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Neural bases of selective attention in action video game players

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Abstract

Over the past few years, the very act of playing action video games has been shown to enhance several different aspects of visual selective attention. Yet little is known about the neural mechanisms that mediate such attentional benefits. A review of the aspects of attention enhanced in action game players suggests there are changes in the mechanisms that control attention allocation and its efficiency (Hubert-Wallander et al., 2010). The present study used brain imaging to test this hypothesis by comparing attentional network recruitment and distractor processing in action gamers versus non-gamers as attentional demands increased. Moving distractors were found to elicit lesser activation of the visual motion-sensitive area (MT/MST) in gamers as compared to non-gamers, suggestive of a better early filtering of irrelevant information in gamers. As expected, a fronto-parietal network of areas showed greater recruitment as attentional demands increased in non-gamers. In contrast, gamers barely engaged this network as attentional demands increased. This reduced activity in the fronto-parietal network that is hypothesized to control the flexible allocation of top-down attention is compatible with the proposal that action game players may allocate attentional resources more automatically, possibly allowing more efficient early filtering of irrelevant information.

Keywords

action video games; brain plasticity; visual attention; fMRI; perceptual load; fronto-parietal network

1. INTRODUCTION

Selective attention is fundamental to allowing task-relevant information to guide behavior, while reducing the impact of irrelevant or distracting information. Many paradigms have been developed with the goal of quantitatively measuring visual selective attention (Carrasco and Yeshurun, 1998; Eckstein et al., 2004; Eriksen and Eriksen, 1974; Lavie, 1997; Treisman and Gelade, 1980). These paradigms range from visual search to flanker compatibility, measuring the efficiency with which targets are selected and irrelevant, potentially distracting, stimuli ignored. Recently, playing fast-paced action video games has been shown to enhance several different aspects of selective visual attention as compared to

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control games (Green and Bavelier, 2003; Hubert-Wallander, Green and Bavelier, 2010 for a review). The present study asks how such changes in behavior may be instantiated at the neural level by comparing action video game players (VGPs) to individuals who do not play such games (NVGPs). We first review the aspects of attention that have been shown to be modified in VGPs as the design of the present study was based on this body of work.

It was first demonstrated that VGPs outperform NVGPs in selective attention by using the Useful Field of View (UFOV) paradigm initially developed by Ball and collaborators. This task requires subjects to distribute their attention widely over the screen and locate a peripheral target while ignoring irrelevant distractors (Feng et al., 2007; Green and Bavelier, 2003; Sekuler and Ball, 1986; Spence et al., 2009). Enhanced spatial selective attention in gamers has been shown more recently using different types of search tasks, such as the Swimmer task (West et al., 2008) or difficult visual search tasks (Hubert-Wallander et al., 2010; but see Castel et al., 2005 for a different result). Interestingly, some of these tasks include a condition where participants perform a peripheral localization task while simultaneously discriminating between two possible shapes located at fixation. This version of the task requires spatial selective attention as well as divided attention. Under such conditions, VGPs outperformed NVGPs on both the peripheral task and the central task (Green and Bavelier, 2006a). Thus, both selective attention over space as well as divided attention is enhanced in VGPs.

VGPs not only exhibit better selective attention over space, they also exhibit enhanced selective attention to objects. For example, VGPs can track a greater number of dynamic, moving objects as compared to NVGPs (Dye and Bavelier, 2010; Green and Bavelier, 2003; Green and Bavelier, 2006b; Trick et al., 2005). This skill requires the ability to allocate attention to several objects and to do so efficiently for several seconds. Another aspect of selective attention also found to change in VGPs is the deployment of attention in time, or the ability to select a target from distractors presented in a temporal sequence. Using an Attentional Blink paradigm (Shapiro, 1994), limits on the dynamic allocation of visual attention were compared in VGPs and NVGPs. VGPs exhibited much less of a blink than NVGPs, with a number of VGPs exhibiting no blink whatsoever, indicating that their attention recovers more quickly over time (Green and Bavelier, 2003).

Importantly, the causal effect of action game play on several of these aspects of visual selective attention has been established through training studies in which naïve subjects are required to play either action-packed, fast-paced video games or control games. Those asked to play action games showed greater attentional gains for pre to post-test than those asked to play control games. This was shown for training spatial selective attention (Feng et al., 2007; Green and Bavelier, 2003; Green and Bavelier, 2006a; Spence et al., 2009), selective attention to objects (Cohen et al., 2007; Green and Bavelier, 2003; Green and Bavelier, 2006b) as well as selective attention over time (Cohen et al., 2007; Green and Bavelier, 2003).

The attentional skills mentioned above primarily involve goal-directed, top-down attention. This begs the question of whether other aspects of attention may be equally modified by action game play. Although stimulus-driven, exogenous attention is certainly engaged while playing action games, it seems that the capacity and dynamics of exogenous attention are less susceptible to the effects of playing action video games. Exogenous cues were found to induce equivalent performance enhancement in VGPs and NVGPs leading to similar cue-validity effects and comparable inhibition of return[1] (Castel et al., 2005; Hubert-Wallander

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[1] Speed and accuracy with which an object is detected are first briefly enhanced after the object is attended, and then hindered. This hindrance has been termed 'inhibition of return'.

et al., in press). Thus, not all aspects of attention are equally modified in VGPs. Reports that VGPs show reduced attentional capture as compared to NVGPs could suggest less exogenous pull in VGPs; however, the available data are also consistent with the proposal that VGPs have better top-down attentional control allowing them to either limit or recover faster from the distracting effect of abrupt onsets (Chisholm et al., 2010; but see West et al., 2008 for a different view). In line with the proposal of greater top-down selective attention in VGPs, a recent electrophysiological study by Mishra et al. (2011) reported greater suppression of distracting, unattended information in VGPs. Participants were presented with four rapid serial visual presentation streams in a steady-state visually evoked potential design allowing one to recover the cortical responses to the task-relevant attended stream as well as to the distracting, unattended streams. Under these high load conditions, VGPs and NVGPs similarly processed the attended streams, but VGPs more efficiently suppressed the unattended streams. Notably, this greater suppression was associated with faster reaction times. Greater distractor suppression may be a possible mechanism for more efficient executive and attentional control (Clapp et al., 2011 in older adults; Serences et al., 2004; Toepper et al., 2010). The present work builds up on the findings of these earlier studies to further our understanding of the mechanisms that may be at play in the attentional enhancements noted in VGPs.

The present study directly compares VGPs and NVGPs by using a visual search paradigm contrasting an easy versus a more difficult search, while concurrently measuring the impact of search difficulty on the processing of irrelevant motion information (Lavie, 2005). As most behavioral changes documented so far point to improvements in top-down attention after action gaming, we expected to observe changes in the dorsal fronto-parietal network, whose role in the control and regulation of attention is well-established (Corbetta and Shulman, 2002; Hopfinger et al., 2000). To recruit this network, the present design varies the difficulty of target selection using small search arrays under two different perceptual load conditions. In addition, the present study takes advantage of the well-documented attentional modulation of neural activity in visuo-perceptual areas such as MT/MST to compare distractor processing in action gamers and non-gamers (Rees et al., 1997).

Subjects were presented with a ring of shapes and asked to decide whether there was a square or a diamond among the shapes presented. On each trial, there could only be one target (either a square or a diamond). By manipulating the homogeneity of the other shapes in the ring, two levels of difficulty were used (see Figure 1). In the low load condition, all non-target shapes were circles allowing the target to pop-out and thus be easily discriminated; in the higher load condition, three different filler shapes were used leading to a more heterogeneous display making the target discrimination more difficult. Under this high load condition, we expected increased recruitment of fronto-parietal networks as compared to the low load condition. Of interest was the difference between VGPs and NVGPs in recruiting this network as search difficulty increased. Importantly, we selected rather easy search tasks (the low load effectively corresponds to a pop-out situation and the high load is just slightly more difficult) as we were aiming for relatively comparable increase in reaction times across groups from low to high attentional load. Indeed, while it is the case that VGPs have faster search rates than NVGPs (Hubert-Wallander, et al., in press), relatively matched increase in RTs between two levels of difficulty can still be found when using very easy searches. By using the low load condition as the baseline, any group differences in BOLD signal between VGPs and NVGPs could then be attributed to their group status, rather than a significantly greater increase in difficulty from low to high load in one group and not the other.

Concurrent to this main search task, irrelevant patches of random dots (either moving or static) were presented to examine distractor suppression. Previous work from Lavie and collaborators has shown that as the perceptual load of the main search task increases, distractors receive fewer processing resources, thereby resulting in smaller activation of MT/MST by irrelevant moving patterns (Lavie, 2005; Rees et al., 1997). While this pattern of results was predicted for both VGPs and NVGPs, the amount of activation in MT/MST triggered by irrelevant moving stimuli was expected to differ across populations. Greater attentional control should allow more efficient suppression of task-irrelevant motion (see for example, Mishra et al., 2011). By contrasting the neural correlates of motion processing in MT/MST in VGPs and NVGPs, the present study allowed us to directly compare how much processing irrelevant distractors may undergo in each population.

2. MATERIAL AND METHODS

2. 1 Participants

Participants were 26 naïve males (18-26 years, mean age 20.5 years) who were trained on the task prior to the scanning session. Participants were placed in one of two groups, video game players (VGPs, n=12) or non-video game players (NVGPs, n=14), according to their responses to a questionnaire designed to establish the frequency of action video game usage in the 12 months prior to testing. For each video game which participants reported playing, they were asked how often they had played that game in the previous 12 months, and for how long they had played it during a typical session. The criterion to be considered a VGP was a minimum of 5 hours per week (on average) of action video game play over the previous year. It is important to note that only experience with *action* video games counted towards this requirement. Action video games are played from the first-person perspective and feature fast motion while requiring vigilant monitoring of the periphery and simultaneous tracking of multiple objects, putting divided attention at a premium. An abridged list of the games reported as played by the VGP group includes *Halo, Counterstrike, Gears of War*, and *Call of Duty*. The criterion to be considered a NVGP was one or less hours per week of action video game play over the previous year. (Note that some NVGPs did play other kinds of games, such as board games, puzzle games, card games, strategy games or social games). All studies were performed with the informed consent of the participants and were approved by the University of Rochester's Research Subject Review Board.

2.2 Behavioral training prior to brain imaging

All participants were trained on the task in a one-hour session in the week prior to their scanning session. The stimulus conditions during the training session were similar to those used in the scanner (described below). This training session was used to familiarize the subjects with the experiment and ensure that they were performing above 90% correct on the task before being scanned. Participants were instructed to be as fast and as accurate as possible. Two of the 14 NVGPs did not meet our performance criteria, leaving 12 NVGPs and 12 VGPs who were scanned. We note that this procedure could only weaken possible differences between groups.

2.3 MR Image acquisition

Magnetic resonance images were acquired with a Siemens Trio 3T MRI and a Siemens CP head coil. To minimize head motion and help reduce cumulative head drift during the scanning session, foam padding was used to support the head and neck.

Thirty-one T2*-weighted gradient echo (GE) echo-planar imaging (EPI) axial slices covering the entire brain were acquired every 3 sec (TE = 51 ms, flip angle = 90°, voxel dimension = 4 mm^3, interleaved slices). One hundred measurements (time frames) were acquired for each run. Nine fMRI scans were performed for each participant.

Three-dimensional, T1-weighted anatomical MR images (aMRI) were acquired in the same session. This aMRI was an MPRAGE sequence (TR = 2020 ms, TE = 3.93 ms, flip angle = 12°, 256 × 256 matrix, 1mm^3 resolution).

2.4 Visual stimuli and procedure

The visual stimuli were generated in MATLAB on a Macintosh G4 running OS9, displayed using a JVC DLA-SXS21E projector and presented on a rear-projection screen placed at the back of the magnet bore. Viewing distance was 0.8 m and the screen was viewed using a mirror mounted above the eyes at an angle of ~45°.

The stimulus was composed of eight shapes (each subtending ~1°) presented along an annulus (5° radius – see Figure 1). Participants were asked to fixate on a centre cross and identify whether a square or diamond target was present in the annulus of shapes. Participants responded by pressing one of two buttons on an MR-compatible response box. Task difficulty was manipulated by increasing the number of *different* shapes while keeping the number of overall shapes constant (eight), so as to control for the number of abrupt onsets in the visual display. We measured accuracy and reaction time during two levels of task difficulty (low/high load). Low load trials consisted of the target (square or diamond) with all other filler shapes being circles. High load trials consisted of the target, 3 different shapes selected randomly from a set of 12 possibilities (e.g., triangles, trapezoids, houses – in various orientations), and four circles. The shapes were presented every 1 sec for 120 ms (inter-trial interval = 880 ms). They were light grey on a dark grey background (contrast 60%).

In the peripheral condition, the distractors (patches of moving or static dots) were positioned on both sides of the central fixation spot, outside the annulus of shapes. The dots in the distractor patches were continuously presented and were alternately moving or static in 18 sec intervals.

A central condition, identical to the peripheral one except that the distractors (patches of moving or static dots) were placed within the annulus of shapes, was also used (see Figure 1). Of interest was the comparison between the processing or suppression of the central and peripheral distractors. Would these distractors be processed to the same extent and in the same way?

The middle of the central and peripheral distractor patches were equally spaced from the target annulus and the size of the patches were scaled according to the nasal cortical magnification factor as calculated by Rovamo and Virsu (1979). Central distractors were positioned 1.6° from fixation with a diameter of 1.8°, peripheral distractors were 8.4° from fixation with a diameter of 4.6°.

Each functional scanning run consisted of both low and high load trials presented in a block design (block length = 36 sec for one load level) with the distractors (patches of dots) alternating from moving to static (or vice versa) every 18 seconds. The block order as well as the initial moving or static state of the distractors for each block was randomized. Each subject performed 8 functional runs – 4 runs of peripheral distractors were intermixed with 4 runs of central distractors. See Figure 2 for time course of sample scanning runs.

We did not record eye movements, but instead trained participants to maintain fixation on a central point. Participants came for a first behavioral session performed outside of the magnet during which they were instructed to fixate. Although the eccentric location of the shapes within the annulus could have triggered eye movements, the use of a search annulus with a central fixation cross presented for only 120 ms ensured that subjects could only perform the task well while fixating the central fixation cross. Along with the behavioral performance, we will see that the brain imaging data show that the subjects were centrally fixated. Indeed, activity along the calcarine sulcus related to the distractors (central/peripheral) was as one might predict and only possible if the subjects were fixating.

In the same scanning session, along with these eight functional scanning runs, each subject also did a separate motion localizer run used to define his area MT/MST, which is sensitive to visual motion. The stimulus for the motion localizer consisted of a full field (12° radius) of white dots on a black background (100% contrast). The dots were alternately moving (radially) or static in 18 sec intervals. Subjects were asked to fixate the centre of the screen (a blue fixation dot) and were not required to make any response.

2.5 Behavioral data analysis

Reaction time (RT) and accuracy measures were collected during the scanning session. RTs from erroneous responses were not included in the behavioral analysis (erroneous responses included incorrect responses as well as trials where RTs < 250 ms - of which there were fewer than 1%). There were no anomalously long RTs as the maximum RT of 1000 ms was determined by the 1 sec inter-trial interval. A repeated measures 2×2×2 analysis of variance (ANOVA) was performed between the groups (VGP/NVGP), with load level (low/high) and distractor eccentricity (central/peripheral) as within group variables.

2.6 MR Image analysis

Image analysis was performed using tools from the FMRIB Software Library (FSL, version 4.0, FMRIB, Oxford, UK, www.fsl.ox.ac.uk/fsl, see also Smith et al., 2004; Woolrich et al., 2009). The first 4 timeframes of each functional run were discarded to remove any start-up magnetization transients in the data. The following preprocessing techniques were applied: motion correction using MCFLIRT (no participant moved more than 2 mm in any direction and rotations were less than 1.3°) (Jenkinson et al., 2002); fieldmap-based EPI unwarping using PRELUDE+FUGUE (Jenkinson, 2003; Jenkinson et al., 2004); slice-timing correction using Fourier-space time-series phase-shifting; non-brain removal using BET (Smith, 2002); spatial smoothing using an isotropic 3D Gaussian kernel (full-width-half-maximum = 5mm) to attenuate high frequency noise; grand mean-based intensity normalisation of all volumes by the same factor; and nonlinear high-pass temporal filtering with a 50 sec cut-off. Statistical analyses were then carried out using FEAT 5.63, the FMRI Expert Analysis Tool.

2.6.1 Single Subject Analyses—For each run within each subject, we first used the FILM (FMRIB's Improvised Linear Model) based on a general linear model (GLM) with prewhitening for correlated errors (Woolrich et al., 2001). Regressors or explanatory variables (EVs) were used to model the following three conditions in the first level model: (i) low load with moving distractors (MotionLow), (ii) high load with moving distractors (MotionHigh), and (iii) high load with static distractors (StaticHigh). The condition of low load with static (StaticLow) distractors was used as the baseline. To identify the brain areas activated under different conditions, a set of contrasts were derived from the EVs. Co-efficients were computed for each contrast for the four peripheral and central runs for each subject. Registration to high-resolution and/or standard images (MNI-152 template) was carried out using FLIRT (Jenkinson and Smith, 2001).

Then, the four peripheral runs within a session for a single subject were combined using general linear model with fixed effects (likewise for the four central runs) for the same set of contrasts. The co-efficient of contrasts was computed using the fixed effects model by forcing the random effects variance to zero with FLAME (FMRIB's Local Analysis of Mixed Effects) (Beckmann et al., 2003; Woolrich et al., 2004). Z (Gaussianized T/F) statistic images were thresholded using clusters determined by Z > 2.3 and a corrected cluster significance threshold of p = 0.05 (Worsley et al., 1992).

2.6.2 Whole-brain Analyses—

We first performed within-group, whole brain analyses by pooling the subjects into two groups, the NVGPs and the VGPs. For each group, we computed the difference in brain activations between high load and low load by defining a contrast of [MotionHigh-StaticLow]-[MotionLow-StaticLow]. The coefficients of the contrast computed for the central and peripheral runs in the single subject analyses were used as inputs to study the load difference effect within each group. Data were modeled with mixed effects using FLAME stage 1 (Beckmann et al., 2003; Woolrich et al., 2004). Z (Gaussianised T/F) statistic images were thresholded using clusters determined by Z > 3.0 and a (corrected) cluster significance threshold of p = 0.05 (Worsley et al., 1992) for each of the group.

We then performed between-group, whole brain analyses to identify those brain areas where high versus low load differences differ across groups. The inputs were the co-efficients of contrast computed using the central and peripheral runs from each group as described in the paragraph above. Again the analysis was carried out using mixed effects model with FLAME stage 1. Z (Gaussianised T/F) statistic images were thresholded using clusters determined by Z > 2.0 and a (corrected) cluster significance threshold of p = 0.05 (Worsley et al., 1992). Here contrast masking was used to make sure to limit group differences to those areas showing significant differences for HighLoad vs. LowLoad in each of the NVGP and the VGP group.

The activations were quite extensive for the high versus low load conditions both within and between groups, with clusters often spanning multiple anatomically and functionally distinct regions. To decompose these large clusters of activation, we first identified all anatomical regions activated in these comparisons, then extracted the results from anatomically-defined regions of interest (ROIs) based on the work of Tzourio-Mazoyer et al. (2002). The boundaries of these areas where slightly distorted to avoid attributing activation at the fringe of a well-delineated cluster to structures other than the main center of mass of the cluster. ROIs from each hemisphere included frontal areas - the superior frontal sulcus encompassing the frontal eye field, the middle frontal gyrus, the inferior frontal gyrus, the supplementary motor area, and the dorsal anteriors cingulate cortex; parietal areas - superior parietal cortex including the dorsal part of the intra-parietal sulcus, the intra-parietal sulcus proper, and the cuneus and precuneus; occipital areas – superior, middle and inferior occipital cortices as well as the cerebellum and basal ganglia structures (see Tables 1 & 2).

Finally, the contrast between central and peripheral distractors conditions were computed separately for VGPs and NVGPs. Conjunction analyses were then performed to determine areas common to these contrasts in VGPs and NVGPs by multiplying binarized versions of the thresholded statistical maps. This analysis was used to verify our analyses as central and peripheral distractors are known to evoke activation at different locations in the visual cortices. Z (Gaussianized T/F) statistic images were thresholded using Z > 3 and a corrected cluster significance threshold of p = 0.05 (Worsley et al., 1992).

2.6.3 Processing of Motion Distractors - Regions of Interest analysis—

Given our design, brain activation differences in area MT/MST were of particular interest. To allow for individual variation in the location and magnitude of response, each subject's MT/MST was functionally defined using his motion localizer scan and an MT/MST region-of-interest (ROI) was drawn based on the functional data and known localization of MT/MST. These ROIs were then applied to each subject's signal change images. %BOLD signal change was computed using StaticLow as a baseline for all contrasts of interest, resulting in two main contrasts for low load and high load, respectively: (1) MotionLow-StaticLow and (2) [MotionHigh-StaticLow] – [StaticHigh-StaticLow]. % BOLD signal change for the different conditions were extracted on an individual subject basis and used as the dependent measure in the statistical analyses reported below.

3. RESULTS

3.1 Behavioral results

A 2×2×2 ANOVA with distractor eccentricity (central/peripheral) and load (low/high) as within-subject variables and group (VGP/NVGP) as the between subject variable was carried out on the percent correct data. The only significant effect was an interaction between eccentricity and group [$F(1, 22) = 11.8$, $p < 0.002$, partial eta squared = 0.36] as NVGPs were slightly less accurate under the peripheral condition whereas VGPs were equally accurate under both conditions (NVGP_Peripheral = 95.2%, NVGP_Central = 96.15%; VGP_ Peripheral = 96.5%; VGP_Central = 96.05% - Figure 3). All other p's > 0.18.

A similar 2×2×2 ANOVA with reaction times as the dependent variable was carried out. Main effects of load [High Load = 574 ms, Low Load = 506 ms, $F(1, 22) = 276.4$, $p < .0001$, partial eta squared = .93] and of group [VGPs = 514ms, NVGPs = 566ms, $F(1, 22) = 10.8$, $p < 0.003$, partial eta squared = .33] confirmed faster RTs in the low load than in the high load condition as well as faster RTs in VGPs as compared to NVGPs (Figure 3). In addition a triple interaction between group, load and eccentricity [$F(1, 22) = 8.9$, $p <0.007$, partial eta squared = 0.29] was significant, indicating differential effects of load and group as a function of eccentricity (Figure 3). The cost of going from low to high load displays was slightly greater under peripheral motion than central motion for NVGPs, whereas VGPs exhibited the opposite pattern. The source of this triple interaction remains unclear; as it was not predicted, it would have to be further confirmed before being interpreted. When considered along with the accuracy data, the overall pattern of results suggests that irrelevant motion in the visual periphery is more disrupting in NVGPs than VGPs. None of the other effects were significant; in particular there was no interaction between load and group ($p > .8$), eccentricity and group ($p > .9$) or load by eccentricity ($p > .7$).

In sum, we found faster RTs in VGPs than NVGPs in the face of comparable accuracy replicating past reports on how action game play affects speed and accuracy (Dye et al., 2009a; Green et al., 2010). In addition, increasing the search difficulty from the low to high load displays increased reaction times by about 70 ms in both VGPs and NVGPs indicating equal increase in difficulty from low to high load in the two populations compared. Equivalent increase in reaction times from low to high load is an important characteristic of this study that asks how VGPs and NVGPs may differ as attentional difficulty increases. Indeed, in the face of a similar change in RTs from low to high load in each group, differences between groups are more likely to arise from group status rather than just a lesser increase in task difficulty for the VGPs group..

3.2 Impact of load increase on attentional networks - fMRI whole brain analysis

The whole brain analyses looked for differences in brain activation as load was increased from low to high between VGPs and NVGPs. This effect was studied by asking which brain structures change their activation level under the high load condition using the low load condition as a baseline. These analyses were first performed separately for VGPs and NVGPs; then between-group analyses were performed to characterize those brain regions that differ between groups. Although separate analyses were performed for peripheral and central distractor runs, the patterns of brain activity were very similar in the two groups across distractors eccentricities. Therefore, the effect of load will be presented averaged across central and peripheral distractors runs.

As expected, NVGPs showed activation in a network of fronto-parietal areas as load increased (Table 1). This network included activation bilaterally in the superior frontal and inferior frontal areas, the pre-central and post-central gyri as well as the SMA (supplementary motor area). Importantly, a large activation was noted in the dorsal anterior cingulate. Thus, both midline and lateral frontal areas showed greater recruitment as task difficulty was increased. Parietal activations were seen bilaterally in the inferior parietal cortex, the superior parietal cortex extending medially to the cuneus/precuneus. Finally, marked activation was noted in visual areas including superior and middle occipital areas bilaterally, as well as along the left inferior and middle temporal gyri. Although a similar network of areas was recruited in VGPs as task difficulty increased (Table 1), the recruitment of the fronto-parietal network was much less marked. Of note, there was no significant activation in frontal areas (medial or lateral, see Figure 4). Bilateral parietal activation was restricted to a smaller region in the inferior and superior parietal lobules. The bulk of the activation in the VGPs was limited to visual areas including superior and middle occipital gyri bilaterally, and the left inferior temporal gyrus.

Importantly, between-group analyses confirmed significantly greater recruitment of the fronto-parietal network in NVGPs than in VGPs as task difficulty increased (Table 2; Figure 5). This difference was especially marked in frontal areas including the superior frontal cortex, inferior and middle frontal gyri, as well as the SMA, and the dorsal anterior cingulate cortex. Greater activation in NVGPs was also noted in parietal areas and especially the right superior parietal lobe and its extension to the right cuneus and precuneus. Finally, visual areas (occipital lobe) themselves were also more active in NVGPs than VGPs as illustrated by the significantly greater activation in right superior and middle occipital gyri. Greater activation in NVGPs was also noted in the right insula and the right putamen.

3.3. Impact of eccentricity on recruitment of visual areas – fMRI whole brain analyses

We performed analyses to confirm the predicted pattern of results as a function of distractor eccentricity. A conjunction analysis of VGP and NVGP data for the contrast between the central versus the peripheral moving distractor conditions confirmed a very similar pattern of results in both groups. Notably, activation along the calcarine fissure was observed and showed a more posterior focus for central than peripheral distractor conditions as expected (Figure 6). Activation was also noted bilaterally in the lingual gyrus. In the case of the central distractors, the activation also extended laterally covering part of the middle and inferior occipital sulcus in both the left and right hemisphere. These analyses confirmed all expected patterns of activation given the known retinotopic organization of visual cortices.

3.4 Processing of motion distractors – Region of interest results

Given our research question, we also characterized how the processing of irrelevant motion was altered from low to high load in VGPs and NVGPs. To do so, we turned to a region-of-interest analysis, known to have greater sensitivity than whole brain analyses. Indeed, the latter require normalizing all brains into a common template, potentially muddying boundaries of areas functionally defined such as MT/MST.

This analysis focused on MT/MST to assess how the irrelevant motion was processed as a function of load and group. A 2×2×2 ANOVA using percent change in MT/MST as the dependent variable showed a main effect of distractor eccentricity [$F(1,22) = 31.58$, $p < 0.0001$, partial eta squared = 0.59] due to lower activation from peripheral than central motion, and a near significant effect of load [$F(1, 22) = 4.13$, $p = 0.054$, partial eta squared =

0.16] reflecting greater activation under low than high load. In addition, eccentricity interacted with load [F(1,22) = 6.06, p = 0.022, partial eta squared = 0.22] as well as with group, albeit weakly so [F(1,22) = 3.53, p < 0.075, partial eta squared = 0.14]. There was a larger effect of load when motion distractors were presented peripherally compared to centrally, as well as a larger group difference under central than peripheral motion distractors (Figure 7). None of the other effects were significant, all ps > .1. The different effects of load as a function of eccentricity led us to carry separate 2×2 analyses for central and peripheral moving distractors.

For peripheral motion, a main effect of load was observed [F(1, 22) = 7.98, p = 0.01, partial eta squared = 0.27] replicating the work of Rees, Frith, and Lavie (1997). No other effect was significant (all p's > 0.5). For central motion, a different pattern of results was observed. A main effect of group was observed [F(1, 22) = 4.55, p = 0.044, partial eta squared = 0.17] reflecting lower activation in VGPs than NVGPs, but no other effects were present (all p's > 0.8), and in particular there was no main effect of load.

Importantly, analysis of motion localizers indicated no difference across groups (mean % BOLD signal change and standard deviation, VGPs = 0.98%, +/-0.38; NVGPs = 1.05%, +/-0.30, t(21) = -0.48, p = 0.64). Thus, it is not the case that VGPs always show reduced activation in MT/MST as compared to NVGPs when viewing a moving stimulus (motion localizer stimulus).

4. GENERAL DISCUSSION

4.1 Summary

The present study was designed to compare the neural networks underlying attentional processing in VGPs and NVGPs. In particular we aimed at identifying the neural networks recruited as attentional load is increased and at characterizing the fate of distractors under different attentional loads in these two groups. For this purpose, a visual search paradigm was used alternating between an easy and a more attentionally demanding task, while distractors, either static or moving random-dot displays, appeared in the visual field.

VGPs were faster at performing the search tasks than NVGPs replicating previous reports in the literature. To more cleanly isolate group effects as attentional demands increase, the two levels of search tasks used in this study were selected to be relatively easy to lead to comparable increase in RTs from low to high load in each population. Indeed, although VGPs show faster search rates than NVGPs (Hubert-Wallander et al., in press), this difference is difficult to capture when only considering easy searches. Therefore, by using the low load condition as our baseline, we could compare the recruitment of the fronto-parietal attentional network in VGPs and NVGPs as attentional demands increased reaction times by about 70 ms in each group. Despite this matched increase in attentional difficulty, we observed a significantly lesser recruitment of the fronto-parietal attentional network in VGPs as compared to NVGPs.

In a separate analysis focused on the motion specific area MT/MST, we evaluated the fate of alternatively moving and static distractors as a function of attentional load in each population. Overall, we found that irrelevant motion leads to lesser activation in VGPs than NVGPs. We discuss these results in more details below.

4.2 Processing of Irrelevant Motion Distractors in Gamers and Non-Gamers

4.2.1 Group Effect—This study takes advantage of the perceptual load paradigm to measure the fate of irrelevant and unattended distractors across eccentricity in different populations. Alternations of static and moving stimuli, although irrelevant to the task, led to activation in MT/MST. Overall, VGPs showed less recruitment of MT/MST than NVGPs during task performance. It is important to note that VGPs showed lesser recruitment of MT/MST than NVGPs during task performance, whereas no difference in activation was noted during the MT/MST localizer. This confirms that the decreased activation in VGPs does not reflect a generalized baseline difference between the two populations. Lesser activation in VGPs suggests that they may suppress irrelevant motion distractors more efficiently than NVGPs. Better suppression of distracting information in VGPs has been reported recently using steady-state evoked potential and a very different design (Mishra et al., 2011). Thus, efficient distractor suppression may be a common mechanism that contributes to the superior attentional capabilities of VGPs.

One may ask how these results relate to the proposal in the literature that VGPs may benefit from greater attentional resources (Green and Bavelier, 2003). As proposed by Lavie and collaborators (Lavie, 2005), irrelevant, peripheral moving distractors tend to produce greater MT/MST activation when they receive more attentional resources. This could have led one to expect greater recruitment of MT/MST in VGPs, rather than lesser recruitment as observed here. Indeed, a number of behavioral studies have reported that distractors typically receive more processing resources in VGPs as exemplified by a greater impact of distractor identity on the main task reaction times in VGPs (Dye et al., 2009b; Green and Bavelier, 2006a). The present study cannot directly address this issue, however, since the motion distractors were not task-relevant, and thus could not compete for responses. This prevented the quantification of distractor identity on reaction times. Further research will be needed to clarify this point.

4.2.2 Eccentricity Effects—As initially shown by Lavie and collaborators (Lavie, 2005), irrelevant, peripheral moving distractors produced greater MT/MST activation when the perceptual load of the target task was low as compared to high. A common interpretation of this effect is that a low perceptual load task does not exhaust all attentional resources, allowing some to spread to irrelevant distractors in the periphery. The present study replicates this effect, which is observed in both VGPs and NVGPs. In addition, Figure 7 illustrates that the high perceptual load task leads to equal activation of MT/MST in all participants, whereas at low load, a (non-significant) trend can be seen for greater activation in NVGPs than in VGPs. This pattern also mirrors a recent report by Forster and Lavie (2007) in which these authors document that a sure way to equate performance across groups that differ in their resources is to use a high perceptual load for all.

Notably, the use of central distractors (as compared to peripheral distractors) led to a different pattern of results. First, central motion led to an overall greater level of activation in MT/MST than peripheral motion. Although the stimuli were corrected for cortical magnification, this was to be expected. Central motion typically elicits greater response in MT/MST than peripheral motion (Bavelier et al., 2000; Beauchamp et al., 1997), and there is ample evidence that foveal and para-foveal vision is functionally unique, both because of its anatomical organization and of its connectivity (Massey, 2006; Ruff et al., 2006). Accordingly, when using distractors that are task-relevant and thus either compatible or incompatible with the target response, greater compatibility effects are typically observed from central as compared to peripheral distractors. This accords with our result of greater activation in MT/MST for central rather than peripheral distractors. Second, there was no effect of load on MT/MST activation when central distractors were used. Thus, unlike the condition with peripheral distractors, activation triggered by central distractors was not modulated by the resources consumed by the primary task. This finding was unexpected. Several behavioral studies have established that varying the perceptual load modulates the size of the compatibility effect for both peripheral as well as central distractors (Beck and Lavie, 2005; Green and Bavelier, 2006a; Proksch and Bavelier, 2002). In the present study, the peripheral condition produces the expected load effect on MT/MST activation in both populations, and the only difference between the central and peripheral conditions is the eccentricity of the distractors. Thus, the lack of modulation by perceptual load for the central condition is unlikely to reflect a problem with the load manipulation or an oddity of the participants studied. It may be that peripheral resources deplete before central ones, and that given an even more challenging target task, a modulation of central distractors by perceptual load would also be observed.

4.3 Attentional Networks in Action Gamers and Non-Gamers

As the perceptual load of the search task was increased, the fronto-parietal network of areas known to be involved in the allocation and control of attention was robustly activated. Perceptual load in this study was manipulated by changing the salience of the target stimulus, but not the number of stimuli presented. Indeed, the number of search elements was kept constant ensuring an equal amount of sensory stimulation across loads, but the heterogeneity of the search array was increased so as to render the search for the target more difficult in the high load condition (Duncan and Humphreys, 1989). This manipulation successfully changed the difficulty of the task as exemplified by longer RTs in the high load condition. Importantly, this manipulation lengthened RTs in NVGPs and VGPs by a similar amount (about 70 ms) suggesting an equivalent increment in difficulty between low and high loads across groups (VGPs – Low Load = 480 ms, High Load = 548 ms; NVGPs – Low Load = 531 ms, High Load = 601 ms). Despite this behavioral similarity, marked differences in brain activation were noted across groups as load increased.

In accordance with the known brain networks of attention, strong activation was noted in both goal-directed and stimulus-driven attentional systems. In particular, NVGPs exhibited strong bilateral recruitment of the superior frontal sulcus as well as parietal areas along the intra-parietal sulcus and the dorsal anterior cingulate gyrus. Recent studies suggest the anterior cingulate gyrus to be involved in stimulus driven shifts of attention and selective target processing (Hopfinger et al., 2000; Shulman et al., 2009; Shulman et al., 2010). Moreover, its fundamental role in cognitive control has been observed in a variety of studies (Braver and Barch, 2006; Dosenbach et al., 2006; Schulz et al., 2011). While this network is typical of goal-directed attentional control, marked activation was also noted in right frontal areas including the middle and inferior frontal gyri which have been associated with sensory salience and its filtering (Corbetta et al., 2008). Crucially, this fronto-parietal network of areas was much less recruited in VGPs who exhibited reduced activation throughout all frontal and parietal areas (Figure 5). This was reflected in the between-group statistics showing that no region was more activated in VGPs than NVGPs as load increased. In contrast, significantly greater activation was noted in NVGPs throughout the network of areas considered as load was increased.

Lesser activation in VGPs is consistent with the proposal that VGPs develop more efficient attentional processes as a result of their gaming activity, allowing them to allocate attention in a less effortful manner (Hubert-Wallander et al., 2010). We acknowledge that the present work only contrasts VGPs and NVGPs, and thus does not directly establish a causal effect of action video game play on the reduced attentional network recruitment noted in VGPs. It is worth noting, however, that the point of departure for this study included several different training studies that established a causal effect of action game play on visuo-spatial selective attention, as engaged in the present fMRI experimental design (Green and Bavelier, 2003; Green and Bavelier, 2006a; Green and Bavelier, 2007). The present aim was to investigate the neural bases of this attentional enhancement. Future training studies will certainly be valuable in consolidating that link. Yet, by characterizing the neural mechanisms by which selective attention enhancement is attained in VGPs (who are likely to have experienced more than the limited training regimen employed by prior training studies), this work documents how a typical action gamer's attentional system ends up benefiting from his/her action game play.

A working hypothesis for future work is that lesser recruitment of attention-related areas is a signature of greater attentional control. A similar proposal was advanced by Brefczynski-Lewis et al. (2007) in a study of the neural bases of meditation, a state known to enhance attention regulation (Jha et al., 2007; Lutz et al., 2008; Tang and Posner, 2009). In the case of the present study, one could object and argue for an alternative account whereby the lesser recruitment of fronto-parietal areas in VGPs as load increased may have been due to the fact that the high load condition was easier for VGPs than NVGPs. It is correct that absolute level of difficulty was not matched across subjects – VGPs were faster than NVGPs, a now well-established signature of performance in the VGPs group (Dye et al., 2009a; Green et al., 2010). However, the use of the low load condition as a baseline in the analyses and the focus of our analyses on the contrast between high and low load should protect against this alternative account. Indeed, the present design ensured that the increase in difficulty between low and high load was matched across groups. Thus although VGPs were faster overall than NVGPs, the two groups were similarly slowed down by the change in perceptual load from low to high. This comparable change in behavior across loads should have led to a comparable change in recruitment of attentional network; yet it did not, supporting the proposal of a change in attentional efficiency.

Preliminary functional connectivity analyses of the fronto-parietal network provide further support for this view (See Supplementary Data). Seeding from parietal areas revealed no major differences in functional connectivity between VGPs and NVGPs. However, seeding from frontal areas (e.g. dorsal anterior cingulate and right middle frontal gyrus) revealed enhanced functional connectivity in VGPs to a distinctive network of areas. A largely overlapping network of areas was observed to be functionally connected to the dorsal anterior cingulate and middle frontral gyrus in VGPs and NVGPs. These included, in addition to the two seed areas, the superior parietal cortex, the supra-marginal gyrus, the SMA, the pre-central gyrus, the insular cortex, and interestingly the anterior prefrontal cortex. Along with the superior parietal cortex, the insula and the precentral gyrus, this anterior prefrontal area showed significantly greater connectivity with the anterior cingulate and the middle frontal gyrus in VGPs than in NVGPs. Higher regulatory cognitive functions have been assigned to the anterior prefrontal cortex (Vincent et al., 2008; Gilbert et al., 2006 for an overview). Koechlin et al. (1999), for example, observed activation in this area when participants were instructed to achieve a main goal that required performing several subgoals along the way. The view that the anterior prefrontal cortex is recruited when participants have to monitor multiple task sets and switch among them is further supported by studies of problem solving (Ramnani and Owen, 2004), decision making (Vincent et al., 2008) or task-set switching (Braver et al., 2003). Whether greater efficiency of this network may account for some of the selective attention enhancement noted in gamers should be a fruitful avenue of research to understand the mechanisms by which attention and executive functions may be enhanced in future studies.

Overall, the results are consistent with the proposal that enhanced attentional skills in VGPs may proceed through an automatization of the resource allocation process, resulting in lesser recruitment of the fronto-parietal network that mediates such attention allocation. The view that automatization of processing results in diminished cortical recruitment is echoed in the literature across domains including those of motor, verbal and perceptual learning as well as learning at a more executive level (Beauchamp et al., 2003; Erickson et al., 2007; Poldrack et al., 2005; Puttemans et al., 2005; Raichle et al., 1994; Shadmehr and Holcomb, 1997; see Clare Kelly and Garavan, 2005 for a review). This is not to say that VGPs would not engage fronto-parietal networks of attention under any circumstance. Rather the working hypothesis is that it would take a much greater burden of task difficulty before they do so. This view is consistent with the behavioral literature on action gamers that documents enhanced performance in tasks that require primarily efficient and flexible allocation of attentional resources (Hubert-Wallander et al., 2010) and indicate that such behavioral enhancement may be mediated through a greater automatization of resource allocation and in turn more efficient suppression of irrelevant or distracting information in VGPs.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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RESEARCH HIGHLIGHTS

- Neural bases of greater attentional control in action videogame players (VGPs)
- Greater suppression of irrelevant information in VGPs
- Efficient distractor suppression may contribute to VGPs superior attention
- Lesser recruitment of areas mediating allocation and control of attention in VGPs
- More automatic and flexible allocation of attentional resources in VGPs

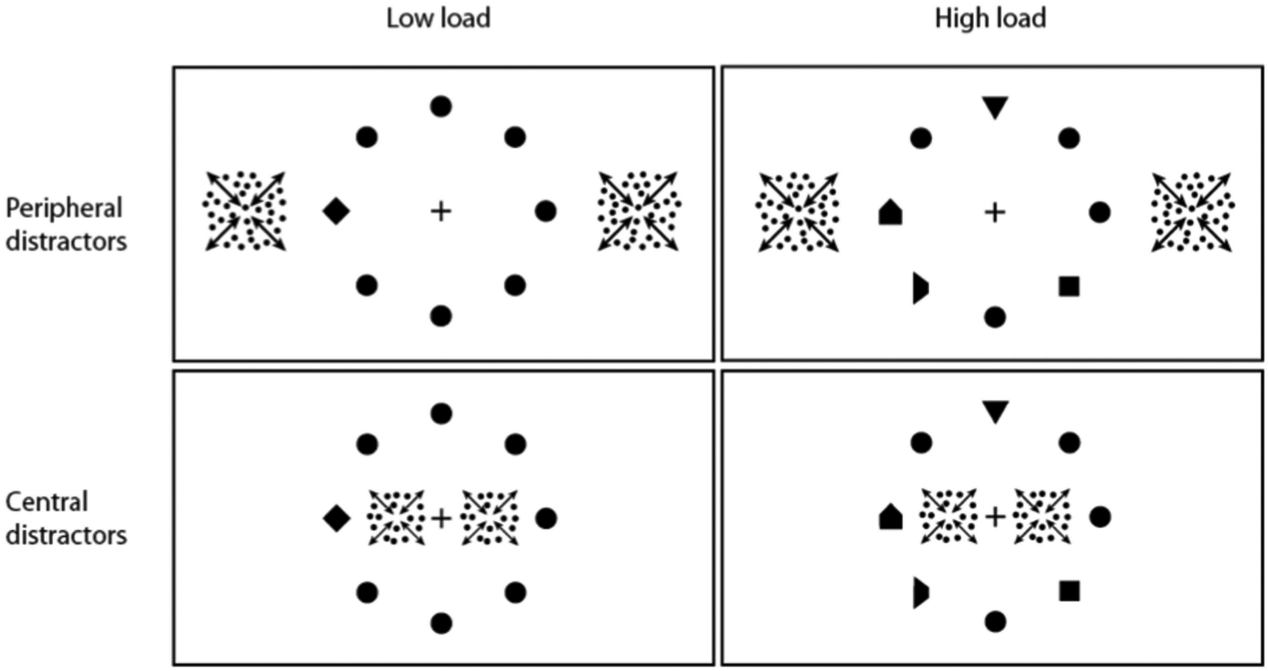

Figure 1.

Example of stimuli. Subjects had to indicate with a button press which of two targets (square or diamond) appeared in the ring of shapes while maintaining fixation on the centre cross. In the low load condition the remaining seven shapes in the annulus were circles and in the high load condition the remaining shapes were a mixture of circles and other shapes (e.g., triangles, trapezoids, houses). The distractors, patches of moving or static dots, were placed on both the left and right, either inside (central distractors) or outside (peripheral distractors) the annulus of shapes.

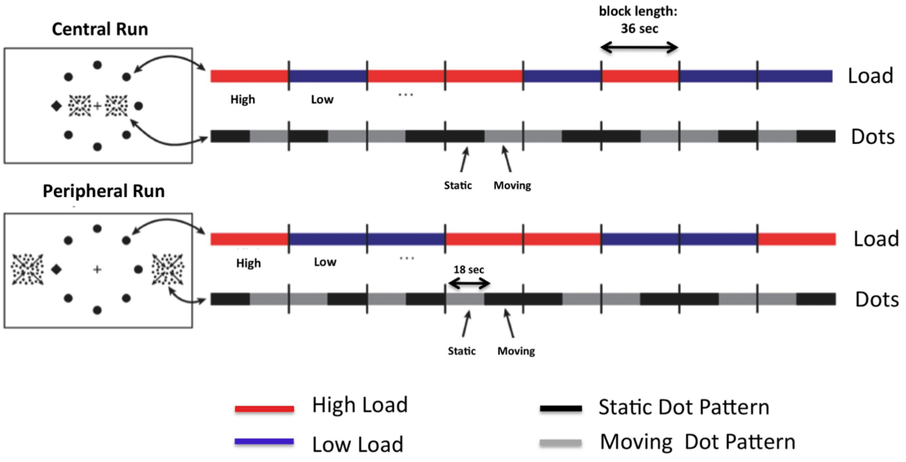

Figure 2.

Sample scanning run. Each scanning run lasted 5 minutes and included eight, 36-second blocks as well as an initial dummy block of 12 seconds (not depicted in the figure). In each run there were four blocks of the two load levels presented in a randomized block order. During each block the distractors (patches of dots) were alternately moving or static in 18-second intervals. The moving or static state of the dots was also randomized within a block. There were eight scanning runs: 4 with central distractors and 4 with peripheral distractors. Run order was randomized across subjects.

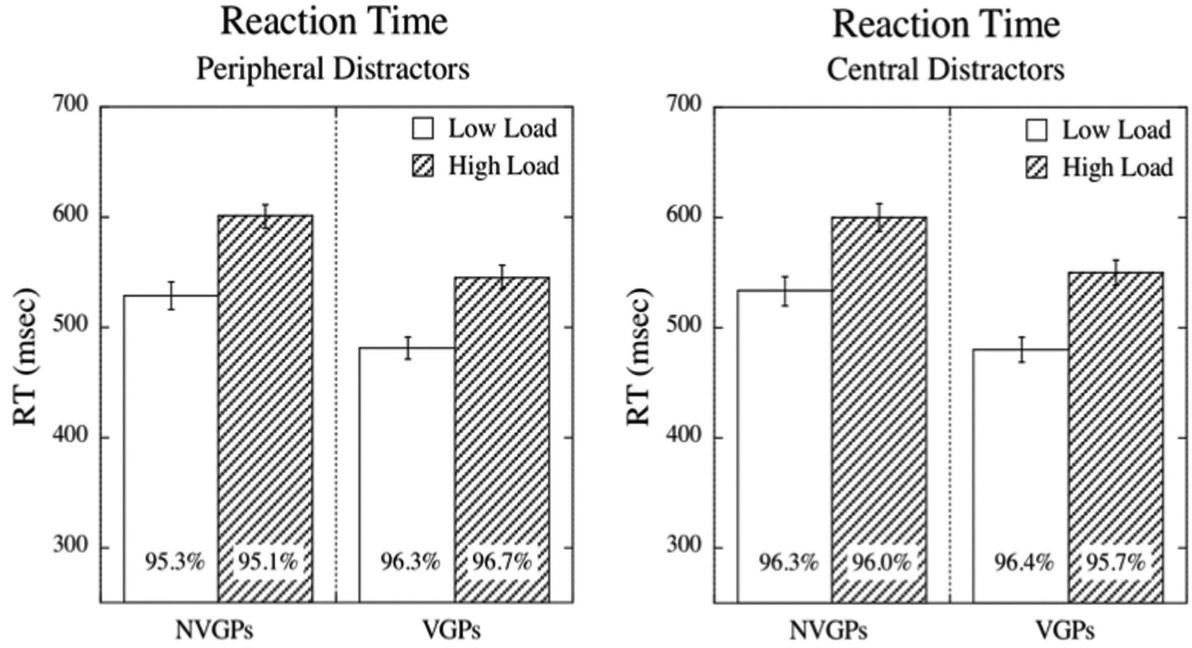

Figure 3.

Behavioral results. RT data plotted by load level with % correct data noted on each bar for the peripheral distractor and the central distractor conditions respectively. There was no significant difference across load level or distractor eccentricity in terms of accuracy (percentages at the base of the histograms), but there was a main effect of load on reaction time. In both experiments, the high load condition produced longer RTs. Importantly, VGPs and NVGPs were comparably slowed down from low to high load, indicating similar increase in difficulty across groups.

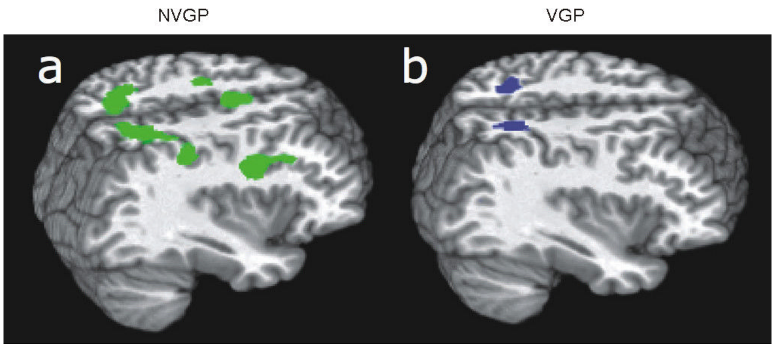

Figure 4.

Pattern of activation as attentional load is increased for NVGPs (a) and for VGPs (b). VGPs show much reduced recruitment of the fronto-parietal network as compared to NVGPs (see p. 11 for statistical parameters).

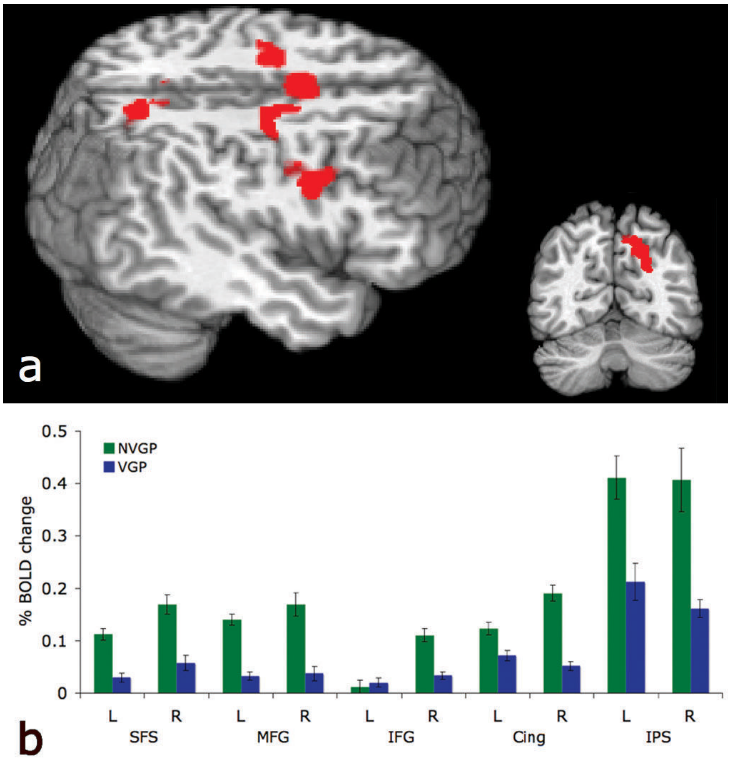

Figure 5.

Greater activation for NVGPs than VGPs was noted as load increased in areas of the fronto-parietal network (a). Difference in percent bold changes between high and low load is plotted for five regions of interest in the attentional network system in NVGPs and in VGPs (b). SFS = Superior Frontal Sulcus, MFG = Middle Frontal Gyrus, IFG = Inferior Frontal Gyrus, Cing = Cingulum, IPS = Intraparietal Sulcus.

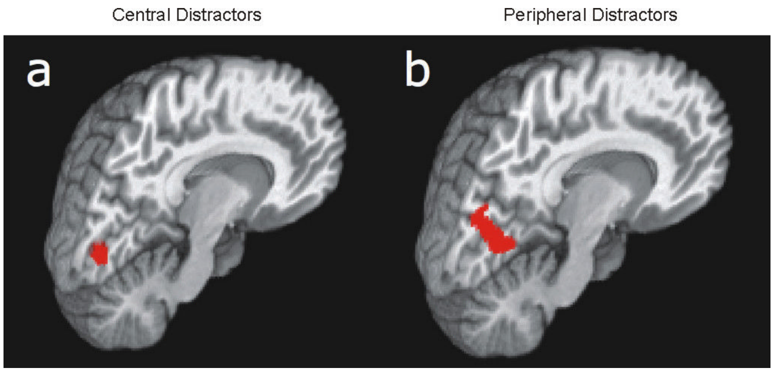

Figure 6.

Pattern of activation for central versus peripheral distractors computed through a conjunction analysis of VGPs and NVGPs activation maps (see p. 12, top paragraph for statistical parameters). Across groups, greater activation for central distractors was noted more posteriorly along the calcarine sulcus, whereas greater activation for peripheral distractors was observed more anteriorly, as predicted by the known retinotopic organization of early visual areas.

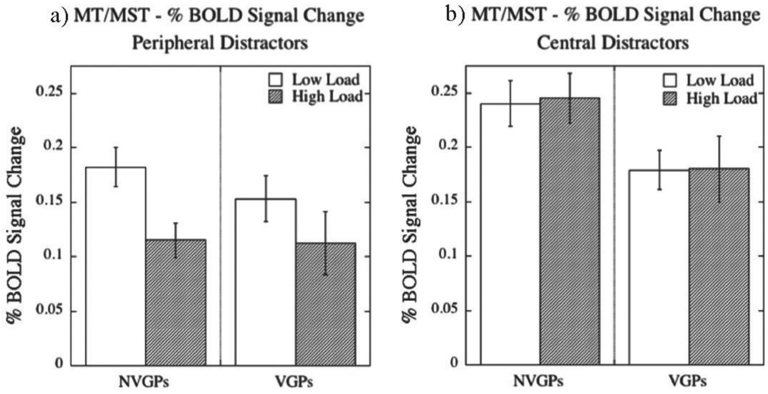

Figure 7.

(a) Percent BOLD signal change in area MT/MST as a function of load and the eccentricity of the irrelevant motion patch. (b) MT/MST ROI for one representative subject.

Table 1

Regions showing greater activation for high load than low load in NVGPs and VGPs.

		NVGP					VGP				
ROI		**X**	**Y**	**Z**	**Max Z**	**Volume (mm^3)**	**X**	**Y**	**Z**	**Max Z**	**Volume (mm^3)**
Frontal											
SFS	**L**	-27	-7	55	4.60	2840					
	R										
Middle Frontal	**L**										
	R	48	8	29	4.64	5872					
SMA	**L**	-3	7	51	4.94	2288					
	R	6	6	54	4.79	2440					
Dorsal Anterior Cingulate	**L**	-6	13	38	3.71	352					
	R	8	14	38	4.32	952					
Parietal											
Superior Parietal/Dorsal IPS	**L**	-23	-65	51	5.27	7248	-22	-61	51	4.41	4256
	R	24	-64	55	4.87	5128	24	-61	54	4.37	2024
IPS	**L**	-35	-51	45	5.24	6032	-30	-54	48	4.16	1744
	R	36	-50	47	4.96	3848	28	-57	48	4.27	776
Cuneus/Precuneus	**L**	-12	-68	56	4.07	1152	-14	-61	50	3.11	48
	R	16	-70	49	4.01	1024	18	-65	45	3.39	72
Occipital											
Superior Occipital	**L**	-22	-76	34	5.04	1888	-24	-73	32	4.32	448
	R	26	- 71	37	4.98	2976	26	-66	42	4.01	648
Middle Occipital	**L**	-28	-76	23	5.55	4432	-31	-78	19	5.18	5288
	R	32	-77	24	5.14	3464	34	-77	21	4.38	1784
Inferior Occipital/Middle Temporal	**L**	-45	-65	-10	4.71	3512	-42	-72	10	4.90	3568
	R										
Cerebellum											
Cerebellum	**L**						5	-76	25	4.09	776
	R						83	-76	25	4.48	1592

SFS: Superior Frontal Sulcus, SMA: Supplementary Motor Area, IPS: Intraparietal Sulcus. ‘L’ and ‘R’ stand for Left and Right respectively. For this and all other tables, coordinates are given in the Montreal Neurological Institute stereotaxic space.

Table 2

Between-group analyses revealed overall greater activation in NVGPs than in VGPs for the high versus low load contrast.

		NVGP > VGP					VGP > NVGP				
ROI		**X**	**Y**	**Z**	**Max Z**	**Vol. (mm^3)**	**X**	**Y**	**Z**	**Max Z**	**Vol. (mm^3)**
Frontal											
SFS	**L**	-27	-8	55	4.26	2776					
	R	33	-10	57	3.08	1904					
Middle Frontal	**L**										
	R	48	7	30	3.74	4904					
IFG/Insula	**L**										
	R	41	20	8	3.44	1024					
Frontal pole	**L**										
	R	42	37	14	2.74	736					
SMA	**L**	-4	4	51	4.09	1800					
	R	6	3	55	3.54	2360					
Dorsal Anterior Cingulate	**L**	-6	13	38	3.53	728					
	R	5	8	43	3.21	224					
Parietal											
Superior Parietal/Dorsal IPS	**L**										
	R	10	-72	52	2.86	864					
Cuneus/Precuneus	**L**	-9	-57	50	2.03	16					
	R	14	-69	50	3.08	712					
Occipital											
Superior Occipital	**L**										
	R	25	-73	38	2.91	1528					
Middle Occipital	**L**										
	R	29	-76	28	2.93	344					
Subcortical											
Putamen/Insula	**L**										
	R	30	13	4	2.93	192					