in Table S1, online only). The data from these participants are also a part of our other study,⁴⁷ but the GMV analyses are unpublished in the case of all of the included participants. The overall video game playing characteristics and average weekly playtime in each video game genre are presented in Table S1 (online only). None of the participants had a history of neurological illness, and they did not declare the use of any psychoactive substances. We also had access to information about each player's overall performance in the game (wins and losses from the last two seasons) and the number of games played.

All subjects participated in additional MRI and cognitive measurement sessions in order to obtain diffusion tensor imaging (DTI) measurements and assess several cognitive functions, which were not related to the project described in this article.

All subjects gave their informed consent to participate in the study, in accordance with the SWPS University Ethical Committee. All participants were male because of difficulties in recruiting female participants with sufficient video game experience. They were paid (approximately 52 USD) for participating in the study.

MRI image acquisition. High-resolution wholebrain images were acquired on a 3-Tesla MRI scanner (Siemens Magnetom Trio TIM, Erlangen, Germany) equipped with a 32-channel phased-array head coil. T1w images were acquired using an MPRAGE sequence with the following specification: repetition time (TR) = 2530 ms, echo time (TE) = 3.32 ms, flip angle (FA) = 7°, field of view (FOV) = 256 mm, inversion time (TI) = 1100 m, and voxel size = $1 \times 1 \times 1 \text{ mm}^3$, 176 axial slices. Foam padding was used around the head to minimize head motion during scanning. During these sequences, subjects were asked to relax and try not to fall asleep or move.

The study was a part of a larger project where participants underwent three more MRI sessions (two functional MRI tasks and DTI session), and a cognitive session on other days.

Data preprocessing. The same approach was used for both studies. For data preprocessing and statistical analyses, we used statistical parametric mapping (SPM8, Wellcome Trust Center for Neuroimaging, London, UK) running on MATLAB R2015 (The Mathworks, Inc., Natick, MA). We applied standard processing steps as proposed by Ashburner and Friston:⁴⁸ (1) checking for anatomical abnormalities and scanner artifacts for each participant, (2) setting the image origin to the anterior commissure (AC), (3) manual reorientation to canonical T1 (canonical\avg152T1.nii), (4) segmentation of tissue classes, (5) normalization using DARTEL, (6) modulation of different tissue segments, and (7) smoothing. A segment algorithm was used in order to obtain basic tissue classes: WM, GM, and cerebrospinal fluid (CSF).48 Next, a study-specific template was computed from all participants using the Diffeomorphic Anatomical Registration through the Exponentiated Lie Algebra (DARTEL) toolbox⁴⁹ to determine the nonlinear deformations for warping all the GM and WM images so that they match each other. This step was followed by an affine registration of the GM maps to the Montreal Neurological Institute (MNI) space. Modulation (Jacobian determinant) of different tissue segments by nonlinear normalization parameters was applied to correct for individual differences in brain sizes. Finally, data were smoothed with an 8-mm isotropic Gaussian kernel. A group-wise brain mask was computed for statistical analysis to decrease false positives occurring outside the brain. Coordinates of significant effects are reported in the MNI space. XjView was used to identify the structures showing effects (http:// www.alivelearn.net/xjview). The results were visualized using BrainNet Viewer software⁵⁰ (http:// www.nitrc.org/projects/bnv/).

Statistical analysis. Differences in GMV between RTS experts and NVGPs were calculated using two-sample *t*-tests. The two-group difference was adjusted for the participant's age. Given that the total intracranial volume (TIV) could affect the relationships between regional BV and measures of skill acquisition, we included TIV in our analyses. An explicit mask was employed (group brain mask with no threshold) to exclude false positives. The group mask was computed by summing GM, WM, and CSF (unmodulated) for each individual and then computing an average mask for the whole group. The masking was performed using MaskingToolbox.⁵¹ The model was computed without an absolute threshold since clusters that include voxels with smaller intensity are excluded from the statistical analysis.⁵¹

Whole-brain voxel maps were thresholded with 5% family-wise error (FWE) cluster size inference, with a P = 0.001 cluster-forming threshold (a minimal cluster size of 2125 voxels).

Next, the average GMV signal from a significant cluster was extracted using the MarsBaR toolbox.⁵² Then, the GMVs (both right and left putamen and the pallidum) were fed to the correlation analysis with our SC experience indicator. The indicator of SC2 experience was calculated using the number of hours spent playing all video games (weekly averaged) over the last 6 months, multiplied by the declared percentage of time spent playing SC2 (e.g.,

when somebody declared playing video games for 30 h a week and 80% of this time spent on RTS, their index was 30×0.8).

Training study

Participants. Twenty subjects (n = 20) participated in the study, but four were excluded from analysis because of low MRI data quality (image artifacts) (n = 2) as well as training dropout (n = 2). The final sample consisted of 16 (n = 16) righthanded participants with a mean age of 22.94 years (SD = 2.11): 5 males (22.20 years, SD = 2.39) and 11 females (23.27 years, SD = 2.01). The mean years of education was 15.10 years (SD = 1.93). All subjects completed the same online questionnaire as described above (cross-sectional study). Their mean OSPAN score was 52.31 (SD = 18.15). We also asked about their video game playing experience, and the number of mean weekly hours spent playing video games over the last 6 months was 0.97 h (SD = 1.16), with no experience in any action video game genres. None of the participants had a history of neurological illness, and they did not report using psychoactive substances.

All subjects provided written informed consent to participate in the experiment, and the study protocol was approved by the SWPS University Ethical Committee. They were paid (approximately 180 USD) for participating in the study.

Experimental task. Sixteen participants carried out 30 h of SC2 gaming in a controlled laboratory setting. The training lasted from 3 to 4 weeks (a minimum of 6 h per week, maximum of 10 h per week), with a prohibition of gaming elsewhere (outside the laboratory). Before participants started the training, they had an introduction session with the SC2 trainer. The training was carried out using dedicated desktop PC running Windows 7 (professional edition, 64-bit operating system) equipped with a dedicated graphic card (NVIDIA GeForce GTX 770), 8GB or RAM and a 24" LED display, allowing to play at high graphic quality (1920 \times 1080 pixels resolution, 60Hz). Participants played the game using a mouse/keyboard/headset setup.

In SC2, game players need to build an economy (gathering resources and building bases) and develop the military resources (training units) in order to beat their opponents (destroying their base and army). Cognitive and motor challenges of the SC2 game are described in the Introduction. The participants played using only one race (Terrans) against AI (artificial intelligence).

There were eight possible difficulty levels in the SC2 matches: very easy, easy, medium, hard, harder, very hard, elite, and cheater. For each victory, the player received 1 point. If the player lost, they lost 1 point (-1). The scoring intervals for each level of difficulty were determined as follows: very easy, 0–4 points; easy, 5–8 points, medium, 9–12 points; hard, 13–16 points; harder, 16–20 points; very hard, 21–24 points; elite, 25–28 points; and cheater, up from 29 points. None of the participants reached the cheater level, so we included seven levels in the analysis.

We computed the variable indexing the weighted time spent on every level of SC2 difficulty (the time spent on the second level was multiplied by 2, the time spent on the third level by 3, and so on) for each participant. The final result is a standardized (group-wise) sum of the time spent on all difficulty levels, reflecting performance in the game.

RTS game skill acquisition indicator =

 $(hrs^{*}1) + (hrs^{*}2) + (hrs^{*}3) + (hrs^{*}4)$ + $(hrs^{*}5) + (hrs^{*}6) + (hrs^{*}7)$

MRI image acquisition. High-resolution T1weighted (T1w) images were collected using the IR-FSPGR sequence performed using a 3T MRI GE Discovery MR750w scanner before RTS training. The MRI scanner was equipped with an 8-channel phased-array head coil. T1w images were acquired with the following specification: TR = 7 ms, TE = 3ms, $FA = 11^\circ$, FOV = 256 mm, TI = 400 ms, and voxel size = $1 \times 1 \times 1 \text{ mm}^3$, 200 axial slices. Foam padding was used around the head to minimize head motion during scanning. Subjects were asked to try and relax but not to fall asleep or move. All participants performed a structural MRI and cognitive assessment consisting of several cognitive tasks at two time points: before (T0) and after 30 h of video game practice (T1). In the current study, we focused on pretraining (T0) MRI scans.

Data preprocessing. The same approach was used for both studies. Details of data processing are described in the Materials and methods, data preprocessing section of the cross-sectional study.

Statistical analysis. We used one-sample *t*-tests with the same steps as described in the Mate-

rials and methods, Statistical analysis section of the cross-sectional study. Next, the putamen and pallidum were defined using the AAL-116⁵³ atlas and on the basis of the results from the crosssectional study. Owing to the fact that it was a group of novices (NVGPs), we decided to check both the putamen and pallidum (bilaterally), and not only within the results obtained from the crosssectional study where expert video game players were recruited. We aimed to explore these data more as a result of different skill levels between our groups in the cross-sectional and training studies. Each ROI was extracted using the MarsBaR toolbox.⁵² Then, the GMV was fed into the correlation analysis. Because our data did not meet the assumptions for regression models, all correlational analyses were conducted using Spearman's correlation coefficient. Correction for multiple comparisons (FDR) for correlation analysis was applied.

Results

The cross-sectional study

Higher GMV in RTS experts compared with NVGPs. Thirty-one RTS experts (in the SC2 game) were compared with 31 NVGPs using highresolution T1w images. GMV differences between players and nonplayers were calculated using whole-brain voxel-based morphometry (VBM) analyses. RTS experts had a significantly higher regional GMV in the right lenticular nucleus (RLN; the putamen and pallidum) compared with nonexperts (peak MNI coordinates: x = 22; y = -11; z = 7; t = 5.54; cluster size = 2125 voxels), P = 0.04corrected for multiple comparisons with an FWE correction at the cluster level using cluster size. The obtained result is in the lenticular nucleus (LN), a structure consisting of the putamen and pallidum (also commonly called the globus pallidus), which are separated by WM tracts called the lateral medullary lamina. In the whole-brain analysis, the RLN was the only area showing a significant difference in RTS experts in comparison with NVGPs (Fig. 2A). There were no significant differences in GMV for the reverse contrast (NVGPs versus RTS experts).

We calculated Cohen's d together with power (Fig. 2B). Cohen's d was 1.061 and using G*Power,⁵⁴ we had 82% power to detect differences between groups.



Figure 2. Differences in GMVs between RTS expert players and nonplayers. (A) Results from VBM analyses showing RTS experts > NVGPs difference in GMV, part of the LN (peak MNI coordinate x = 22; y = -11; z = 7; t = 5.54; cluster size = 2125 voxels; P = 0.04). Clusters from the whole-brain exploratory analysis using FWE cluster correction. The LN is a collective name given to the putamen and pallidum (also commonly called the globus pallidus); both are nuclei in the basal ganglia. (B) Presentation of differences in GM between RTS experts and NVGPs. Cohen's *d* presented to show the effect size of the difference (d = 1.06). GMV, gray matter volume; NVGPs, non-video game players; ROIs, regions of interest; L, left; R, right.

No significant Spearman's correlation was observed between the GMV within the LN and the index of experience in SC2 (hours spent playing SC2, the RTS expert group only), r = 0.19, P = 0.32.

The training study

Regional GMV as a predictor of RTS game skill acquisition. In the next study, we used the RTS game SC2 as a tool to study complex skill learning in a longitudinal setup. We computed the variable indexing the weighted time spent on every level of SC2 difficulty, which reflects performance in the game. Figure 3 represents the time (hours) spent on each level for all participants.

To specifically target our hypothesis, we employed the ROI analysis method for longitudinal data. Our ROIs were defined on the basis of the results from our cross-sectional study, which showed that SC2 performance was associated with volumes of the ventral striatum (the putamen and pallidum).

We used anatomical ROIs based on GMV differences in areas that were related to RTS gaming activity in our first cross-sectional independent study. We found that the volume of both putamens (left: r = 0.67, P = 0.01; and right: r = 0.57, P = 0.02) (Fig. 4A) and both pallidums (left: r = 0.62, P = 0.01; and right: r = 0.62, P = 0.01) correlated positively with RTS game skill acquisition (Spearman's correlation, see Fig. 4B). No correlation metrics survived the false discovery rate (FDR) P < 0.05correction for multiple comparisons, so the results presented here are uncorrected for multiple comparisons. There were no training-related changes in the GVM of the examined brain structures.

Regional GMV and PAC latency in RTS skill acquisition. Our next step was to check what type of in-game behavior correlates with VBM assessments of GMV. Using measures of cognitive-motor abilities extracted from SC2 game replay data from 16 participants, we constructed three indicators based on in-game actions performed by trainees: (1) PAC latency, time (in milliseconds) from a pointof-view (PoV) change (switch in focus of attention) to the occurrence of the first action issued by the player (indexing motor reaction); (2) HS usage, expressed as the average number of hotkey presses per minute in each game, where each such action represents an automated selection of multiple units or buildings; hotkeys are used to aid in the management of dispersed elements of the game; and (3) APM, the average number of actions performed during each minute of the game (a measure of



Figure 3. Distribution of the average time (hours) spent on each difficulty level in SC2 for all participants. Presentation of possible difficulty levels in the SC2 matches: very easy, easy, medium, hard, harder, very hard, and elite. None of the participants reached the cheater level, so we included only seven levels. The weighted time spent on each level of SC2 difficulty (the time spent on the second level was multiplied by two, the time spent on the third level by three, and so on) was computed for each participant. The final result is a standardized (group-wise) sum of the time spent on all difficulty levels, which reflects performance in the game. This indicator was used in the correlational analyses. Presentation of average time (M) and standard errors (SE) for the number of hours played for each difficulty level in SC2.

cognitive–motor speed). We defined PAC latency as a cognitive marker of SC2 expertise, and APM and HS usage as the motor markers of SC2 expertise.⁴² We divided the whole training time of each trainee into quartiles and computed PAC latency, HS usage, and APM for each quartile (within-subject).⁴²

We found a significantly negative correlation between PAC latency in the first quartile and GMV in all of our predefined ROIs (the left and right putamen (left: r = -0.58, P = 0.02; and right: r = -0.43, P = 0.10 tendency level; Fig. 5A), as well as both pallidums (left: r = -0.57, P = 0.02; and right: r = -0.54, P = 0.03; Fig. 5B). No correlation analysis survived the FDR P < 0.05 correction for multiple comparisons, so the results presented here are uncorrected for multiple comparisons. Correlations between PAC latency and ROIs volume for the second, third, and fourth quartiles were not found. We also conducted correlational analyses for all quartiles for HS usage, APM, and all predefined ROIs, but there were no significant correlations. All correlation coefficients and significance levels are provided in Table S2 (online only). PAC latency distribution for each participant is presented in Figure 6.

Discussion

In training-related plasticity studies, interindividual differences in learning performance have not received much attention. A large number of publications focused on behavioral improvement and experience-dependent structural changes in the brain. However, neural factors of predisposing to complex skill learning, such as video game acquisition, appear to play an important role in optimizing the training paradigms dedicated to increasing the subject's efficiency and brain plasticity.

In the two studies described here, using VBM, we observed that the volume of the RLN (part of the BG) was predictive of success in the complex RTS game SC2. Experts in SC2 (players from the top five leagues) had the larger BG compared with people who do not play RTS games. When we took into consideration the volume of the areas identified in the first study in a completely new, unrelated sample of individuals who were naive to RTS games, we were able to predict the quality of learning in SC2. The regional differences in the volume of the BG (BGV) correlated with the pace at which participants learned to play this complex video game. In our opinion, the results presented here provide new insights into how BV measurements can be utilized to predict the success of the skill learning process and can be applied to a much broader than just video game context.

The cross-sectional study showed more GMV in the RLN (putamen and pallidum) in RTS experts when compared with NVGPs. In the training study, we explored whether the preexisting volume of the putamen and pallidum can predict improvement in the RTS skill acquisition in novice players. We, in fact, confirmed that the GMV of predefined ROIs was correlated with complex skill acquisition, measured as time spent on more demanding game levels, which is treated here as a proxy of complex skill learning. The correlation was found in both the right and left LN (the putamen and pallidum), whereas, in the cross-sectional study, we found differences between experts and nonplayers in the RLN only. The LN is a subcortical structure within the BG, composed of the putamen and pallidum, and constitutes a relay station,



Figure 4. Predefined ROIs (the right/left putamen (A) and pallidum (B)) and scatterplots portraying the relationship between GMV in ROIs and RTS game skill acquisition. On the basis of the significant difference in both the putamen and pallidum (part of the LN from Fig. 3) in the cross-sectional study, we chose those areas as ROIs for the training study to evaluate the patterns of RTS game skill acquisition. Panels show areas with a significant (bolded) positive correlation between mean GMVs in the ROIs with SC2 game performance. The blue color represents the results for the putamen, and the pink color represents the results for the pallidum. The results of correlation analyses are uncorrected for multiple comparisons. ROIs, regions of interest; L, left; R, right.

conveying information between different subcortical areas and the cerebral cortex (mainly the primary motor cortex and supplementary motor area).55 Both the pallidum and putamen play an important role in a variety of motor acts, such as sequential motor learning⁵⁶ and movement control,^{57–59} including the operation of a joystick.⁶⁰ It is also abundantly clear that pallidum and putamen neurons are involved in more than just the organization and/or execution of movements. They are also actively involved in a variety of cognitive functions, such as visual attention,⁶¹ working memory,^{62,63} and cognitive control.⁶⁴ Additionally, pallidum neurons encode actions such as the actual location of the target on a screen, as well as monitor behavioral goals (spatial or object), indicating that this region is involved in goal-directed decisions and action selection.⁶⁵ We did not find any GM alterations in attention- or perception-related brain areas, such as the occiptioparietal loop, which we observed and described in our previous study on

DTI.⁴⁷ Changes in GM and WM microstructure associated with learning do not always occur within the same brain areas. Acquiring new skills can simultaneously affect distinct structural properties of multiple brain areas, which could be detected by different MRI-related methods with different sensitivities.^{66,67}

To properly understand the results from the two studies presented here, we need to take into consideration the dynamics of the learning process and expertise levels. Playing a demanding RTS game like SC2 requires the engagement of a wide range of cognitive and motor functions.^{42,68,69} However, the degree to which each of these functions is engaged is not likely to be equally engaged across all stages of SC2 learning. Specifically, early attempts to acquire a novel skill, especially as complex as learning to play SC2, are characterized by effortful, explicit information processing, which proceeds under executive control functions (especially working memory). As the practice advances, the



Figure 5. Predefined ROIs (the right/left putamen (A) and pallidum (B)) and scatterplots portraying the relationship between GMVs in ROIs and PAC latency in the first quartile. The brain area with a significant difference (part of the LN from Fig. 3.) was the data point to choose the GMVs in the ROIs (both the putamen and pallidum), which were included to evaluate the patterns of PAC latency in the first quartile (Q1). The panels show areas with a significant (bolded) negative correlation between the mean GMVs in the ROIs with PAC latency in Q1. The blue color represents the results for the putamen, and the pink color represents the results for the pallidum. The results for correlation analyses are uncorrected for multiple comparisons. ROIs, regions of interest; PAC, perception–action cycle, Q, quartile.

skill becomes less effortful and more proceduralized, with almost complete automaticity attained at the expert levels of performance.43 Our observations paint a pattern of results, suggesting that such a process is taking place within BG structures. The result of more GMV in the RLN of expert RTS players may stem from the effective use of learned motor sequences (especially automatic movements). On the road to success in most RTS games, including SC2, the expertise level is commonly multistaged and connected with acquiring an increasingly higher degree of automatization of specific sequences of movements. Such automatization allows expert players (like those in our first study) to perform actions that were at first (in novice players, like in our training study) complicated and cognitively demanding, with minimal effort.⁴³ SC2 has an economic component, which means that players have to spend resources on the production of military units and structures. Hence, many of the player's decisions/strategies are related

to the balancing of expenses on military and economic strength. Second, the game board, called the map, is much larger than what the player can see at one time. Third, players do not have to wait for the opponent to play their turn, so the pace of the game is incomparably faster than in, for example, chess. Players who can more effectively and quickly implement their strategy have a huge advantage. Therefore, motor skills, mainly related to handling the keyboard, are an integral part of the game that leads to victory. And thus, the growth of the subcortical structure is probably the result of the above-described experience. We know from other studies that the putamen plays a special role in game-related processes and is also important for movement preparation, learning, and motor sequence control.^{59,70–72} An additional confirmation that video games strongly stimulate motor skills, especially those that are highly specialized and automated, was conducted by Borecki et al.73 Their study assessed a wide range of hand



Figure 6. PAC latency distribution for each participant. Additionally, the plot represents PAC latency distribution in the first quartile (Q1) separately for participants below and above the median: computed from the average GMV for all the ROIs (both the right/left putamen and pallidum). ROIs, regions of interest; PAC, perception–action cycle; Q, quartile.

movement coordination skills and demonstrated that FPS players were able to use motor skills more effectively than control subjects, and the scope of these skills included improved targeting accuracy, reduced tremors, more effective eye-hand coordination, and an increased speed of wrist movements. This range of motor skills has been investigated using the game Counter-Strike[®], owing to its interactive nature. In Counter-Strike, players perceive battlefield-like conditions from the first-person perspective, which forces them to engage in various military activities requiring an immediate response. The biggest advantage of the top video game players over other opponents is speed, which develops toward expertise.

It should also be added that all subjects in our first study were right-handed, but their left hand, for many years, was extensively used during gaming. It can be seen as intensive training of the left hand, and what we see on the level of VBM are differences in the right hemisphere. Evidence for lateralization related to specific movement has already been well described in the literature.^{74,75} What is more, there is a study showing that action video game players are characterized by faster reaction times in tasks that measure visual and spatial abilities (in comparison with nonplayers), but only when responses were given using the nondominant hand.⁷⁶ It should be

mentioned that we did not observe a relationship between the size of the LN and experience with RTS games. Other studies^{12,77,78} have similarly failed to show such correlations, suggesting that the relationship between anatomical plasticity measured using VBM methods and behavior may be more complex and mediated by other variables.⁷⁹ There was also low variability in SC2 experience among our participants, which may explain the lack of correlation. The lack of correlation can also be interpreted as an argument for the existence of certain predispositions in complex video game skill acquisition, which we tested and confirmed in our second training study. Because of the correlational nature of the first study, we cannot determine whether the structural differences between the RTS and NVGP groups were the result of extensive video game experience or because RTS players have brain structure characteristics that predispose them to engage in activities like playing RTS video games. We designed our longitudinal study, which followed a cross-validation procedure44 and introduced a training regimen with the same RTS game as in the first study with a group of NVGPs, to shed some light on this conundrum.

On the basis of the dominant theory concerning BG involvement in motor skills, we assumed that the differences seen in our cross-sectional study were driven mainly by the motor component of the prolonged SC2 usage. To test that, we followed the methodological approach proposed by Thompson and others⁴² and focused on the game telemetry. We performed an analysis of both more cognitive game indicators, namely PAC latency, and more motorrelated game characteristics, that is, APM and HS usage. We found a negative correlation between the GMV of the left putamen and both the left and right pallidum, and PAC latency at the beginning of RTS game skill acquisition. From the cognitive perspective, PACs represent shifts in attention focus followed by a set of motor actions, as SC2 players have to constantly relocate a narrow PoV window over a large map area to attend to different locations and execute actions associated with the current state of the game. Technically, each PAC is a PoV that contains one or more actions. PACs encompass roughly 87% of player game time⁴² and closely resemble the structure of individual trials in experimental tasks that record the set of participant's reactions to presented stimuli. We found that PAC latency was relevant to game performance at the beginning of RTS skill acquisition among novice players. This advantage in the early stage of training can be explained by better attentional filtering of relevant game objects. This edge diminishes in the later stages of learning, as the game has a finite number of visual elements with meaningful affordances that can be learned over time. For new players, most of the work being done is within an individual PAC. To engage a PAC, players have to first attend to a cue, assess what they are looking at within that region of interest, and then start producing actions. PACs latency represents the time it takes for perceptual abilities to paint a picture of the situation and for attentional abilities to pick through the relevant stimuli. As players accumulate experience and game knowledge, the attentional demands within a PAC should decrease. A larger pretraining BGV could boost attention by focally releasing the inhibition of task-relevant representations⁸⁰ at the beginning of learning how to play RTS games. That demand is constantly being stressed through each cycle and should improve up to some biological limits, if game knowledge permits. However, in contrast to our predictions, correlations between HS usage, APM, and BGV were not found. The usage of HS speeds execution and the speed of execution is represented by APM. However, speed plays a very crucial role at the top level of players, but not in novice players, and

30 h of training was likely not enough to develop automatization.

From the perspective of a novice player, success in most RTS video games is by design based on tactical planning, which involves the memory functions and attention of players in many ways. As in almost all strategy games, players devise the most optimal game-opening strategies and counterstrategies and commit them to memory. For players learning a game like SC2, the most challenging aspect involves memorizing the visuals of interactive game elements and the complex mechanics associated with particular units (e.g., What can that building produce? What types of special actions can this unit make?). Moreover, as the underlying concept of SC2 gameplay is the counterplay mechanic, it forces players to memorize complex interactions between units (e.g., Which unit will be most effective against a specific threat?), and as the game progresses, players need to constantly monitor and update their internal representation of the opponent's unit composition to react accordingly. On a higher strategic level, RTS video games require players to be able to memorize many game states from their past experience, as this allows for a more accurate prediction of the opponents' intentions. The putamen and pallidum were shown as uniquely sensitive brain structures in the abovementioned situations.81

It needs to be added that the obtained results of a greater GMV in the RTS group (our crosssectional study) may be interpreted as the effect of long-term training in the planning and execution of motor sequences (as it has been discussed earlier), but the GMV of the LN as a neural predictor of RTS training outcomes should be also considered. And the interaction of these two factors seems to be the most probable, as people who engage in intensive and effective video game playing probably have some structural brain predispositions to take such actions and be good at them (which, in turn, motivates them to engage even more). This does not mean that there is no effect of training, but that the correlational nature of our study does not allow us to conclude whether people who start playing video games have different brain structure characteristics in comparison with nongamers. This unresolved question about brain predispositions in acquiring new skills motivated us to perform a training study.

Our results are in line with Erickson and others,³⁹ who showed that putamen volumes were positively correlated with learning new procedures and developing new strategies in a noncommercial RTS video game designed by psychologists. Additionally, Vo and collaborators⁴¹ found that patterns of time-averaged T2*-weighted signal in the dorsal striatum recorded before the start of extensive training were predictive of future learning success in the same game. Other regions were recognized as predictors of RTS skill acquisition in an elderly population, such as the prefrontal and frontal regions, including the frontal gyrus, AC, central gyrus, cerebellum, precentral gyrus, and premotor cortex.⁴⁰

It needs to be added that owing to the fact that we did not include any active control training experience group, we cannot determine whether the mechanism of action is motivational or driven by the capacity to learn. A future longitudinal study with active control training groups, motivation questionnaires, and flow measures would be necessary to determine the mechanism of action.

Furthermore, some behavioral predictors should also be investigated, as they have been shown to explain a significant amount of variance in video game performance, such as intelligence level⁸² or early game learning rate.⁸³ It would be ideal to combine different measures of brain characteristics with behavioral measures in the identification of video game skill acquisition potential.

Additionally, we found no effects of training on brain structures in the longitudinal study. This result does not support the hypothesis that shortterm RTS video game training (30 h in total) causes alterations in GMV. This does not rule out the possibility that there were changes in GMV, but they are too small to detect using the VBM method.⁸⁴ Using diffusion-weighted MRI to study WM can provide complementary information about neuroplastic changes after video game training.

Conclusions and future directions

This paper presents novel findings showing that RTS video game players have a larger LN than NVGPs. The greater volume of the LN can be explained as a result of intensive and complex motor sequence learning (especially automated movements) by our group of RTS experts. However, the counterargument is supported by the assumption that people with specific brain structure characteristics (a larger LN) have predispositions to become good video game players. To resolve it, we conducted a training study and checked if there are some neural predispositions that define the manner in which playing a game is learned. We showed that regional differences in the volumes of brain areas identified in the crosssectional study (on expert RTS players) correlated with the learning pace observed in the training study conducted on a completely new, unrelated, and naive to RTS game participants. The present study provides new insights into how skill learning success can depend on brain characteristics. Our results show the importance of individual features of the brain in the effectiveness of training, and in the case of our study, learning to play a new video game. The conclusion that comes to mind is that people with a specific brain structure have a better chance of acquiring new skills. In our study, we showed this in relation to learning a video game, but there is a good chance that it is a more general attribute of the human brain. These findings also point to the usefulness of MRI brain structure characteristics in predicting relevant intervention outcomes and greatly improve the practicability and effectiveness of those interventions. On the level of a more direct application, our results may open the window to identifying the structural characteristics of successful professional eSports players, much like physical measurements are used in professional sports.

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Author contributions

N.K.-G. designed the study and methods, collected the structural imaging data, collected the behavioral data, analyzed and interpreted data, wrote the manuscript, and obtained funding. M.S. designed the experiment and performed SC2 training. P.D. designed the experiment and corrected the manuscript. B.K. prepared the MRI sequence and contributed to the interpretation. M.M. and N.H. were involved in structural imaging data collection. M.G. was involved in behavioral data analysis. A.M. was involved in structural imaging data analysis and revising the manuscript. M.K. contributed to the data interpretation. A.B. designed the study and methods, interpreted data, wrote the manuscript, and obtained funding.

Data and materials availability

All data needed to evaluate the conclusions in the paper are presented in the paper. Additional data related to this paper and custom analysis scripts are available upon reasonable request.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1. Mean weekly hours of video games playedin the last 6 months, by genre.

Table S2. Correlation coefficient (r) from Spearman's correlation analyses between ROIs GMW (the left and right putamen, and the pallidum) and PAC latency, actions per minute, and hotkey select usage.

Competing interests

The authors declare no competing interests.

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