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Research report

Videogame training strategy-induced change in brain function during a complex visuomotor task

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ABSTRACT

Although changes in brain function induced by cognitive training have been examined, functional plasticity associated with specific training strategies is still relatively unexplored. In this study, we examined changes in brain function during a complex visuomotor task following training using the Space Fortress video game [22]. To assess brain function, participants completed functional magnetic resonance imaging (fMRI) before and after 30 h of training with one of two training regimens: Hybrid Variable-Priority Training (HVT), with a focus on improving specific skills and managing task priority, or Full Emphasis Training (FET), in which participants simply practiced the game to obtain the highest overall score. Control participants received only 6 h of FET. Compared to FET, HVT learners reached higher performance on the game and showed less brain activation in areas related to visuo-spatial attention and goal-directed movement after training. Compared to the control group, HVT exhibited less brain activation in right dorsolateral prefrontal cortex (DLPFC), coupled with greater performance improvement. Region-of-interest analysis revealed that the reduction in brain activation was correlated with improved performance on the task. This study sheds light on the neurobiological mechanisms of improved learning from directed training (HVT) over non-directed training (FET), which is related to visuo-spatial attention and goal-directed motor planning, while separating the practice-based benefit, which is related to executive control and rule management.

1. Introduction

Practicing and learning new skills changes brain structure and function [1–5]. However, how you learn may be just as important as what you learn, in determining how the brain will respond to learning new skills. A recent study by Voss et al. [6] examined changes in brain network interaction dependent on training strategy. A strategy focused on improving separate components of a complex videogame within the context of the whole task (i.e., Variable Priority Training) resulted in network interactions that reflected flexible skill learning and retrieval, compared to a strategy focused on all aspects of the game at the same time (i.e., Full Emphasis Training) that resulted in network interactions reflective of procedural learning and skill implementation. Additionally, only network interactions associated with flexible learning and retrieval were associated with improved learning. In the present study, we extend these findings by examining changes in the magnitude of functional brain activation during a complex visuomotor task as a result of extensive training with strategies similar to those used in Voss et al. [6]. Furthermore, we included a control group that received only limited training, allowing us to dissociate practice- and strategy-related changes in brain function.

Visuomotor skills, or the ability to control muscles in coordination with visual inputs, are crucial for everyday tasks such as driving, sports, and typing. Theories of skill acquisition posit that skill learning progresses with practice through an ordered series of stages [7–10]. The initial stage, called the *cognitive*, *declarative*, or *controlled processing* stage, is characterized by slow, effortful, and error-prone performance as rules are learned and strategies are explored. The second stage, referred to as the *associative*, *procedural*, or *mixed controlled/automatic* stage, involves

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the refinement and proceduralization of declarative knowledge gained in the initial stage. Finally, after extensive practice, the *autonomous* or *automatic* stage is reached, characterized by little cognitive effort or attention being required to maintain skilled performance.

Considering the complex stages of skill acquisition, developing and applying effective learning strategies is of theoretical as well as practical importance. Several cognitive training programs have demonstrated that some training strategies are more effective than others for learning new skills [11–13]. Variable Priority Training (VPT) emphasizes different task components at different times in the context of the whole task, and can enhance task performance, retention, and transfer to other tasks compared to training without emphasis manipulation (Full Emphasis Training, FET [11–15]).

Although behavioral effectiveness of VPT regimens has been well documented, the neural mechanisms involved in functional brain plasticity as a result of training strategy have not been fully investigated. Neuroimaging studies have demonstrated that extensive practice with a visuomotor skill can improve performance and also modify underlying patterns of neural activation [16–18]. The most consistent finding is that visuomotor task practice leads to a reduction in overall cortical activity in those areas responsible for the control of basic movement [16–18], suggesting neural efficiency has been gained (see also [19,20] as examples reporting increased activation in primary sensory or motor cortex after practicing).

Recently, Voss et al. [6] demonstrated learning-induced plasticity of the interaction of brain networks as a function of training strategy. Using the Space Fortress video game, Voss et al. [6] showed that the advantage of VPT was linked to the interaction of the declarative learning system with a fronto-parietal network implicated in the allocation of attention and working memory. In contrast, a training strategy focusing on all aspects of the game at the same time (FET) was linked to the interaction of the procedural learning system with the fronto-parietal network and enhanced interaction between the fronto-executive and declarative systems. In another study, Kantak et al. [21] demonstrated that the neural substrates of motor-memory consolidation are modulated by practice structure; learning with variable practice depended on higher-order motor areas such as DLPFC, whereas learning with a fixed practice structure relied on primary motor cortex to mediate motor-memory consolidation.

Yet the question of how guided strategy during training affects patterns of task-related brain activation involved in complex visuomotor tasks remains poorly understood. The training regimen-based difference found in Kantak et al. [21] was only present during the motor memory consolidation period after short-term motor control training, and brain activation during motor task performance was not examined. Although Voss et al. [6] demonstrated differences between VPT and FET after longer-term training, this study examined plasticity among pre-defined brain networks and did not examine change in the magnitude of evoked, task-related brain activation. Also, because there was no no-contact control group included in Voss et al. [6], the study could not dissociate practice effects from the manipulation of strategy. Finally, Voss et al. examined functional connectivity during a complex videogame (Space Fortress), which involves not only motor control but also working memory and resource management. Therefore, brain processes specific to visuomotor control could not be disentangled from other cognitive demands involved in the game.

Thus, we sought to characterize the effect of training strategy on *functional brain activation changes* during a complex visuomotor task. Changes in brain function were assessed while participants played only the visuomotor component of the Space Fortress game.[1] The Space Fortress game requires complex manual control, in which the alignment of visual information and that of the required motor output is a non-standard mapping (players have to navigate their ship with precise control using a joystick). The ship moves in a frictionless environment, and players can rotate the ship by moving the joystick left or right, or apply a thrust by pushing forward on the joystick [22]. Change in the position of the joystick results in a change in the acceleration of the spaceship being controlled. Non-video game players were trained with the Space Fortress game for 15 2-h sessions during a 7–8 week period and were scanned before and after training using functional magnetic resonance imaging (fMRI). One group of participants received directed training, which combines part-task training and Variable Priority Training (see [23] for an earlier implementation of a similar strategy). We named this training Hybrid Variable-Priority Training (HVT). Early in HVT, component tasks were trained in isolation and gradually increased in complexity, approaching the whole task. This progressive part-task training was included to enhance learning by reducing the complexity of the whole task. After part-task training, blocks of Variable Priority Training (i.e., emphasizing different sub-tasks in the context of the whole task, VPT) were also included to provide learners an opportunity to integrate the skills acquired from the part-task training into the whole task. Later in training, focus is fully shifted to VPT so that they can continue to explore ways to integrate and coordinate sub-tasks.

Another group of participants received non-directed training, which asked participants to focus on all aspects of the game throughout training (Full Emphasis Training, FET). Furthermore, we included a control group that received only limited game experience, but whose brain function was assessed with fMRI with the same interval between assessments as the HVT and FET groups.

Using whole-brain exploratory analyses, we first examined the effect of practice on functional brain activation (HVT vs. control group and FET vs. control group). According to the stage model of skill acquisition [7–10], HVT and FET training groups might be in the later stage of skill acquisition, which requires little cognitive effort or explicit control compared to the control group. Therefore, we expected to see differences in brain regions related to executive control and working memory between the training and control groups.

Next, we investigated the effect of training strategy (HVT vs. FET). Using functional connectivity analysis, Voss et al. [6] demonstrated that a strategy similar to HVT showed changes in brain network interaction reflective of more flexible skill learning and retrieval compared to procedural learning and skill implementation with FET. Since we were measuring brain activation changes after extensive training (30 h), we expected to see differences in brain activation changes between HVT and FET in brain regions separating the levels of skill acquisition at the later stages (associative, procedural, or mixed, followed by automatic). The relationship between brain and behavior was assessed with a region-of-interest analysis by examining the correlation between brain activation changes after training and performance gain. Finally, we tested for strategy-related changes in motor-areas. We localized individual ROIs with a right-wrist movement localizer and examined if these traditional motor-related areas showed brain activation changes after training.

[1] Changes in brain function while participants played the whole game of the Space Fortress including memory and attention components was also examined and presented in another study [40].

Table 1
Descriptive characteristics of participants in the three groups (FET, HVT, and control), standard deviations are within parentheses.

	Full Emphasis Training (FET)	Hybrid Variable-Priority Training (HVT)	Control
N	25	25	25
Age	21.91 (2.77)	20.88 (2.06)	21.44 (2.52)
Proportion male	.30	.33	.37
Self-rated health	5	5	5
Years of education	15.52 (2.19)	14.68 (1.85)	15.28 (2.25)
Baseline game score	−844.45 (2086.81)	−1034.78 (1907.14)	−988.38 (1916.30)
Participants for fMRI analysis			
N	23	22	20
Age	22 (2.89)	21.09 (2.09)	21.6 (2.77)
Proportion male	34.78	45.45	45
Self-rated health	5	5	5
Years of education	15.61 (2.27)	14.81 (1.88)	15.42 (2.46)
Baseline game score	−788.63 (2024.53)	−876.95 (1951.79)	−885.5 (1646.49)

Note: For self-related health, the scale was ranging from 1 for poor to 5 for excellent.

2. Experimental procedures

2.1. Participants

Seventy-five participants (ages 18–30, 29 males) were recruited from the Urbana-Champaign community and were paid fifteen dollars an hour for completing game training and imaging sessions. All participants reported normal or corrected-to-normal vision and were right-handed. Twenty-five participants were assigned to the Hybrid Variable-Priority Training group (HVT), 25 were assigned to the Full Emphasis Training group (FET), and 25 were assigned to the control group. Initially participants were randomly assigned to each group, and halfway through the recruitment processes demographic characteristics of each group were checked and used as a guideline for group assignment to ensure groups did not differ in terms of gender composition or age. Demographics for all participants are provided in Table 1.

Participants were recruited through flyers posted in campus buildings and businesses or through advertisements posted to online bulletin boards. Individuals responding to these flyers and advertisements were then asked to complete a survey of their video game habits and to return this survey via e-mail. To determine their final qualification for the study, potential participants were invited to the lab to complete an in-person interview. This interview assessed detailed video game habits and health status.

Eligible participants had to (1) be between the ages of 18 and 30, (2) have video game experience of less than 4 h per week, (3) be free of neurological disease, psychiatric disorders, or metallic implant (4) be right handed, (5) have normal color-vision, (6) have a corrected visual acuity of at least 20/20, and (7) sign an informed consent form.

2.2. Space Fortress game

Complete details of the Space Fortress game are reported elsewhere [22,11], but here we summarize the game briefly. The main goal of the game is for players to destroy the Space Fortress (at the center of the screen) as many times as possible by hitting 10 missiles followed by double-shots while avoiding damage to their own ship (see Fig. 1A). In order to do so, players have to navigate their ship with precise control using a joystick. The ship moves in a frictionless environment, and players can rotate the ship by moving the joystick left or right, or apply a thrust by pushing forward on the joystick. The ship has no braking system. In order for players to

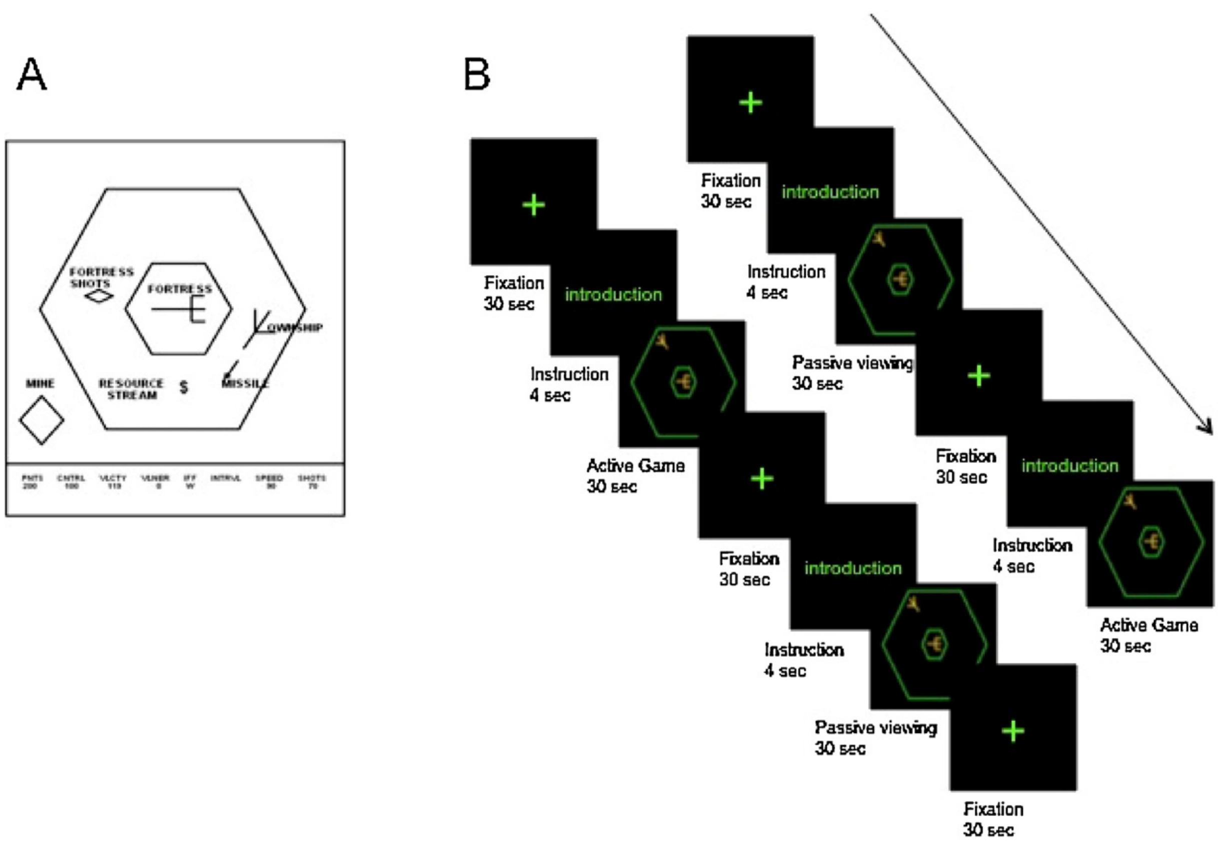

Fig. 1. (A) Schematic diagram of the Space Fortress display seen by the participants. (B) A depiction of ship control MRI task design.

Table 2
Details of Space Fortress training procedures.

	FET	HVT	Control
2 h		Game Instruction/Mock Magnet, for all groups	
4 h		Cognitive Battery 1, for all groups	
3.5 h		ERP 1, for all groups	
2 h		fMRI 1, for all groups	
Session 1	Full Emphasis Training	Part-task/Variable Priority Training	Full Emphasis Training
Session 2	Full Emphasis Training	Part-task/Variable Priority Training	
Session 3	Full Emphasis Training	Part-task/Variable Priority Training	
Session 4	Full Emphasis Training	Part-task/Variable Priority Training	
Session 5	Full Emphasis Training	Part-task/Variable Priority Training	
4 h		Cognitive Battery 2, for all groups	
3.5 h		ERP 2, for all groups	
Session 6	Full Emphasis Training	Variable Priority Training	Full Emphasis Training
Session 7	Full Emphasis Training	Variable Priority Training	
Session 8	Full Emphasis Training	Variable Priority Training	
Session 9	Full Emphasis Training	Variable Priority Training	
Session 10	Full Emphasis Training	Variable Priority Training	
Session 11	Full Emphasis Training	Variable Priority Training	
Session 12	Full Emphasis Training	Variable Priority Training	
Session 13	Full Emphasis Training	Variable Priority Training	
Session 14	Full Emphasis Training	Variable Priority Training	
Session 15	Full Emphasis Training	Variable Priority Training	Full Emphasis Training
3.5 h		ERP 3, for all groups	
2 h		fMRI 2, for all groups	
4 h		Cognitive Battery 3, for all groups	

slow or stop the ship they must rotate the ship so that it faces the opposite of its current motion and apply a thrust. This makes control of the ship a challenging and demanding task. Participants are asked to keep their ship within the two hexagons on the screen (see Fig. 1A). Doing so increases the Control sub-score. Flying the ship outside of the large hexagon or leaving the screen entirely (going into hyperspace) subtracts from the Control sub-score. The Velocity sub-score rewards participants for going slowly and punishes participants for flying at high speeds.

In addition to tasks related to ship control, “mines” and “bonus symbols” appear on the screen at regular intervals. The mines serve as a working memory task. At the start of each game, participants are presented with three letters representing foe mines, and are asked to remember these three letters. Throughout the game, diamond-shaped mines appear on the screen with a corresponding letter that is displayed on the bottom of the screen. If the corresponding letter is one of the remembered letters, then the mine is a foe; otherwise the mine is friend. Participants are instructed to correctly recognize the mines and take appropriate action. The bonus symbols serve as a continual monitoring task embedded in the game. Participants monitored a stream of symbols on the screen to get either bonus points or missiles. The bonus was rewarded when participants made a response on the second dollar sign in a row. Participants respond to mines and bonus symbols with a button press on a mouse in their left hand. The speed sub-score rewards or punishes participants for how quickly they deal with mines. The points sub-score rewards participants for shooting and destroying the fortress, but it subtracts points for damage and destruction of the player’s ship. Total score is calculated by summing all four sub-scores.

2.3. Training procedure

Table 2 shows a schematic depiction of the training group and timeline. The project included the game training, cognitive battery, and event related potential (ERP) and functional magnetic resonance imaging (fMRI) sessions, but here we describe the procedure related to the current fMRI study (game training and fMRI sessions). Cognitive battery and ERP imaging data will be presented in separate publications.

Participants were taught to play the game by watching a 20-min instructional video that explained all the details of the Space Fortress game, followed by another 5-min summary video that summarized the most important rules. After participants fully understood the game rules, they played six 3-min games to familiarize them with the game.

After the initial game familiarization, participants in the two training groups (FET and HVT) completed 15 2-h training sessions. For the FET group, each session consisted of 36 3-min games, in which participants were asked to maximize performance and focus on obtaining the highest total score by emphasizing each task component equally.

For the HVT group, the first 5 sessions were a combination of part-task training and Variable Priority Training. Each session was composed of 1 h and 10 min of part-task training and 50 min of Variable Priority Training. Part-task training was used to train the components of the game independently, starting from a simple sub-task such as rotating the ship and the complexity of the sub-tasks increased as training progressed. After the part-task training, 50 min of VPT were presented to provide participants a chance to integrate the skills learned from part-task training into the context of whole game. After the first 5 sessions, participants completed 10 sessions of VPT. The block and trial structure was identical with FET, and the only aspect that differed was the instructions the groups received before each block of trials. Participants were asked to focus on improving and monitoring different sub-scores of the game during practice. The control group played the Space Fortress game for only 3 sessions, once at the beginning of the training, once at the average time-point after which training groups had completed 10 h of training, and once at the end of training, in order to compare their game scores with other training (FET and HVT) groups. For all game trials, identical feedback was given regarding total score and all sub-scores for FET and HVT. During part-task training of HVT, each part-task specific results were presented as a feedback. Participants generally completed 3–5 sessions a week. In general, the entire study including familiarization session, ERP and fMRI scanning, training, and cognitive battery took about 8–10 weeks.

2.4. Tasks: fMRI session

2.4.1. Ship-control

In this task, participants only played the ship-control component of the Space Fortress game without the tasks of destroying the fortress, management of mines, and continual monitoring of bonus symbols. Participants were instructed to navigate a ship between the hexagons in a clockwise direction. The task was presented as a block design, where participants either watched a pre-recorded video of the ship-control game (passive view) or played the ship-control game with a joystick in their right hand (active game). Both blocks were presented twice in a run for 30 s each, interspersed with 10 s of fixation and 4 s of instructions. The order of blocks for all participants was passive view, active game, active game, passive view, and the run started and ended with a 30-s fixation block. Participants completed three ship-control runs. The ship control MRI task design is depicted in Fig. 1B. The two runs with the least amount of motion were included in the analysis for all subjects. We excluded one run with the lowest signal to noise ratio (SNR) and motion greater than 1 functional voxel space (3.475 mm) in 3 or more volumes.

2.4.2. Motor-localizer

Following the ship-control task, participants performed self-paced wrist- or finger-movement tasks. Based on a command shown on the projector screen, participants either moved the joystick with their wrist or pressed buttons on a keypad with their fingers. Wrist-movement and finger-movement conditions were presented in a block design, such that there were three 30-s blocks of wrist-movement and three 30-s blocks of finger-movement that alternated with 30-s fixation blocks. The order of blocks for all participants was fixed as wrist–finger–wrist–finger–wrist–finger, and the run started and ended with a 30-s fixation block. Participants completed one run with right-wrist and left-finger movement and then completed another run with left-wrist and right-finger movement. For our analyses, we predominantly focused on the right-wrist, and the left-wrist conditions.

2.5. Imaging procedures and processing

All participants completed a mock MRI session, wherein they were screened for their ability to complete an experiment in an MRI environment. Participants who passed the mock screening subsequently completed a series of structural and functional MRI scans before and after Space Fortress game training.

2.5.1. Structural MRI

High resolution T1-weighted brain images were acquired using a 3D MPRAGE (Magnetization Prepared Rapid Gradient Echo Imaging) protocol with 144 contiguous axial slices, collected in ascending fashion parallel to the anterior and posterior commissures, echo time (TE) = 3.87 ms, repetition time (TR) = 1800 ms, field of view (FOV) = 256 mm, acquisition matrix 192 mm × 192 mm, slice thickness = 1.3 mm, and flip angle = 8°. All images were collected on a 3 T head-only Siemens Allegra MRI scanner.

2.5.2. Functional MRI

For all functional scans, T2* weighted images were acquired using a fast echo-planar imaging (EPI) sequence with Blood Oxygenation Level Dependant (BOLD) contrast (TR = 2000 ms, TE = 25 ms, flip angle = 80°, BOLD repetitions in ship-control run = 115 volumes, BOLD repetitions in motor-localizer run = 195 volumes). All ship-control videos, games, fixation, and movement command displays were projected onto a screen and presented to participants via a 45° angled mirror fixed on the head coil; this mirror was adjusted for each participant to enable view of the screen without head movement. During the ship-control session, the joystick for the right hand was taped to the scanner bed in a position adjusted individually for each participant.

fMRI preprocessing was carried out using FSL 4.1.2 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The following pre-statistics processing were applied: rigid body motion correction using MCFLIRT [24], removal of non-brain structures using BET [25], spatial smoothing using a Gaussian kernel of FWHM 6.0-mm, grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor, and temporal filtering with a high pass frequency cut-off of 100 s. Regression-based analysis of fMRI data was carried out using FSL's FEAT Version 5.98. Of primary interest to this study was the contrast of active game > passive view. For the first individual-level analyses, the hemodynamic response to targeted contrast (active game > passive view) was convolved with a double-gamma HRF function in each run. Next, the contrasts were combined across the two runs with smaller motion on a subject-by-subject basis using fixed-effect analysis for each pre- and post-training. In the third level, we contrasted pre- and post-training within subject using the second-level contrast images (pre-training mean, post-training mean, pre-training > post-training, post-training > pre-training). Finally in the fourth level, the third level images were submitted to a mixed-effects group analysis. Higher-level mixed-effects analyses were carried out using FLAME [41]. We tested for between group differences on these contrasts with all three groups, HVT vs. control, FET vs. control, and HVT vs. FET comparisons, while co-varying for pre-training activation. All maps were thresholded at a voxel-wise Z-score of 2.33 ($p < .01$) and a cluster-wise threshold of $p < .05$.

2.5.3. ROI analysis: association between brain activation change and performance

To identify regions showing changes after visuomotor skill acquisition, the third level contrast (the contrast of pre-training vs. post-training on the active game > passive view) images were averaged across all participants in order to prevent bias from skewed sampling. Statistical peaks in this contrast were taken to create regions of interest (ROIs) for examining brain–behavior associations. We created a 14-mm sphere around each of the statistical peaks and extracted % signal change of active game and passive view blocks from pre- and post-training sessions respectively and contrasted pre- and post-training of active game–passive view using difference scores. We investigated the correlation between the difference scores of % signal change in the ROIs and ship-control score improvement for games performed during scanning.

2.5.4. ROI analysis: motor localizer analysis

The motor localizer scan was presented to the participants in order to localize areas of the motor cortex that were sensitive to right-wrist movement. Each participant's hemodynamic response function was modeled for task-dependent change using a double-gamma convolution. This first-level analysis resulted in voxel-wise parameter estimate maps for the entire brain for each condition (right-wrist, left-wrist, right-finger, and left-finger) and for the direct comparison between these conditions. These parameter estimate maps and variance maps were then forwarded to a whole-head second level analysis whereby inter-participant variability was treated as a random variable. The higher-level analysis was thresholded at $Z > 2.33$ voxel-wise, with a $p < .05$ cluster correction.

Given that the ship-control task only required right-wrist movement, in order to localize areas of the motor cortex that were sensitive to right wrist movement, we examined the contrast of right-wrist > left-wrist. This resulted in a left lateralized area of activation in the sensory-motor cortex. This was done separately for pre-training and post-training, and as can be seen in Fig. 2, cortical activation in the contrast of right-wrist > left-wrist was highly overlapping between pre- and post-training. This region of interest (ROI) was thus found to be sensitive to right wrist movement, and was used as a mask to locate subject-specific peaks in functional space. That is, for each of the participants in the study, we took a local maxima defined in functional space in this ROI and created a 14-mm sphere around that peak in order to obtain a participant-specific right-wrist sensitive area. This was done separately for pre-training and post-training sessions. These regions of interest were then used to extract mean percent signal change in the Ship Control task to investigate the modulation of the sensory-motor regions as a function of training strategy. That is, with the individual ROIs, we pulled out % signal change in the active game and passive viewing conditions, and performed an ANOVA with the % signal change difference (active game > passive view) with group (HVT, FET, and control) as a between-subjects factor, and time (T1 and T2) as a within-subject factor.

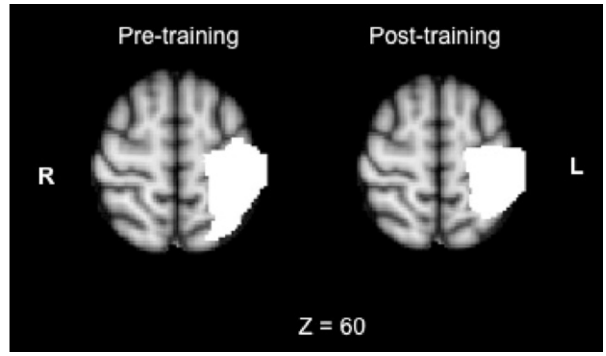

Fig. 2. Global right-wrist ROI.

3. Results

3.1. Ship-control training performance

The ship control scores were calculated by combining Control and Velocity sub-scores of the Space Fortress game. First, we compared ship-control performance between training (HVT and FET) and control groups by conducting an ANOVA with assessment session (3 sessions) as a within-subject factor and training group (training group, and control group) as a between-subject factor. Gender and baseline game performance (average ship-control score of initial test block at session 1) were included as covariates. The main effect of session was not significant, $F(2,142) = 1.49$, $p = .229$. The main effect of training group was marginally significant, $F(1,72) = 3.32$, $p = .073$. The training groups (681 points) showed higher ship-control performance than the control group (523 points). Importantly, the interaction between session and training group was significant, $F = (2,142) = 17.79$, $p < .01$.

Next, we compared training strategy groups by conducting an ANOVA with training sessions (15 sessions) as a within-subject factor and training strategy (FET, and HVT) as a between-subject factor. Gender and baseline game performance (average ship-control score of initial test block at session 1) were included as covariates. The main effect of session was significant, $F(14,644) = 2.80$, $p < .001$. The main effect of strategy group was also significant, $F(1,46) = 5.29$, $p = .026$; HVT reached higher levels of mastery on the ship-control performance. The interaction between session and strategy group was not significant, $F(14,644) = .808$, p = n.s. (see Fig. 3A).

A similar pattern was found for ship-control performance improvement during scanning. Three participants did not finish fMRI sessions due to technical problems. Since there were only two sessions (pre-training and post-training), we used the performance improvement (post-training–pre-training) as a dependent measure. We performed one-way ANOVA with group as a between-subject factor. Results showed a significant main effect of group, $F(2,69) = 5.32$, $p = .007$. HVT showed the highest score improvement (545 points) followed by FET (493 points) and control (217 points). Planned comparisons demonstrated that the two training groups (HVT and FET) showed greater score improvement compared to

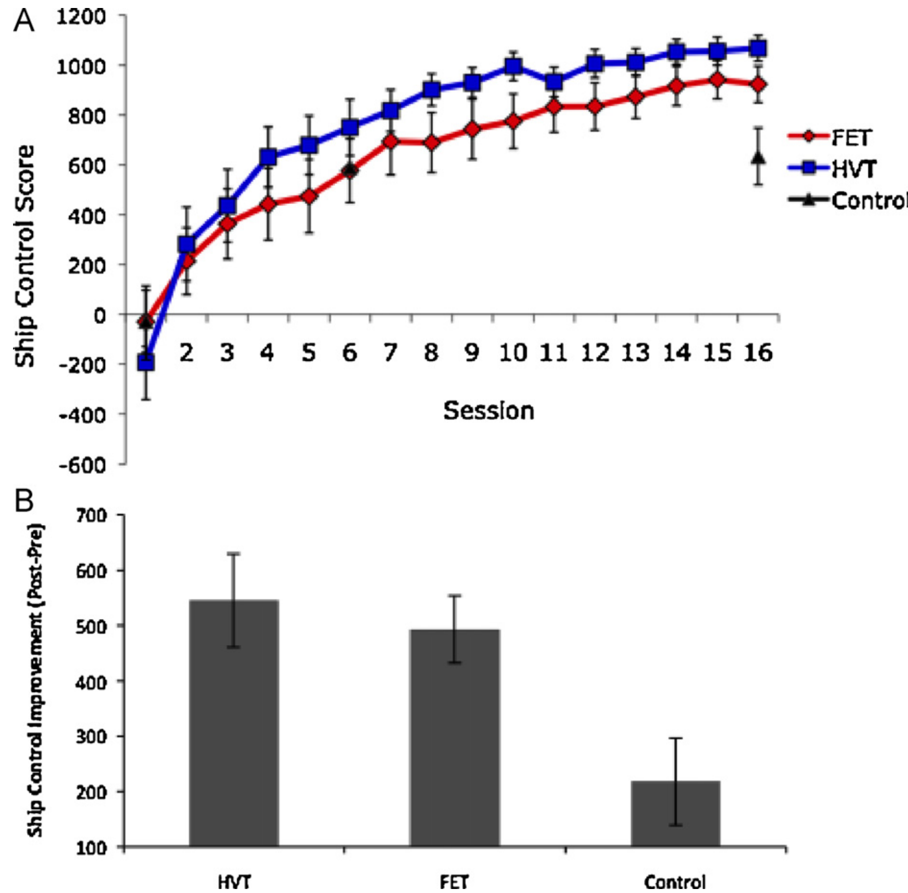

Fig. 3. (A) Change in ship control score for the FET, HVT and control group in training sessions. All groups showed significant improvement in performance on the Space Fortress game. HVT demonstrated superior performance compared to FET and control. (B) Ship control score improvement for the games performed during scanning. Similar to results in training session, HVT demonstrated the greatest score improvement followed by FET and control.

the control group, $t(70) = 3.24$, $p = .002$. However, the two training groups did not differ significantly, $t(47) = .497$, p = n.s. (see Fig. 3B).

3.1.1. *fMRI activation*

Behavioral performance results indicate that ship-control performance improves with training and that performance is sensitive to training strategy, such that HVT reaches higher game performance score than FET. To further understand how training and strategy influences brain function, fMRI analysis focused on examining differences in task-related brain activation changes: (1) between HVT and control group and FET and control group and (2) between HVT and FET after the training. Eight participants' data were excluded from analysis due to excessive motion using an exclusion criterion of motion greater than 1 functional voxel space (3.475 mm) in 3 or more volumes.

3.1.2. *Whole-brain analysis: HVT vs. control group and FET vs. control group*

First, we compared changes in brain activation between the training groups (FET and HVT) and the control group. The control group showed greater activation than the HVT group in the right dorsolateral prefrontal cortex (DLPFC), including frontal pole, superior frontal gyrus, and precentral gyrus (Fig. 4A). Clusters showing significant differences in brain activation changes between HVT and control group are listed in Table 3. The percent signal changes in ROIs from the statistical peak are presented in Fig. 4B. The contrasts of HVT > control, FET > control and control > FET did not result in any significant clusters of activation.

Table 3
Task activation foci for brain activation change (pre-training > post-training for active game > passive view) between HVT and control, FET and control and between HVT and FET.

Cluster anatomical description Active game > passive view Group contrast	MNI coordinates (x, y, z)	Z score	Voxels	p-Value
HVT > control				
Right superior frontal gyrus, extending into right middle frontal gyrus, right precentral gyrus, and right frontal pole	28, −4, 56	3.95	1021	0.007
HVT > FET				
Left precuneus cortex, extending into left lateral occipital and left intracalcarine cortex	−18, −58, 4	3.81	1814	0.0001
Right superior frontal gyrus, extending into juxtapositional lobule cortex, and right precentral gyrus	28, −4, 56	4.18	1056	0.006
FET > control				
None				
FET > HVT				
None				
Control > HVT				
None				
Control > FET				
None				

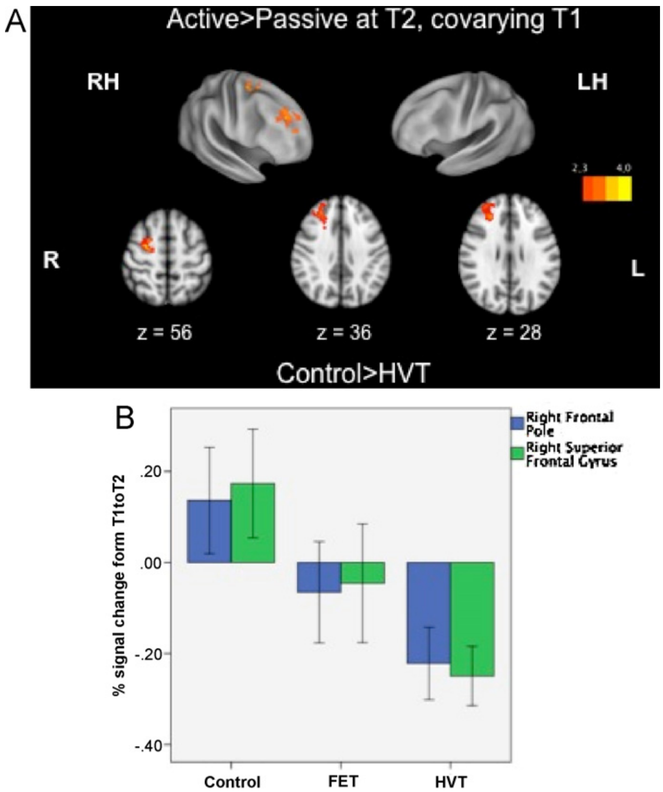

Fig. 4. (A) Cortical regions showing greater activation in control group over HVT at post-training for the contrast of active game > passive view, while covarying out pre-training activation. (B) % signal change from pre-training to post-training on the ROIs from peaks of the contrast between Control group and HVT. Error bars are ±1 standard errors.

3.1.3. *Whole-brain analysis: HVT vs. FET*

Next, we compared HVT and FET to examine the effect of training strategy. FET showed greater activation in left precuneus cortex extending into left lateral occipital cortex and left intracalcarine cortex and in right superior frontal gyrus, compared to HVT at post-training (Fig. 5A). Clusters showing significant differences in change in brain activation between HVT and FET are listed in Table 3. The percent signal changes in ROIs from the statistical peaks are presented in Fig. 5B. The contrast of HVT > FET did not result in any significant clusters of activation.

3.1.4. *ROI analysis: association between brain activation change and performance change*

If lower cortical recruitment after training were related to learning, we would expect the reduction of cortical recruitment to be related to improvements in behavioral performance. We first established ROIs showing reduction of activation after training across all participants, including the control group. A contrast of Time 1 > Time 2 across all participants showed decreased activation of the right intracalcarine cortex, extending into left intracalcarine cortex, bilateral lingual gyrus and bilateral lateral occipital cortex (Fig. 6). Table 4 provides the maximum *Z*-stat values in MNI space for the peak voxels in this contrast.

Next, we conducted a partial correlation between the game improvement from pre- to post-training and the time contrast of % signal change in the peak ROI (right intracalcarine cortex) controlling for the effects of gender. We found a negative relationship between game improvement and activation in the right intracalcarine cortex ($r = -0.49$, $p < .01$), such that individuals showing a greater decrease of activation in those areas also demonstrated higher gains in game improvement.

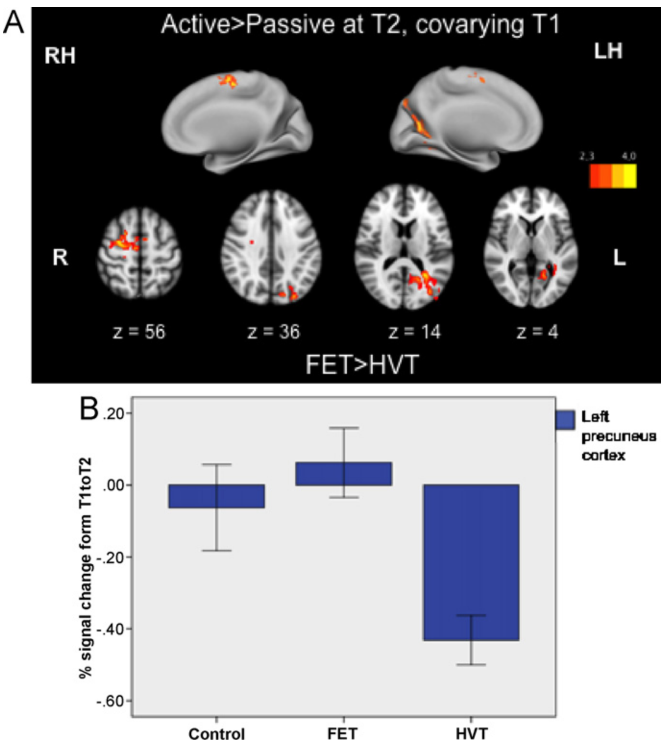

Fig. 5. (A) Cortical regions showing greater activation in FET over HVT at post-training for the contrast of active game > passive view, while covarying out pre-training activation. (B) % signal change from pre-training to post-training on the ROIs from peaks of the contrast between FET and HVT. Error bars are ±1 standard errors.

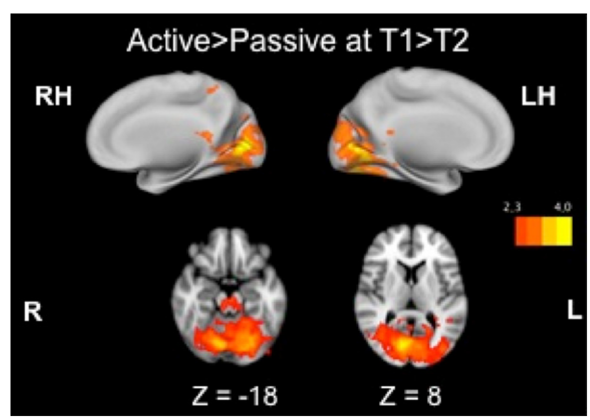

Fig. 6. Cortical regions active during the pre-training > post-training for the contrast of active game > passive view in all participants.

3.1.5. *ROI analysis: motor localizer analysis*

It is interesting that cortical changes from the complex visuomotor training are mainly in the visual cortex in areas that represent higher-order relationships between motor actions and their outcomes. To compare the pattern of these effects to plasticity in specialized motor processing regions, we used a motor localizer to generate an individual right-wrist ROI.

We performed an ANOVA with the % signal change difference (active game > passive view) in the individual right-wrist ROI with time (pre-training and post-training) and group (HVT, FET and control) as factors. The main effect of time was not significant, $F(1,62) = .289$, $p > .1$. The main effect of group was not significant, $F(2,62) = .576$, $p > .1$. The interaction between time and group was also not significant, $F(2,62) = .952$, $p > .1$ (see Table 5).

Table 4
Task activation foci for pre-training vs. post-training for the contrast of active game > passive view from all participants.

Cluster anatomical description Active game > passive view Task contrast	MNI coordinates (x, y, z)	Z score	Voxels	p-Value
Pre-training > post-training				
Right intracalcarin cortex, extending into left intracalcarine cortex, bilateral lingual gyrus and bilateral lateral occipital cortex	10, −78, 8	4.5	18,333	4.8×10^{-16}
Post-training > pre-training				
None				

Statistical parametric map threshold set at $Z > 2.33$ voxel, $p < .05$ cluster-correction; MNI coordinates are for statistical peaks in cluster and Z score is for corresponding coordinate location; voxels refer to the number of standard space voxels in the cluster; p-value is the p-value significance for the cluster.

Table 5
Summary of % signal changes for motor localizer ROI analysis between groups.

	% signal change					
	Pre-training			Post-training		
Cluster ROI	Control	FET	HVT	Control	FET	HVT
Right wrist	2.31	2.42	2.48	1.84	2.77	2.17

4. Discussion

In the present study, we investigated changes in functional brain activation patterns following complex visuomotor training. Several conclusions can be drawn from the results of this study. First, brain processes associated with performing a complex visuomotor task can be modified by training. Especially when comparing HVT to the control group, HVT showed less activity in the right dorsal lateral prefrontal cortex after the training. The difference between FET and control groups was not statistically significant. Second, training strategy influenced visuomotor task performance. HVT demonstrated greater visuomotor skill acquisition than FET. Similarly, we found that the training strategy showing the largest behavioral improvement (HVT) resulted in less brain activation after training. Comparing to FET, HVT showed less brain activity in the left precuneus cortex and left lateral occipital cortex, along with right superior frontal cortex after training.

Additionally, the cortical changes that occurred following training were associated with performance gain. To understand the behavioral relevance of training-induced changes in brain function, we assessed the association between changes in brain activation in ROIs that showed activation changes after training in all groups and performance gain. Results showed decreased activation in lateral and medial occipital areas extending into posterior parietal areas after the training. The decrease of activation in those areas was associated with improved visuomotor task performance. These results suggest that the reduced brain activation after training is reflecting the degree to which the training successfully reduces cognitive costs or workload as a consequence of skill acquisition.

4.1. Practice-induced changes

In this section, we focus mainly on the results from the Time × Practice interactions in brain activation changes. Similar to previous training studies of visuomotor tasks with relatively simple stimuli, we found a reliable improvement in performance with training. Neuroimaging results revealed that HVT showed greater reduction of activation than the control group in right dorsolateral prefrontal cortex (DLPFC) including frontal pole, and superior frontal gyrus, usually known for the regulation of executive control and working memory [26–33]. Especially, compared to the left DLPFC, right DLPFC has been suggested to be involved in the process of decision-making [42,43], and error checking [44,45]. This finding is consistent with the stage model of skill acquisition that has shown transition from the initial controlled processes to later automatic processes. The control group likely is in the initial stage in skill acquisition that requires controlled processing of memory, attention and decision-making to perform the task as rules are learned and strategies are explored. In contrast, the training groups might be in the more automatic stage which requires less effort to remember rules and to explore strategy, and as a consequence of the advanced stage of skill learning, less cortical resources for executive control and working memory are utilized compared to the control group.

4.2. Strategy-related changes

When comparing two training groups as a function of training strategy, HVT showed less activation in left precuneus cortex, extending into left lateral occipital cortex, and in right superior frontal cortex compared to FET, coupled with better task performance. These results suggest that the HVT training strategy could be more efficient compared to FET both in behavioral performance and in neurological processes. Unlike the comparison between training and control groups, the difference in activation changes between directed and non-directed training strategies was mainly in brain regions related to planning motor action and allocating attention to visuo-spatial processing. Activation in the lateral and medial occipital areas has been associated not only with visual representation but also with planning, executing, and imagining movement of the observer's limb [34]. Also posterior parietal areas including the precuneus cortex are involved in directing attention in space during making or planning movements [35,36]. We speculate that both training groups might reach the stage requiring less explicit control and memory of specific rules as a result of training, but HVT might reach a more associative, automatic, and advanced stage that requires less visuo-spatial attention and task-specific motor planning resources compared to FET group. Other studies have documented the benefit of training [16–18] and training structure on cortical activation in short-term, motor control training [21], but our study is the first to identify a training strategy (rather than unsupervised practice) benefit after longer-term training on beyond behavioral assessment.

The efficient visuo-spatial attention and motor planning in HVT over FET is consistent with the connectivity results from 20 h of Space Fortress training [6]. Voss et al. demonstrated that the advantage of VPT was linked to the interaction between the MTL and the fronto-parietal system, which is implicated in the increased capacity of working memory and attention [37,38]. With VPT training involving more flexible allocation of attention to different aspects of the SF game, the attentional brain network might be able to efficiently utilize attention resources. In contrast, FET was linked to enhanced interaction of two different cognitive control systems: interaction between the MTL and the fronto-executive system and interaction between basal ganglia and the fronto-parietal system. The enhanced functional connectivity in the two attention systems might be an indicator of an attention load and, as a consequence, an inefficient modulation of neural activity relative to VPT.

It is also interesting that many changes in brain activation as a result of training strategy occurred in the occipital and posterior parietal areas, rather than sensory-motor areas. One possible explanation for this finding stems from the complexity of the Space Fortress game. The Space Fortress game requires non-standard mapping of sensory input and motor control. Therefore, the skills acquired from training might not be related to specific movement of finger or wrist but may instead be related to effective planning of motor control and visuo-spatial attention. The motor ROI analysis confirmed this idea by demonstrating no changes in right-wrist areas after training.

One potential caveat of this study and any other neuroimaging studies that assess training-related changes in brain activation are that they typically only assess brain activation change at a certain point during skill acquisition (e.g., pre- and post-training). Classic models of skill acquisition [9,10,8,7] posit that skill acquisition progresses with practice through an ordered series of stages. However, the current study only assessed the functional changes after 30 h of training, which would be the autonomous or automatic stage. Therefore, the reduction of brain activity after training might be characteristically only applicable to the final stage of skill learning. It is possible that increase of cortical activation is happening at the initial or middle stages of skill learning in order to accommodate the task rules and strategies. In fact, Shadmehr and Holcomb [39] demonstrated that the brain engaged new regions to perform a trained task after the completion of short-term training of motor control. Whether the training- and strategy-induced changes could be modified by the level of skill acquisition is an important question that deserves future research.

In sum, we find that many of the areas that were involved in complex visuomotor processing decrease in activity as a result of training. It is likely that this change in activity represents an increase in neural efficiency such that fewer brain regions are required to perform the complex visuomotor task. The correlation between the magnitude of brain activity and performance improvement supports this claim. However, the decreased cortical activity depended on both the amount of training and training strategy. Compared to the control group, HVT showed greater decrease of activity in the right DLPFC areas, suggesting improved efficiency of goal-directed processes such as explicit and rule-based management of motor control as a result of prolonged practice. Among the two strategy groups, HVT showed greater decrease of activation in left precuneus cortex, left lateral occipital and right superior frontal gyrus coupled with better behavioral performance, suggesting that the benefit from specific training strategy might be based on the efficiency of visuospatial attention and goal-directed planning of motor control. Interestingly, our complex visuomotor training did not induce changes in wrist-related areas, demonstrating that observed learning of the complex visuomotor tasks is not attributable to fine motor control, but instead to the effective control of action planning.

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