CORTEX 46 (2010) 1165–1177

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Research report

Extensive video-game experience alters cortical networks for complex visuomotor transformations

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A R T I C L E I N F O

Article history:
Received 28 April 2009
Reviewed 28 August 2009
Revised 24 September 2009
Accepted 23 October 2009
Action editor Henry Buchtel
Published online 4 November 2009

Keywords:
Eye-hand coordination
fMRI
Human cortex
Reaching
Skill

A B S T R A C T

Using event-related functional magnetic resonance imaging (fMRI), we examined the effect of video-game experience on the neural control of increasingly complex visuomotor tasks. Previously, skilled individuals have demonstrated the use of a more efficient movement control brain network, including the prefrontal, premotor, primary sensorimotor and parietal cortices. Our results extend and generalize this finding by documenting additional prefrontal cortex activity in experienced video gamers planning for complex eye-hand coordination tasks that are distinct from actual video-game play. These changes in activation between non-gamers and extensive gamers are putatively related to the increased online control and spatial attention required for complex visually guided reaching. These data suggest that the basic cortical network for processing complex visually guided reaching is altered by extensive video-game play.

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1. Introduction

It has been established that extensive experience with a visuomotor skill can alter brain activity for the subsequent performance of that skill (Haslinger et al., 2004; Jancke et al., 2000; Krings et al., 2000; Norton et al., 2005; Smith et al., 1999). Even on a shorter time scale, cortical changes can be observed from the early to the late stages of novel skill learning (Jenkins et al., 1994). A variety of imaging techniques have been used to examine the phenomenon of experienced-based plasticity in the adult brain with respect to the neural representation of visuomotor skill, including electroencephalography, magnetoencephalography, and functional magnetic resonance imaging (fMRI). Professional musicians have been used as the hallmark for investigating long-term effects of motor expertise. The most consistent finding to date is that experience leads to a reduction in overall cortical activity in those areas responsible for the control of basic movement, during the performance of the specific skilled activity. These brain areas include the medial motor areas, primary sensorimotor areas, lateral premotor, parietal and cingulate cortices (Haslinger et al., 2004; Jancke et al., 2000; Krings et al., 2000; Norton et al.,

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doi:10.1016/j.cortex.2009.10.009

2005). Less cortical activation without a behavioral deficit implies that fewer neurons are necessary to produce the same response.

Tasks such as action video games, in which the guiding visual information differs from the required motor actions, have been used to understand how the brain controls complex visuomotor situations (Haier et al., 1992; Hoeft et al., 2008; Matsuda and Hiraki, 2006; Nagamitsu et al., 2006). With the evolution of tool-use, we deal with complex visuomotor situations in everyday life. Complex situations can include those where the visual information guiding an action is dissociated from both the spatial location and the direction of that action (i.e., has a non-standard mapping Wise et al., 1996). The common example for non-standard mapping is the use of a computer mouse: in order to displace a cursor upward on a vertical monitor, one must move the mouse forward in the horizontal plane. Previous work in our laboratory has shown that the preparation for different types of non-standard visuomotor transformations utilizes a common cortical network including the prefrontal, premotor, parietal and temporal cortices (Gorbet et al., 2004). While such tasks are fairly effortless for the healthy adult, the ability to control these types of non-standard skills is not innate (Bo et al., 2006; Piaget, 1965), and can deteriorate with disease (Carey et al., 1997; Ghilardi et al., 1999; Pisella et al., 2006; Tippett and Sergio, 2006).

While studies of experience-based plasticity provide insight into basic visuomotor control, it remains poorly understood how the brain changes its activity over the long-term as a result of motor expertise for a) more generalized movements (i.e., not the specific skill leading to the plasticity) and b) non-standard situations. Adults with extensive video-game experience offer an ideal population to examine the effects of experience on cortical activity for complex situations; the eye-hand coordination involved in video-game performance comprises a discrepancy between the alignment of the guiding visual information and that of the required motor output. Previous imaging studies on video gamers revealed a common cortical network throughout all of the cortices during actual video-game play (Haier et al., 1992; Hoeft et al., 2008; Nagamitsu et al., 2006). As in studies on experienced musicians, less overall cerebral glucose metabolism was seen in the experienced video gamers compared to naïve controls (Haier et al., 1992). These findings, however, do not provide insight into how the brain of a skilled performer controls more general types of non-standard visuomotor transformations.

In the present study, we use event-related fMRI to examine directly the effect of video-game experience on cortical activity during the preparation of visually guided movements. To prevent the false interpretation of potential movement artifacts associated with whole-hand movements, we focus on movement preparation rather than movement execution (Beurze et al., 2007; Cavina-Pratesi et al., 2006; Gorbet et al., 2004; Toni et al., 2001). We employ a series of visuomotor tasks, where the guiding visual information is increasingly dissociated from the required motor action (Gorbet et al., 2004), in order to examine how skill is represented within the cortical networks for non-standard eye-hand coordination. Our hypothesis is that extensive video gaming experience leads to a reduction in the brain activity associated with planning general complex eye-hand coordination tasks other than video gaming, relative to that observed in adult humans with little video gaming experience. Based on this hypothesis, our previous research, and the design of the present experiment, we make the following prediction: video-game experience in young adult males will lead to a decrease in activation of the parietal, prefrontal, and premotor cortices when planning increasingly more dissociated visuomotor tasks, relative to age-matched controls. Importantly, this difference will occur in the absence of any behavioral differences in task performance. This would suggest that any brain activity changes would be related to information processing differences, not particular movement-based differences.

2. Materials and methods

2.1. Subjects

Thirteen right-handed male video gamers (mean age 24 ± 3.1) and thirteen right-handed male controls (mean age 26 ± 4.6) participated in the study, and received financial compensation. Males were used exclusively due to the sex-related activity pattern differences observed previously for the experimental tasks (Gorbet and Sergio, 2007), as well as during actual video-game play (Hoeft et al., 2008). The inclusion criteria for the video gamers were a minimum of 4 h/week of practice (mean of 12.8 ± 8.6 h/week) over the last three years, as well, all subjects reported a high proficiency on action video-game skill (using a custom-written questionnaire). All subjects provided informed consent, and handedness was verified using the Edinburgh inventory (Oldfield, 1971). None of the subjects had a history of neurological problems. All subjects had normal or contact-lens-corrected vision.

2.2. Experimental paradigm

The paradigm is identical to one used previously (Gorbet et al., 2004; Gorbet and Sergio, 2007). Briefly, event-related fMRI was used such that the upcoming condition and visual target were cued. Subjects then had a ten second delay period to allow for the hemodynamic level to stabilize during the movement-planning phase. We employed four visuomotor conditions: one standard condition and three non-standard conditions (Fig. 1). These conditions involved one hand movement (HM) condition, where subjects directly looked at and touched targets, and three eye-hand dissociated conditions: A) a rotated hand movement (RHM), where the eye looked at the target and the hand moved in the opposite direction, B) a joystick movement (JM), where the eye looked at the target and a joystick at the subject's side was used to displace a cursor to the target, and C) a rotated joystick movement (RJM), where the eye looked at the target and a joystick was moved in the opposite direction in order to displace a cursor to the target. Subjects also performed two further conditions (eye movement only and central fixation only; Fig. 1). Each subject performed three consecutive imaging runs, consisting of 30 sec of baseline measurement (subjects were instructed to rest with their eyes open) followed by six conditions. The

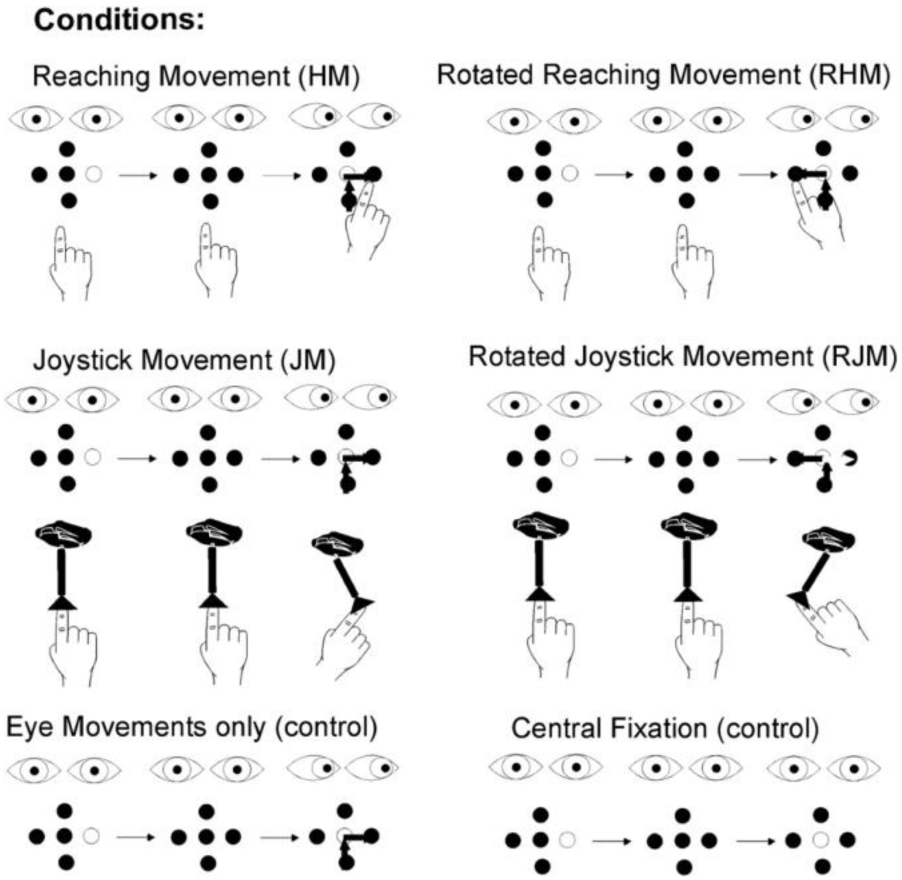

Fig. 1 – An illustrated representation of the experimental and control conditions performed in each imaging run. Reprinted from NeuroImage, 23/3, Brain mechanisms for preparing increasingly complex sensory to motor transformations. Gorbet, D., Staines, W. & Sergio, L., 110–1111, 2004, with permission from Elsevier.

instructions were to move very carefully during the task to avoid any overt movements which would cause movement related artifacts. Each subject was assigned a semi-counterbalanced order of the six conditions to control for order effects, where hand and joystick conditions were blocked together to minimize movement within the scanner. Subjects used only their right hand and performed five trials in each of the six conditions, in three functional runs. Thus, there were a total of 90 trials. Each imaging run was approximately 18 min long. T1-weighted anatomical images were collected immediately before collection of functional images.

2.3. *Training*

In this study it was important that the behavioral performance between groups was equivalent. Therefore, subjects were trained extensively at least one day before imaging data collection to ensure that activity reflected a learned paradigm rather than motor learning. Training was performed first at a desktop and then in a simulated scanner. The simulated scanner matched the dimensions of the actual imaging environment as closely as possible. Training lasted approximately 2 h/subject (or until subjects could perform all tasks repeatedly without error). Subjects also practiced all conditions from within the magnet immediately before scanning.

2.4. *Apparatus*

Event-related cortical activity was measured using fMRI. A 4.0 T, Varian/Siemens Unity Inova whole-body scanner (Robarts Research Institute, London, ON) was used to measure blood oxygen level dependent activity (BOLD) signals and to perform anatomical cortical scans. A birdcage radio frequency (RF) head coil was used (Barberi et al., 2000). Subjects lay supine in the bore with their heads flexed forward approximately 30° using a 'tilt-board' in order to directly interact with the screen. In order to minimize head motion artifacts, subjects' heads were secured using foam padding, and a piece of tape was laid across their forehead to provide the subjects with feedback about head movement. In addition, subjects' upper right arm was strapped to their bodies to eliminate large arm movements that could translate to their head. A plastic screen was suspended vertically at a distance that allowed subjects to directly see and touch back-projected targets. Motion about the wrist to acquire targets was approximately 30° for the HM conditions and 15° for the joystick conditions; however, these values varied by subject ±5° depending on projection distance (which was an average of 58.5 cm away from subject's eyes). The subjects' saccades towards the peripheral targets were an average of 12.5°. Visual stimuli were generated using custom-written software (Matlab, Mathworks Inc.) run from a portable computer. An interface was created which allowed subjects to control a joystick (Mag Design and Engineering, Sunnyvale, CA) using their right index finger. The joystick was attached to the scanner bed such that subjects could control it with their arm resting comfortably beside them. Four bend sensors (Images SI, New York, NY) were sewn into a thin, flexible glove (on the medial, lateral, dorsal, and ventral aspects), which subjects wore on their right hand. This allowed us to record the kinematics of the HMs made from within the bore of the magnet.

2.5. *fMRI parameters*

Functional imaging of the cortex was done using T2*-weighted, gradient echoplanar imaging, 64 × 64 resolution, time to echo (TE) = 12.0 msec, volume acquisition time = 2.0 sec, flip angle = 40°. Fifteen 5-mm thick slices oriented along the anterior commisure to posterior commisure (AC–PC) plane were used, giving voxel dimension of 3 × 3 × 5 mm. The bottom slice was positioned along the AC–PC plane. Acquisition of data from each slice was interleaved. Anatomical imaging was performed using turbo-FLASH, T1-weighted acquisition with 128 slices, TE = 5.5 msec, repetition time = 640 msec, flip angle of 11°, and a resolution of .8 × .8 × 1.25 mm.

2.6. *fMRI data analysis*

Due to the 30° tilt board, we positioned our RF coil and the functional slices to capture predominantly the frontal and parietal cortices. We focused our analysis on the BOLD signal above the AC–PC plane (the lowest functional slice collected), since we were interested in analyzing the known motor-related cortical areas; analyzing subcortical areas was beyond the scope of the current study.

2.6.1. *Preprocessing*

Analysis of the fMRI data of the individual subjects was performed using Brain Voyager QX 1.10 (Brain Innovation, Maastricht, The Netherlands). Each anatomical scan was converted from .8 × .8 × 1.25 mm voxel dimensions to 1 × 1 × 1 mm isovoxels. For each subject, successive functional images from all three runs were co-registered to the first image of their first run to compensate for movement. The functional data were then run through high-pass temporal filtering (at .0028 Hz) and linear trend removal. Each subject's data were also aligned to their corresponding T1-weighted anatomical data. For the prevention of confounding movement artifacts, any subject who moved more than 2 mm in any direction was eliminated from further analysis. A total of 70/78 (90%) of the functional runs were retained for further analyses. Scanning runs involved 534 image volumes, but the first two volumes of each run were discarded allowing for T1 stabilization.

2.6.2. *Inter-group analysis of fMRI data*

Inter-group analyses focused on movement preparation and excluded volumes during which subjects produced an overt movement. Random-effect general linear model analyses were performed on the 26 anatomical data sets, which had been normalized to Talairach space, were run to directly compare the video gamer and control groups. Design matrices, consisting of each subject's stimulation protocol, were convolved using a hemodynamic response function. Predictors were defined for the baseline and the delay periods for each condition. To directly test the hypothesis that male video gamers and male controls showed different patterns of cortical activity while preparing non-standard movements, main effect analyses were used to compare the BOLD signal during the preparation of each condition over baseline data at each voxel, using paired student *t* tests ($p_{\text{uncorrected}} < .005$). Additional main effect analyses between the video gamer group and the control group were performed on the two 'rotated'

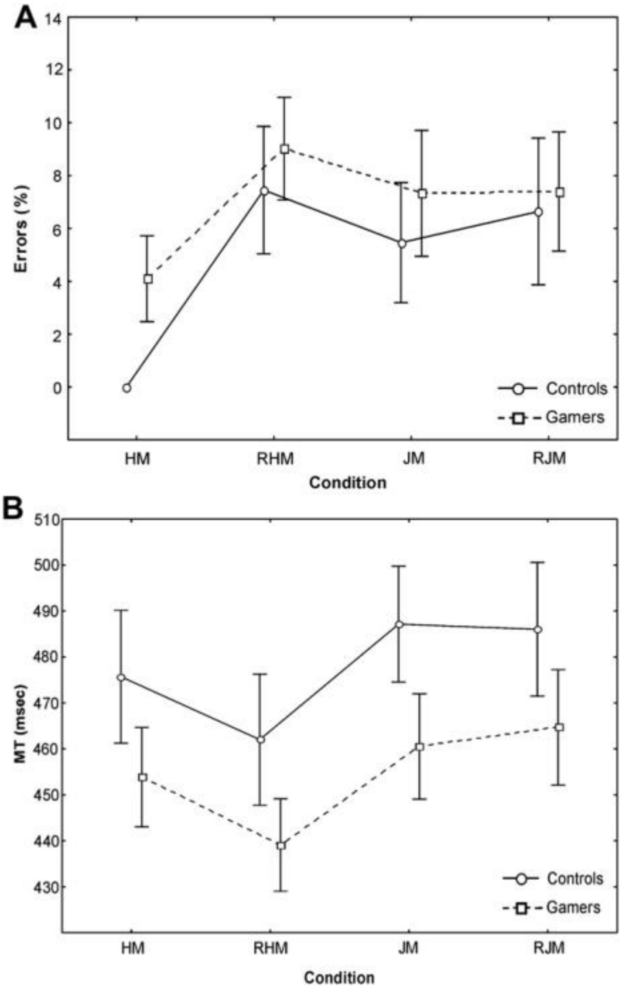

Fig. 2 – A) Mean percentage of errors made by the gamer (dashed line with squares) and control (solid line with circles) groups during performance of the experimental conditions. The percentages between groups were not significantly different: $F_{3,68} = .49$, $p = .87$. B) Mean MT for the gamers (dashed line with squares) and the controls (solid line with circles) during the performance of the four experimental conditions. MTs were not significantly different between groups: $F_{3,1012} = .19$, $p = .99$. Vertical bars denote standard error of the mean.

conditions (RJM and RHM) in order to compare the preparation for the *rotation* component of the tasks between groups. Specifically, the delay period of the JM condition was subtracted from the delay period of the RJM condition, while the HM delay period was subtracted from the RHM condition. To correct for multiple comparisons for all analyses, only clusters containing at least ten consecutive 'active' voxels were considered. Locations of clusters of activity were confirmed using Brain Voyager Brain Tutor 2.0 and the Damasio Atlas (1995).

2.7. *Behavioral data analysis*

The behavioral data were analyzed using MATLAB 7.0.4 using a custom-written scoring program. The HM data were examined for number of errors in movement direction and movement time (MT). Reaction time was not analyzed since the subjects were not instructed to begin movement as quickly as possible, to avoid any overt movements while in scanner. The behavioral data were only analyzed if the corresponding functional run could be analyzed. Due to technical reasons

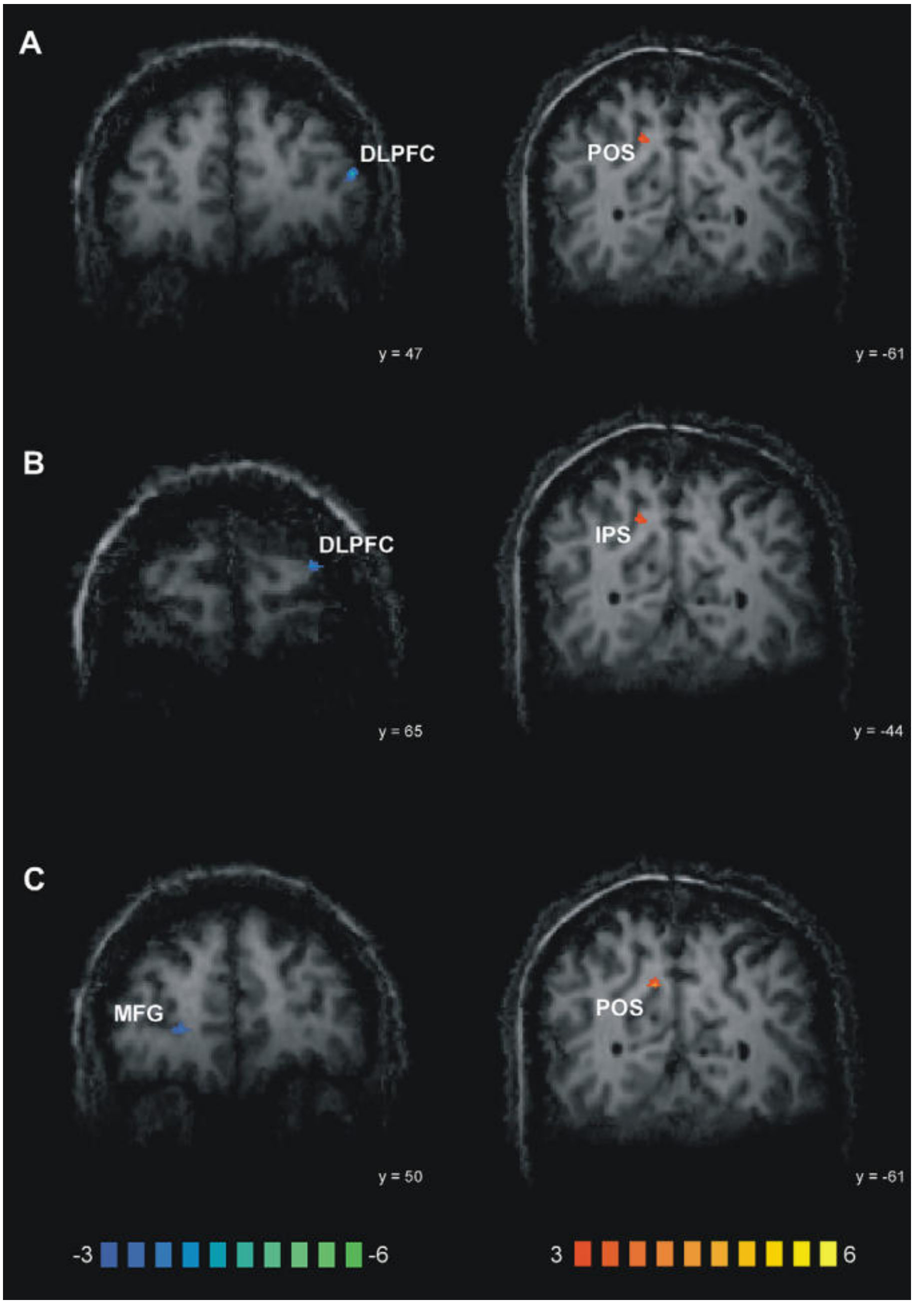

Fig. 3 – Data illustrating the areas of activation as a result of a main effect analyses during the delay period of the RJM (A), JM (B), and RHM (C) conditions over baseline, for the control subjects contrasted with the video gamer subjects. Functional data are superimposed on normalized and smoothed brains constructed from 26 subjects and are displayed as coronal slices. Y-values indicate the level of the coronal slice in Talairach space. Color bar represents *t*(24)-values in significant voxels, $p_{\text{uncorrected}} < .005$. Images are shown using neurological convention (left = left).

Table 1 – Differential cortical activation between the video gamers and the controls over baseline during the planning of the RJM condition.

Group	Cortical region	Coordinates	Extent	t-Value
Gamers	*Prefrontal cortex*			
	Right SFG (BA 10)	(16, 62, 7)	14	−4.16
	Right SFG (BA 10)	(9, 57, 1)	11	−3.60
	Left ventro-orbital prefrontal cortex (BA 47)	(−18, 59, −3)	10	−3.36
	Right DLPFC (BA 46)	(28, 64, 16)	14	−3.86
	Right DLPFC (BA 46)	(42, 53, 17)	61*	−4.38
	Right DLPFC (BA 46)	(36, 50, 6)	13	−3.78
	Right DLPFC (BA 46)	(48, 48, 12)	67*	−4.98
	Right DLPFC (BA 46)	(45, 36, 6)	30	−4.05
	Right IFG (BA 45)	(46, 51, 8)	37	−4.04
	Right IFG (BA 45)	(47, 27, 1)	59	−3.63
	Left IFG (BA 45)	(−52, 26, 11)	88*	−4.27
	Left LS (BA 45)	(−28, 21, 16)	20	−4.19
	Cingulate cortex			
	Left anterior cingulate cortex (BA 24)	(−3, 35, 13)	12	−3.81
	Premotor cortex			
	Left ventral premotor cortex (BA 6)	(−55, −2, 14)	61	−3.76
	Temporal cortex			
	Right superior temporal gyrus (BA 38)	(5, 18, −2)	90*	−4.51
	Occipital cortex			
	Left calcarine sulcus (BA 17)	(−5, −84, 12)	112**	−4.69
Controls	*Parietal cortex*			
	Left IPL (BA 19)	(−35, −62, 29)	13	3.53
	Left IPL (BA 19)	(−35, −56, 37)	35	3.52
	Left IPL (BA 7)	(−29, −55, 41)	37	3.73
	Left POS (BA 7)	(−14, −60, 39)	32	3.43
	Left precuneus (BA 7)	(−15, −52, 41)	63	3.41
	Premotor cortex			
	Right dorsal premotor cortex (BA 6)	(32, −7, 39)	14	3.42

Note: Coordinates (x, y, z) are given in Talairach space. Peak t(24)-values ($p_{\text{uncorrected}} < .005$) are presented when a minimum of ten contiguous voxels were simultaneously active as a result of a main effect analysis during preparatory period of the RJM condition over baseline activity, between the video gamer and control groups. Single asterisks denote ($p_{\text{uncorrected}} < .001$) and double asterisks denote ($p_{\text{uncorrected}} < .0005$). The anatomical names and areas (BAs) of the active regions have been identified.

(faulty bend sensor function/collection), only seven control subjects and twelve video gamer subjects had analyzable behavioral data. Number of errors and MT were analyzed using a factorial Analysis of Variance (ANOVA) and planned contrasts were performed within each movement condition and between subject groups.

3. Results

3.1. *Behavioral data*

3.1.1. *Movement errors*

The number of errors within each condition and between each group was analyzed from the output of the bend sensors. Importantly, while there was a main effect of condition across both groups, the behavioral performance across the four conditions did not differ between groups (Fig. 2A). After training, the non-video gamer controls were equally proficient when compared to the video gamers (4.9% and 7.0% error rates; ANOVA, $F_{3,68} = .24$, $p = .87$; contrasts: HM, $p = .16$, RHM, $p = .59$, JM, $p = .52$, RJM, $p = .79$).

3.1.2. *MT*

Task performance within each group and between each condition was also analyzed from the MT displayed by the output of the bend sensors. Importantly, there was no difference between the MT of each group across the four conditions (Fig. 2B). As a result of previous training on the task, there was no condition by group interaction (ANOVA, $F_{3,1012} = .19$, $p = .99$; contrasts: HM, $p = .11$, RHM, $p = .19$, JM, $p = .12$, RJM, $p = .22$).

Since the training was sufficient for there to be no behavioral differences (in both MT and number of errors) between the video gamer and control groups, one can then interpret cortical activity alterations in terms of neural processing differences between groups.

3.2. *fMRI data*

Our previous work revealed a basic network for visuomotor control, which changed as the eye and HMs were increasingly dissociated (Gorbet et al., 2004; Gorbet and Sergio, 2007). Here, we also observed cortical activation in these same prefrontal, premotor, sensorimotor, and parietal regions.

Table 2 – Differential cortical activation between the video gamers and the controls over baseline during the planning of the JM condition.

Group	Cortical region	Coordinates	Extent	t-Value
Gamers	*Prefrontal cortex*			
	Right SFG (BA 10)	(6, 59, 2)	12	−3.31
	Right DLPFC (BA 46)	(29, 64, 17)	35*	−4.38
	Right DLPFC (BA 46)	(48, 27, 5)	104*	−4.66
	Cingulate cortex			
	Left anterior cingulate cortex (BA 24)	(−3, 35, 13)	20	−4.32
	Temporal cortex			
	Right superior temporal gyrus (BA 38)	(49, 18, −2)	42	−4.23
	Premotor cortex			
	Left ventral premotor cortex (BA 6)	(−56, −2, 19)	22	−3.91
	Occipital cortex			
	Left calcarine sulcus (BA 17)	(−6, −83, 11)	47	−4.17
Controls	*Parietal cortex*			
	Left superior parietal lobule (BA 7)	(−14, −60, 39)	31	3.69
	Right superior parietal lobule (BA 7)	(28, −33, 37)	176*	4.09
	Left IPL (BA 7)	(−45, −46, 43)	18	3.68
	Right IPS (BA 7)	(32, −44, 39)	311*	4.36
	Right primary somatosensory cortex (BA 3)	(29, −26, 42)	337*	4.07
	Motor/premotor cortex			
	Right primary motor cortex (BA 4)	(27, −10, 37)	182**	5.05
	Right dorsal premotor cortex (BA 6)	(36, −8, 36)	84	3.82
	Right dorsal premotor cortex (BA 6)	(33, −2, 38)	41	3.92

Note: Coordinates (x, y, z) are given in Talairach space. Peak $t(24)$-values ($p_{\text{uncorrected}} < .005$) are presented when a minimum of ten contiguous voxels were simultaneously active as a result of a main effect analysis during the preparatory period of the JM condition over baseline activity, between the video gamer and control groups. Single asterisks denote ($p_{\text{uncorrected}} < .001$) and double asterisks denote ($p_{\text{uncorrected}} < .0005$). The anatomical names and areas (BAs) of the active regions have been identified.

3.2.1. *Movement planning over baseline*

The main effect analyses between the video gamers and the controls, over baseline brain activity, revealed an overall trend in all three non-standard tasks. Our principal novel finding was that video gamers utilized an altered weighting within the cortical visuomotor network responsible for complex movement planning. During the planning of the three non-standard visuomotor conditions, not only did experienced video gamers show less parieto-frontal cortical activation, but they also showed an increase in prefrontal activation (Fig. 3; Tables 1–3).

The increased prefrontal activity seen in the video gamer group was most obvious during the preparation of the most complex condition (RJM; Fig. 3A; Table 1). Specifically, during the planning of the RJM condition, compared with the controls, the video gamers utilized more rostral prefrontal cortex activity, including ipsilateral superior frontal gyrus (SFG; Brodmann Area – BA 10). As well, video gamers exhibited a marked increase in dorsolateral prefrontal cortex (DLPFC) activity, including the middle frontal gyrus (MFG; BA 46) and the inferior frontal gyrus (IFG; BA 46). We also observed increased bilateral ventrolateral prefrontal cortex (VLPFC) activity, including the IFG (BA 45), the ventro-orbital frontal gyrus (PFv+o; BA 47), and the rostral lateral sulcus (LS; BA 45).

The increased parietal cortex activity displayed by the control group was most apparent during the preparation of the RHM condition (Fig. 3C; Table 3). Specifically, the control group, as compared with the video gamer group, utilized greater posterior parietal cortex (PPC) activity including greater bilateral parieto-occipital sulcus (POS; BA 7, 19), precuneus (BA 7), intraparietal sulcus (IPS; BA 7), and inferior parietal lobule (IPL; BA 7) activity.

3.2.2. *Rotated visual feedback planning*

The main effect analyses between the video gamer and control groups for the ‘rotated’ conditions across effectors (hand or joystick), revealed a similar altered weighting between the prefrontal and parietal cortices (Fig. 4; Table 4). When planning for the 180° rotation using either effector, the

Table 3 – Differential cortical activation between the video gamers and the controls over baseline during the planning of the RHM condition.

Group	Cortical region	Coordinates	Extent	t-Value
Gamers	*Prefrontal cortex*			
	Left MFG (BA 10)	(−23, 49, 1)	64	−3.84
	Right MFG (BA 44)	(42, 37, 30)	27	−3.54
	Right IFG (BA 45)	(49, 21, 0)	213***	−5.27
	Temporal cortex			
	Right superior temporal sulcus (BA 22)	(52, −5, −8)	94*	−4.08
Controls	*Parietal cortex*			
	Right POS (BA 7)	(11, −68, 41)	37	3.34
	Left POS (BA 7)	(−12, −60, 38)	23	3.65
	Left POS (BA 7)	(−9, −58, 33)	116**	4.50
	Left POS (BA 19)	(−14, −51, 15)	55	4.23
	Right precuneus (BA 7)	(4, −62, 31)	18	3.71
	Left precuneus (BA 7)	(−16, −52, 38)	15	3.16
	Left IPS (BA 7)	(−21, −52, 35)	33	3.75
	Right IPS (BA 7)	(29, −41, 31)	106*	4.64
	Left IPL (BA 7)	(−33, −50, 37)	30	3.76
	Left IPL (BA 7)	(−28, −41, 33)	169*	4.32
	Right IPL (BA 7)	(36, −45, 41)	13	3.47
	Cingulate cortex			
	Left posterior cingulate cortex (BA 31)	(−8, −48, 37)	198*	4.19
	Left posterior cingulate cortex (BA 31)	(−1, −46, 29)	73	3.80
	Right posterior cingulate cortex (BA 23)	(1, −23, 37)	16	3.61
	Left anterior cingulate cortex (BA 24)	(−4, −8, 35)	32	3.52
	Prefrontal cortex			
	Left superior frontal sulcus (BA 9)	(−24, 44, 32)	32	3.96

Note: Coordinates (x, y, z) are given in Talairach space. Peak t(24)-values ($p_{\mathrm{uncorrected}} < .005$) are presented when a minimum of ten contiguous voxels were simultaneously active as a result of a main effect analysis during the preparatory period of the RHM condition over baseline activity, between the video gamer and control groups. Single asterisks denote ($p_{\mathrm{uncorrected}} < .001$), double asterisks denote ($p_{\mathrm{uncorrected}} < .0005$), and triple asterisks denote ($p_{\mathrm{uncorrected}} < .0001$). The anatomical names and areas (BAs) of the active regions have been identified.

video gamers recruited additional prefrontal cortices relative to the controls. These additional areas included rostral SFG (BA 10), PFv+o (BA 47, 10), and IFG (BA 45, 44). Again in contrast, the controls relied predominantly on parietal activity including bilateral superior parietal lobule (SPL; BA 19), contralateral IPL (BA 19), IPS (BA 19), as well as supramarginal gyrus (SMG; BA 40). Overall, a prefronto-parietal activation dichotomy was observed between groups during the preparation of a 180° rotation, regardless of the end-effector utilized.

4. Discussion

These findings demonstrate how long-term, heavy experience with video games can alter the brain activity involved in controlling other types of visually guided movements. Specifically, as the spatial location of the visual stimulus differed from the location of the motor target, as in the non-standard visuomotor conditions, an altered weighting within the preparatory cortical visuomotor network became apparent. When planning this type of dissociated movement, video gamers displayed a reduction in parieto-frontal cortical activity with a concomitant increased recruitment of prefrontal cortical areas, relative to non-gamers. Even when planning for the rotational aspect of the non-standard tasks regardless of the effector (joystick or hand), the altered weighting between the prefrontal and parietal cortices was preserved. These findings support our hypothesis that extensive video gaming experience would lead to a relative reduction in the parieto-frontal activity associated with performing more general classes of visuomotor tasks. However, we extend previous findings by quantifying additional loci of brain activity related to the extent of video-game experience. Together, these changes represent an alteration within the cortical network for different levels of non-standard visually guided action. This alteration was seen in the video gamers despite the equivalent sensory input, and despite the absence of any behavioral performance differences between the two groups. Thus, our observations reflect the neural processes which underlie the planning of the visually guided movements.

4.1. *Prefrontal cortex and experience*

Within the prefrontal cortex, increased DLPFC (BA46) activation was observed in experienced video gamers compared to age- and sex-matched controls in all three non-standard tasks. The DLPFC is widely known as an area associated with inhibitory attention (Hoshi and Tanji, 2006; Leung and Cai, 2007), specifically during the preparation and switching of motor programs incorporating tool-use (Moll et al., 2000; Saito

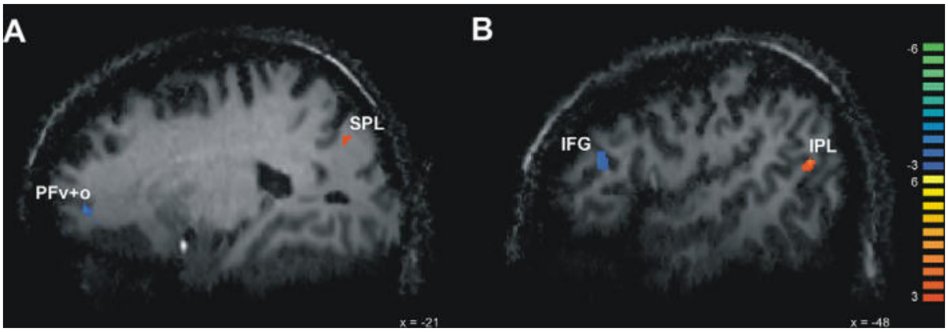

Fig. 4 – Data illustrating the areas of activation as a result of main effect analyses during the delay period of the RJM condition over JM (A) and the RHM condition over HM (B), for control subjects contrasted with the video gamer subjects. Functional data are superimposed on normalized and smoothed brains constructed from 26 subjects and are displayed as sagittal slices. *X*-values indicate the level of the sagittal slice in Talairach space. Color bar represents *t*(24)-values in significant voxels, $p_{\text{uncorrected}} < .005$. Images are shown as (anterior = left). PFv+o, ventro-orbital prefrontal cortex.

et al., 2005). Our non-standard JM task required halting the natural spatial linkage of eye and HMs (Gielen et al., 1984; Gorbet et al., 2004; Neggers and Bekkering, 2000, 2001) in order to use a joystick. Similarly, it has been proposed that prefronto-striatal connectivity, specifically deriving from the DLPFC, is necessary for the decision to inhibit natural tendencies such as in the case of performing anti-saccades (Bertolino et al., 2009; Durston et al., 2005). We suggest that the increased DLPFC activity seen in our video gamer group may be one of the brain areas which function to break apart eye and HMs in order to incorporate non-standard mapping into an ongoing movement plan.

We also found increased rostral prefrontal activation in all three non-standard tasks, in the video gaming group compared with controls. The rostral SFG is known to be involved in rule-based decision making (Leung and Cai, 2007; Murray et al., 2000; Rowe et al., 2008) and it is strongly interconnected with the dorsal premotor cortex (PMd) (Tomassini et al., 2007), a brain area known to be active in non-standard movement control (Batista et al., 1999; Battaglia-Mayer et al., 2001; Boussaoud et al., 1998; Crammond and Kalaska, 1994; Johnson et al., 1999; Shen and Alexander, 1997; Snyder et al., 2000). In the present context, video gamers may rely on prefrontal activation to recruit consolidated motor plans within premotor cortex – learned from video-game training – in order to integrate the rule-based behavior required for non-standard visuomotor mapping. In contrast, previous studies (Debaere et al., 2004; Sakai et al., 1998; Shadmehr and Holcomb, 1997) have reported that as performance improves during a learning paradigm, less prefrontal activation is required. What differentiates the results in the present study is the number of trials performed by the subjects. It has been shown that prefrontal cortices may not be necessary for automation of a specific skill (Doyon et al., 1998). It may be that in the present study, the video gamers did not perform enough trials in the general non-standard tasks for the performance to become completely automated.

The video gamers also displayed additional loci of activity throughout the VLPFC as compared to the controls. Specifically, the lateral PFv+o was also more strongly recruited in the video gamers for all three non-standard tasks. The PFv+o has been implicated in learning new non-standard visuomotor transformations involving joysticks (Murray et al., 2000) and in the acquisition of arbitrary visuomotor associations where the visual information required for guiding a motor response must be learned (Rushworth et al., 2005). As well, the PFv+o is required for learning the reward value of a visual stimulus (Hornak et al., 2004). This suggests that the increased PFv+o activation seen here for the video gamer group might be associated with the video gamers' increased motivation towards the successful completion the task (Hoeft et al., 2008). In addition, IFG and the inferior portion of MFG were additionally active in the video gamers relative to the controls. IFG has been shown to be involved in working memory and attention during planning for visuomotor transformations (Brass and von Cramon, 2002; Derrfuss et al., 2004) as a part of a conflict control network (Petrides and Pandya, 1999). This implies that the video gamers utilized increased active conflict control processing during non-standard visuomotor transformations.

In summary, the increase in prefrontal cortex activity observed in the video gamers, relative to the controls, putatively reflects the generalization of a specific non-standard visuomotor skill towards other types on non-standard visuomotor transformations.

4.2. *Less experience requires more sensorimotor processing*

The altered weighting within the cortical network controlling dissociated visuomotor transformations in non-video gamers, relative to video gamers, consisted of less prefrontal activity and more activity in the primary motor, lateral premotor, posterior parietal, and parietal association areas. The additional sensorimotor activation seen in non-video gamer controls confirmed past studies on skill and cortical activity reduction in skilled performers (Haslinger et al., 2004; Jancke et al., 2000; Krings et al., 2000; Norton et al., 2005). The primary sensorimotor area (M1/S1) is well known throughout the literature for the planning and execution of all types of sensorimotor transformations. The increased ipsilateral premotor activity seen in the controls during the preparation of both joystick conditions (RJM/JM), specifically in the caudal

Table 4 – Differential cortical preparatory activation between the video gamers and the controls for the rotated conditions (RJM and RHM) over the non-rotated conditions (JM and HM).

Condition	Group	Cortical region	Coordinates	Extent	t-Value
RJM	Gamers	*Prefrontal cortex*			
		Left SFG (BA 10)	(−2, 53, −6)	81*	−4.08
		Left ventro-orbital prefrontal cortex (BA 10)	(−17, 50, −4)	87	−3.98
		Left ventro-orbital prefrontal cortex (BA 47)	(−32, 40, −2)	48	−3.87
		Left IFG (BA 45)	(−47, 32, 6)	12	−3.68
		Premotor cortex			
		Left ventral premotor cortex (BA 6)	(−58, 8, 18)	37*	−4.21
		Parietal cortex			
		Right IPS (BA 7)	(21, −46, 45)	19	−3.63
	Controls	*Parietal cortex*			
		Left superior parietal lobule (BA 19)	(−21, −74, 32)	13	3.21
		Right superior parietal lobule (BA 19)	(27, −63, 38)	10	3.62
		Cingulate cortex			
		Right anterior cingulate cortex	(4, −3, 30)	32	4.19
RHM	Gamers	*Prefrontal cortex*			
		Left ventro-orbital prefrontal cortex (BA 10)	(−23, 49, 2)	13	−3.79
		Right ventro-orbital prefrontal cortex (BA 47)	(42, 23, −6)	24	−3.62
		Left IFG (BA 44)	(−45, 34, 17)	186*	−4.37
		Right MFG (BA 44)	(38, 20, 33)	113*	−4.48
		Temporal cortex			
		Right superior temporal gyrus (BA 41)	(46, −22, 8)	17	−3.81
	Controls	*Parietal cortex*			
		Left IPL (BA 19)	(−47, −58, 16)	37	4.46
		Left IPS (BA 19)	(−28, −47, 31)	40	3.50
		Left SMG (BA 40)	(−53, −27, 40)	28	3.62
		Cingulate cortex			
		Left anterior cingulate cortex	(−2, 3, 35)	191*	4.00

Note: Coordinates (x, y, z) are given in Talairach space. Peak t(24)-values ($p_{\text{uncorrected}} < .005$) are presented when a minimum of ten contiguous voxels were simultaneously active. The main effect analyses were applied to the planning period of the RJM condition contrasted with the JM planning period, and the RHM condition contrasted with the HM planning period. All values represent a contrast between the video gamer and control groups. Single asterisks denote ($p_{\text{uncorrected}} < .001$). The anatomical names and areas (BAs) of the active regions have been identified.

portion of PMd (PMdc), likely reflects the formulation of a less practiced motor plan. PMdc is known for its arm movement planning (Picard and Strick, 2001; Tachibana et al., 2004; Weinrich and Wise, 1982) and has been shown to suppress movements that have been prepared, but are not going to be used (Koch et al., 2006). Given the right PMd's role in movement suppression and contralateral arm control (Koch et al., 2006; Kurata, 1994), we suggest that the greater right PMdc activation seen in our control group reflects an inhibition of their natural tendency to reach towards the direction of gaze. As discussed above for experienced video gamers, this inhibition was reflected in the cortex as additional prefrontal activity.

Our control subjects also had an increase in parietal BOLD activity in the preparation of all three non-standard conditions, as well as the 180° rotation. These parietal loci were in IPL, SPL, IPS, POS, precuneus, and SMG, which are areas that may be related to processing the disparate spatial alignment between vision and proprioception during these non-standard tasks (Caminiti et al., 1996; Leung and Cai, 2007; Moll et al., 2000). The IPL and its connections with the DLPFC have been shown to be involved in cognitive control during visuomotor tasks involving increased inhibitory attention (Leung and Cai, 2007). An intact left IPL has been shown to be required for proper tool manipulation (Buxbaum et al., 2007). Further, SPL activity, has been regarded as integral for covert spatial attention (Caminiti et al., 1996) and an intact SPL has been implied in the role of extrafoveal reaching implied by the gaze-biased misreaching seen in optic ataxics (Blangero et al., 2010; Jackson et al., 2005; Khan et al., 2007). In addition, area V6A within the SPL of non-human primates, has been shown to be involved in the dissociation between the eye and the hand during visually guided reaching movements (Marzocchi et al., 2008). Areas within the IPS have been shown to integrate both proprioception and vision (Beurze et al., 2007; Lewis and Van Essen, 2000a) and can incorporate a tool as an extension of the end-effector (Obayashi et al., 2001). Specifically, the posterior superior, middle inferior and anterior inferior part of the IPS are involved with anti-pointing during central fixation (Connolly et al., 2000). The POS connects the parietal to the occipital lobe (Lewis and Van Essen, 2000b) and has been shown to be involved in the integration of visual information into a motor output when a visual target is within reach (Gallivan et al., 2009). Therefore, the POS is crucial for visuomotor control and an intact POS appears to be integral for extrafoveal reaching (Clavagnier et al., 2007; Prado et al., 2005; Trillenberg et al., 2007). In the lower medial parietal cortex, the precuneus is implicated in shifting attention between different spatial locations (Ogiso et al., 2000) and in the working memory of an upcoming movement (Luber et al., 2007). In the lateral parietal cortex, the SMG is a secondary somatosensory area, activated during reaching tasks towards remembered targets (Lacquaniti et al., 1997) and during tool-use (Johnson-Frey et al., 2005). In summary, the increased BOLD response seen throughout the parietal cortex in the control group suggests that additional bottom-up processes are required by a non-experienced individual. We suggest that these greater activity levels in less experienced subjects reflect the natural recruitment of parietal areas needed to process non-standard visuomotor tasks.

From the opposite perspective, we observed *less* sensorimotor cortical activation in experienced video gamers in the three non-standard conditions. This relatively lower sensorimotor activation, despite the equivalent behavioral performance with the control subjects, may be a neural consequence of their experience with situations where there is a discrepancy between the direction of the eye and the hand, especially when using a tool such as a joystick. One consistent exception was observed in the ipsilateral superior temporal cortex. The video gamers utilized additional right superior temporal activation during the preparation of all non-standard conditions. Right superior temporal gyrus (STG) activation has been implied in the role of spatial attention during visuomotor transformations (Karnath et al., 2001). The activation of the prefrontal, premotor, motor, posterior parietal and temporal lobes seen in the current study overlap with areas known as cortical hubs of connectivity (Buckner et al., 2009; Hagmann et al., 2008), implying these areas as communicative nodes involved in different types of transformations.

4.3. *Caveats and future considerations*

A limitation of our study is that we were unable to track the eye movements of the subjects from within the scanner. Eye tracking would also enable us to confirm that they did always look towards the target after movement onset, although it would be unlikely that they would not foveate a bright green flashed target while lying in a dark room. Further, since we confirmed that they were doing the task correctly during the training sessions, we were confident that our subjects were all sufficiently motivated and trained to perform the task correctly during the scanning.

Due to the liberal statistical threshold used to identify the differences between groups in this study, future prefrontal and parietal region of interest fMRI experiments, utilizing appropriate localizer protocols, would be of use to confirm the present findings.

With a larger sample of video gamers, it would be interesting to analyze whether there was an effect of *amount* of experience as well as video-game *type* on the pattern of brain activity changes during more general dissociated visuomotor transformations. For example, would experience exclusively with Wii™ (which employs standard mapping) versus action (which employs non-standard mapping) video games have different effects on brain activity? As well, since significant sex differences have been observed in brain activity during non-standard reaching (Gorbet and Sergio, 2007), it would be of interest to see if our findings of increased efficiency applied to the activation pattern seen in females video gamers while planning for dissociated visuomotor transformations.

Lastly, an additional direction for this work would be to combine the present video gaming/experience related approach to another line of study characterizing dissociated performance deficits in early Alzheimer's disease (AD). Past studies (Ghilardi et al., 1999; Tippett and Sergio, 2006; Tippett et al., 2007) have shown that early AD patients display increased reaction times and MTs as well as an increased amount of errors when performing different levels of dissociated visuomotor transformations. One could speculate that if video-game experience has the ability to alter the weighting within the cortical network responsible for planning for different levels of non-standard visuomotor situations, perhaps it could delay the behavioral deficits seen in early AD patients.

5. Conclusions

In summary, we offer two important contributions to the concept of neural efficiency. First, we characterize an altered prefronto-parietal weighting of activity in the movement-planning brain network as a result of extensive, long-term video-game experience. Second, using a task that was different from the particular skill of our "expert" group, we found that video-game experienced adults were able to use an altered cortical network to control *other* dissociated visuomotor tasks. Thus, the brain reorganization that occurred with skill development is not exhibited solely while playing video games, but has been generalized to other types of non-standard visually guided movement.

Acknowledgements

The authors wish to acknowledge the invaluable contributions of Joy Williams, Adam McLean, Lan Nguyen, and Dr. Denise Henriques. This work was supported by an operating grant from the Canadian Institutes for Health Research, MOP-74634.

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