Gaming is related to enhanced working memory performance and task-related cortical activity

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Keywords: working memory, functional MRI, gaming, adolescence, dorsolateral prefrontal cortex

Abstract

Gaming experience has been suggested to lead to performance enhancements in a wide variety of working memory tasks. Previous studies have, however, mostly focused on adult expert gamers and have not included measurements of both behavioral performance and brain activity. In the current study, 167 adolescents and young adults (aged 13–24 years) with different amounts of gaming experience performed an *n*-back working memory task with

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[1] Abbreviations: DA = digital activity; GPA = grade point average; WM = working memory; LH = left hemisphere; RH = right hemisphere; MFG = middle frontal gyrus; SPL = superior parietal lobe; Prc = precuneus; SFG = superior frontal gyrus; SMA = supplementary motor area; SDP = sociodigital participation.

vowels, with the sensory modality of the vowel stream switching between audition and vision at random intervals. We studied the relationship between self-reported daily gaming activity, working memory (*n*-back) task performance and related brain activity measured using functional magnetic resonance imaging (fMRI). The results revealed that the extent of daily gaming activity was related to enhancements in both performance accuracy and speed during the most demanding (2-back) level of the working memory task. This improved working memory performance was accompanied by enhanced recruitment of a fronto-parietal cortical network, especially the dorsolateral prefrontal cortex. In contrast, during the less demanding (1-back) level of the task, gaming was associated with decreased activity in the same cortical regions. Our results suggest that a greater degree of daily gaming experience is associated with better working memory functioning and task difficulty-dependent modulation in fronto-parietal brain activity already in adolescence and even when non-expert gamers are studied. The direction of causality within this association cannot be inferred with certainty due to the correlational nature of the current study.

1. Introduction

A substantial amount of evidence has accumulated suggesting that extensive experience with computer and video game playing is associated with enhancements in a wide variety of cognitive domains (for reviews, see Connolly et al., 2012; Green & Bavelier, 2012; Powers e al., 2013). It has been proposed that since gaming requires the player to react rapidly, monitor fast-paced concurrent visual and auditory stimuli and switch flexibly between subtasks while holding information in memory, this might lead to improved attentional and working memory abilities in gamers. Games may, in other words, act as a cognitive enhancement tool, even though that is not their primary purpose (Anguera & Gazzaley, 2015). Experimental studies focusing on attentional abilities have indeed shown that gamers outperform non-gamers in tasks measuring, for example, visual selective attention and the spatial distribution of visuospatial attention (Green & Bavelier, 2003), as well as multiple object tracking (Trick et al., 2005; Green & Bavelier, 2006). The ability to switch flexibly between tasks (Colzato et al., 2010; Karle et al., 2010; Cain et al., 2012; Green et al., 2012) and perform multiple simultaneous tasks (Strobach et al., 2012) has also been shown to be superior in video game players, suggesting that experience with gaming can generalize to improvements in cognitive control. However, some studies have shown that gaming can have negative effects on executive functions (Bailey et al., 2010). Moreover, a recent meta-analysis found negligible associations between gaming experience and executive functions when only experimental studies with a video-game training paradigm were taken into consideration (Powers et al., 2013).

In the domain of working memory, gaming has been linked to improved performance in standard visual *n*-back tasks both in terms of reaction times (McDermott et al., 2014) and performance accuracy (Colzato et al., 2013). Similar results have been obtained using other working memory paradigms (Boot et al., 2008), and with both stationary and dynamic stimuli (Sungur & Boduroglu, 2012). In addition, the advantage of gaming on working memory performance seems to hold irrespective of the complexity of the used stimuli or the time allotted to memory encoding (Blacker & Curby, 2013). Taken together, these results suggest that gaming is linked to an improved ability to maintain and flexibly update information in working memory.

Whether the evidence outlined above allows for any causal inferences to be made about the relationship between gaming and cognition is still under debate. Some evidence exists for the notion that cognitive benefits can be obtained by training non-gamers on action video games (Green & Bavelier, 2003) even when the participants are older adults (Anguera et al., 2013; Belchior et al., 2013). Yet, such training studies have also produced null findings (Boot et al., 2008). Further, it remains unclear whether different types of games produce similar effects on cognition, as most studies to date have been conducted on action video game players. The specific effects of different game genres (such as strategic or roleplaying games) remains understudied, but some evidence suggests that the unique aspect of each game genre may enhance different aspect of cognition (Oei

& Patterson, 2013). For example, it has been shown that training on spatially-orientated games enhances visual cognition, while non-spatially orientated games have no such effect (Subrahmanyam & Greenfield, 1994; DeLisi &Wolford, 2002).

The aim of the current study was to examine whether the amount of daily gaming activity affects adolescents' and young adults' (aged 13-24) performance and brain activity during an *n*-back task. We devised an *n*-back task which required the participants to report whether a presented vowel matched a stimulus presented *n* trials previously, with the modality of the vowel switching between the auditory and visual modalities at unpredictable intervals. With this task we were able to measure not only working memory capacity within one sensory modality, but also the ability to switch attention between sensory modalities while maintaining vowel representations in working memory. We reasoned that in addition to working memory performance such cognitive flexibility might be entrained by computer gaming. Our bimodal task also allowed us to determine whether gaming activity affects both visual and auditory working memory. The specific effects of different game types on working memory performance were also examined. Brain activity during task performance was recorded using event-related functional magnetic resonance imaging (fMRI) in order to determine the effects of gaming on brain activity associated with working memory or modality switching.

Although the cognitive effects of gaming have been studied extensively, the current study provides a valuable addition to this line of research for several reasons. Firstly, the participants in our study were sampled from a wide age range of adolescents and young adults, whereas previous studies have mostly been conducted on adults. This allowed us to examine possible age-related effects contributing to the association between cognitive changes and gaming. Furthermore, our study did not recruit avid or expert gamers and compare them to non-gamers, as most previous studies have done. The amount of daily gaming of our participants varied from little gaming to moderate amounts of gaming, meaning that our results are more generalizable to adolescents and young adults in general instead of only to individuals at the extreme ends of the gaming spectrum. Finally, our study incorporated not only behavioral measures but also the measurement of task-related brain activity which allowed us to determine the neural underpinnings of the possible cognitive benefits related to gaming. Although gamers have previously been shown to perform better at working memory tasks, the cortical underpinnings of this behavioral advantage have not been studied before. In fact, to our knowledge our study is the first ever to combine behavioral measures and fMRI when studying the link between gaming activity and working memory performance in healthy participants.

2. Results

2.1. Gaming Score and Digital Activity Score

The ages and grade point averages (GPA) per age cohort and gender are displayed in **Table 1**. Boxplots of the Gaming Scores for females and males in each of the three age cohorts can be seen in **Figure 2A**. The Gaming Score did not differ significantly between age cohorts ($p=0.09$) but it was significantly higher for males than females ($F(1,161)=6.74$, $p<0.05$, $\eta^2=0.04$). Gaming Score and Digital Activity (DA) Score (i.e., the self-reported amount of daily technologically mediated activity) showed a strong and significant correlation ($r=0.36$, $p<0.001$) when Age Cohort and Gender were controlled for.

Table 1. Participant characteristics.

Age Cohort	Gender	Age (±SD)	GPA (±SD)
13-14 yrs (n=57)	**F** (n=25)	**13.1** (±0.4)	**8.6** (±0.5)
	M (n=32)	**13.3**. (±0.5)	**8.4** (±0.7)
16-17 yrs (n=57)	**F** (n=31)	**16.6** (±0.5)	**9.1** (±0.5)
	M (n=26)	**16.6** (±0.5)	**8.8** (±0.7)
20-24 yrs (n=53)	**F** (n=24)	**20.6** (±1.3)	**8.9** (±0.7)
	M (n=29)	**21.9** (±0.9)	**8.3** (±0.9)

The latent variable structure of the Gaming Scale was explored using a multidimensional item response theory (MIRT) model, which produced three latent variables explaining a total of 58% of the variance. Variable 1 (explaining 25% of the variance) was labeled Serious Games due to the high loadings of the following game genres: role playing games, adventure games, strategic games, and shooter games. Variable 2 (explaining 20% of the variance) was labeled Fun Games, as the items loading most strongly onto this latent variable were: music games, exercise games, party games and puzzle games. The final variable (explaining 13% of the variance) was labeled Sports games, due to the high loadings of sports games and racing games onto this latent variable. The loadings and communalities for the items of the Gaming scale are listed in **Table 2**. Internal consistency for each of the scales was examined using Cronbach's alpha. The alphas were moderate: 0.79 for Serious Games (4 items), 0.70 for Fun Games (4 items), and 0.63 for Sports Games (2 items). The resulting three latent variables were used in subsequent statistical analyses as a between-subjects variable in order to further examine significant effects related to Gaming Score. Boxplots depicting the distribution of scores for the three latent gaming variables are presented in **Figure 2B**.

Table 2. The communalities and loadings onto the three latent gaming variables for the 10 items of the Gaming scale

		Loadings		
	Variable 1: **Serious Games**	Variable 2: **Fun Games**	Variable 3: **Sports Games**	**Communality**
Role playing games (e.g., World of Warcraft, Mass Effect, The Elder Scrolls, Fallout)	0.87			0.73
Adventure games (e.g., Legend of Zelda, Minecraft, Tomb Raider, Uncharted)	0.76			0.64
Strategic games (e.g., Starcraft, Civilization, Age of Empires, Total War, The Sims)	0.73			0.58
Shooter games (e.g., Grand Theft Auto, Call of Duty, Battlefield, Far Cry)	0.59			0.50
Music/dance games (e.g., Just Dance, Singstar, Rock Band)		0.79		0.62
Exercise games (e.g., Wii, MS Kinetic, Wii Sports, Your Shape)		0.68		0.51
Party games (e.g., Mario Party, Start the party)		0.58		0.43
Puzzle games (e.g., Angry Birds, Bejeweld, Tetris, Most Pogo, Puzzle Quest)		0.52		0.36
Sports games (e.g., NHL, FIFA, Tiger Woods, Madden, Football Manager)			0.94	0.87
Racing games (e.g., Gran Turismo, Mario Kart, GRID, Need for Speed)			0.45	0.52

Note. Loadings <0.4 are suppressed.

2.2. Behavioral results

The overall mean percentage of correct responses (± standard error of the mean, SEM) was 92.0% ± 0.4%. In 3% (32/1020) of the blocks the percentage of correct responses were three standard deviations lower than the mean (below 57.2%), and these blocks were excluded from further analyses. General performance effects related to increasing task difficulty and modality switching were studied by conducting a repeated-measures ANOVA with Memory Load (0-back, 1-back and 2-back) and Modality Switch (switch and no switch) as the within-subjects variables. A main effect of Memory Load on performance accuracy was observed ($F(2,332)=126.06$, $p<0.001$, $\eta^2=0.34$, $\varepsilon=0.75$). Performance accuracy decreased with increasing Memory Load, and it was 97.4 ± 0.3% for

0-back, 94.7 ± 0.4% for 1-back and 86.2 ± 0.8% for 2-back ($p<0.001$ for all pairwise comparisons). Modality Switch also had a main effect on performance ($F(1,166)=6.54$, $p<0.05$, $\eta^2=0.003$). Performance accuracy was slightly lower after a modality switch (92.3 ± 0.4%) than if no switch had occurred (93.2 ± 0.3%). There was also an interaction between Memory Load and Modality Switch ($F(2,332)= 4.16$, $p<0.05$, $\eta^2=0.003$, $\varepsilon=0.88$), because Modality Switch had a main effect on 0-back ($F(1,166)=9.33$, $p<0.005$, $\eta^2=0.05$) and 1-back ($F(1,166)=13.63$, $p<0.001$, $\eta^2=0.07$), but not the 2-back ($F(1,166)=0.31$, $p=0.58$) task.

When response times were studied, a main effect of Memory Load was observed ($F(2,332)=346.24$, $p<0.001$, $\eta^2=0.59$, $\varepsilon=0.84$). Response times increased with increasing Memory Load, so that they were 0.75 ± 0.01s for 0-back, 0.95 ± 0.01s for 1-back and 1.10 ± 0.02s for 2-back ($p<0.001$ for all pairwise comparisons). Modality Switch also had a main effect on performance ($F(1,166)=87.78$, $p<0.001$, $\eta^2=0.02$), so that response times were slightly longer after a modality switch (0.95 ± 0.01s) than if no switch had occurred (0.90 ± 0.01s). There was also an interaction between Memory Load and Modality Switch ($F(2,332)= 5.96$, $p<0.005$, $\eta^2=0.002$, $\varepsilon=0.96$), but subsequent ANOVAs revealed that Modality Switch had a main effect on 0-back ($F(1,166)=21.11$, $p<0.001$, $\eta^2=0.11$), 1-back ($F(1,166)=47.28$, $p<0.001$, $\eta^2=0.22$), and 2-back ($F(1,166)=40.46$, $p<0.001$, $\eta^2=0.20$) tasks.

Next, the effects of the between-subjects variables on both the percentage of correct responses and response times were examined by conducting a repeated measures ANOVA with Memory Load (1-back, 0-back and 2-back) as the within-subject variable. In this ANOVA, as well as in all subsequent ANOVAs, Age Cohort and Gender were included as between-subjects factors, and Gaming Score, DA Score and GPA as covariates. When performance accuracy was examined, no significant main effect of Gaming Score ($F(1,157)=0.51$, $p=0.47$) or interaction with Memory Load ($F(2,314)=2.10$, $p=0.14$, $\varepsilon=0.70$) was observed. Partial correlations were also calculated in order to produce correlation coefficients between Gaming Score and task performance. All reported partial correlations are controlled for Age Cohort, Gender, DA Score and GPA. Partial correlations suggested that there was no association between performance and Gaming Score during the 0-back (r=0.06, p=0.44) or 1-back (r=-0.07, p=0.40) conditions. There was, however, a non-significant trend for Gaming Score to be associated with better performance during the 2-back condition (r=0.15, p=0.06). In order to study whether the trend for gaming to be associated with better performance specifically during the 2-back task might be explained by increased attention and vigilance during this task type, the amount of misses as well as the effects of run number during 1- and 2-back tasks were studied by conducting a repeated-measures ANOVA with Run number and Memory Load (1-back and 2-back) as the within-subject variables. The results showed no significant interaction between Run number, Task type (1- and 2-back) and Gaming Score for either the percentage of correct trials (F(1,157)=0.68, p=0.41) or misses (F(1,157)=0.76, p=0.39), nor was the interaction between Task type (1- and 2-back) and Gaming Score significant for the amount of miss trials (F(1,157)=0.96, p=0.33). When an ANOVA with Memory Load (1-back, 0-back and 2-back) as the within-subject variable was carried out for response times, an significant interaction between Gaming Score and Memory Load (F(2,314)=3.68, $p<0.05$, $\eta^2=0.02$, $\varepsilon=0.85$) was revealed. Partial correlations confirmed this interaction to be due to the fact that Gaming Score was associated with shorter response times only during 2-back (r=-0.23, $p<0.005$), but not during 0-back (r=-0.11, p=0.16) or 1-back (r=-0.10, p=0.20). When the analysis was repeated so that the three latent gaming variables were used as between-subjects variables instead of Gaming Score, no interactions between Memory Load and any of the latent variables were observed.

Next, difference measures between the n-back levels were examined. When a repeated measures ANOVA for the percentage of correct responses was conducted with Memory Load (1-back vs. 0-back, 2-back vs. 0-back and 2-back vs. 1-back) as the within-subject variable, a significant interaction between Gaming Score and Memory Load was observed (F(2,314)=3.77, $p<0.05$, $\eta^2=0.02$, $\varepsilon=0.62$): As seen in **Figure 3A,** partial correlation calculations revealed that Gaming Score was positively associated with the change in the percentage of correct responses from 1-back to 2-

back ($r=0.17$, $p<0.05$), but not with the change in the percentage of correct responses form 0-back to 1-back ($r=-0.11$, $p=0.17$) or from 2-back to 0-back ($r=0.12$, $p=0.14$). In other words, as the difficulty of the *n*-back task increased from 1-back to 2-back, Gaming Score was associated with smaller decrements on performance accuracy. An identical ANOVA to the previous one, but with mean response times as the dependent variable, did not show a significant interaction between Gaming Score and Memory Load ($F(2,314)=0.97$, $p=0.33$). However, partial correlations revealed that, as seen in **Figure 3B,** the association between Gaming Score and the change in response times from 1-back to 2-back was significantly negative ($r=-0.17$, $p<0.05$; the higher the Gaming Score was, the smaller the 2-back minus 1-back difference was), but not between Gaming Score and the change in response times from 0-back to 1-back ($r=-0.03$, $p=0.73$) or from 2-back to 0-back ($r=0.12$, $p=0.14$). When analyses of difference measures on performance accuracy and response times were repeated using the latent gaming variables instead of Gaming Score, no significant interactions were observed between Memory Load and any of the three latent variables.

The relationship between Gaming Score and the difference measures between *n*-back levels were further studied by specifically examining trials directly following a modality switch (i.e., switch trials). When switch trials were analyzed with Memory Load (1-back vs. 0-back, 2-back vs. 0-back and 2-back vs. 1-back) as the within-subjects variable in the ANOVA, Gaming Score did not demonstrate a significant main effect ($F(1,157)=0.18$, $p=0.68$) or interactions with any of the other variables for the percentage of correct responses, but analysis of response times revealed an interaction between Gaming Score and Memory Load ($F(2,314)=3.75$, $p<0.05$, $\eta^2=0.02$, $\varepsilon=0.74$). Partial correlations showed that on trials following a modality switch, Gaming Score was negatively associated with the change in response times form 1-back to 2-back ($r=-0.23$, $p<0.005$; **Figure 3C**) as well as from 2-back to 0-back ($r=-0.16$, $p<0.05$) but not with the change in response times form 0-back to 1-back ($r=0.03$, $p=0.75$). Again, when the three latent gaming variables were studied, no effects on response times for the difference measures including only switch trials were observed.

An identical ANOVA as the previous one was conducted for trials that had not been preceded by a modality switch (i.e., non-switch trials), which revealed a significant interaction between Gaming Score and Memory Load ($F(2,314)=4.44$, $p<0.05$, $\eta^2=0.03$, $\varepsilon=0.60$): Gaming Score was positively associated with the change in the percentage of correct responses from 1-back to 2-back ($r=0.18$, $p<0.05$), but not with the change form 0-back to 1-back ($r=-0.13$, $p=0.10$) or 2-back to 0-back ($r=0.12$, $p=0.12$). No such interaction was found when the analysis was repeated for the three latent gaming variables. Analysis of response times for non-switch trials revealed no significant main effect of Gaming score ($F(1,157)=1.36$, $p=0.25$) or interactions of Gaming Score with any of the other variables.

The modality of the working memory task did not affect the relationship between Gaming score and task performance when comparing the *n*-back levels, as revealed by an ANOVA with Modality (visual and auditory) and Memory Load (1-back vs. 0-back, 2-back vs. 0-back and 2-back vs. 1-back) as the within-subject variables. That is, no significant interactions were observed between Modality, Memory Load and Gaming score on the percentage of correct responses ($F(2,314)=0.18$, $p=0.73$, $\varepsilon=0.64$) or response times ($F(2,314)=0.36$, $p=0.60$, $\varepsilon=0.65$). The DA score demonstrated no significant effects on any of the indices of behavioral performance.

Age cohort was included in all ANOVAs as a between-subjects factor, so that interactions between gaming and age could further be examined. However, there was no significant interaction between Gaming Score and Age Cohort on performance accuracy ($F(2,157)=1.02$, $p=0.36$) or response times ($F(2,157)=0.53$, $p=0.59$) when absolute values were examined, or on performance accuracy ($F(2,157)=0.26$, $p=0.77$) or response times ($F(2,157)=0.27$, $p=0.76$) when relative values were examined. Further, no such effects on performance accuracy or speed were observed when only switch or non-switch trials were examined, or when the modality of the presented letter was considered.

2.3. fMRI results

Cortical regions showing greater activation during 1- and 2-back than during 0-back task are depicted in **Figure 4A.** Ten Working Memory regions-of-interest (WM ROIs) were subsequently drawn to cover the regions showing maximal activity (threshold t=5.26, cluster size > 100, voxel-level Familywise error corrected p <0.05): left and right middle frontal gyrus (MFG; BA9), left and right superior frontal gyrus (SFG; BA6), left and right superior parietal lobe (SPL; BA7), left and right medial supplementary motor area (SMA; BA6) and left and right precuneus (Prc; BA7) ROIs. Coordinates of peak signal changes for each of the ten WM ROIs are presented in **Table 3**.

Table 3. Peak coordinates for the ten Working Memory regions-of-interest (WM ROIs). Coordinates of peak signal changes refer to the MNI coordinate system. (MFG = middle frontal gyrus, SPL = superior parietal lobe, Prc = precuneus, SFG = superior frontal gyrus, SMA = supplementary motor area, prefix r = right hemisphere, prefix l = left hemisphere)

ROI label name	**x**	**y**	**z**
lMFG	-42	22	30
lSPL	-40	-44	50
lPrc	-4	-64	52
lSFG	-26	8	52
lSMA	-6	18	46
rMFG	44	30	30
rSPL	34	-42	42
rPrc	8	-64	54
rSFG	28	2	52
rSMA	6	18	48

Subsequent analyses were performed for all voxels within the WM ROIs.

The effects of Gaming Score and the other between-subjects variables on cortical recruitment within the WM ROIs were then examined. The three latent gaming variables were not included in the ROI analyses because they had no significant effects on any of the key performance measures, and the aim of the current study was specifically to examine how cognitive benefits related to gaming are reflected in cortical activity. Standardized beta values for Gaming Score produced by the GLM for activity in each of the WM ROIs (while controlling for Age Cohort, Gender, DA Score and GPA) are depicted in **Figure 4B.** When task-related activity modulations in the WM ROIs across all trials were examined, a three-way interaction between ROI, Memory Load (1-back vs. 0-back, 2-back vs. 0-back and 2-back vs. 1-back) and Gaming Score was observed (F(18,2826)=2.82, $p<0.01$, $\eta^2=0.004$, $\varepsilon=0.41$). When an ANOVA was conducted for each WM ROI separately, an interaction between Gaming Score and Memory Load (1-back vs. 0-back, 2-back vs. 0-back and 2-back vs. 1-back) was observed specifically in the left MFG (F(2,314)=5.75, $p<0.01$, $\eta^2=0.03$) and right MFG (F(2,314)=5.28, $p<0.05$, $\eta^2=0.03$) ROIs. Gaming Score was negatively associated with the 1-back vs. 0-back activity differences in both the left and right MFG (b=-0.07, t(157)=2.44, $p<0.05$ and b=-0.08, t(157)=2.31, $p<0.05$, respectively). Conversely, Gaming Score was positively associated with the 2-back vs. 1-back activity difference in the same ROIs (b=0.09, t(157)=2.81, $p<0.01$ and b=0.10, t(157)=2.70, $p<0.01$, respectively). For the subtraction between 2- and 0-back, no effect of Gaming score was observed for either the left or right MFG (b=0.03, t(157)=0.63, p=0.68 and b=0.01, t(157)=0.29, p=0.77, respectively). In other words, the higher the Gaming Score of a participant, the smaller the change in MFG activity from 0-back to 1-back, but the greater the change in MFG activity from 1-back to 2-back. There was a significant correlation between activity and task performance during 2-back task in the left and right MFG (r=0.18, $p<0.05$ and r=0.25, $p<0.005$, respectively) as well as the left and right SPL (r=0.16, $p<0.05$ and r=0.26, $p<0.005$, respectively), when controlling for Age Cohort, Gender, DA Score and GPA. Mediation analysis was therefore conducted for the left and right MFG ROIs, since they showed an association between both Gaming Score and activity, as well as performance accuracy and activity. The mediation analysis revealed that for the left MFG, the model with both Gaming Score and performance accuracy predicting activity in the ROI during 2-back was not significant (F(5,161)=1.30, p=0.27) and there was no indirect effect of Gaming Score on ROI activity mediated by performance accuracy as demonstrated by the Sobel test (Z=0.80, p=0.43). For the right MFG, the model with both Gaming Score and performance accuracy predicting activity in the ROI during 2-back was significant ($F(5,161)=2.31$, $p<0.05$, $R^2=0.07$) so that Gaming Score remained a significant predictor in this model ($\beta=0.04$, $t(161)=2.10$, $p<0.05$) and no indirect effect of Gaming Score on ROI activity was observed ($Z=1.29$, $p=0.19$).

When only switch trials were included in the analyses, a three-way interaction between ROI, Memory Load and Gaming Score was observed ($F(18,2826)=2.28$, $p<0.05$, $\eta^2=0.003$, $\varepsilon=0.45$). ANOVAs conducted separately for each WM ROI showed an interaction between Gaming Score and Memory Load (1-back vs. 0-back, 2-back vs. 0-back and 2-back vs. 1-back) specifically in the left MFG ($F(2,314)=3.96$, $p<0.05$, $\eta^2=0.02$, $\varepsilon=0.84$) and right MFG ($F(2,314)=3.60$, $p<0.05$, $\eta^2=0.02$, $\varepsilon=0.88$) ROIs. A similar result was obtained when only non-switch trials were taken into consideration: a three-way interaction between ROI, Memory Load and Gaming Score was again observed ($F(18,2826)=2.21$, $p<0.05$, $\eta^2=0.003$, $\varepsilon=0.40$), and ANOVAs conducted for each WM ROI separately showed an interaction between Gaming Score and Memory Load specifically in the left MFG ($F(2,314)=4.56$, $p<0.05$, $\eta^2=0.03$, $\varepsilon=0.73$) and right MFG ($F(2,314)=4.83$, $p<0.05$, $\eta^2=0.03$, $\varepsilon=0.70$) ROIs.

The modality of the working memory task did not affect the relationship between Gaming Score and activity in the WM ROIs, as no significant interactions were observed between Modality, Memory Load (1-back vs. 0-back, 2-back vs. 0-back and 2-back vs. 1-back) and Gaming Score ($F(2,314)=0.85$, $p=0.39$, $\varepsilon=0.65$), or Modality, Memory Load, Gaming Score and ROI ($F(18,2826)=0.50$, $p=0.84$, $\varepsilon=0.39$). Also, Gaming Score did not demonstrate a significant effect on the gray matter volume in the WM ROIs ($F(10,148)=0.96$, $p=0.48$).

3. Discussion

In the current study, gaming experience was observed to be related to enhancements in working memory functioning. More specifically, a positive association was found between gaming and performance accuracy, so that the higher the Gaming Score, the less performance was affected by an increase in working memory load from 1-back to 2-back. Gaming was found to be associated with faster response times during the 2-back task along with a nonsignificant trend for better performance, but the majority of significant behavioral findings relate specifically to the difference in performance as working memory load was increased from 1- to 2-back. This suggests that in the current study, gaming was a significant factor in determining how performance changes as the burden on working memory functioning increases. Improved performance accuracy related to gaming was observed both for trials which had been preceded by a modality switch and for trials without a preceding modality switch. In addition, gaming was associated with smaller increases in response times when working memory load was increased from 1-back to 2-back. Closer inspection revealed that these faster response times were specific to trials immediately following a modality switch. The modality in which the working memory task was performed did not affect the relationship between gaming and task performance. Overall, these behavioral findings suggest that gaming is related to improvements in both response speed and the ability to monitor and update information in working memory irrespective of the presentation modality of the task, as well as to the ability to switch between the auditory and visual modalities in response to an unexpected cue while performing a working memory task. This lends support to the notion that gaming affects more general aspects of working memory such as the ability to effectively remove irrelevant items from working memory and update its' content effectively (Colzato et al., 2013), as well as the ability to recover from attention shifts (Colzato et al., 2010; Karle et al., 2010; Cain et al., 2010; Green et al., 2012) while performing a working memory task. The behavioral benefits noted in the current study were not specific to any certain type of game, but to the extent of gaming activity in general. This suggests that although unique aspects of different types of games may train at least partially distinct facets of cognition (Oei & Patterson, 2013), common features of the gaming experience are most relevant to the more general aspects of working memory functioning observed here.

On a more general level, the behavioral findings of our study can tentatively be seen to endorse the notion that games can exercise cognitive faculties (Anguera & Gazzaley, 2015), although a direct causal relationship cannot be inferred solely based on our results. It is important to note that due to the cross-sectional nature of the current study, the observed association between working memory functioning and gaming could be explained by pre-existing differences between participants, and not by training effects induced by gaming per se. There is evidence, however, that working memory capacity can be trained with computerized regimes (Harrison et al., 2013; Toril et al., 2016; von Bastian & Oberauer, 2013), suggesting that a direct causal relationship between gaming and working memory enhancements could exist. Another pitfall of cross-sectional studies on gaming is related to subject recruitment: gamers might perform better simply because they are expected to (Boot et al., 2011). This confounding factor can be ruled out in the current study, however, because our participants were not grouped into expert gamers and novices and they were not aware of the precise purpose of the study, and they could therefore not be influenced by knowing their group membership. A significant finding in the present study was also the lack of age-related influence on the relationship between gaming and improved working memory. Age was not a significant interacting factor with gaming experience for any of the performance indices, suggesting that the coupling between gaming and cognition is detectable already in adolescence. This presents a valuable extension to previous gaming studies, which have almost exclusive recruited adult participants. Future research would likely benefit from recruiting even younger participants in order to determine at what age the benefits of gaming become detectable. If no pattern of linear increase in the correlation between gaming and performance is observed with age even when recruiting younger participants, this would suggest that inborn differences in cognitive capacity may underlie the performance benefits of gamers.

Our study is the first of its kind to examine not only the behavioral benefits related to gaming, but also the cortical underpinnings of these benefits. When brain activity was examined, a fronto-parietal network was consistently activated across participants when the task conditions taxing working memory (1- and 2-back) were compared with the control condition (0-back). This network has repeatedly been shown to be involved in a wide variety of versions of the *n*-back working memory paradigm (for a meta-analyses, see Owen et al., 2005; Rottschy et al., 2012). When the relationship between gaming and activity within the fronto-parietal network was studied, the results revealed that this relationship differed according to task difficulty. During the less demanding *n*-back task level (1-back), gaming was associated with a smaller increase in activity especially in dorsolateral prefrontal regions when compared to the control condition. In contrast, as the difficulty of the task was increased from 1-back to 2-back, gaming was associated with a significantly greater increase in activity in the same cortical regions, coupled with enhanced behavioral performance. This effect did not depend on whether a modality switch had or had not occurred prior to the trial, or on the modality of the working memory task. Our study is therefore the first to demonstrate that gamers might show improved working memory performance due to a "boost" specifically in prefrontal recruitment when task conditions become adequately challenging.

The relationship between the extent of neural recruitment and cognitive performance is still unclear, and therefore the effects of gaming experience on fronto-parietal recruitment during the working memory task observed in the current study cannot be interpreted in a straightforward manner. According to the neural efficiency hypothesis, greater individual cognitive capacity as well as repeated training is coupled with lesser cortical activity during problem solving, reflecting more efficient recruitment of the cortex (Haier et al., 1988). In line with this hypothesis, Bavelier et al. (2012) found reduced activity in the fronto-parietal network for gamers during a visual selective attention task. Likewise, Heinzel et al. (2016) observed decreased activity in right prefrontal regions in older adults during an *n*-back task as a result of repeated training on the task. On the other hand, training on a working memory task has been associated both with increased activity in prefrontal and parietal cortices (Olesen et al., 2004), as well as with no changes in cortical activity at all

(Nussbaumer et al., 2015). These apparently contradictory findings as well as the results of the current study may be explained by the moderating effect of task difficulty. During only moderately difficult tasks, individuals with a greater cognitive capacity or better cognitive skills may need to recruit less cortical resources to achieve the same behavioral performance level as other individuals. In contrast, when more effort is required, these individuals recruit task-relevant brain regions to a greater extent and exhibit superior performance, perhaps because a different cognitive strategy is used to accomplish the task (Rypma et al., 2002). The use of an alternate strategy is supported by the fact that in the current study, gaming-related differences were noted only in lateral prefrontal regions. Although the fronto-parietal cortical network recruited by the working memory task in the current study comprises of domain-general regions activated by a wide range of cognitively demanding tasks (Duncan, 2010), specialized functions have nevertheless been assigned to subregions of the frontal and parietal lobes. The specific contribution of dorsolateral prefrontal regions to working memory remains a topic of debate, but it has been suggested that these regions play an essential role in organizing working memory content. For example, organizing working memory items into higher-level groups in order to aid memorization has been shown to produce activity specifically in the lateral frontal cortex (Bor et al., 2003, 2004) and patients with lesions to these same regions have exhibited inefficient use of organizational strategies during working memory tasks (Owen et al., 1996). It is therefore possible that gaming experience translates into better working memory performance because of the use of more efficient organization strategies, seen as changes in the recruitment of frontal regions exclusively. An alternative explanation for the observed results is that highly functioning individuals may become inattentive during unchallenging tasks and therefore display heightened vigilance and more focused attention during more demanding tasks, thus leading to the observed pattern of cortical activity in response to changes in task demands. Our behavioral results do not support this explanation, however, as gaming was not linked to more misses (reflecting inattentiveness) or to decrements in performance from the first task block to the second (reflecting difficulties in sustaining attention on the task over longer time periods) during the easier *n*-back task condition. Taken together, our results provide evidence for a more complex relationship between neural recruitment and cognitive performance than outlined by the neural efficiency hypothesis (Haier et al., 1988). Both the underlying cognitive capacity of the individual and the level of challenge offered by the cognitive task should be considered, as it is not either factor alone which affects neural recruitment, but rather their interaction and the cognitive strategies used to accomplish the task.

In sum, the current study replicates previous findings linking gaming to improved working memory functioning (e.g., Blacker & Curby, 2013; Boot et al., 2008; McDermott et al., 2014; Sungur & Boduroglu, 2012), and extends these findings to apply not only to adults but also to adolescents, and to participants representing a much broader spectrum of gaming experience than just expert gamers and novices. Furthermore, the current study provides novel insight into the neural basis of working memory enhancements in gamers by demonstrating that the pattern of prefrontal recruitment is significantly altered when working memory load is increased in participants with more gaming experience. Future studies would benefit greatly from utilizing similar task-related fMRI measurements as in the current study, but in a pre-post game training paradigm where cortical activity during a working memory task would be recorded both before and after game training. This would help to determine whether gaming really causally alters how the fronto-parietal network is recruited when working memory is heavily taxed, and it would further elucidate the relationship between neural recruitment and cognitive performance.

4. Conclusions

A positive association between daily gaming activity and working memory performance of adolescent and young adult participants was demonstrated in the current study. More specifically, higher levels of self-reported daily gaming activity were linked to smaller performance decrements when working memory load was increased, both in terms of performance accuracy and response times. In addition, response times during the working memory task were less affected by a modality switch the higher the gaming activity level of the participant was. When brain activity was measured, gaming was associated with a smaller increase in activity especially in dorsolateral prefrontal regions when working memory was only moderately taxed. As the difficulty of the working memory task was increased, gaming was associated with a significantly greater increase in activity in the same cortical regions, possibly reflecting an alternative cognitive strategy used to perform the task. The results of the current study extend previous findings on gaming and working memory enhancements to apply to adolescents and young adults with moderate levels of gaming activity, and elucidate the neural underpinnings of the observed cognitive benefits linked to gaming.

5. Experimental procedure

5.1. Participants

The participants were selected from a sample of 2977 respondents, who had filled out a questionnaire including a wide variety of questions relating to the daily use of digital technologies as a part of the research project titled Mind the Gap between Digital Natives and Educational Practices (2013–2016) (http://wiredminds.fi/projects/mind-the-gap/). The respondents belonged to three different age cohorts: 13–14- and 16–17-year-old lower and upper secondary students and 20–24-year-old university students (cohorts 1, 2, and 3, respectively). The questionnaire included a Sociodigital Participation (SDP) inventory (Hietajärvi et al., 2015) assessing various dimensions of technology-mediated practices in everyday life. The participants (each cohort separately) were first grouped into profiles representing their SDP practices using a latent profile analysis (Vermunt & Magidson, 2002). The identified profiles (across cohorts) were then interpreted as basic participators (control; n=1925 in total, n=59 in the current study) who demonstrated the least technologically-mediated activity, gaming-oriented participators (n=656 in total, n=54 in the current study), who focused especially on action and social gaming as separated from recreational gaming, and creative participators (n=388 in total, n=54 in the current study) characterized by intensive engagement in socio-digital activities in general and creative use of knowledge and media in particular. Respondents who demonstrated the highest likelihood of belonging to their respective profiles were then asked to participate in the fMRI study. **Figure 1** depicts all of the questionnaire respondents in a scatterplot so that the colors of the circles denote the SDP profile of each respondent, and filled circles denote respondents who are included in the analyses of the current study. The respondents are plotted against two discriminant functions produced by a linear discriminant function analysis (conducted for the purpose of this data visualization), where SDP profile was the grouping variable, and the predictor variables were a total of 27 items from the SDP inventory assessing technology-mediated activities (e.g., the use of social media, playing different genres of computer games, creating content to share online). Both functions produced by the discriminant analysis were significant (Wilks Lambda=0.17, $\chi 2(78)= 5220.42$, $p<0.001$ and Wilks Lambda=0.58, $\chi 2(38)=1582.81$, $p<0.001$), which was to be expected since the majority of the predictor variables were used when conducting the original SPD grouping. The first function was principally explained by playing various genres of computer games, online gaming activity and considering gaming as one’s hobby, so this function was termed Gaming activity. The second function was principally explained by sharing content such as videos, photos or status updates online, so this function was termed Creative activity. The SDP profiles were only used to sample participants but not in any further analyses, as all participants demonstrated some level of gaming or socio-digital activity. Although the purpose of the current study was to examine gaming-related effects, representative creative participators were recruited as participants due to the fact that the current study is part of a larger effort to investigate a variety of technology-related activities (such as media multitasking; Moisala et al., 2016). It also enabled us to recruit participants exhibiting varying degrees of gaming activity instead of only including participants from the far ends of the gaming spectrum, thus strengthening the generalizability of our results. Respondents ineligible for an fMRI measurement and respondents with any learning difficulties or notably poor school performance with a self-reported grade point average (GPA) below 7 on a 4-to-10 point scale system were screened out. In total, brain activity and performance of 173 participants were measured for the study. Out of the measured participants, 6 participants were discarded from further analyses due to technical difficulties in data measurement or bad data quality. As a result, a total of 167 healthy volunteers were included in the analyses (**Table 1**), with 57 participants in cohort 1, 57 in cohort 2 and 53 in cohort 3. A subset (n=149) of these same participants were used in a previously published study linking media multitasking activity to increased distractibility and right prefrontal cortical activity (Moisala et al., 2016). All participants were native Finnish speakers with normal hearing, normal or corrected-to-normal vision, and no self-reported history of psychiatric or neurological illnesses. An informed written consent was obtained from each participant (and from a guardian in the case of underage participants) before the experiment. The experimental protocol was approved by the Ethics Committee for Gynaecology and Obstetrics, Pediatrics and Psychiatry of The Hospital District of Helsinki and Uusimaa, Finland.

5.2. Gaming Score

A sum of scores from 10 items comprising a Gaming scale was calculated based on the SDP inventory and used as the Gaming Score. The Gaming scale probed how often the participants play different types of computer and video games. These 10 gaming types were: Fun (e.g., Mario Party, Start the Party), Exercise (e.g., Wii Sports, MS Kinetic), Music/dance (e.g., Just Dance, Singstar), Puzzle (e.g., Angry Birds, Bejeweled), Sports (e.g., NHL, FIFA), Racing (e.g., Gran Turismo, Mario Kart), Role playing (e.g.,World of Warcraft, Fallout), Strategic (e.g., Starcraft, Civilization), Shooter (e.g., Call of Duty, Battlefield) and Adventure (e.g., Minecraft, Uncharted) games. Participants were asked how much time the they spend playing each game type on either a mobile device, gaming console or computer, and responses were given on a 7 point Likert scale (1=never, 2=a few times a month, 3=monthly, 4=weekly, 5=daily, 6=multiple times a day, 7=all the time). The Gaming scale is included in the supplementary material. A univariate analysis of variance (ANOVA) with the between subject factors Age Cohort and Gender was conducted with Gaming Score as the dependent variable. In order to examine whether any significant findings related to Gaming Score were explained specifically by certain types of games instead of overall gaming activity, the latent variable structure of the data was examined in order to group gaming genres. The factorability of the Gaming scale items were deemed sufficient, as i) all items correlated at least 0.3 with at least one other item, ii) the Kaiser-Meyer-Olkin measure of sampling adequacy (0.77) was above the commonly recommended value of 0.60, iii) Bartlett's test of sphericity was significant ($\chi2(45)=459.44$, $p<0.001$), and iv) the diagonals of the anti-image correlation matrix were all over 0.50. Since the Gaming scale used a Likert response scale producing mostly non-normally distributed ordinal data, its latent variable structure was modeled using a multidimensional item response theory (MIRT) model (the graded response model using polychoric correlations; Holgado–Tello et al., 2010; Rigdon & Ferguson, 1991), which is thought of as an equivalent to nonlinear factor analysis (Takane & De Leeuw, 1987). The last five response categories in the 7-point Likert scale of the Gaming scale were collapsed due to small number of data points in these three categories. MIRT analysis was conducted using the statistical software R (R Core Team, 2016) and its Psych toolbox (Revelle, 2016).

5.3. Digital Activity Score

A sum of scores from 17 items probing the amount of time spent using digital technologies was calculated based on the SDP inventory and used as the DA Score. Examples of these items are: "I send text messages", "I talk on the phone", "I watch movies on the computer", "I send e-mails" and "I play games on the computer". Participants indicated how much time they spent with each activity on a 7-point scale. Partial correlations between Gaming Score and DA Score controlling for Gender and Age Cohort were calculated. The DA Score was used in all ANOVAs as a covariate in order to ensure that any observed effects related to gaming would not be explained by the level of overall daily digitally mediated activity.

5.4. Stimuli

The visual stimuli used in the *n*-back task were vowels (the Finnish vowels a, e, u and y), presented in the middle of a video screen. The vowels were presented in four different fonts (Arial, Castellar, Comic Sans MS and Bradley Hand ITC). The font of each vowel was assigned randomly, but if the vowel in the 1- or 2-back condition matched a vowel presented 1 or 2 trials back, respectively, it was never written in the same font as the vowel preceding it *n* trials back so that vowels could not be matched purely based on their physical properties. The size of the vowels was 1.43° horizontally and vertically. The vowel was surrounded by a square (2.86° horizontally and vertically) with a fixation point in the center, both of which were on the screen throughout the entire block. The vowels, surrounding square and fixation point were all white, while the background was grey. The video screen where the visual stimuli were displayed was projected onto a mirror mounted on the head coil.

The auditory stimuli in the *n*-back task were spoken Finnish vowels (/a/, /e/, /u/ and /y/).The vowels were spoken by four different native Finnish speakers (2 males, 2 females). The voice in which each vowel was spoken was assigned randomly, but if the vowel in the 1- or 2-back condition matched a spoken vowel presented 1 or 2 trials back, respectively, it was never spoken by the same person as the *n*-back vowel. The spoken vowels were presented binaurally through insert earphones (Sensimetrics model S14; Sensimetrics, Malden, MA, USA). All spoken vowels were high-pass filtered with a cut-off at 100 Hz and low-pass filtered with a cut-off at 7000 Hz. The intensity of the spoken vowels was adjusted so that their total power in RMS units, the square root of the mean of the squared signal, was similar (0.1). The intensity of the spoken vowels was individually set to a loud, but pleasant level, and it was ~80 dB SPL as measured from the tip of the earphones, while noise from the MRI scanner (maximum ~130 dB) was attenuated by the earplugs, circumaural ear protectors (Bilsom Mach 1, Bacou-Dalloz Inc., Smithfield, Rhode Island, USA), and viscoelastic mattresses around the head coil. All adjustments to the auditory stimuli were made using Audacity (http://audacity.sourceforge.net) and Matlab (Mathworks Inc., Natick, MA, USA) softwares.

5.5. fMRI/MRI data acquisition

A 3 T MAGNETOM Skyra whole-body scanner (Siemens Healthcare, Erlangen, Germany) with a 20-channel head coil was used for functional brain imaging. The functional echo planar (EPI) images were acquired using a gradient echo sequence with an imaging area consisting of 43 contiguous oblique axial slices (TR 2500 ms, TE 32 ms, flip angle 75°, voxel matrix 64 x 64, field of view 20 cm, slice thickness 3.0 mm, in-plane resolution 3.1 mm x 3.1 mm x 3.0 mm). Image acquisition was performed at a constant rate (i.e., image acquisition was not jittered), but was asynchronized with stimulus onsets. Two functional runs of 155 volumes (including 4 initial dummy volumes) were measured. The duration of one block was 7 minutes, so during a total of 14 minutes, 310 functional volumes were obtained.

High-resolution anatomical images (voxel matrix 256 x 256, in-plane resolution 1 mm x 1 mm x 1 mm) were acquired from each participant before the *n*-back task blocks began.

5.6. Procedure

Participants performed three levels of the *n*-back task in separate blocks: 0-, 1- and 2-back. **Figure 5** depicts the experimental setup of the *n*-back task. In the beginning of each block, instructions for the current *n*-back task level were shown for 6 s. In subsequent task blocks, 32 vowels (visual or auditory) were presented, each with a duration of 500 ms. The modality of the presented vowel was switched randomly on every 3rd, 4th , 5th or 7th vowel, so that participants were not able to anticipate a modality switch. Seven modality switches occurred in a block. Each vowel was followed by a 2500-ms retention period during which the participants were instructed to respond. In the control

(0-back) condition, this meant responding with the appropriate button press whether the presented vowel had been presented visually or auditorily using their right index or middle finger, respectively. In the 1-back and 2-back conditions, this meant responding with an appropriate button press on each trial whether the vowel did or did not match the vowel presented *n* trials back (irrespective of whether the preceding vowel *n* trials back was a written or a spoken one) using their right index or middle finger, respectively. There were 10 match trials in each block of 32 trials. The guess level (i.e., if the participant responds randomly) was 50 %. In turn, by adopting a strategy of consistently responding that the vowel was not a match would have led to a correct response percentage of 22/32 = 68.75 %. During the retention period or when only auditory stimuli were presented, only the square surrounding the vowels and the fixation point remained on the screen. At the end of each block, the participant was shown the percentage of correct responses in that block. The score was shown for 3 s.

There were two functional runs, 3 blocks in each run, and 32 trials (i.e., vowels) in each block. Each run included one block of each *n*-back task level presented in a random order. This resulted in a total of 64 trials for each *n*-back task level. Before beginning the *n*-back task, the participants had performed an unrelated attention task described in Moisala et al. (2016) and had, therefore, already spent around 30 minutes in the scanner. Although all of the participants completed both the attention and the working memory task, the two tasks were specifically designed to study media multitasking and gaming, respectively, according to a priori hypotheses based on existing literature. The aim of the attention task was to see if a relationship between media multitasking and distractibility could be detected by using a more ecologically valid experimental task than the standard attention tasks used previously. Associations between working memory and media multitasking were not explored, as the existing literature did not provide basis to assume that such associations would exist. The working memory task, in turn, was used to study cognitive performance exclusively in relation to gaming. A more standard working memory task was used in this case to ensure that the neural basis of performance enhancements related to gaming could be explored.

5.7. Analysis of behavioral data

The total percentage of correct responses for each *n*-back task level was calculated. Blocks where the percentage of correct responses was more than three standard deviations below average were removed from all further analyses. General task-related effects were examined by conducting a repeated-measures ANOVA with Memory Load (0-back, 1-back and 2-back) and Modality Switch (switch and no switch) as the within-subjects variables. A repeated measures ANOVA was then conducted for both the percentage of correct responses as well as response times with Memory Load (1-back, 0-back and 2-back) as the within-subject variable, Age Cohort and Gender as between-subjects factors, and Gaming Score, DA Score and GPA as covariates. Partial correlation coefficients were calculated between Gaming Score and the percentage of correct responses, response times and the percentage of misses (i.e., not detecting a match), while controlling for Age Cohort, Gender, DA Score and GPA. The same ANOVA and partial correlation calculations were also conducted for difference measures between *n*-back levels (i.e., by subtracting the percentage of correct responses between 1- and 0-back, 2- and 0-back, and 2- and 1-back). Further, the same ANOVA was conducted separately for switch trials and for non-switch trials. In addition, a repeated-measures ANOVA was conducted for the percentage of correct responses and response times for non-switch trials with Modality (visual and auditory) and Memory Load (1-back vs. 0-back, 2-back vs. 0-back and 2-back vs. 1-back) as within-subject variables, Age Cohort and Gender as between-subjects factors, and Gaming Score, DA Score and GPA as covariates. A repeated-measures ANOVA was also carried out for both the percentage of correct responses as well as misses with Run number and Memory Load (1-back and 2-back) as the within-subject variables, Age Cohort and Gender as between-subjects factors, and Gaming Score, DA Score and GPA as covariates. ANOVAs and partial correlation calculations producing significant main effects or interactions relating to Gaming Score were repeated using the latent variable scores extracted from the 10 items of the Gaming scale. These analyses were conducted so that the Gaming Score was replaced as the between-subjects variable by the three latent gaming variable scores, so that all three latent variable scores were included in the same ANOVA/partial correlation calculation.

Eta squared (η^2) was calculated for all conducted ANOVAs as a measure of effect size. For all conducted ANOVAs the Greenhouse-Geisser p-value was used (as indicated by the correction value ε) if the Mauchly's test of sphericity showed a significant result for a variable with more than two levels. However, original degrees of freedom will be reported with the F-value even in these cases. A 95% confidence interval was used in all ANOVAs. When an ANOVA yielded a significant result, Bonferroni post hoc tests were conducted. IBM SPSS Statistics 21 for Windows (IBM SPSS, Armonk, NY, USA) was used for statistical analyses.

5.8. fMRI data analysis

The preprocessing and statistical analysis of fMRI data was performed using Statistical Parametric Mapping (SPM12) analysis package (Wellcome Department of Cognitive Neurology, London, UK; Friston et al., 1994) as implemented in Matlab. The first four dummy volumes were excluded from analysis to allow for initial stabilization of the fMRI signal. During pre-processing, the slice timing was corrected, data were motion corrected, high-pass filtered (cut-off at 1/128 Hz), and spatially smoothed (6 mm Gaussian kernel). The EPI images were intra-individually realigned to the middle image in each time series and un-warping was performed. Then the anatomical images were normalized to a canonical T1 template (MNI standard space) provided by SPM12 and the transformations were then used as a template to normalize the functional volumes for each participant (tri-linear interpolation, 3 mm x 3 mm x 3 mm using 16 nonlinear iterations).

The regressors included in the GLM for the first-level statistical analysis are listed in **Table 4**.

Table 4. List of the regressors included in the GLM for the first-level statistical analysis of fMRI data.

Task-related regressors:

1) 0-back trials immediately preceding a modality switch with vowel presented visually
2) 0-back trials immediately following a modality switch with vowel presented visually
3) All other 0-back trials with vowel presented visually
4) 0-back trials immediately preceding a modality switch with vowel presented auditorily
5) 0-back trials immediately following a modality switch with vowel presented auditorily
6) All other 0-back trials with vowel presented auditorily
7) 1-back trials immediately preceding a modality switch with vowel presented visually
8) 1-back trials immediately following a modality switch with vowel presented visually
9) All other 1-back trials with vowel presented visually
10) 1-back trials immediately preceding a modality switch with vowel presented auditorily
11) 1-back trials immediately following a modality switch with vowel presented auditorily
12) All other 1-back trials with vowel presented auditorily
13) 2-back trials immediately preceding a modality switch with vowel presented visually
14) 2-back trials immediately following a modality switch with vowel presented visually
15) All other 2-back trials with vowel presented visually
16) 2-back trials immediately preceding a modality switch with vowel presented auditorily
17) 2-back trials immediately following a modality switch with vowel presented auditorily
18) All other 2-back trials with vowel presented auditorily

Nuisance regressors:
19) Participant’s responses
20) Instructions (2.5-s periods between the blocks and a 6-s period at the beginning of each run)
21) – 26) Six movement parameters (movement along three orthogonal axes, pitch, roll and yaw)
27) Blocks where the percentage of correct responses was more than three standard deviations below average

In total, 27 regressors [3(memory load) × 6 (trial type) + 8 (nuisance) + 1 (bad blocks)] were included. The regressors were convoluted with the canonical hemodynamic response function.

In the second-level analysis, statistical parametric maps of individual contrasts between the *n*-back task levels and between switch and non-switch trials were averaged across participants. Working Memory regions-of-interest (WM ROIs) were constructed by drawing ROIs to cover the regions demonstrating greater activity (threshold t=5.26, cluster size > 100, voxel-level Familywise error corrected p <0.05) during the 1- and 2-back tasks than during the 0-back task. Subsequent analyses were performed for all voxels within the WM ROIs.

5.9. Region-of-interest analysis

ROI analysis was conducted in order to study the effects of gaming in cortical regions recruited more extensively by the working memory (1- and 2-back) than the control condition (0-back). WM ROIs were defined as regions showing greater activity during a combination of activity during 1- and 2-back than during 0-back in the whole-head analysis. The WM ROIs were drawn manually using Freesurfer software, and their exact locations were extracted using xjView toolbox (http://www.alivelearn.net/xjview). Two types of repeated measures ANOVA was conducted for mean signal changes within the WM ROIs. First, an ANOVA with ROI and Memory Load as within-subject variables, Age Cohort and Gender as between-subjects factors, and Gaming Score, DA Score and GPA as covariates was conducted. The purpose of this ANOVA was to study whether gaming is associated with ROI activity, and how this might interact with task difficulty and ROI location. This ANOVA was also repeated separately for switch and non-switch trials, in order to examine whether any gaming-related significant effects from the first ANOVA applied exclusively to either trials following a modality switch, or to non-switch trials. A second type of repeated measures ANOVA was then conducted where only non-switch trials were included, and Modality (visual and auditory) was added as a within-subjects variable. Similarly to the first ANOVA, ROI and Memory Load were included as within-subject variables, Age Cohort and Gender as between-subjects factors, and Gaming Score, DA Score and GPA as covariates. The purpose of this ANOVA was to study how the modality of the presented letter might affect any observed relationship between gaming and ROI activity. Switch trials were not included in this ANOVA in order to minimize any “spill-over” effects in the fMRI data resulting from a recent modality switch. Partial correlations (controlling for Age Cohort, Gender, DA Score and GPA) were calculated between task performance and activity in the WM ROIs separately for the 1- and 2-back tasks. Mediation analysis using the Process macro for SPSS (http://www.processmacro.org/index.html) was used to examine possible mediating effects of performance accuracy on the relationship between Gaming Score and activity in the WM ROIs showing a significant correlation between task performance and activity, while controlling for Age Cohort, Gender and DA Score. In the mediation analysis, 1000 bootstrap samples for bias-corrected bootstrap confidence intervals was used, and a 95% confidence level was used. The grey matter volume within each ROI was examined by using Freesurfer's automatic processing stream for volume and thickness estimates (Reuter et al., 2012), and by subjecting the grey matter volume estimates of the ROIs to a multivariate ANOVA with the between-subject factors Age Cohort and Gender, and with Gaming Score, DA Score and GPA as covariates.

Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgments

This research was funded by the Academy of Finland Mind Program project "Mind the Gap - between digital natives and educational Practices" [grant number 265528]; the Academy of Finland [grant numbers 259752, 273147]; the Antti and Jenny Wihuri foundation; the Emil Aaltonen foundation; and the Päivikki and Sakari Sohlberg Foundation. We warmly thank Mr. Jari Lipsanen, MA, for statistical consultation.

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Figure 1. The distribution of all questionnaire respondents into the Sociodigital Participation (SDP) profiles. The three SDP profiles are basic participators (blue circles), gaming-oriented participators (green circles), and creative participators (green circles). Filled circles denote the participants (n=167) of the current study. The data is plotted against two standardized discriminant functions: Gaming activity (i.e., playing various genres of computer games, online gaming activity and considering gaming as one's hobby) and Creative activity (i.e., sharing content such as videos, photos or status updates online).

Figure 2. Boxplots of Gaming Scores and scores for three latent gaming variables. Gaming Scores are presented separately for females and males in each of the three age cohorts **(A)**. Gaming Score was defined as the sum of scores from all 10 items of the Gaming scale, probing how often the participants play 10 different types of computer and video games on a 7-point response scale (1=never, 2=a few times a month, 3=monthly, 4=weekly, 5=daily, 6=multiple times a day, 7=all the time). Scores for the three latent variables extracted from all 10 items of the Gaming Scale **(B)**, with data pooled across all participants. The three latent gaming variables were labeled Serious Games, Fun Games and Sports Games. Each boxplot has lines at the lower quartile, median, and upper quartile values, and the whiskers show the extent of data. Outliers (>1.5 times the interquartile range) are marked with crosses.

Figure 3. Associations between task performance and Gaming Score. The difference in **(A)** the percentage of correct responses and **(B)** response times between 2-back and 1-back tasks, and the difference in **(C)** response times following a modality switch between 2-back and 1-back tasks is plotted against Gaming Score. The data in all figures are adjusted for Age cohort and Gender. The fitted regression slope (a bright red line) and 95% confidence interval bounds (light red lines) are shown in each figure.

Figure 4. Whole-head and region-of-interest fMRI results of cortical regions related to working memory. A) Cortical regions showing greater activity during a conjunction of 2-back and 1-back activity than during 0-back (i.e., WM ROIs; voxel-wise height threshold t=5.26, cluster size > 100, voxel-level Familywise error corrected p <0.05). **B)** Standardized beta values for Gaming Score produced by the General Linear Model (GLM) for activity in each of the WM ROIs (while controlling for Age Cohort, Gender, DA Score and GPA). The activity values used in the GLM represent subtractions between 1- and 0-back (left), 2- and 0-back (middle) and 2- and 1-back (right) conditions. Significant beta values for the Gaming Score are indicated with asterisks (* p<0.05). Error bars represent 95% confidence intervals. (LH = left hemisphere, RH = right hemisphere, MFG = middle frontal gyrus, SPL = superior parietal lobe, Prc = precuneus, SFG = superior frontal gyrus, SMA = supplementary motor area, prefix r = right hemisphere, prefix l = left hemisphere)

Figure 5. The experimental setup of the *n*-back task. Illustration of the *n*-back task showing six trials of the 2-back condition including one vowel matching with a vowel delivered 2 trials back.