Functional Intergation Between the Salience and Central Executive Networks: A Role for Action Video Game Experience

Diankun Gong, University of Electronic Science and Technology of China, China

Asian Conference on Psychology and Behavioral Sciences 2015
Official Conference Proceedings

Abstract
Using resting-state fMRI, this study examined the influence of action video game (AVG) experience on two canonical brain functional networks – Salience Network (SN) and Central Executive Network (CEN). Based on the proposition that SN and CEN interacted with each other to support attention and working memory, we explored whether AVG playing, which required high load of attention and working memory, was related to enhancements of SN and CEN. We found that compared AVG amateurs, AVG experts had an enhanced functional integration between SN and CEN, which was further supported by results of the graph theoretical analysis. Thus, this study is the first to show the relation between AVG playing and the plasticity of SN and CEN. The results also support the cognitive benefits of AVG experience on attention and working memory.

Keywords: functional connectivity, central executive network, salience network, learning, action video game

Introduction

As a major type of virtual environment for social interaction in the modern world, the action video game (AVG) emphasizes physical and mental challenges (Latham, Patston, & Tippett, 2013), and requires various cognitive functions such as hand-eye coordination, memory, and attention. Thus, as it becomes increasingly popular worldwide across different age ranges, the AVG has attracted growing research attention on its cognitive influences (Daphne Bavelier et al., 2011).

Behavioral studies revealed that the AVG experience is related to enhancements of both primary (e.g., visual processing (Green & Bavelier, 2007; R. Li, Polat, Makous, & Bavelier, 2009; R. W. Li, Ngo, Nguyen, & Levi, 2011), eye-hand coordination (Jones, Burton, Saper, & Swanson, 1976), contrast sensitivity (R. Li et al., 2009), oculomotor performance (West, Al-Aidroos, & Pratt, 2013), body movement (Kennedy, Boyle, Traynor, Walsh, & Hill, 2011)) and higher-level cognitive functions (e.g., attention, working memory). Green et al. found that compared to amateurs, experienced AVG players had better selective attention; furthermore, AVG training improved the amateurs' performance on attentional tasks, thereby suggesting the attentional effects of AVG playing (Green & Bavelier, 2003). AVG experience was also associated with enhancements of spatial distribution of visuospatial attention (Green & Bavelier, 2006), attentional capture (Chisholm, Hickey, Theeuwes, & Kingstone, 2010), and attention shifting at switching tasks (Cain, Landau, & Shimamura, 2012). Furthermore, by manipulating the visual complexity of stimuli, Blacker et al. found that experienced AVG players had improved visual short-term memory (Blacker & Curby, 2013).

Researchers have also started to examine the neural basis of cognitive effects of AVG experience. For example, Bavelier et al. found that compared to amateurs, AVG experts had better early filtering of irrelevant information and selective attention as measured by activities in the fronto-parietal areas (D Bavelier, Achtman, Mani, & Föcker, 2012). Furthermore, AVG experience was associated with gray matter volume (GMV) in certain brain areas responsible for attention and working memory (e.g., dorsal striatum (Erickson et al., 2010), right posterior parietal (Tanaka et al., 2013), entorhinal, hippocampal and occipital (Kühn & Gallinat, 2013), dorsolateral prefrontal cortex (Kühn, Gleich, Lorenz, Lindenberger, & Gallinat, 2013)). In addition, a recent study showed that AVG training improved older adults' cognitive control by reducing the multi-tasking cost as measured by electrophysiological signatures; furthermore, the benefit of AVG training extended to untrained cognitive control abilities (e.g., enhanced sustained attention and working memory), thus, suggesting the effects of AVG experience on attention and working memory (Anguera et al., 2013).

It, however, still remains unclear whether AVG experience is related to enhancement of the functional networks of attention and working memory as measured by resting-state fMRI, a method commonly used to evaluate the interaction among different brain regions when subjects are not performing an explicit task (Connolly et al., 2013; Fox & Raichle, 2007). Since the resting-state functional network indicates the *underlying* pattern of neuronal modulations (Damoiseaux et al., 2006), it offers us a strong case to test the relation between AVG experience and neuroplasticity.

This study examines whether AVG experience is related to an enhanced integration between the functional networks of attention and working memory, which are essential for AVG playing. Research on resting-state functional connectivity (FC, a dynamic coordinated activity for communicating information on connected brain regions (Freyer et al., 2011)) has revealed separate functional networks for attention and working memory (Beckmann, DeLuca, Devlin, & Smith, 2005; Cocchi, Zalesky, Fornito, & Mattingley, 2013; Seeley et al., 2007; Sridharan, Levitin, & Menon, 2008): *i*) Salience Network (SN), which typically includes anterior cingulate cortex (ACC) and anterior insula, supporting the detection of salient events; *ii*) Central Executive Network (CEN), which typically includes the dorsolateral prefrontal cortex (DLPFC) and posterior parietal cortex (PPC), supporting attentional control and working memory (see Table 1 for nodal information of the networks). The identification of the two networks is further supported by the results of the structural connectivity analysis (Montembeault et al., 2012; Zielinski, Gennatas, Zhou, & Seeley, 2010).

Researchers have proposed that SN and CEN interact with each other to support attention and working memory respectively (Cocchi et al., 2013; Elton & Gao, 2013). SN receives and provides selective amplification of silent information, thereafter, generates a top-down control signal initiating CEN to respond to salient information for attentional shift and control execution (Menon & Uddin, 2010). More importantly, this proposition suggests a task-dependent functional integration between SN and CEN, which facilitates one's performance on the tasks requiring a high attentional and working memory load (Cocchi et al., 2013). We thus would hypothesize that habitual AVG playing should enhance the integration between SN and CEN, which may be observable by comparing experienced and amateur AVG players using resting-state fMRI.

To evaluate the hypothesis, the present study compared AVG experts and amateurs. We first examined the functional integration between SN and CEN using FC analysis. Then, we performed a quantitative analysis of the functional integration by examining the network and nodal characteristics based on the graph-theoretical analysis.

Method

There were 23 male participants ($M = 23.3 \pm 4.3$ yrs) in the expert group, who were highly experienced players of real-time strategy video games (i.e., League of Legends [LOL] or Defense of the Ancient [DOTA]). They had received AVG training for at least four years and were recognized as either regional or world champions in international AVG competitions. Their AVG experience was quantifiable based on Elo's rating scale (Elo, 1978), ranging from 1800 to 2600 ladder points. There were 22 male participants, who did not play AVG habitually, in the amateur group ($M = 22.3 \pm 3.46$ yrs), whose ladder points were less than 1200. The two groups were matched in years of school education, Raven's Progressive Matrices (91 ± 10.8 vs. 91.6 ± 9.8), and the onset age of video game playing (8 years of age). All the participants were right-handed basing on the Edinburgh Inventory (Oldfield, 1971), reported normal or corrected-to-normal vision, and presented no history of neurological illnesses. Participants gave written consent to participate in this study, which was approved by the Ethics Board of the University of Electronic Science and Technology of China (UESTC).

To allow for an examination of the relation between behavioral and fMRI data, the participants were administered a digital n-back task and a spatial memory task before the fMRI session. In the digital n-back test, they were presented with a sequence of digits and then were asked to indicate whether a digit matches the one from n steps earlier in the sequence. The difficulty of the task was adjustable according to the load factor –n, ranging from 0 to 2 (Jaeggi, Buschkuehl, Perrig, & Meier, 2010). The spatial memory task prompted the participants to memorize a sequence of blocks lit up and then to repeat the sequence in order. Starting with a small number of blocks and then increasing to fifteen blocks maximally, the task measured the longest sequence one could remember (Kessels, van Zandvoort, Postma, Kappelle, & de Haan, 2000).

Images were collected on a 3T MRI scanner (GE Discovery MR750) at the MRI Research Center of UESTC. Resting-state fMRI data were acquired using gradient-echo EPI sequences (repetition time [TR] = 2000 msec, echo time [TE] = 30 msec, flap angle [FA] = 90°, matrix = 64 × 64, 3×3×3 mm voxels, field of view [FOV] = 24 × 24 cm^2, slice thickness/gap = 4 msec/0.4 mm), with an eight channel-phased array head coil. All the participants underwent a 510-second resting-state scanning to yield 255 volumes (32 slices per volume). High-resolution T1-weighted images were acquired using a 3-dimensional fast spoiled gradient echo (T1-3D FSPGR) sequence (TR = 6.008msec, TE = 1.984msec, FA = 90°, matrix = 256 × 256, FOV = 25.6 × 20 cm^2 (80 %), slice thickness (no gap) = 1 mm) to generate 152 slices.

The fMRI data were processed through typical preprocessing procedures using SPM8 software (Wellcome Department of Cognitive Neurology, London, UK) (Cauda et al., 2011; Jenkinson, Bannister, Brady, & Smith, 2002), including the first five volumes of each run discarded, slice scan time correction, head motion correction, normalized images with a BOLD EPI template in the Montreal Neurological Institute (MNI) atlas space and spacial smoothing with Gaussian kernel of 8 mm full-width half-maximum (FWHM). Temporal filtering (band-pass) was then performed between 0.01- 0.08 Hz. The mean signal was removed. BOLD time courses were extracted from each ROI by averaging 27 voxels. The linear regression was used to reduce the effects of physiological processes such as fluctuations related to cardiac and respiratory cycles, or to motion, and 9 noise covariates included White Matter (WM), Cerebro-Spinal Fluid (CSF), Global Signal (GS), as well as from 6 motion parameters (3 rotations and 3 translations as saved by the 3D motion correction). We derived the GS/WM/CSF nuisance signals averaging the time courses of the voxels in each subject's whole brain / WM / CSF masks. These masks were produced by the segmentation process of each participant's T1 image.

Based on previous research (Cauda et al., 2011; Seeley et al., 2007; Spreng et al., 2013; Sridharan et al., 2008), we selected 23 MNI coordinates as the center positions of functional network nodes (ROIs). Functional network edges were defined by Pearson's correlation coefficients, which were computed between the extracted signals of ROIs for each participant. Then the correlation coefficients were performed with Fisher's *r*-to-*z* transformation (Fox & Raichle, 2007). For each edge, the independent samples *t*-tests was used to analyze the difference between groups and corrected the multiple comparisons with False Discovery Rate (FDR, $p < 0.05$). To reveal the relation between SN and CEN, we calculated the average nodal signal across all the nodes within SN and CEN respectively.

The quantitative metrics of SN and CEN were analyzed based on the graph-theoretical method for the full correlation matrix using the Brain Connectivity Toolbox (http://www.brainconnectivity-toolbox.net) (Rubinov & Sporns, 2010).

Results

The average nodal signal was calculated across all the nodes within SN and CEN respectively. Then, we examined the inter-network FC through the correlation between the average nodal signal of SN and CEN. The experts had a significantly enhanced inter-network FC between SN and CEN than the amateurs (t = 3.91, $p < 0.001$, Fig. 1a). The enhanced inter-network FC was largely evident in bilateral DLPFC and SMA in CEN, while SN showed a more even spatial distribution since the majority of the nodes were related to the enhancement of inter-network FC. Furthermore, the experts also had a higher level of enhancement of intra-network FC in SN than in CEN (Fig. 1b). Furthermore, the experts did not have decreased FC compared to the amateurs.

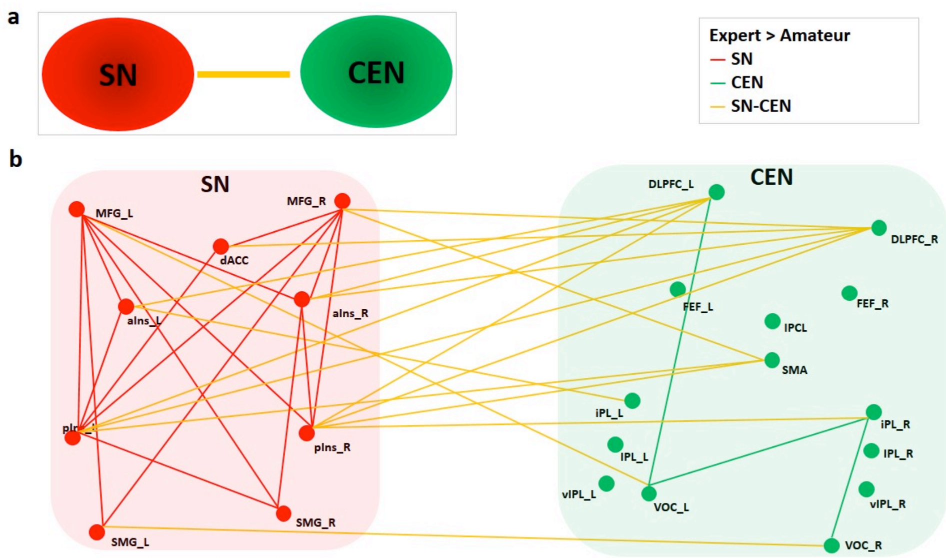

Fig. 1 - The significantly enhanced FC in the experts.

Sub-Fig (a) indicates enhanced FC between SN and CEN based on the correlational analysis between the average nodal signal of SN and CEN (yellow lines indicate $p < 0.001$). Sub-Fig (b) indicates enhanced FC at the nodal level (FDR, $p < 0.05$). Red dots are the nodes of SN; red lines are the edges of SN; green dots are the nodes of CEN; green lines are the edges of CEN, yellow lines are edges of inter-network.

For quantitative metric of the integration between SN and CEN, we constituted the nodes of both SN and CEN into a multi-system network. At different threshold levels as shown in Figure 2a, the graph-theoretical analysis showed significant increases in the three global characteristics (i.e., global efficiency, connection cost, and the mean clustering coefficients in the multi-system network) in the experts compared to the amateurs (see Fig. 2).

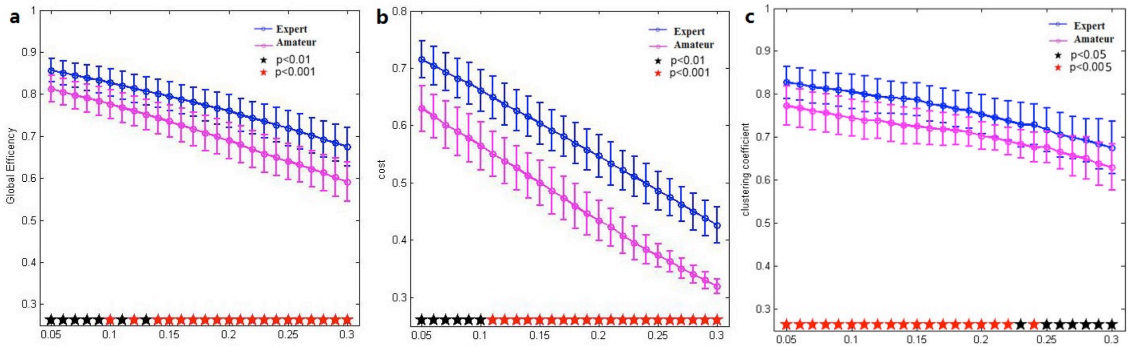

Fig. 2 - Increased global characteristics in AVG experts over amateurs.

Sub-Fig. (a), (b) and (c) indicate global efficiency, connection cost and mean clustering coefficient respectively. The abscissa indicated step-by-step thresholds (correlation coefficient) to establish network.

In the new network, we found significantly enhanced nodal characteristics in the experts compared to the amateurs (Fig. 3). Fig. 3a showed that DLPFC.L of CEN and four nodes of SN had increased nodal clustering coefficient (bilateral aIns, pIns.L and SMG.L.). Fig. 3b showed a significantly increased nodal degree in most of the SN and CEN nodes. Fig. 3c revealed a pattern of results similar to Fig. 3a except IPCL and SMA of CEN in nodal efficiency.

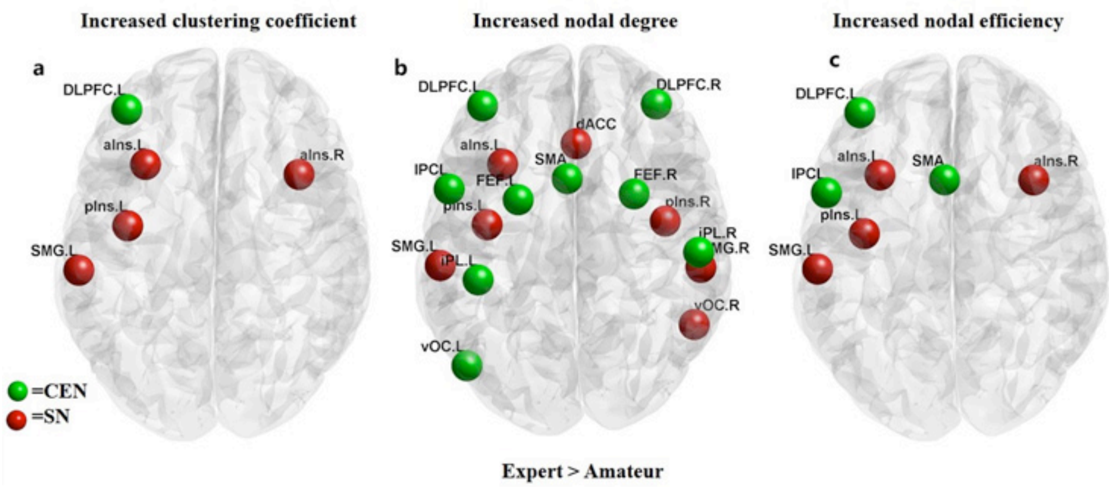

Fig. 3 - Increased nodal characteristics in the experts over the amateurs.
Sub-Fig. (a), (b) and (c) indicate significantly increased nodal clustering coefficient, degree and efficiency, respectively. Green dots are the nodes of CEN, while red dots are the nodes of SN

The experts outperformed the amateurs at the spatial memory task (t = 4.07, p < 0.001) and the response time of 2-back task (t = - 2.08, p = 0.04). We found that the performance on the spatial memory task was positively correlated to the global efficiency (r = 0.47, p = 0.04) and the connection cost (r = 0.48, p = 0.03), respectively. Furthermore, results showed that the response time at the 2-back task was negatively correlated to the nodal efficiency of DLPFC.L (r = - 0.51, p = 0.02). However, results did not reveal significant correlations between behavioral data and graph theoretical characteristics in the amateurs.

Discussion

This study examined the relation between AVG experience and the functional integration between SN and CEN using resting-state FC analysis. We also explored the graph theoretical characteristics of the integration between SN and CEN. Results showed that compared to the amateurs, the AVG experts had significantly enhanced FC, global characteristics, and nodal characteristics both within and between the networks.

We found significantly enhanced intra-network and inter-network FC in the experts compared to the amateurs (Fig. 1). The finding that there was a higher level of enhancement in SN than in CEN suggested that SN might be more sensitive to AVG experience than CEN. The stronger sensitivity of SN to adaptive environment may be related to its role in the cognitive processes (Menon & Uddin, 2010). SN receives and selectively amplifies the salient information, thereafter, generates a top-down control signal prompting CEN to respond to salient information through more advanced cognitive activities, such as decision-making, planning, and action execution (Cocchi et al., 2013). Thus, SN appears to be responsible for more primary cognitions than CEN. Perhaps, the network responsible for more primary cognitions (i.e., SN) has a higher level of plasticity than the network responsible for more advanced cognitions (i.e., CEN). However, this conjecture needs a further examination by future studies.

Furthermore, the enhanced FC between the nodes of SN and CEN (e.g., dACC, iPL_L, bilateral AI, PI, DLPFC and MFG) suggests an enhanced functional integration between SN and CEN, which in turn may facilitate attention and working memory at a cognitively demanding task (Seeley et al., 2007; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013). The enhanced functional integration between SN and CEN observed in the experts might serve as the neural basis supporting their advanced attention and working memory during an AVG session (Colzato, van den Wildenberg, Zmigrod, & Hommel, 2012; Green & Bavelier, 2003; Powers, Brooks, Aldrich, Palladino, & Alfieri, 2013). This study is the first to show that long-term AVG playing is related to enhanced functional integration that is observable even under the resting-state.

Past research showed that both SN and CEN were positively activated at certain cognitive tasks, and thus considered as task-positive network (Cocchi et al., 2013). Using graph-theoretical analysis, we examined the multi-system network (SN and CEN combined) and we found significantly increased global characteristics in the AVG experts compared to the amateurs, including global efficiency, mean clustering coefficient, and connections cost (Fig. 2). Global efficiency reflects the ability to integrate the nodal information; mean clustering coefficient indicates nodal information processing; connection cost denotes the resource consumption in maintaining the function of the network (Rubinov & Sporns, 2010; Xue et al., 2014). Thus, the results suggested that the experts might be advanced at integrating nodal information and nodal information processing.

Furthermore, these enhancements were realized at the cost of increased resource consumption in maintaining the function of networks, which was consistent with the previous findings on the neural network (van den Heuvel, Kahn, Goñi, & Sporns, 2012). The correlation between behavioral data (performance of the spatial memory) and global efficiency (global efficiency, connection cost) further supported the relation between AVG experience and the functional enhancements of SN and CEN. The increased efficiency of global network might improve one's performance on an AVG session.

Increased nodal characteristics were also observed in the AVG experts. We evaluated three nodal characteristics: clustering coefficient, degree, and efficiency. Nodal clustering coefficient indicates the ability of information processing of a node; nodal degree reflects the number of connections of a node, a basic nodal characteristic to which other nodal characteristics are related; nodal efficiency reflects the ability of a node to integrate specialized information from other nodes (Rubinov & Sporns, 2010; Zhang et al., 2011). Thus, the increased nodal characteristics in the experts suggested that they had enhanced information processing ability at local regions of CEN and SN. These regions shown in Fig. 3, especially nodes with enhancement in all of three characteristics (i.e. DLPFC, Insula and SMG) might have a close relation to AVG experience. As an important node in CEN, DLPFC.L is related to attentional control and working memory (Cocchi et al., 2013; Seeley et al., 2007).

Similar to a recent study on the effect of AVG experience (increased GMV in DLPFC), the present study showed an enhanced DLPFC.L (Kühn et al., 2013). Furthermore, the nodal efficiency of DLPFC.L was correlated to the response time at the 2-back task in the AVG experts but not in the amateurs. Furthermore, the AVG experts also showed better work memory than amateurs. Therefore, the left DLPFC might play an important role in the cognitive effects of AVG experience. Moreover, we also found that the bilateral DLPFC, which were also main nodes in CEN, had more enhanced FC between CEN and SN than other nodes, thus suggesting that DLPFC might be associated with the integration of both CEN and SN.

In addition, bilateral aIns receives salient information and initiating CEN. According to recent resting-state studies, bilateral pIns and SMG.L are related to the sensorimotor network (Cauda et al., 2011) which charge input and output information to support attentional and working memory. Thus, these enhanced nodal characteristics support the behavioral finding that AVG playing is related to advanced attention and working memory (Colzato et al., 2012; Green & Bavelier, 2003; Powers et al., 2013).

Conclusion

In general, by comparing AVG experts with amateurs, this study investigated AVG experience-related functional improvement in human brain. Results showed that AVG experts had significantly enhanced FC between SN and CEN, increased global characteristics and nodal characteristics in SN and CEN. Thus, frequent AVG playing might integrate AVG players' SN and CEN, which implicated the plasticity of brain responded to AVG. The integration may is related to the experts' advanced attention and working memory in a game session, which need a longitudinal study for further examination.

References

Anguera, J., Boccanfuso, J., Rintoul, J., Al-Hashimi, O., Faraji, F., Janowich, J., Johnston, E. (2013). Video game training enhances cognitive control in older adults. Nature, 501(7465), 97-101. doi: 10.1038/nature12486

Bavelier, D., Achtman, R., Mani, M., & Föcker, J. (2012). Neural bases of selective attention in action video game players. Vision Research, 61, 132-143. doi: 10.1016/j.visres.2011.08.007

Bavelier, D., Green, C. S., Han, D. H., Renshaw, P. F., Merzenich, M. M., & Gentile, D. A. (2011). Brains on video games. Nature Reviews Neuroscience, 12(12), 763-768. doi: 10.1038/nrn3135

Beckmann, C. F., DeLuca, M., Devlin, J. T., & Smith, S. M. (2005). Investigations into resting-state connectivity using independent component analysis. Philosophical Transactions of the Royal Society B: Biological Sciences, 360(1457), 1001-1013. doi: DOI 10.1098/rstb.2005.1634

Blacker, K. J., & Curby, K. M. (2013). Enhanced visual short-term memory in action video game players. Attention, Perception, & Psychophysics, 75(6), 1128-1136. doi: 10.3758/s13414-013-0487-0

Cain, M. S., Landau, A. N., & Shimamura, A. P. (2012). Action video game experience reduces the cost of switching tasks. Attention, Perception, & Psychophysics, 74(4), 641-647. doi: 10.3758/s13414-012-0284-1

Cauda, F., D'Agata, F., Sacco, K., Duca, S., Geminiani, G., & Vercelli, A. (2011). Functional connectivity of the insula in the resting brain. NeuroImage, 55(1), 8-23. doi: 10.1016/j.neuroimage.2010.11.049

Chisholm, J. D., Hickey, C., Theeuwes, J., & Kingstone, A. (2010). Reduced attentional capture in action video game players. Attention, Perception and Psychophysics, 72(3), 667-671. doi: 10.3758/APP.72.3.667

Cocchi, L., Zalesky, A., Fornito, A., & Mattingley, J. B. (2013). Dynamic cooperation and competition between brain systems during cognitive control. Trends in cognitive sciences, 17(10), 493-501. doi: DOI 10.1016/j.tics.2013.08.006

Colzato, L. S., van den Wildenberg, W. P., Zmigrod, S., & Hommel, B. (2012). Action video gaming and cognitive control: playing first person shooter games is associated with improvement in working memory but not action inhibition. Psychological Research, 77(2), 1237-1239. doi: 10.1007/s00426-012-0415-2

Connolly, C. G., Wu, J., Ho, T. C., Hoeft, F., Wolkowitz, O., Eisendrath, S., Paulus, M. P. (2013). Resting-State Functional Connectivity of Subgenual Anterior Cingulate Cortex in Depressed Adolescents. Biological Psychiatry, 74(12), 898-907. doi: 10.1016/j.biopsych.2013.05.036

Damoiseaux, J. S., Rombouts, S. A., Barkhof, F., Scheltens, P., Stam, C. J., Smith, S. M., & Beckmann, C. F. (2006). Consistent resting-state networks across healthy subjects. Proceedings of the National Academy of Sciences of the United States of America, 103(37), 13848-13853. doi: 10.1073/pnas.0601417103

Elo, A. E. (1978). The rating of chessplayers, past and present (Vol. 3). New York: Arco Pub.

Elton, A., & Gao, W. (2013). Divergent task-dependent functional connectivity of executive control and salience networks. Cortex, 51, 56-66.

Erickson, K. I., Boot, W. R., Basak, C., Neider, M. B., Prakash, R. S., Voss, M. W., Gratton, G. (2010). Striatal volume predicts level of video game skill acquisition. Cerebral Cortex, 20(11), 2522-2530. doi: 10.1093/cercor/bhp293

Fox, M. D., & Raichle, M. E. (2007). Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. Nature Reviews Neuroscience, 8(9), 700-711. doi: 10.1038/nrn2201

Freyer, F., Roberts, J. A., Becker, R., Robinson, P. A., Ritter, P., & Breakspear, M. (2011). Biophysical mechanisms of multistability in resting-state cortical rhythms. Journal of Neuroscience, 31(17), 6353-6361. doi: 10.1523/JNEUROSCI.6693-10.2011

Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. Nature, 423(6939), 534-537. doi: 10.1038/nature01647

Green, C. S., & Bavelier, D. (2006). Effect of action video games on the spatial distribution of visuospatial attention. Journal of Experimental Psychology: Human Perception and Performance, 32(6), 1465-1478. doi: 10.1037/0096-1523.32.6.1465

Green, C. S., & Bavelier, D. (2007). Action-video-game experience alters the spatial resolution of vision. Psychological Science, 18(1), 88-94. doi: 10.1111/j.1467-9280.2007.01853.x

Jaeggi, S. M., Buschkuehl, M., Perrig, W. J., & Meier, B. (2010). The concurrent validity of the N-back task as a working memory measure. Memory, 18(4), 394-412. doi: 10.1080/09658211003702171

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. NeuroImage, 17(2), 825-841.

Jones, E., Burton, H., Saper, C., & Swanson, L. (1976). Midbrain, diencephalic and cortical relationships of the basal nucleus of Meynert and associated structures in primates. Journal of Comparative Neurology, 167(4), 385-419. doi: 10.1002/cne.901670402

Kühn, S., & Gallinat, J. (2013). Amount of lifetime video gaming is positively associated with entorhinal, hippocampal and occipital volume. Molecular Psychiatry, 19(7), 842-847. doi: 10.1038/mp.2013.100

Kühn, S., Gleich, T., Lorenz, R., Lindenberger, U., & Gallinat, J. (2013). Playing Super Mario induces structural brain plasticity: gray matter changes resulting from training with a commercial video game. Molecular Psychiatry, 19(2), 265-271. doi: 10.1038/mp.2013.120

Kennedy, A. M., Boyle, E. M., Traynor, O., Walsh, T., & Hill, A. D. K. (2011). Video Gaming Enhances Psychomotor Skills But Not Visuospatial and Perceptual Abilities in Surgical Trainees. Journal of Surgical Education, 68(5), 414-420. doi: 10.1016/j.jsurg.2011.03.009

Kessels, R. P., van Zandvoort, M. J., Postma, A., Kappelle, L. J., & de Haan, E. H. (2000). The Corsi block-tapping task: standardization and normative data. Applied Neuropsychology, 7(4), 252-258. doi: 10.1207/S15324826AN0704_8

Latham, A. J., Patston, L. L., & Tippett, L. J. (2013). The virtual brain: 30 years of video-game play and cognitive abilities. Front Psychol, 4, 629. doi: 10.3389/fpsyg.2013.00629

Li, R., Polat, U., Makous, W., & Bavelier, D. (2009). Enhancing the contrast sensitivity function through action video game training. Nature Neuroscience, 12(5), 549-551. doi: 10.1038/Nn.2296

Li, R. W., Ngo, C., Nguyen, J., & Levi, D. M. (2011). Video-game play induces plasticity in the visual system of adults with amblyopia. PLoS Biology, 9(8), e1001135. doi: 10.1371/journal.pbio.1001135

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: a network model of insula function. Brain Structure and Function, 214(5-6), 655-667.

Montembeault, M., Joubert, S., Doyon, J., Carrier, J., Gagnon, J.-F., Monchi, O., Brambati, S. M. (2012). The impact of aging on gray matter structural covariance networks. NeuroImage, 63(2), 754-759. doi: 10.1016/j.neuroimage.2012.06.052

Nichols, T., & Hayasaka, S. (2003). Controlling the familywise error rate in functional neuroimaging: a comparative review. Statistical Methods in Medical Research, 12(5), 419-446.

Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: a primer with examples. Human Brain Mapping, 15(1), 1-25.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9(1), 97-113. doi: 10.1016/0028-3932(71)90067-4

Powers, K. L., Brooks, P. J., Aldrich, N. J., Palladino, M. A., & Alfieri, L. (2013). Effects of video-game play on information processing: A meta-analytic investigation. Psychonomic Bulletin & Review, 20(6), 1055-1079. doi: 10.3758/s13423-013-0418-z

Rubinov, M., & Sporns, O. (2010). Complex network measures of brain connectivity: Uses and interpretations. NeuroImage, 52(3), 1059-1069. doi: 10.1016/j.neuroimage.2009.10.003

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. Journal of Neuroscience, 27(9), 2349-2356. doi: 10.1523/JNEUROSCI.5587-06.2007

Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. Journal of Cognitive Neuroscience, 25(1), 74-86. doi: 10.1162/jocn_a_00281

Sridharan, D., Levitin, D. J., & Menon, V. (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. Proceedings of the National Academy of Sciences of the United States of America, 105(34), 12569-12574. doi: 10.1073/pnas.0800005105

Tanaka, S., Ikeda, H., Kasahara, K., Kato, R., Tsubomi, H., Sugawara, S. K., . . . Honda, M. (2013). Larger Right Posterior Parietal Volume in Action Video Game Experts: A Behavioral and Voxel-Based Morphometry (VBM) Study. PLoS ONE, 8(6), e66998. doi: 10.1371/journal.pone.0066998

van den Heuvel, M. P., Kahn, R. S., Goñi, J., & Sporns, O. (2012). High-cost, high-capacity backbone for global brain communication. Proceedings of the National Academy of Sciences of the United States of America, 109(28), 11372-11377. doi: 10.1073/pnas.1203593109

West, G. L., Al-Aidroos, N., & Pratt, J. (2013). Action video game experience affects oculomotor performance. Acta Psychologica, 142(1), 38-42. doi: 10.1016/j.actpsy.2011.08.005

Xue, K., Luo, C., Zhang, D., Yang, T., Li, J., Gong, D., Zhou, D. (2014). Diffusion tensor tractography reveals disrupted structural connectivity in childhood absence epilepsy. Epilepsy Research, 108(1), 125-138. doi: 10.1016/j.eplepsyres.2013.10.002

Zhang, J., Wang, J., Wu, Q., Kuang, W., Huang, X., He, Y., & Gong, Q. (2011). Disrupted brain connectivity networks in drug-naive, first-episode major depressive disorder. Biological Psychiatry, 70(4), 334-342. doi: 10.1016/j.biopsych.2011.05.018

Zielinski, B. A., Gennatas, E. D., Zhou, J., & Seeley, W. W. (2010). Network-level structural covariance in the developing brain. Proceedings of the National Academy of Sciences of the United States of America, 107(42), 18191-18196. doi: 10.1073/pnas.1003109107

Contact email: gdk2010@gmail.com