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Author for correspondence:
Greg L. West
e-mail: gregory.west@umontreal.ca

Habitual action video game playing is associated with caudate nucleus-dependent navigational strategies

Greg L. West[1], Brandi Lee Drisdelle[1], Kyoko Konishi[2], Jonathan Jackson[1], Pierre Jolicoeur[1] and Veronique D. Bohbot[2]

[1]Université de Montréal, Montréal, Québec, Canada H3C 3J7
[2]Douglas Hospital Research Centre, Department of Psychiatry, McGill University, Verdun, Québec, Canada H4H 1R3

The habitual playing of video games is associated with increased grey matter and activity in the striatum. Studies in humans and rodents have shown an inverse relationship between grey matter in the striatum and hippocampus. We investigated whether action video game playing is also associated with increased use of response learning strategies during navigation, known to be dependent on the caudate nucleus of the striatum, when presented in a dual solution task. We tested 26 action video game players (actionVGPs) and 33 non-action video game players (nonVGPs) on the 4-on-8 virtual maze and a visual attention event-related potential (ERP) task, which elicits a robust N-2-posterior-controlateral (N2pc) component. We found that actionVGPs had a significantly higher likelihood of using a response learning strategy (80.76%) compared to nonVGPs (42.42%). Consistent with previous evidence, actionVGPs and nonVGPs differed in the way they deployed visual attention to central and peripheral targets as observed in the elicited N2pc component during an ERP visual attention task. Increased use of the response strategy in actionVGPs is consistent with previously observed increases in striatal volume in video game players (VGPs). Using response strategies is associated with decreased grey matter in the hippocampus. Previous studies have shown that decreased volume in the hippocampus precedes the onset of many neurological and psychiatric disorders. If actionVGPs have lower grey matter in the hippocampus, as response learners normally do, then these individuals could be at increased risk of developing neurological and psychiatric disorders during their lifetime.

1. Introduction

People now spend a collective 3 billion hours per week playing video games [1], and it is estimated that the average young person will now spend nearly 10 000 h gaming by the time they are 21 [2]. As video game playing becomes more and more ubiquitous, it is increasingly important to better understand the impact of this intense exposure on cognitive and neural functioning. Currently, the literature reports many favourable cognitive improvements associated with action video game playing (e.g. first- or third-person shooting games) [3–6]. For example, action video game players (actionVGPs) have been shown to have faster response times when detecting visual targets [7] and have a larger useful field of view suitable for accurate peripheral target detection [3,6,8], when compared with non-video game players (nonVGPs). More recently, electrophysiological measures have demonstrated differences in attentional orienting and selection, as measured by the P3 component, which is an index of attentional allocation, where actionVGPs were found to elicit a larger P3 amplitude in response to targets compared with nonVGPs [9,10].

Video game playing is also associated with greater volume and activity in the striatum [11,12]. The striatum is part of the brain's reward pathway and has been implicated in the formation of habits [13] and procedural memory (e.g. riding a bicycle) [14]. The striatum also plays a role in stimulus–response

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learning, which involves making a particular action when faced with an environmental trigger that acts as a stimulus [15,16]. Increased striatal volume and activity are also associated with decreased volume and activity in the hippocampus [17,18]. The striatum, which is significantly larger in video game players (VGPs) [11,12], shares an inverse relationship with the hippocampus [16,19]. In contrast to the striatum's critical role in response learning and memory, and habit formation by making rigid stimulus–response associations [15,20–23], the hippocampus is critical for allocentric spatial learning and memory, and the formation of a cognitive map (i.e. learning and memory for the relationships between environmental landmarks) irrespective of the position of the observer [24–27]. When navigating, distinct strategies rely on either the hippocampus or the striatum in both humans [28] and rodents [20,29]. Specifically, the *spatial strategy* involves building relationships between landmarks in an environment to create a cognitive map, and relies on the hippocampus [25]. The *response strategy*, by contrast, entails learning a series of movements (e.g. left and right turns) from given positions that act as stimuli (e.g. post office) and relies on the striatum [29]. When these series of movements are learned, they are known to become part of the procedural memory system.

There is a large amount of evidence that supports the hypothesis that the use of spatial strategies is associated with increased hippocampal grey matter and activity, while the use of response strategies is associated with increased grey matter and activity in the striatum [16,18,19,30–32]. For example, in a dual solution task, which allows the use of both spatial and response navigational strategies, studies in rodents have shown increased basal levels of acetylcholine in the hippocampus prior to the spontaneous use of the spatial strategy. In comparison, rodents that spontaneously used a response strategy in the dual solution task had increased basal levels of acetylcholine in the striatum [33]. Corroborating evidence from the rodent literature has been reported by Lerch *et al.* [16], who trained mice on the Morris Water Maze to find a target platform by either using distinct visual landmarks (spatial training) or a single 'beacon' stimulus that directly indicated the location of the platform (response training). They found that mice in the spatial training group showed increased hippocampal volume after training, whereas mice in the response group instead showed increased striatal volume.

In humans, Schinazi *et al.* [34] found that right posterior hippocampal volume positively correlated with people's ability to identify the relative locations of buildings on a university campus while blindfolded (i.e. relying on a cognitive map). Conversely, accuracy on this task was negatively correlated with both left and right caudate nucleus volume. Further, Head & Isom [35] found that wayfinding using landmarks (spatial learning) and route memorizing (response learning) performance were, respectively, related to baseline hippocampal and caudate nucleus volumes.

In addition to these findings, it has been shown that young adults who navigated using a spatial strategy showed greater fMRI activity [18] and grey matter [19] in the hippocampus. Conversely, young adults who navigated using response strategies showed increased fMRI activity [18] and grey matter [19] in the caudate nucleus of the striatum. These findings were also replicated in older adults such that those using a spatial strategy had more fMRI activity [36] and grey matter [32] in the hippocampus than those using the response strategy. These results are consistent with those of Poldrack *et al.* [37], where

a declarative and non-declarative classification learning task was used in the scanner to show that medial temporal lobe activity occurs early in learning, whereas caudate nucleus activity occurs in later phases when subjects make faster classification responses. Together, these results provide convincing evidence that the use of response-based navigation strategies are associated with increased development and activation of the striatum and a reduction of hippocampal volume and activity across the lifespan [38].

As with the response strategy, video game playing is also associated with increased development and activation of the striatum. For example, when recording functional brain activity during the Monetary Incentive Delay task, researchers found that adolescents who engaged in increased video game playing had increased activity in the left ventral striatum when given feedback stating a loss of income [12]. Dopamine release in the ventral striatum was also shown to be associated with increased video game performance [39]. Another study reported both increased visual–cognitive performance (increased visual working memory accuracy) and increased striatum volume in the same cohort of actionVGPs [11]. Further linking video game playing and response strategies, Kuhn & Gallinat [40] showed a negative correlation between playing certain types of action video games (e.g. Ego shooters with role-playing game design elements, such as Borderlands, Fallout 3 and Dead Island) and volume of the entorhinal cortex, a region highly interconnected with the hippocampus. Conversely, the study reported a positive correlation between time playing certain logic and puzzle video games (e.g. Tetris; Professor Layton) and platformer games (e.g. Super Mario 64) and volume of the entorhinal cortex. Together, these data suggest that experience specifically with certain action video games is associated with decreased entorhinal cortex volume and that video game playing increased volume and activation of the ventral and dorsal regions of the striatum. Furthermore, these data also suggest that cognitive performance enhancements associated with actionVGPs may be, at least in part, related to procedural learning and error/reward feedback mediated by the striatum.

In addition to promoting habit formation and task perceptual–motor task efficiency, response learning is also related to various forms of impulsivity and sensation-seeking behaviours and has been shown to be associated with cue sensitivity mediated within the striatum [41]. Further, cue sensitivity and substance abuse are both associated with increased striatal grey matter [42]. Fitting with this notion, recent evidence from Bohbot *et al.* [43] has shown that response learners as determined by a virtual dual solution task, the 4-on-8 Virtual Maze (4/8VM), show greater levels of substance abuse, such as higher lifetime use of tobacco, greater cannabis and double the alcohol use, relative to spatial learners. In a separate study, it was also demonstrated that, in people who engage in higher levels of video game playing, there was a significant correlation between time playing video games and alcohol use, as well as Internet addiction [40]. As actionVGPs have larger striatal volume and playing video games is associated with increased striatal activity and engagement in other sensation-seeking activities related to response learning, we predicted that actionVGPs would be more likely to spontaneously adopt a response strategy when navigating compared with nonVGPs.

To investigate the relationship between actionVGP experience and navigation strategies, we tested a group of healthy young adults with no substance use disorders on a virtual

navigation task that can be solved using either a spatial or a response learning strategy and assessed their video game playing habits. To further qualify our results, we also tested actionVGPs and nonVGPs on a separate visual attention event-related potential (ERP) task. This allowed us to compare our cohort of actionVGPs and nonVGPs in the context of previous reports citing differences in visual attention processes between these two groups, and further explore the neural mechanisms that drive these differences (e.g.[3–6,8,9]). As visual attention differences between actionVGPs and nonVGPs have been the literature's primary focus until this point, we felt that the inclusion of a visual attention task was important to ensure that our current sample did not significantly differ from those of previous studies that focused on differences in visual attention and short-term memory.

The target detection paradigm we chose to use was designed to show no behavioural differences (e.g. accuracy and reaction times); however, it elicits a robust ERP component, the N2pc (N-2-posterior-controlateral), a lateralized component thought to be modulated by target selection and distractor inhibition in the visual domain [44]. The N2pc is defined as an increased negativity at posterior electrode sites contralateral to the position of an attended visual target, relative to ipsilateral electrodes, typically occurs about 200–260 ms after target onset and is thought to index covert visuo-spatial attention [45]. We sought to detect existing between-group differences by using the N2pc to measure the moment-by-moment deployment of attention during target detection [46,47].

We had two central hypotheses. Specific to action video game playing and navigation strategies, we hypothesized that, owing to higher striatal activation and volume associated with video game playing [11,12], actionVGPs would spontaneously adopt a response strategy to a greater proportion while navigating compared with nonVGPs. We also hypothesized that actionVGPs would show results similar to previous cohorts in visual attention processing [3,5,6,8–10] and display differences in the electrophysiological activity associated with the deployment of selective attention.

2. Material and methods

(a) Participants

Fifty-nine healthy young adult participants (13 female) who were an average of 24.15 ($\pm$3.77) years of age were screened into the study. An extensive phone questionnaire that included various components such as demographic information, vision, motion sickness, medical history, cardiovascular diseases, neurological disorders, medical conditions, psychiatric disorders, substance abuse, general medication, family history and handedness was administered to potential participants. Participants were excluded from the study if they had a history of neurological or psychiatric disorders, including depression and anxiety. Participants were also excluded if they have a history of substance abuse (recreational drugs, alcohol consumption that exceeds 10 alcoholic beverages per week, and cigarette use that exceeds 10 cigarettes per day) or a history of medical conditions that include hormone disorders, cancer, cardiovascular disease and diabetes. Owing to the use of virtual reality, if participants experience motion sickness or are colour-blind then they were also excluded from the study. Participants for both groups were recruited with the same methods and from the same population through campus advertisements and word of mouth. Informed consent was obtained in conformity with the local ethics committee requirements.

To classify participants as actionVGPs or nonVGPs, the same criteria were used as have been used in past studies examining differences between these groups [3,5,6,48,49]. Participants were placed into the actionVGP or nonVGP group on the basis of a questionnaire about their action video game playing habits. To be considered an actionVGP, a participant needed to report a minimum of 6 h a week of *action* video game usage during the previous six months. An abridged list of the action video games participants reported playing includes first-person shooters such as Fallout 3, Borderlands 2, Counterstrike and Call of Duty and third-person shooter/adventure games such as Grand Theft Auto V, Tomb Raider (2012) and Gears of War. The criterion to be considered a nonVGP was a report of little or no action game playing for at least the previous six months [3,5,6,48,49]. This resulted in 26 participants (four female) being placed into the actionVGP group and 33 participants (nine female) being placed into the nonVGP group. The actionVGP group had an average age of 23.88 ($\pm$3.94) and reported playing an average of 17.9 ($\pm$10.44) hours per week during the past six months, while the nonVGP group had an average age of 24.36 ($\pm$3.68) and played 0 h per week of action games during this time.

(b) Tasks

(i) 4-on-8 virtual maze

The 4/8VM is a virtual reality task that was created using programming software from a commercially available computer game (Unreal Tournament; Epic Games, Raleigh, NC, USA; figure 1). The 4/8VM is a behavioural task that provides an indirect measure of hippocampus and striatum volume and function during navigation [18,19]. The virtual reality task consists of an eight arm radial maze situated in an enriched environment. The environment contains both distal and proximal landmarks: two trees, a rock and mountains.

The task comprises several trials, which consisted of two parts. In Part 1, a set of barriers block four of the eight arms. The participant is instructed to pick up objects located at the end of the four open arms. Additionally, the participant is told to remember which pathways they visited because, in Part 2, all of the pathways are accessible and the objects that they must retrieve are situated in the pathways that were previously inaccessible. Participants always begin the task facing the same direction. All landmarks are visible during Part 1 and Part 2 of a trial. Participants are administered a minimum of three trials. If participants do not reach criterion within the first three trials, a maximum of five extra trials are given until participants reach criterion. The criterion on the 4/8VM is no errors on part 2 for a single trial. This criterion ensures that all participants have learned the task.

Once this criterion is reached, a probe trial is administered. During Part 1 of the probe trial, the participants still collect the objects from the open arms and all landmarks are present, however, in Part 2, when all of the arms are accessible, a wall is erected around the maze so that the participants cannot see the environment and all landmarks are removed. Participants can solve the 4/8VM using either of two strategies. The first, a 'spatial' strategy, depends on learning the relationship between the target objects and the landmarks in the environment. For example, a participant would remember the position of an object relative to the trees and the mountain. The second is a 'response' strategy, where a counting or patterning system is used to remember the sequence of rewarded arms. The probe trial does not disturb the performance of participants using a response strategy as their sequence does not depend on the environmental landmarks. Conversely, participants using a spatial strategy have difficulty on Part 2 of the probe trial because they require the landmarks to properly retrieve the objects [18,43]. At the end of the task, participants were asked to report how they knew which pathways contained objects and which were empty in the Part 2 trials.
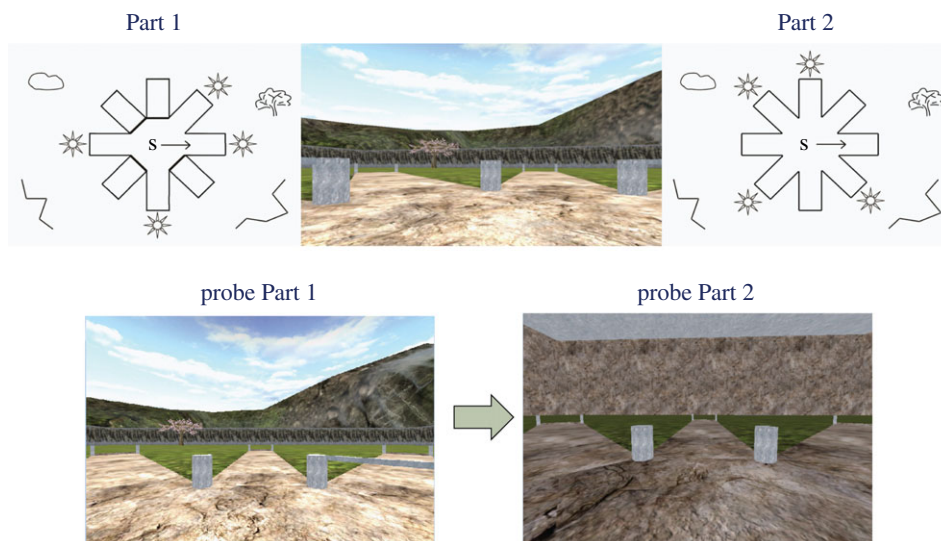
Part 1   Part 2

probe Part 1   probe Part 2

Figure 1. A view of the virtual environment used in the 4-on-8 virtual maze. Note the tree and mountains that form part of the landscape. A rock and meadow were also present in the virtual environment. In Part 1, participants retrieve 4 objects at the end of 4 available paths out of 8 that extend from a central platform. In Part 2, participants remember which pathways they have already visited and avoid these in order to find the remaining objects. Probe: After acquisition, in Part 2, a wall is erected around the radial maze after learning, blocking the participants' view of landmarks in the environment. (Online version in colour.)
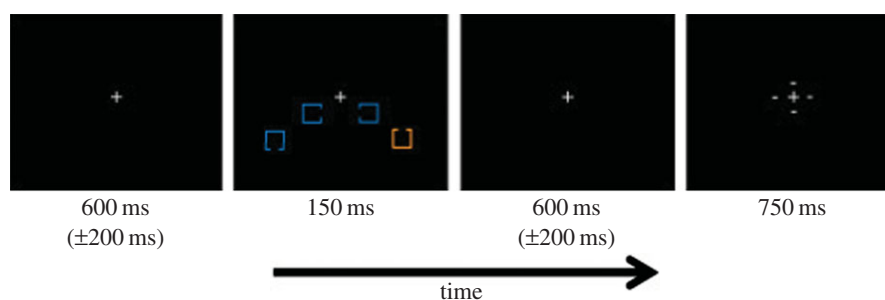

| 600 ms | 150 ms | 600 ms | 750 ms |
| (±200 ms) | | (±200 ms) | |

time

Figure 2. Trial sequence of the visual search paradigm used for ERPs recordings. (Online version in colour.)

Using a specific objective questioning procedure, we asked about their initial method of navigation during the very first trial. This has previously been shown to be a reliable measure of initial spontaneous navigation strategy. Based on their description, participants were categorized as using either a spatial strategy or a response strategy [17–19,38,43,50]. On the first trial, if participants reported using two or more landmarks at the same time to remember the location of the objects, and avoided reporting using a sequence from a single starting point, they were categorized as using a spatial strategy. If the participant reported using a sequence or pattern on the first trial, counting from a single starting point to remember the locations of the objects, they were categorized as using a response strategy. The experimenter who administered the virtual reality task was blind to the video game playing status of each participant.

(ii) N2pc visual attention task

To investigate whether our cohort of actionVGPs and nonVGPs differed in visual attentional processes as previously reported (e.g. [3,5,6,48,49]), participants completed a visual spatial attention task while an electroencephalogram (EEG) was recorded (see Brisson & Jolicoeur [46] for full method details). Participants completed 768 experimental trials (figure 2; [44,46]). They were asked to fixate on a point at the centre of the screen that remained on screen for the remainder of the trial. After 600 ms (±200 ms), a 150 ms bilateral visual display appeared. The display consisted of four coloured squares (two on each side of fixation in the lower quadrants), each with a gap in one of their four sides. When present, the target stimulus was orange (frequent colour) or green (rare colour) among blue distractors. All colours were

adjusted to be equiluminant using a chromometre (Minolta CS100) to control for low-level sensory responses. In addition to the target-present trials, 128 no go trials were included where no target appeared and participants had to inhibit their response. Target colour squares were presented with equal probability to all four possible positions ($p = 0.25$ all locations). The probability of each gap location (top, bottom, left and right) was equal ($p = 0.25$). Both a frequent and an infrequent target condition were also created. When the target square had a gap on its left, right or bottom side (frequent condition, $p = 0.75$) participants responded by pressing the 'V' key on a keyboard, whereas they pressed the 'N' key only when the target square had a gap on the top side (infrequent condition, $p = 0.25$). After a 600 ms (±200 ms) delay, accuracy feedback was given by displaying either four minus or four plus signs around the fixation cross for 750 ms.

(c) Electrophysiological recordings and data analysis

The EEG was recorded from 64 active Ag/AgCl electrodes (Biosemi Active Two system) with positions corresponding to the International 10–10 System [51] mounted on an elastic cap, as well as five external electrodes. The signal was re-referenced offline to the average of the left and right mastoids. The horizontal electrooculogram (HEOG), recorded as the voltage difference between two electrodes placed lateral to the external canthi, was used to measure horizontal eye movements. The vertical electrooculogram (VEOG), recorded as the voltage difference between two electrodes placed below the left eye and Fp1 (above the left eye), was used to detect eye blinks. The EEG and EOG were digitized at 512 Hz. EEG data were high-pass filtered at 0.1 Hz, low-pass filtered at 30 Hz and

averaged offline. EOG data were high-pass filtered at 0.1 Hz, low-pass filtered at 10 Hz and averaged offline. Trials with artefacts (± 100 mV from baseline) and horizontal eye movements (saccades; HEOG >35 mV over 300 ms) were excluded from final analysis. Eye blinks (VEOG >50 mV over 150 ms) were removed from the data of all participants using the independent component analysis technique. When more than 50% of the data were removed from a condition following artefacts and ocular movement rejection, subjects were discarded from further analyses. This resulted in two actionVGPs and six nonVGPs being removed from the EEG analysis, giving a final total of 24 actionVGPs and 27 nonVGPs being kept for final analysis.

EEG epochs of 1000 ms (including 200 ms pre-stimulus onset) were averaged after artefact rejection, separately for trials with a left visual field target and trials with a right visual field target and baseline-corrected based on the 200 ms pre-target period. To isolate the N2pc component from non-lateralized perceptual processes, averaged ipsilateral waveforms (activity over the left hemisphere when the target stimulus was presented in the left visual field and activity over the right hemisphere when the target was presented in the right visual field) is subtracted from the averaged contralateral waveforms (activity over left hemisphere to a right visual field target and activity over right hemisphere to a left visual field target). The remaining activity is then subsequently averaged (i.e. [contralateral activity–ipsilateral activity]/2). N2pc measurements (mean amplitude recorded during the 200–260 ms post-stimulus onset) were then made on the contralateral minus ipsilateral difference waveforms. Separate averaged ERP waveforms were computed for near and far target conditions and were compared between actionVGPs and nonVPG groups.

3. Results

(a) 4-on-8 virtual maze

Twenty-six actionVGPs and 33 nonVGPs were tested on the 4/8VM. No group difference was found on the number of trials needed to reach criterion ($p > 0.8$). Spontaneous navigational strategy use during the first trail was assessed for each participant according to verbal reports. Importantly, raters were blind to the participants' video game playing status, as was the experimenter administering the 4/8VM. Two raters evaluated the strategy used by each participant and classified them as initially using either a response or spatial strategy to complete the 4/8VM. There was a 91.5% inter-rater concordance for participants in both groups. When there was discrepancy between both raters' evaluation, a third rater's evaluation was employed.

As can be seen in figure 3, results from the 4/8VM show that a higher proportion of actionVGPs were found to spontaneously use a response strategy (80.76%) compared to nonVGPs, where 57.58% used a spatial strategy and 42.42% used a response strategy. This difference in spontaneous strategy use between both groups was confirmed to be significant using a χ^2-test: $\chi^2_{(58)} = 8.86$, $p < 0.005$. As observed in previous studies (e.g. [18,50]), spatial learners made significantly more probe errors (mean = 1.5) compared to response learners (mean = 0.94; $t = 1.78$, $p < 0.05$, one-tailed).

(b) N2pc visual attention task
(i) Behavioural and electrophysiological results
Twenty-four actionVGPs and 27 nonVGPs were kept for final analysis in the N2pc visuo-spatial attention task. Reaction times and accuracy scores were submitted to a 2 (VGP Group: actionVGP; nonVGP) × 2 (Target Distance: near
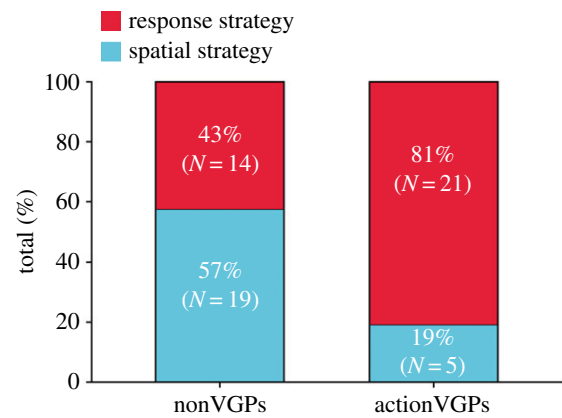

Figure 3. A higher proportion actionVGPs spontaneously used a response strategy compared to nonVGPs. (Online version in colour.)

target; far target) mixed factorial ANOVA. Small, but reliable main effects of target distance were found for both reaction times (near target = 638 ms; far target = 678 ms; $F_{1,49} = 128.02$; $p < 0.01$; $\eta^2 = 0.723$) and accuracy (near target = 97% correct; far target = 96% correct; $F_{1,49} = 22.01$; $p < 0.01$; $\eta^2 = 0.310$). As expected, there were no group differences in reaction time (actionVGPs = 657 ms; nonVGPs = 659 ms; $p > 0.05$) nor accuracy scores (actionVGPs = 96% correct; nonVGP = 97% correct; $p > 0.05$).

The grand averaged waveforms of both groups in each distance condition can be seen in figure 4. Mean N2pc amplitudes recorded at PO7/PO8 electrode sites were submitted to a 2 (VGP Group: actionVGP; nonVGP) × 2 (Target Distance: near target; far target) mixed factorial ANOVA. This revealed a main effect of target distance ($F_{1,49} = 15.19$; $p < 0.001$; $\eta^2 = 0.24$). A planned paired t-test revealed that, overall, the N2pc amplitude for targets near fixation was larger (-1.34 µV) than for targets further from fixation (-0.63 µV; $t_{50} = 3.80$, $p < 0.001$). The ANOVA also revealed a significant VGP Group × Target Distance interaction ($F_{1,49} = 6.38$; $p < 0.01$; $\eta^2 = 0.14$). Planned independent t-tests were conducted to compare both groups' N2pc amplitudes elicited by target distance from fixation (near or far). This revealed a significant difference for targets near fixation, where nonVGPs produced a larger N2pc amplitude (-1.67 µV) compared with actionVGPs (-0.98 µV; $t_{49} = 2.21$; $p < 0.05$). The opposite pattern was observed for targets far from fixation, where nonVGPs produced a smaller N2pc amplitude (-0.49 µV) compared to actionVGPs (-0.80 µV), however, this difference was non-significant ($t < 1$). To further qualify this interaction, paired t-tests were conducted comparing within-group differences between N2pc amplitudes for targets near and far from fixation. This revealed that N2pc amplitudes produced by near and far targets differed significantly in the nonVGP group (-1.67 versus -0.49 µV; $t = 4.39$; $p < 0.001$) but not in the actionVGP group (-0.98 versus -0.80 µV; $t < 1$).

4. Discussion

This study investigated whether action video game experience was associated with different spontaneous navigational strategies in healthy young adults. Using a dual solution task in the virtual maze (4/8VM), our results indicated that 80% of actionVGPs spontaneously used a response strategy, which earlier studies indicate are striatum dependent [16,18,19], when navigating in a virtual maze. Conversely, nonVGPs
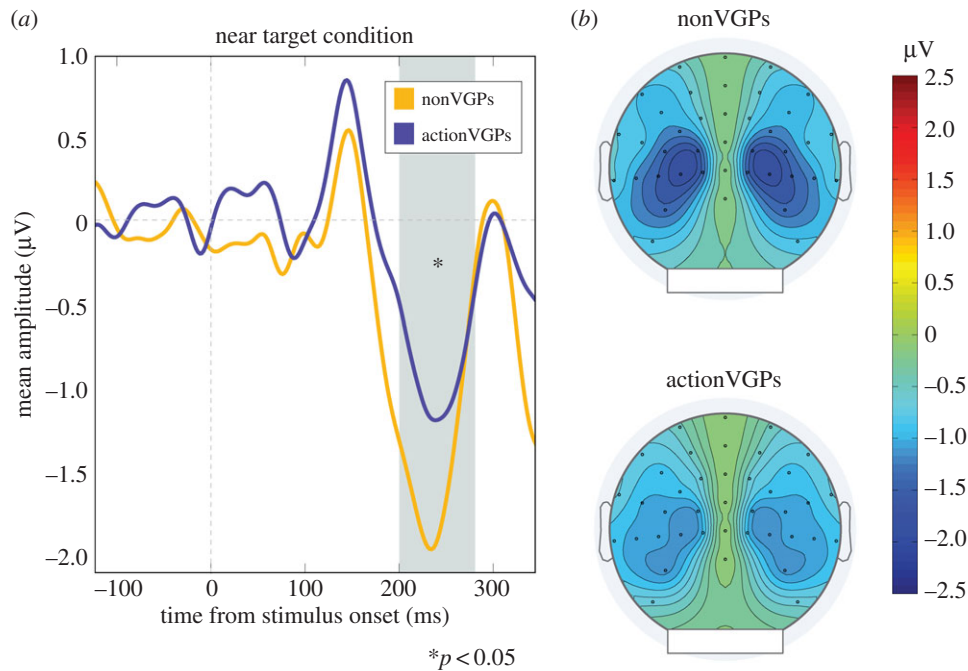
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Figure 4. (a) Grand average N2pc component recorded at PO7/PO8 for the near target condition. NonVGPs produced a larger N2pc negativity (approx. 200–260 ms post-stimulus) in response to near targets, compared with actionVGPs. No significant between-group difference was found in the far target condition. (b) Scalp topographies at peak N2pc amplitude for nonVGPs and actionVGPs. Both nonVGPs and actionVGPs show negativity near electrode sites PO7 and PO8 that represents the N2pc activity. As can be observed in the nonVGP distribution, there is a relative increase in negativity in the scalp distribution that underlies the N2pc compared with the actionVGP group. (Online version in colour.)

showed the proportion of strategy adoption typically observed in normal healthy young adults, with nearly half spontaneously using a response strategy and half spontaneously using a spatial strategy, which previous studies indicate are hippocampus-dependent. Consistent with previous results, we observed that people who spontaneously used a spatial strategy made significantly more probe errors than those who used a response strategy. We did not hypothesize a difference in probe scores taken at the end of the experiment between actionVGP and nonVGPs, because there is a mix of both spatial and response learners in the nonVGP group.

Importantly, although the 4/8VM is an indirect behavioural measure, previous reports using this virtual reality task have shown that young adults who spontaneously solved the maze using response strategies have increased striatal grey matter and fMRI activity, while people who used spatial strategies have increased grey matter and fMRI activity in the hippocampus [18,19]. Our current results, based on the 4/8VM, that actionVGPs are significantly more likely to spontaneously adopt navigation strategies associated with increased caudate nucleus volume are consistent with previous evidence showing that video game playing is associated with more grey matter volume and activity in both the dorsal and ventral striatum [11,12,39,40].

Consistent with previous behavioural and electrophysiological studies, our cohort of actionVGPs and nonVGPs displayed differences in the engagement and processing of selected target stimuli. An interaction between group and target location was observed for the amplitude of the N2pc, where nonVGPs showed a significantly larger N2pc in the near condition. This pattern was reversed in the far condition, where actionVGPs produced a larger N2pc. Within-group comparisons revealed a significant difference between near and far conditions only in the nonVGP group; no significant difference in the actionVGP group was observed.

Previous reports comparing ERPs of actionVGPs and NVGPs examined the P3 component, which is thought to correlate with the amount of attentional resources allocated to a target and occurs later in the processing stream (approx. 300 ms after stimulus onset) [52]. Similar to our current task, previous studies required participants to detect targets while suppressing distracting peripheral information [9,10]. In these reports, ERPs time-locked to targets elicited by the actionVGP group generated a significantly larger P3 component compared with nonVGPs [9,10], which is indicative of increased perceptual discrimination and ability to suppress distracting non-target stimuli [53].

With respect to our current ERP results, there are two possible interpretations for the observed patterns that are supported by previous findings. First, it is possible that a similar interpretation to the fMRI results of Bavelier et al. [54] can be made. In this study, participants performed a high-load/low-load target detection task in a scanner. The results revealed that actionVGPs recruited fewer fronto-parietal structures to complete the task [54]. This reduced level of activity in the fronto-parietal network is consistent with the proposal that actionVGPs show increased automatization and efficiency during procedural task learning [5,55,56]. In a similar manner, it is possible that actionVGPs also required fewer attentional resources to resolve our current target detection task, thus producing a reduced N2pc in the near (i.e. easier) condition. By contrast, nonVGPs needed to deploy more attention to targets to maintain the same level of accuracy, thus producing a larger N2pc. Another possible interpretation is that actionVGPs were able to more efficiently deploy attention to all target locations (near and far) on both the left and right sides of the display [3,6,8]. When attention is more evenly deployed to both left and right hemifields, the amplitude of the N2pc is reduced owing to the nature of its computation (activity ipsilateral

to target subtracted from activity contralateral to target). Both of these possible explanations, nonetheless, support previous reports that actionVGPs more efficiently deploy attention to resolve target detection tasks compared to nonVGPs.

When examining the spatial memory and visual attention data together, our data suggest that people who play action video games benefit from a more efficient perceptual system but do not show an advantage in hippocampal function. It is also possible that a more general relationship between response strategies and visual attention performance exists. Erickson *et al.* [57] 's findings demonstrating that striatal volume predicted performance on a video game supports this notion. This finding together with our current data presents a possible alternative hypothesis regarding spatial memory strategies and visual attention. It is possible that our current between-group visual attention results are, in fact, driven by the large difference in response learners in each group. More research specifically examining the effect of navigation strategies on visual attention without the confounding factor of video game experience is needed to further address this question.

Why do we observe differences in navigation strategies and neural responses in the striatum between actionVGPs and nonVGPS? We speculate, drawing on earlier research, that these differences have their basis in anatomically distinct and dissociable learning systems that are differentially engaged by actionVGPs. For example, it is possible that regularly playing action video games engages the striatal reward system in a similar manner to other rewarding activities. Specifically, dopamine release has been measured in the caudate nucleus of the striatum of participants not only in response to behaviours considered to be maladaptive, such as exposure to amphetamines [58], cocaine [59] and alcohol [60], but also to other types of rewards that are more common, such as chocolate [61]. Related to this, adolescents engaging in 9 h of video games per week or more were shown to have a significantly larger striatum (including the nucleus accumbens and caudate nucleus; [12]). In another study, the volume of the entorhinal cortex, which sends afferent projections to the hippocampus, negatively correlated with playing action-RPG ego shooter video games [40]. It should be noted that this same relationship was not observed for ego-shooting and third-person shooting games, highlighting the need for more research on the effects of specific types of video games on the brain. The entorhinal cortex was also found to positively correlate with time playing logic and puzzle games. This positive correlation is also consistent with the hypotheses put forth by Foerde & Shohamy [62] showing that delaying feedback timing will shift from learning based on the striatum to hippocampus. Therefore, in the case of action video games, the presence of immediate rewards may stimulate the striatum to grow and the entorhinal cortex to shrink, whereas the presence of delayed rewards in puzzles or logic games would stimulate the entorhinal cortex to grow [62,63].

Previous results using the 4/8VM have demonstrated that healthy young participants who employ spatial strategies specifically show increased activity and grey matter in the hippocampus. Response learners, by contrast, show increased activity and grey matter in the caudate nucleus and decreased grey matter and activity in the hippocampus [18,19]. Our current 4/8VM data suggest that the high rate of response strategy use in actionVGPs compared with nonVGPs could also indicate a reduction in hippocampus integrity in actionVGPs. This possibility needs further research as reduced grey matter in the hippocampus has been associated with an increased risk for numerous neurological and psychiatric disorders across the lifespan such as schizophrenia [64], post-traumatic stress disorder [65], depression [66] and Alzheimer's disease [67,68], and cognitive deficits in normal ageing [69] and non-hippocampus-dependent response strategies are associated with addiction [43]. Since our current results did not directly measure hippocampal function, further research on the specific effects of action video games on this system is needed.

It is possible that our current results could reflect a self-selection effect, where actionVGPs in our sample were predisposed to action video game playing owing to higher pre-existing levels of grey matter in striatum. In fact, Erickson *et al.* [57] found that grey matter in the striatum at baseline predicted the level of video game skill acquired by their participants. As a result, people with higher pre-existing striatal functioning might find video games to be more rewarding and continue playing during their lifetime. It is therefore plausible that people who use response strategies find action video games more pleasurable than spatial learners. While this may be true, time spent playing certain action video games is associated with entorhinal cortex atrophy [40] and this kind of effect during childhood could possibly alter medial temporal lobe development [70]. If this is the case, children exposed to action video games during development could adopt response learning strategies even if they were not response learners to begin with. In other words, engaging with action video games may promote the striatum during development and thus lead to increased use of response strategies. Further research investigating the direct impact of different genres of video games (e.g. first-person shooters; action-role playing games; three-dimensional platform games) on the striatum and hippocampus must be conducted to better understand how and when video games could encourage response learning.

In summary, our current results suggest that while actionVGPs show more efficient visual attention abilities, they are also much more likely to rely on response strategies that are associated with increased grey matter and activity of the caudate nucleus. Future research using neuroimaging is necessary to further qualify these initial findings and should investigate the direct effects of action video games on hippocampal integrity.

References

1. Zimbardo PG, Duncan N. 2012 The demise of guys: why boys are struggling and what we can do about it. New York, NY: TED Conferences.

2. McGonigal J. 2011 *Reality is broken*. New York, NY: Penguin Books.

3. Green CS, Bavelier D. 2003 Action video game modifies visual selective attention.

Nature **423**, 534–537. (doi:10.1038/nature01647)

4. Li R, Polat U, Makous W, Bavelier D. 2009 Enhancing the contrast sensitivity function through action

video game training. *Nat. Neurosci.* **12**, 549–551. (doi:10.1038/nn.2296)

5. West GL, Al-Aidroos N, Pratt J. 2013 Action video game experience affects oculomotor performance. *Acta Psychol.* (*Amst*). **142**, 38–42. (doi:10.1016/j.actpsy.2011.08.005)

6. West GL *et al.* 2008 Visuospatial experience modulates attentional capture: evidence from action video game players. *J. Vis.* **8**, 1–9. (doi:10.1167/8.16.13)

7. Castel AD, Pratt J, Drummond E. 2005 The effects of action video game experience on the time course of inhibition of return and the efficiency of visual search. *Acta Psychol.* (*Amst*). **119**, 217–230. (doi:10.1016/j.actpsy.2005.02.004)

8. Feng J, Spence I, Pratt J. 2007 Playing an action video game reduces gender differences in spatial cognition. *Psychol. Sci.* **18**, 850–855. (doi:10.1111/j.1467-9280.2007.01990.x)

9. Wu S, Cheng CK, Feng J, D'Angelo L, Alain C, Spence I 2012 Playing a first-person shooter video game induces neuroplastic change. *J. Cogn. Neurosci.* **24**, 1286–1293. (doi:10.1162/jocn_a_00192)

10. Mishra J, Zinni M, Bavelier D, Hillyard SA. 2011 Neural basis of superior performance of action videogame players in an attention-demanding task. *J. Neurosci.* **31**, 992–998. (doi:10.1523/JNEUROSCI.4834-10.2011)

11. Tanaka S *et al.* 2013 Larger right posterior parietal volume in action video game experts: a behavioral and voxel-based morphometry (VBM) study. *PLoS ONE* **8**, e66998. (doi:10.1371/journal.pone.0066998)

12. Kuhn S *et al.* 2011 The neural basis of video gaming. *Transl. Psychiatry* **1**, e53. (doi:10.1038/tp.2011.53)

13. Mishkin M, Petri HL. 1984 Memories and habits: some implications for the analysis of learning and retention. In *Neuropsychology of memory* (ed. I Butters), pp. 287–296. New York, NY: Guilford.

14. Squire LR, Zola SM. 1996 Structure and function of declarative and nondeclarative memory systems. *Proc. Natl Acad. Sci. USA* **93**, 13 515–13 522. (doi:10.1073/pnas.93.24.13515)

15. McDonald RJ, White NM. 1993 A triple dissociation of memory systems: hippocampus, amygdala, and dorsal striatum. *Behav. Neurosci.* **107**, 3–22. (doi:10.1037/0735-7044.107.1.3)

16. Lerch JP *et al.* 2011 Maze training in mice induces MRI-detectable brain shape changes specific to the type of learning. *Neuroimage* **54**, 2086–2095. (doi:10.1016/j.neuroimage.2010.09.086)

17. Bohbot VD, Iaria G, Petrides M. 2004 Hippocampal function and spatial memory: evidence from functional neuroimaging in healthy participants and performance of patients with medial temporal lobe resections. *Neuropsychology* **18**, 418–425. (doi:10.1037/0894-4105.18.3.418)

18. Iaria G *et al.* 2003 Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *J. Neurosci.* **23**, 5945–5952.

19. Bohbot VD *et al.* 2007 Gray matter differences correlate with spontaneous strategies in a human virtual navigation task. *J. Neurosci.* **27**, 10 078–10 083. (doi:10.1523/JNEUROSCI.1763-07.2007)

20. Packard MG, Hirsh R, White NM. 1989 Differential effects of fornix and caudate nucleus lesions on two radial maze tasks: evidence for multiple memory systems. *J. Neurosci.* **9**, 1465–1472.

21. Alvarez P, Zola-Morgan S, Squire LR. 1995 Damage limited to the hippocampal region produces long-lasting memory impairment in monkeys. *J. Neurosci.* **15**, 3796–3807.

22. Packard MG, McGaugh JL. 1996 Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiol. Learn. Mem.* **65**, 65–72. (doi:10.1006/nlme.1996.0007)

23. Wolbers T, Weiller C, Buchel C. 2004 Neural foundations of emerging route knowledge in complex spatial environments. *Brain Res. Cogn. Brain Res.* **21**, 401–411. (doi:10.1016/j.cogbrainres.2004.06.013)

24. Scoville WB, Milner B. 1957 Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiatry* **20**, 11–21. (doi:10.1136/jnnp.20.1.11)

25. O'Keefe J, Nadel L. 1978 *The hippocampus as a cognitive map.* Oxford, UK: Clarendon.

26. Eichenbaum H, Stewart C, Morris RG. 1990 Hippocampal representation in place learning. *J. Neurosci.* **10**, 3531–3542.

27. Bohbot VD, Kalina M, Stepankova K, Spackova N, Petrides M, Nadel LYNN. 1998 Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia* **36**, 1217–1238. (doi:10.1016/S0028-3932(97)00161-9)

28. Etchamendy N, Bohbot VD. 2007 Spontaneous navigational strategies and performance in the virtual town. *Hippocampus* **17**, 595–599. (doi:10.1002/hipo.20303)

29. Packard MG, McGaugh JL. 1992 Double dissociation of fornix and caudate nucleus lesions on acquisition of two water maze tasks: further evidence for multiple memory systems. *Behav. Neurosci.* **106**, 439–446. (doi:10.1037/0735-7044.106.3.439)

30. Lin SY *et al.* 2012 *Decreased use of hippocampus-dependent spatial strategy in favor of caudate nucleus-dependent response strategy from childhood to adolescence.* Society for Neuroscience 2012 Abstracts, New Orleans, LA, USA.

31. Etchamendy N, Konishi K, Pike GB, Marighetto A, Bohbot VD. 2012 Evidence for a virtual human analog of a rodent relational memory task: a study of aging and fMRI in young adults. *Hippocampus* **22**, 869–880. (doi:10.1002/hipo.20948)

32. Konishi K, Bohbot VD. 2013 Spatial navigational strategies correlate with gray matter in the hippocampus of healthy older adults tested in a virtual maze. *Front. Aging Neurosci.* **5**, 1. (doi:10.3389/fnagi.2013.00001)

33. Chang Q, Gold PE. 2003 Switching memory systems during learning: changes in patterns of brain acetylcholine release in the hippocampus and striatum in rats. *J. Neurosci.* **23**, 3001–3005.

34. Schinazi VR, Nardi D, Newcombe NS, Shipley TF, Epstein RA. 2013 Hippocampal size predicts rapid learning of a cognitive map in humans. *Hippocampus* **23**, 515–528. (doi:10.1002/hipo.22111)

35. Head D, Isom M. 2010 Age effects on wayfinding and route learning skills. *Behav. Brain Res.* **209**, 49–58. (doi:10.1016/j.bbr.2010.01.012)

36. Konishi K, Etchamendy N, Roy S, Marighetto A, Rajah N, Bohbot VD. 2013 Decreased functional magnetic resonance imaging activity in the hippocampus in favor of the caudate nucleus in older adults tested in a virtual navigation task. *Hippocampus* **23**, 1005–1014. (doi:10.1002/hipo.22181)

37. Poldrack RA, Clark J, Paré-Blagoev EJ, Shohamy D, Creso Moyano J, Myers C, Gluck MA. 2001 Interactive memory systems in the human brain. *Nature* **414**, 546–550. (doi:10.1038/35107080)

38. Bohbot VD *et al.* 2012 Virtual navigation strategies from childhood to senescence: evidence for changes across the life span. *Front. Aging Neurosci.* **4**, 28. (doi:10.3389/fnagi.2012.00028)

39. Koepp MJ *et al.* 1998 Evidence for striatal dopamine release during a video game. *Nature* **393**, 266–268. (doi:10.1038/30498)

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

41. Gray JA. 1987 Perspectives on anxiety and impulsivity: a commentary. *J. Res. Pers.* **21**, 493–509. (doi:10.1016/0092-6566(87)90036-5)

42. Ersche KD, Barnes A, Jones PS, Morein-Zamir S, Robbins TW, Bullmore ET. 2011 Abnormal structure of frontostriatal brain systems is associated with aspects of impulsivity and compulsivity in cocaine dependence. *Brain* **134**, 2013–2024. (doi:10.1093/brain/awr138)

43. Bohbot VD, Del Balso D, Conrad K, Konishi K, Leyton M. 2013 Caudate nucleus-dependent navigational strategies are associated with increased use of addictive drugs. *Hippocampus* **23**, 973–984. (doi:10.1002/hipo.22187)

44. Luck SJ, Hillyard SA. 1994 Spatial filtering during visual search: evidence from human electrophysiology. *J. Exp. Psychol. Hum. Percept. Perform.* **20**, 1000–1014. (doi:10.1037/0096-1523.20.5.1000)

45. Woodman GF, Luck SJ. 2003 Serial deployment of attention during visual search. *J. Exp. Psychol. Hum. Percept. Perform.* **29**, 121–138. (doi:10.1037/0096-1523.29.1.121)

46. Brisson B, Jolicoeur P. 2007 Electrophysiological evidence of central interference in the control of visuospatial attention. *Psychon. Bull. Rev.* **14**, 126–132. (doi:10.3758/BF03194039)

47. De Beaumont L, Brisson B, Lassonde M, Jolicoeur P. 2007 Long-term electrophysiological changes in athletes with a history of multiple concussions. *Brain Inj.* **21**, 631–644. (doi:10.1080/02699050701426931)

48. Green CS, Bavelier D. 2006 Enumeration versus multiple object tracking: the case of action video game players. *Cognition* **101**, 217–245. (doi:10.1016/j.cognition.2005.10.004)

49. Green CS, Bavelier D. 2007 Action-video-game experience alters the spatial resolution of vision. *Psychol. Sci.* **18**, 88–94. (doi:10.1111/j.1467-9280.2007.01853.x)

50. Bohbot VD, Gupta M, Banner H, Dahmani L. 2011 Caudate nucleus-dependent response strategies in a virtual navigation task are associated with lower basal cortisol and impaired episodic memory. *Neurobiol. Learn. Mem.* **96**, 173–180. (doi:10.1016/j.nlm.2011.04.007)

51. Sharbrough F, Chatrian GE, Lesser RP, Luders H, Nuwer M, Picton TW. 1991 American Electroencephalographic Society guidelines for standard electrode position nomenclature. *J. Clin. Neurophysiol.* **8**, 200–202. (doi:10.1097/00004691-199104000-00007)

52. Kramer AF, Strayer DL. 1988 Assessing the development of automatic processing: an application of dual-task and event-related brain potential methodologies. *Biol. Psychol.* **26**, 231–267. (doi:10.1016/0301-0511(88)90022-1)

53. Polich J. 2007 Updating P300: an integrative theory of P3a and P3b. *Clin. Neurophysiol.* **118**, 2128–2148. (doi:10.1016/j.clinph.2007.04.019)

54. Bavelier D, Achtman RL, Mani M, Föcker J. 2012 Neural bases of selective attention in action video game players. *Vis. Res.* **61**, 132–143. (doi:10.1016/j.visres.2011.08.007)

55. Gozli DG, Bavelier D, Pratt J. 2014 The effect of action video game playing on sensorimotor learning: evidence from a movement tracking task. *Hum. Mov. Sci.* **38C**, 152–162. (doi:10.1016/j.humov.2014.09.004)

56. Bavelier D, Green CS, Pouget A, Schrater P. 2012 Brain plasticity through the life span: learning to learn and action video games. *Annu. Rev. Neurosci.* **35**, 391–416. (doi:10.1146/annurev-neuro-060909-152832)

57. Erickson KI et al. 2010 Striatal volume predicts level of video game skill acquisition. *Cereb. Cortex* **20**, 2522–2530. (doi:10.1093/cercor/bhp293)

58. Boileau I, Dagher A, Leyton M, Welfeld K, Booij L, Diksic M, Benkelfat C. 2007 Conditioned dopamine release in humans: a positron emission tomography [11]Craclopride study with amphetamine. *J. Neurosci.* **27**, 3998–4003. (doi:10.1523/JNEUROSCI.4370-06.2007)

59. Cox SM et al. 2009 Striatal dopamine responses to intranasal cocaine self-administration in humans. *Biol. Psychiatry* **65**, 846–850. (doi:10.1016/j.biopsych.2009.01.021)

60. Barrett SP, Pihl RO, Benkelfat C, Brunelle C, Young SN, Leyton M. 2008 The role of dopamine in alcohol self-administration in humans: individual differences. *Eur. Neuropsychopharmacol.* **18**, 439–447. (doi:10.1016/j.euroneuro.2008.01.008)

61. Small DM et al. 2001 Changes in brain activity related to eating chocolate: from pleasure to aversion. *Brain* **124**, 1720–1733. (doi:10.1093/brain/124.9.1720)

62. Foerde K, Shohamy D. 2011 Feedback timing modulates brain systems for learning in humans. *J. Neurosci.* **31**, 13157–13167. (doi:10.1523/JNEUROSCI.2701-11.2011)

63. Shohamy D, Adcock RA. 2010 Dopamine and adaptive memory. *Trends Cogn. Sci.* **14**, 464–472. (doi:10.1016/j.tics.2010.08.002)

64. Pantelis C et al. 2003 Neuroanatomical abnormalities before and after onset of psychosis: a cross-sectional and longitudinal MRI comparison. *Lancet* **361**, 281–288. (doi:10.1016/S0140-6736(03)12323-9)

65. Gilbertson MW, Shenton ME, Ciszewski A, Kasai K, Lasko NB, Orr SP, Pitman RK. 2002 Smaller hippocampal volume predicts pathologic vulnerability to psychological trauma. *Nat. Neurosci.* **5**, 1242–1247. (doi:10.1038/nn958)

66. Amico F et al. 2011 Structural MRI correlates for vulnerability and resilience to major depressive disorder. *J. Psychiatry Neurosci.* **36**, 15–22. (doi:10.1503/jpn.090186)

67. Apostolova LG, Dutton RA, Dinov ID, Hayashi KM, Toga AW, Cummings JL, Thompson PM. 2006 Conversion of mild cognitive impairment to Alzheimer disease predicted by hippocampal atrophy maps. *Arch. Neurol.* **63**, 693–699. (doi:10.1001/archneur.63.5.693)

68. Swan GE, Lessov-Schlaggar CN. 2007 The effects of tobacco smoke and nicotine on cognition and the brain. *Neuropsychol. Rev.* **17**, 259–273. (doi:10.1007/s11065-007-9035-9)

69. Lupien SJ et al. 1998 Cortisol levels during human aging predict hippocampal atrophy and memory deficits. *Nat. Neurosci.* **1**, 69–73. (doi:10.1038/271)

70. Giedd JN et al. 1999 Brain development during childhood and adolescence: a longitudinal MRI study. *Nat. Neurosci.* **2**, 861–863. (doi:10.1038/13158)