Increased flanker task and forward digit span performance in caudate-nucleus-dependent response strategies

Étienne Aumont[1], Martin Arguin[1], Véronique Bohbot[2] & Greg L. West[1]

[1] Center of Research in neuropsychology and cognition, Department of Psychology, University of Montreal, Montreal, Quebec, Canada.

[2] Douglas mental health university institute, Department of Psychiatry, McGill University, Verdun, Quebec, Canada.

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Address for Correspondence:
Étienne Aumont
University of Montreal
Department of Psychology
Pavillon Marie-Victorin
90, avenue Vincent d'Indy
Montreal QC
H2V 2S9
email: etienne.aumont.1@gmail.com

Abstract

One of two memory systems can be used to navigate in a new environment. Hippocampus-dependent spatial strategy consists of creating a cognitive map of an environment and caudate nucleus-dependent response strategy consists of memorizing a rigid sequence of turns. Spontaneous use of the response strategy is associated with greater activity and grey matter within the caudate nucleus while the spatial strategy is associated with greater activity and grey matter in the hippocampus. The caudate nucleus is involved in executive functions such as working memory, cognitive control and certain aspects of attention such as attentional disengaging. This study therefore aimed to investigate whether response learners would display better performance on tests of executive and attention functioning compared to spatial learners.

Fifty participants completed the 4/8 virtual maze to assess navigational strategy, the forward and backward visual digit span and the Attention Network Test – Revised to assess both attention disengagement and cognitive control. Results revealed that response learners showed significantly higher working memory capacity, more efficient attention disengagement and better cognitive control. Results suggest that response learners, who putatively display more grey matter and activity in the caudate nucleus, are associated with better working memory span, cognitive control and attentional disengagement.

Keywords: Navigation, cognitive control, flanker, working memory, digit span, caudate nucleus

Highlights:

- Caudate nucleus-based navigation is associated with better cognitive control
- Learning curve in flanker task was more abrupt in response learners
- Navigating using response strategy is linked to longer forward digit span
- Working memory errors in a navigation task was linked to digit span performance
- Use of caudate nucleus-based navigation is linked to better attention disengagement

1. Introduction

The hippocampus and the caudate nucleus are each central to two distinct memory systems involved in navigation that are in competition for the ability to influence behaviour (Bohbot, Iaria, & Petrides, 2004; Mark G. Packard, 1999). During navigation in a new environment, the hippocampus supports the formation of a cognitive map, establishing relationship between environmental landmarks in a process called spatial learning (O’Keefe & Nadel, 1978). In contrast, the caudate nucleus supports learning through the encoding of an environment through a rigid series of turns in a process called response learning (Mark G. Packard & Knowlton, 2002). While cooperation between both systems was observed in various contexts (Müller et al., 2018; Daphna Shohamy & Wagner, 2008; Voermans et al., 2004), navigational strategy is one example of competition between both memory systems (A. S. Lee, Duman, & Pittenger, 2008; M. G. Packard, Hirsh, & White, 1989; West et al., 2018), alternatively people could use the two memory systems in parallel, independently of each other, by using one system or the other, but not both at the same time(Doeller, King, & Burgess, 2008). People who navigate using the spatial strategy display increased grey matter and activity in the hippocampus (Bohbot, Lerch, Thorndycraft, Iaria, & Zijdenbos, 2007; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Konishi & Bohbot, 2013; West et al., 2018). Similarly, people who navigate using the response strategy display increased grey matter and activity in the caudate nucleus (Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013; West et al., 2018). Further, rodents trained to navigate using the spatial strategy displayed increased grey matter in the hippocampus while those that trained to navigate using the response strategy showed increased grey matter volume in the caudate nucleus (Lerch et al., 2011). Thus, navigation strategies are well-established predictors of functional activity and grey matter volume ratios between the caudate nucleus and hippocampus memory systems. Specifically, spatial learning is associated with greater grey matter in the hippocampus and lower grey matter volume in the caudate nucleus whereas the opposite is true of response learners.

In addition to its impact on brain structures, navigational strategies are associated with distinct cognitive processes. Both navigation systems, the hippocampus and caudate nucleus, have different anatomical connections to the rest of the brain (Bohbot et al., 2007; Dahmani & Bohbot, 2015; Konishi & Bohbot, 2013; D. Shohamy & Turk-Browne, 2013). These different brain circuits serve different cognitive functions. As such, hippocampus and caudate nucleus-dependent strategies may lead to differences in cognitive performances in different domains. For example, in older adults, hippocampus-dependent spatial strategies were associated with higher Montreal Cognitive Assessment scores, which reflect general cognitive health in aging, compared to caudate nucleus-dependent response learners (Konishi, Mckenzie, Etchamendy, Roy, & Bohbot, 2017). Spatial learners also display greater amounts of spatial attention directed to targets as reflected in the N2pc event-related potential component (Drisdelle et al., 2017), were found to make more saccades towards landmarks when learning a new environment (Andersen, Dahmani, Konishi, & Bohbot, 2012) and had faster saccadic reaction times during an oculomotor task (Aumont, Bohbot, & West, 2019). Spatial learning therefore appears to benefit certain cognitive processes.

Executive functions are known to be primarily dependent on the prefrontal cortex (Fuster, 2015; Miller & Cohen, 2001; Miyake et al., 2000). However, dopamine release in the caudate nucleus also support executive functions, and specifically working memory and cognitive control, by interacting with dopaminergic transmission in the prefrontal cortex through mesocortical pathways (Cools, 2011; Cools & D’Esposito, 2011). While dopamine transmission has previously been reported in the hippocampus, it is not as predominant as in the caudate nucleus (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006). We therefore hypothesized that, compared to spatial learners, response learners, who display more grey matter and activity in the caudate nucleus, would show better performance on these functions.

1.1 Working memory

Working memory is defined as the temporary conservation and manipulation of information (Miyake et al., 2000). The modulating role of dopamine transmission from the caudate nucleus to the prefrontal cortex is supported by the finding that increased dopamine transmission in the caudate nucleus was found to be associated with better working memory performance (Bäckman et al., 2011; Landau, Lal, O’Neil, Baker, & Jagust, 2009). This is further supported by studies in which the caudate nucleus was observed to be active specifically during working memory tasks, and this activity has been correlated with behavioural working memory performance (Gazzaley, Rissman, & D’Esposito, 2004; Lewis, Dove, Robbins, Barker, & Owen, 2004; Podell et al., 2012; Robbins, 1996). There is also evidence of a direct role of the caudate nucleus in working memory by the observation of a differential impact of dopamine antagonists that target either the prefrontal cortex or striatum on working memory performance. The attention deficit disorder

(ADHD) medication methylphenidate which preferentially raises dopamine levels in the prefrontal cortex does not improve working memory performance (Prehn-Kristensen et al., 2011). Parkinson’s disease medication levodopa, on the other hand, increases dopamine in the striatum and is associated to increased working memory performance (Costa et al., 2003; Lewis, Slabosz, Robbins, Barker, & Owen, 2005; Simioni, Dagher, & Fellows, 2017).It is therefore expected that through increased activity in the caudate nucleus (Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013; West et al., 2018), response learners would perform better on working memory tasks.

1.2 Cognitive control

Cognitive control, as measured in flanker tasks, is defined as the ability to resolve conflicts between target and task irrelevant stimuli in the environment (Eriksen & Eriksen, 1974). A common task used to measure cognitive control is the flanker task, where a target stimulus competes with adjacent task irrelevant stimuli (i.e., flankers) for attention. Cools and D’Esposito (2011) assembled many studies suggesting that the caudate nucleus is important for cognitive control. This is supported by more recent studies where the caudate nucleus was shown to be involved during the flanker task through the observation that dopaminergic activity in the caudate increased when people had to resolve the competition between the target and flanker stimuli (Badgaiyan, Sinha, Sajjad, & Wack, 2015; Badgaiyan & Wack, 2011; Korsch, Frühholz, & Herrmann, 2014). Further, activity in the caudate nucleus has also been shown to correlate with interference suppression during inhibition tasks, suggesting that the caudate nucleus may play a specific role of interference control (Chaddock et al., 2010, 2012; Fall, Querne, Le Moing, & Berquin, 2015; Vaidya et al., 2005). Consequently, we hypothesized that response learners, who show increased activity and grey matter in the caudate nucleus (Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013; West et al., 2018), would show better cognitive control as measured by flanker task performance (Eriksen & Eriksen, 1974).

1.3 Attention disengagement

The ability to move attention away from a stimulus after it has been engaged on a target is called attention disengagement and is often regarded as an important component of attentional processes (read Toffanin, de Jong, & Johnson, 2011 for more details). It is suggested that this process is supported by activity in the caudate nucleus. A study on the effects of dopamine depletion in rats described improved attentional disengagement when administering Parkinson's disease medication levodopa (Smith, Hardy, Schallert, & Lee, 2016). Similarly, in humans, successful attention disengagement from thermally-induced pain was related to activity in the caudate nucleus (Freund et al., 2009). In oculomotor paradigms, attention disengagement is measured using the gap manipulation, where SRTs are faster following the removal of a central fixation stimulus before the target is displayed (Jin & Reeves, 2009), and is the result of the deactivation of the superior colliculus that provides tonic inhibition of eye movements (de Araujo, Matsumoto, Ono, & Nishijo, 2015). The inhibitory signal directed towards the superior colliculi, reducing its tonic inhibition, therefore allowing for improved attention disengagement takes its origin in specific neurons in the caudate nucleus (Hikosaka & Sakamoto, 1986; Hikosaka, Sakamoto, & Usui, 1989). Further, a study comparing response and spatial learners found that response learners displayed a larger gap effect magnitude, suggesting that increased activity in the caudate nucleus is related to a strengthened ability to disengage attention (Aumont et al., 2019). Based on this evidence, we hypothesized that, response learners, who display increased grey matter and activity in the caudate nucleus (Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013; West et al., 2018), will show superior attention disengagement performance.

Participants were defined as spatial or response learners using the 4 on 8 virtual maze, which has been found to be sensitive to hippocampal and caudate nucleus grey matter volume (Bohbot et al., 2007). To test both cognitive control and attention disengagement performance, the revised Attention Network Test (ANT-R) was used (Fan et al., 2009). This offers measurements for the three main attention networks: Cognitive control, orienting (including disengagement) and alerting. Flanker interference cost served as an index of cognitive control. Attention disengagement was assessed using the indicators first described by Posner and colleagues (1984, 1987). i.e. by subtracting reaction time in an invalid cue condition with the double cue condition. Forward and backward visual digit spans were used to measure working memory capacity and updating (Lumley & Calhoon, 1934). This task allows for simple and reliable measurements of working memory, and is widely used in clinical context (Benson, Hulac, & Kranzler, 2010). Spatial learners were expected to have lower digit span and attention disengagement performances, while exhibiting an increased flanker interference cost.

2. Methods

2.1 Participants

Fifty healthy participants (12 males) were recruited for this study. They were aged between 18 and 35 years (M = 23.98 SD = 4.43 years) with at least 14 years of education (M = 15.82 SD = 1.91 years). Participants were non-smokers, had an alcohol intake of less than 10 drinks per month and did not use other psychoactive drugs on a regular basis. Participants did not have history of psychiatric or neurological disorder. Additionally, no participants reported playing video games more than three hours weekly during the year preceding participation. A monetary compensation equivalent to 15 CAD per hour was offered at the end of the study. Recruitment was made via word of mouth and internet ads. Informed written consent was given to participants before the beginning their participation. The study was approved by the University of Montreal Faculty of Arts and Science Ethics committee and was executed in accordance to their recommendations.

2.2 4 on 8 virtual maze (4/8 VM)

The participants' spontaneous navigation strategy when exploring a novel environment was assessed using the 4/8 VM (Andersen et al., 2012; Aumont et al., 2019; Bohbot, Del Balso, Conrad, Konishi, & Leyton, 2013; Bohbot et al., 2007; Dahmani & Bohbot, 2015; Drisdelle et al., 2017; West et al., 2015, 2018) (Figure 1). In this task, participants are placed at the center of a platform surrounded by eight pathways ending with a small pit, making it impossible to see whether an item is present at the end of it. A tree, a rock, a mountain and a valley are positioned outside of the accessible area, serving as proximal and distal landmarks and being visible in all trials except for part 2 of the probe trial. The task comprises several trials each divided in two parts. At the beginning of each part, the participant is relocated at the center of the maze, always facing the same pathway.

Part 1: Four pathways are blocked by barriers; the participant has to collect items at the end of each accessible pathways.

Part 2: All the pathways are accessible; the participant has to collect the items located at the end of the four pathways that were previously blocked and avoid the pathway that were open during part 1.

Probe trial: The probe trial starts off with part 1 that is the same as a normal trial. However, the part 2 which follows contains no visible landmarks. Like in part 2 of a normal trial, participants are instructed to collect the items in the previously blocked pathways.

A criterion needs to be achieved for the probe trial to be started. The criterion is defined as the completion of part 2 without making any errors. If it is not achieved after the three first mandatory trials, up to five extra trials are administered until it is attained, following which the probe trial is administered. A final regular trial is passed after the probe trial.

A semi-structured interview is administered at the end of the final trial in order to assess the spontaneous strategy used during the first trial. Participants were asked to report how they knew which pathways contained objects and which were did not during part 2 of the trial. Based on their description, participants were categorized as using either using a spatial strategy or response strategy. If participants reported using two or more landmarks to remember the location of the objects in the first trial and did not report using a sequence from a single starting point, they were categorized as spatial learners. If participants 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 response learners (Andersen et al., 2012; Aumont et al., 2019; Bohbot et al., 2013, 2007; Dahmani & Bohbot, 2015; Drisdelle et al., 2017; West et al., 2015, 2018). Importantly, this categorization is based on qualitative assessment of navigation strategy and is entirely independent from performance on the 4 on 8 VM task.

The probe trial allows to for the confirmation of the navigational strategy used by measuring errors made. A probe error is defined as an error in the sequence of pathways chosen, where the removal of the landmarks in part 2 will perturb performance of those using a spatial strategy while not affecting the performance of those using a response strategy. Therefore, a lower number of probe errors is indicative of using a response strategy. Probe error, have been shown to predict grey matter volume and activity in the hippocampus and the caudate nucleus as well as navigation strategies (Bohbot et al., 2007; Iaria et al., 2003).

Working memory errors (WME) in the 4/8 VM are made by entering the same pathway for a second time in a single part 2. It can be used as a measure of navigation abilities. WME are divided between WME-correct – revisiting a correct pathway; and WME-incorrect – revisiting an incorrect pathway. An average number of WME trials before the probe test is calculated (Bohbot, Gupta, Banner, & Dahmani, 2011).

2.3 Digit span

A classic task measuring working memory, the digit span was first published by Lumley and Calhoon (1934). A modified computerized version of the task was used. Digits are presented visually in sequences that vary in length, following which the participant must enter the sequence in the correct order. The task is divided in two subtasks: forward and backward, the former requiring the participant to enter the sequence in the same order as presented, and the latter, in the reversed order. The forward recall starts at a length of three while the backward recall starts at two. The length increases by one digit when the participant succeeds, and two consecutive errors result in the shortening of the sequence by a single digit. A total of 14 trials are presented for each subtask. This paradigm allows the calculation of the mean span, which is the approximated length at which the participant has 50 percent chances to successfully recall the sequence. This measure was recommended by Woods et al., (2011) for its superior sensitivity when compared to regular measures of digit span.

2.4 Revised Attention Network Test (ANT-R)

A revised version of the attention network test (ANT-R) was created by Fan et al., (2009) allowing to measure multiple attention networks in a 288-trial test (Figure 2). A fixation cross is present at the center of the screen for the whole duration of the task. At the beginning of each trial, one of four cue conditions are presented: valid cue, invalid cue, no cue or double cue. Cues consist of increasing the luminance of a box for 100 ms that are presented on either side of the central fixation cross. A cue is valid when it predicts the location of the target, while it is invalid when the cue indicated the wrong location. Within each box, additional stimuli can be presented. These stimuli consisted of five arrows pointing either to the right or to the left and situated either to the right or to the left side of the target, which consisted of the middle arrow. The other four arrows were flankers (i.e., distractors). The four distractors always pointed in a congruent direction, but their direction was opposite to that of the target in half of the trials. The stimuli remained visible for a duration of 500 ms.

There were three times as many valid cue trials compared to each invalid cue, no cue or double cue trials. The stimulus onset asynchrony (SOA) separating the offset of the cue and the onset of the target stimulus was either of 0 ms, 400 ms or 800 ms. The response collection window closed 1700 ms after the onset of the target. The participant had to answer as fast as possible according to the direction pointed by the target using a right and a left key. The disappearance of the target and the onset of the next trial were separated by a jittered interval ranging between 2000 and 12 000 ms and averaging 4000 ms. The experiment started with a 36-trial practice block, followed by four 72-trial experimental blocks (see Fan et al. (2009) for complete details).

Performance within multiple attentional networks can be extracted based on RT and accuracy measured in the ANT-R (Fan et al., 2009). The attention disengagement cost is measured as the RT cost of an invalid cue and is calculated by subtracting invalid cue mean RTs from double cue mean RTs. The flanker conflict cost measured as both the increase in RTs and the reduction in accuracy within trials where the flankers are incongruent with the target. It is calculated by subtracting both RTs and accuracy rates of incongruent flanker trials with congruent flanker trials. Other possible measures derived from the ANT-R RTs such as validity (invalid cue - valid cue), inhibition of return ((invalid cue at 0 ms SOA - valid cue at 0 ms SOA) - (invalid cue at 400 ms SOA - valid cue at 400 ms SOA)), moving + engaging (double cue - valid cue), orientating time (Valid cue at 0 ms SOA - valid cue at 800 ms SOA), location conflict cost (location incongruent - location congruent) as well as alerting (no cue - double cue) were calculated.

2.5 Statistical analyses

The kappa test was used to evaluate the inter-rater reliability for the assessment of navigation strategy. The numbers of men and women were compared between groups defined according to either strategy or probe error using the Chi-square test. T-tests served to compare groups on age, education, forward and backward digit span performances, flanker interference on accuracy and the cost of attention disengagement. Chi-square were also used to compare the effect of probe error grouping variable on age, sex and attention disengagement test. The effect of flanker interference on reaction time was examined using analyses of covariance (ANCOVA), with strategy as the fixed factor and the number of years of education as a covariable. Correlations were used to link digit span measures and working memory errors from the 4/8 VM.

An alpha threshold of .05 was used to consider a difference as statistically significant. Since no analyses included three or more groups, no post-hoc tests were required. Since the dependent variables used in the present study are considered to measure different constructs, we considered the statistical tests conducted to be independent from one another, therefore not requiring correction for multiple tests.

3. Results

3.1 Navigation

Twenty-five (five males) of the 50 participants were classified as spatial learners while 25 (seven males) were classified as response learners. Of the 25 spatial learners, 14 “shifted” from an initial spatial strategy to a response strategy with practice. This shift is thought to occur through repetition of a behavior (Packard and McGaugh, 1996; Gold, 2004). Inter-rater reliability was high (κ(50)=.960, p < .0001). A third rater was consulted in the single case where the two main raters disagreed. Age (spatial: M = 22.68, SD = 3.91 years; response: M = 24.28, SD = 4.96 years; *t* (48) = 1.266, *p* = .212), sex (χ^2 (1, N = 50) = 0.439, *p* = .508) and education (spatial: M = 15.60, SD = 1.89; response: M = 16.04, SD = 1.93; *t* (48) = .815, *p* = .419) did not significantly differ between both groups. Response learners were significantly less likely than spatial learners to make at least one probe error in the probe trial: 12 percent of response learners and 68 percent of spatial learners made a probe error (χ^2 (1, N = 50) = 16.333, *p* < .0001, Cramer's φ = .572). This is evidence that response learners had a reduced reliance on landmarks during navigation (Bohbot et al., 2007; Drisdelle et al., 2017; Iaria et al., 2003; Konishi & Bohbot, 2013; West et al., 2015, 2018). Similarly, the incorrect and correct probe groups did not differ in terms of age (correct: M = 24.63, SD = 4.97 years; incorrect: M = 22.3, SD = 3.78 years; *t* (48) = 1.781, *p* = .081), sex (χ^2 (1, N = 50) = 1.480, *p* = .224) and education (correct: M = 16.10, SD = 1.77 years; incorrect: M = 15.55, SD = 2.14 years; *t* (48) = .990, *p* = .327).

3.2 Digit span

Response learners had a significantly longer forward mean span than spatial learners (spatial: M = 6.236, SD = 1.077; response: M = 6.916, SD = 1.152; *T*(48) = 2.158, *p* = .036, Cohen's *d* = .623), but the backward mean span difference did not achieve statistical significance (spatial: M = 6.020, SD = .944; response: M = 6.434, SD = 1.462; *T*(48) = 1.193, *p* = .240). This suggests that the response learners were able to memorize longer digit sequences active in their working memory. Additionally, mean WME correct, which is the average number of times per trials where a participant enters a correct pathway for a second time, was found to be significantly negatively correlated with the forward mean span (R = -.392, p = .008) and non-significantly with the backward mean span (R = -.262, p = .082) (figure 3 & 4). Correlations between mean WME incorrect and digit span measures were null (R < ±.05).

3.3 Revised Attention Network Test

Trials resulting in an incorrect response, representing 7.81% of the total number of trials, were not considered in the RT analyses. Outliers were removed using an iterative method based on a ±2.5 SD interval around the group means, where trials were grouped based on the cue type. Because of this, 3.95% of the correct trials were removed from the data.

Distributions for each measure proposed by Fan et al. (2009) were all found to be closely resembling distributions found in their original article. Means for average RT, alerting, validity, moving + engaging, disengaging, orienting time, flanker conflict cost, inhibition of return and location conflict cost were all found to be within ±.5 standard deviation from Fan et al., (2009)'s distributions (See Table 1 for descriptive statistics). Alerting, validity, moving + engaging, orientating time, inhibition of return and location conflict cost were not significantly different between spatial and response learners when using a T-test.

3.3.1 Flanker conflict reaction time cost

Since education was found to be significantly correlated with the flanker effect on RT (R = .390, p = .005), it was used as a control variable for the following analyses. Overall flanker RT cost was found to be significantly higher in spatial learners when compared to response learners (spatial: M = 134.10, SD = 60.40; response: M = 110.52, SD = 35.71, F(1) = 4.395, p = .041, partial η^2 = .086) (Figure 5). When breaking down results by blocks, differences between spatial and response learners differed significantly only in the first block (spatial: M = 152.70, SD = 65.07; response: M = 123.28, SD = 39.59, F(1) = 4.789, p = .034, partial η^2 = .092). This means that response learners' RTs were less affected by the flanker congruence with the target, and that this difference was concentrated in the first block.

3.3.2 Flanker conflict accuracy cost

Flanker conflict accuracy cost was not correlated with demographic variables. The overall accuracy cost from flanker conflict was not found to significantly differ between spatial and response learners (spatial: M = .143, SD = .086; response: M = .129, SD = .089, *T*(48) = -.551, *p* = .584). However, block breakdown revealed that spatial learners had a higher accuracy cost than response learners in the first block (spatial: M = .192, SD = .099; response: M = .134, SD = .095, *T*(48) = 2.106, *p* = .040, *d* = .598), but not in later blocks (Figure 6). In other words, the accuracy of response learners was less affected by the flanker congruence in the first block.

3.3.3 Attentional disengagement cost

Attentional disengagement cost was not significantly correlated with demographic variables. The attentional disengagement cost was not found to be significantly different when comparing spatial and response learners (Spatial: M = 60.78, SD = 39.85; Response: M = 55.00, SD = 26.06, T(48) = .607, p = .547). However, attentional disengagement cost was significantly shorter amongst those who made a probe error compared to those who did not (No error: M = 49.93, SD = 25.76; Error: M = 69.81, SD = 40.29, T(48) = -2.131, p = .038, *d* = .588). Therefore, participants did not make a probe error were able to disengage from the incorrect cue more quickly on average than those who made a probe error.

4. Discussion

The present study examined differences in working memory, cognitive control and attention disengagement between response and spatial learners. Response learners showed significantly higher forward digit span compared to spatial learners. Analyses of the ANT-R data showed that cognitive control as measured by the RT difference between congruent and incongruent flanker condition was significantly higher in spatial learners when compared to response learners, however, these differences were concentrated in the first block of the task. Disengagement was also found to be significantly more effective in people who did not make a probe error, i.e. those who did not rely on landmarks when navigating in the environment.

4.1 Digit span

We showed that response learning was linked with improved performance in the forward component of the digit span task. Working memory had repeatedly been associated with dopamine function in the caudate nucleus (Bäckman et al., 2011; Landau et al., 2009; Lewis et al., 2004; Podell et al., 2012). Additionally, increased functional activity in the caudate nucleus had also been associated with better working memory task performance (Costa et al., 2003; Lewis et al., 2005; Simioni et al., 2017). Therefore, our current results support the hypothesis that response learners would have longer digit spans. However, our results do not involve a direct measure of the caudate nucleus' contribution to working memory processes. Previous researchers have suggested that the caudate nucleus might contribute to information selection, allowing for more efficient working memory, and interference control, allowing to better maintain items in sequence in the face of distractions (Chatham, Frank, & Badre, 2014; Diamond, 2013; Prehn-Kristensen et al., 2011; Provost, Petrides, & Monchi, 2010). Interestingly, other lines of research have shown that the medial temporal lobes, including the hippocampus, are also critical for certain types of working memory (Ezzyat & Olson, 2008). However, working memory tasks dependent on the medial temporal lobes are very different from the working memory task reported in the current paper. Specifically, the medial temporal lobes were found to be required in a working memory tasks for items that involve discrimination from a study probe (Ezzyat & Olson, 2008; Graham, Barense, & Lee, 2010; Hartley et al., 2007; A. C. H. Lee & Rudebeck, 2010). In the current paper, working memory did not require memory of items that closely matched a study probe but involved repetition of known items instead. The fact that spatial and response learners showed no significant differences in performance on the backward component of the digit span task, is intriguing. This suggests that the increased working memory ability in response learners may be specific to a domain. An important difference between forward and backward digit span, is that the forward digit span may be more prone to the effects of practice for the simple reason that repeat information in the order it is received more often than we repeat information backwards (Antonova Ünlü & Sağın Şimşek, 2018). Since response learning develops with practice and engages the caudate nucleus with repetition, habit or automatization of behavior, it may be no coincidence that the advantage of response learners in the working memory domain, may be more specific to the modality and type of material that is more often practiced (Andersen, 2011; Johnson, van der Meer, & Redish, 2007; Knowlton, Mangels, & Squire, 1996; Rangel, Camerer, & Montague, 2008; Samejima, Ueda, Doya, & Kimura, 2005; Squire & Zola, 1996; West, Konishi, & Bohbot, 2017; West et al., 2018).

Another interpretation is that the forward digit span, on top of measuring working memory capacity, is thought to have more of its variance explained by the efficiency of attention, i.e. being less vulnerable to distractions. It is therefore possible that a higher cognitive control could explain a longer forward, but not backward digit span in response learners (Cools & D'Esposito, 2011; Fowler, Richards, Berent, & Boll, 1987; Kaufman, McLean, & Reynolds, 1991). Future studies are needed to further elucidate the working memory advantages associated with higher functioning in the caudate nucleus.

The digit span results also showed that the WME, for correct pathways, negatively correlate to forward digit span abilities while WME, for incorrect pathways, was not. These results suggest that participants with the best performance on the 4/8VM in terms of least errors committed during acquisition of the task, are also those with the highest forward digit span. Together with the above-mentioned results, these results are coherent with our earlier reports whereby response learners were previously shown to make significantly fewer errors than spatial learners during acquisition of the task (Iaria et al., 2003).

4.2 Flanker Task

The flanker task results showed an association between response learners' lower performance cost from incongruent flankers. This supports our hypothesis based on the previous literature, as cognitive control was associated with activity in the caudate nucleus (Badgaiyan et al., 2015; Badgaiyan & Wack, 2011; Korsch et al., 2014). Further, greater cognitive control performance is correlated with functional activity within the caudate nucleus (Chaddock et al., 2010, 2012; Fall et al., 2015; Vaidya et al., 2005). In other words, previously observed increases in functional activity within the caudate nucleus amongst response learners (e.g., Iaria et al., 2003) could be associated with increased ability to ignore incongruent flankers, which rests on cognitive control.

Interestingly, group comparisons by blocks consistently show that response learning was mainly linked to lower incongruent flanker RT and accuracy cost at the beginning of the task. This is of particular interest since Lungu et al. (2007) found that caudate nucleus activity replaced prefrontal activity as participants progress through a flanker task while performance increases. The caudate nucleus has even been described as a locus of control implementation once a task is well performed (Knowlton et al., 1996; Lungu et al., 2007; Yin & Knowlton, 2006). Therefore, the increased performance of response learners being concentrated in the first block might indicate a faster and more efficient learning and automation of the flanker task. This could be related to increased caudate nucleus volume and activity associated with the response strategy which was also associated with decreased in latency in the 4/8VM (Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013; West et al., 2018).

4.3 Attention disengagement

We found evidence of a shorter attention disengagement cost amongst people who made no probe error when landmarks were removed, which is associated with response learning. This is consistent with our previous findings where the gap effect was stronger in response learners, indicating a more efficient attention disengagement (Aumont et al., 2019). Additionally, activity in the caudate nucleus has been linked to multiple forms of attentional disengaging such as rats disengaging from food stimuli, humans disengaging attention from painful stimuli and the disengagement from a fixation point (Freund et al., 2009; Hikosaka & Sakamoto, 1986; Hikosaka et al., 1989; Smith et al., 2016). Therefore, our interpretation of our results is that the caudate nucleus’ increased functional activity previously found in those who do not make probe errors (Iaria et al., 2003) would be associated with increased ability to disengage attention from an invalid cue. Both attentional disengagement and cognitive control are important in daily functioning, as they allow for better self-control, monitoring of the environment and sustained attention on the task at hand (Diamond, 2013; Muraven & Baumeister, 2000).

4.4 General Discussion

Previous studies showed that spatial and response learners tend to use different brain circuits, serving different functions (Bohbot et al., 2007; Dahmani & Bohbot, 2015; Konishi & Bohbot, 2013; D. Shohamy & Turk-Browne, 2013). This idea predicts that performance in functions supported by these different circuits would differ between both groups. Working memory, cognitive control and attention disengagement are good examples of such functions supported by circuits in which the caudate nucleus plays an important role. This means that our results are in line with these previous studies.

Our results suggest that caution should be exerted when stimulating a specific brain function to improve specific cognitive domains such as navigation strategies, as it could come at a cost in other domains. For example, increasing the use of a response strategy could be accompanied with the cost of a smaller hippocampus, being associated with an increased risk of Alzheimer’s disease (Apostolova et al., 2006; Bohbot, Lerch, Thorndycraft, Iaria, & Zijdenbos, 2007; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Konishi & Bohbot, 2013; West et al., 2018). Similar studies in older adults would be of interest to further validate the current results and examine the interaction between navigation strategy, executive function and cognitive health outcomes (Troyer, Graves, & Cullum, 1994).

4.5 Conclusion

The present study supports that response learning is associated with better working memory for forward material, cognitive control in terms of flanker reaction times and accuracy costs, and attentional disengagement for the task at hand. Our current findings are of importance since recent researchers have shown that the use of technology such as action video games affect the brain by favouring the use of response strategies at the cost of a reduced hippocampal volume (West et al., 2015, 2017, 2018). On the other hand, intervention programs are currently being developed to stimulate the hippocampus in hope to slow cognitive decline in older adults (Andersen, 2011). Therefore, a better understanding of strengths and weaknesses of particular brain areas of specific individuals is required before cognitive training targeting specific neural circuits is to be implemented.

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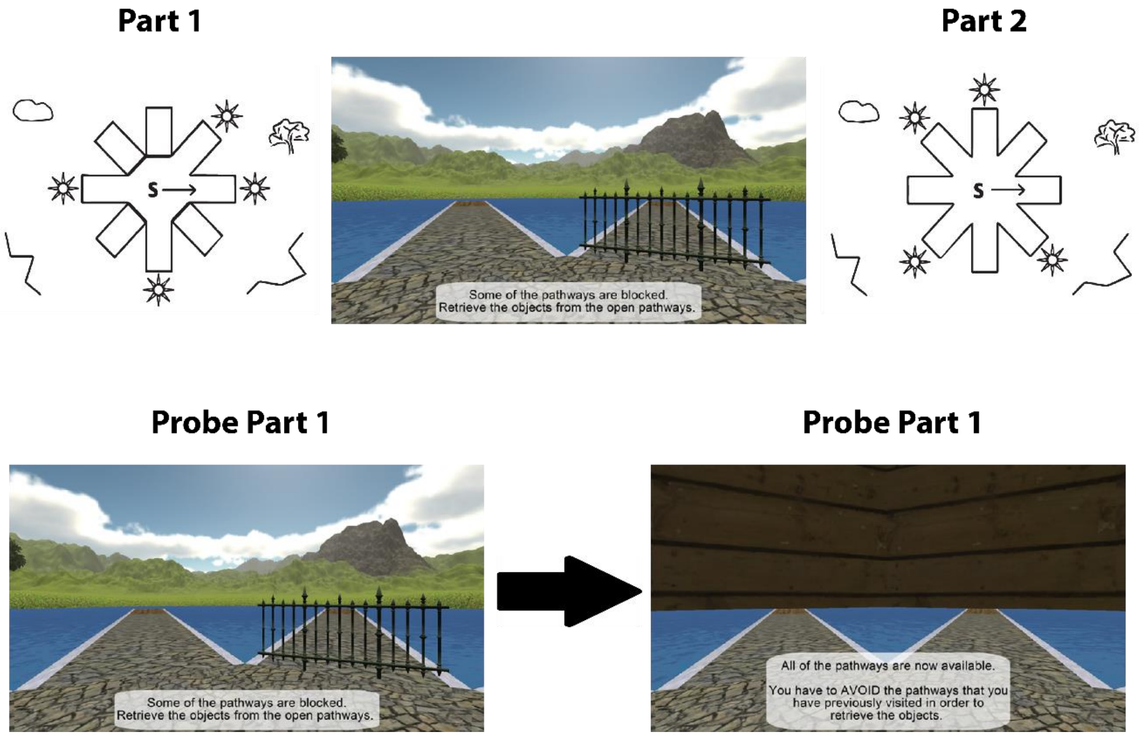
Figures and tables

	Results from present study		Results from Fan et al. 2009	
	Mean RT (MS)	SD	Mean	SD
Average RT	632	76	604	59
Alerting	34	33	29	24
Validity	102	30	95	32
Moving + engaging	44	29	41	21
Disengaging	58	33	54	24
Orienting time	68	30	57	31
Flanker conflict cost	122	51	137	43
Inhibition of return	-78	44	-60	39
Location conflict cost	-7	23	-11	27

Table 1. Attention Network Test – Revised overall RT results compared to those obtained by Fan et al. (2009) using the same metrics. All results fall close to those obtained in the original article.



Some of the pathways are blocked.
Retrieve the objects from the open pathways.

Some of the pathways are blocked.
Retrieve the objects from the open pathways.

All of the pathways are now available.
You have to AVOID the pathways that you have previously visited in order to retrieve the objects.

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.

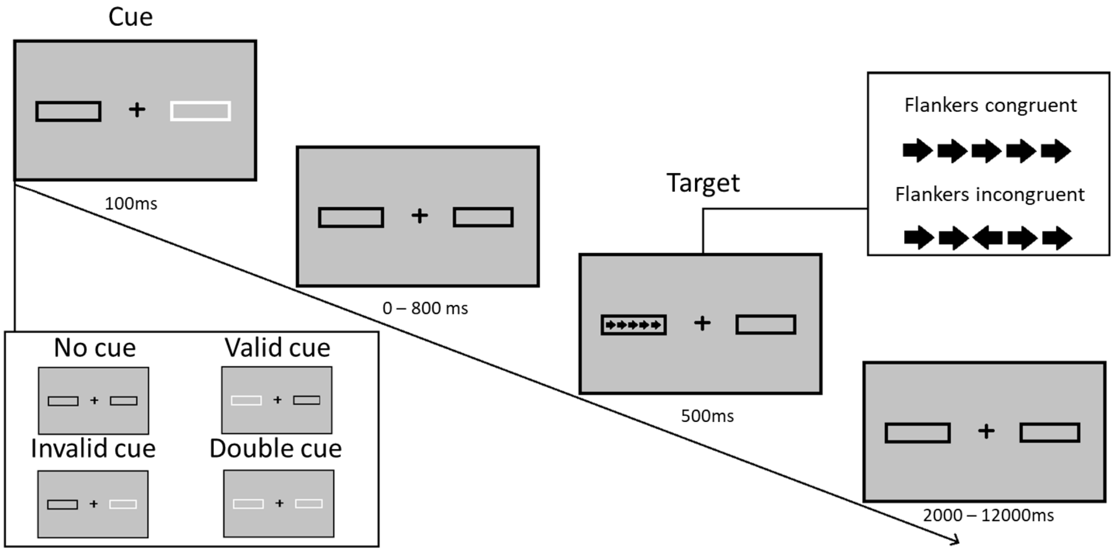


Figure 2. Attention Network Test – Revised. Each trial begins with a cue (or the absence of cue) presentation for 100ms. This is followed by a 0, 400 or 800ms stimulus onset asynchrony, followed by a target presentation for 500ms. The target has either congruent or incongruent flanker. Cognitive control is measures by subtracting performance in incongruent trials to performance in congruent trials. Attention disengagement is measured by subtracting performance in invalid cue trials with performance in double cue trials. Participants respond by pressing the key corresponding to the central arrow’s direction.

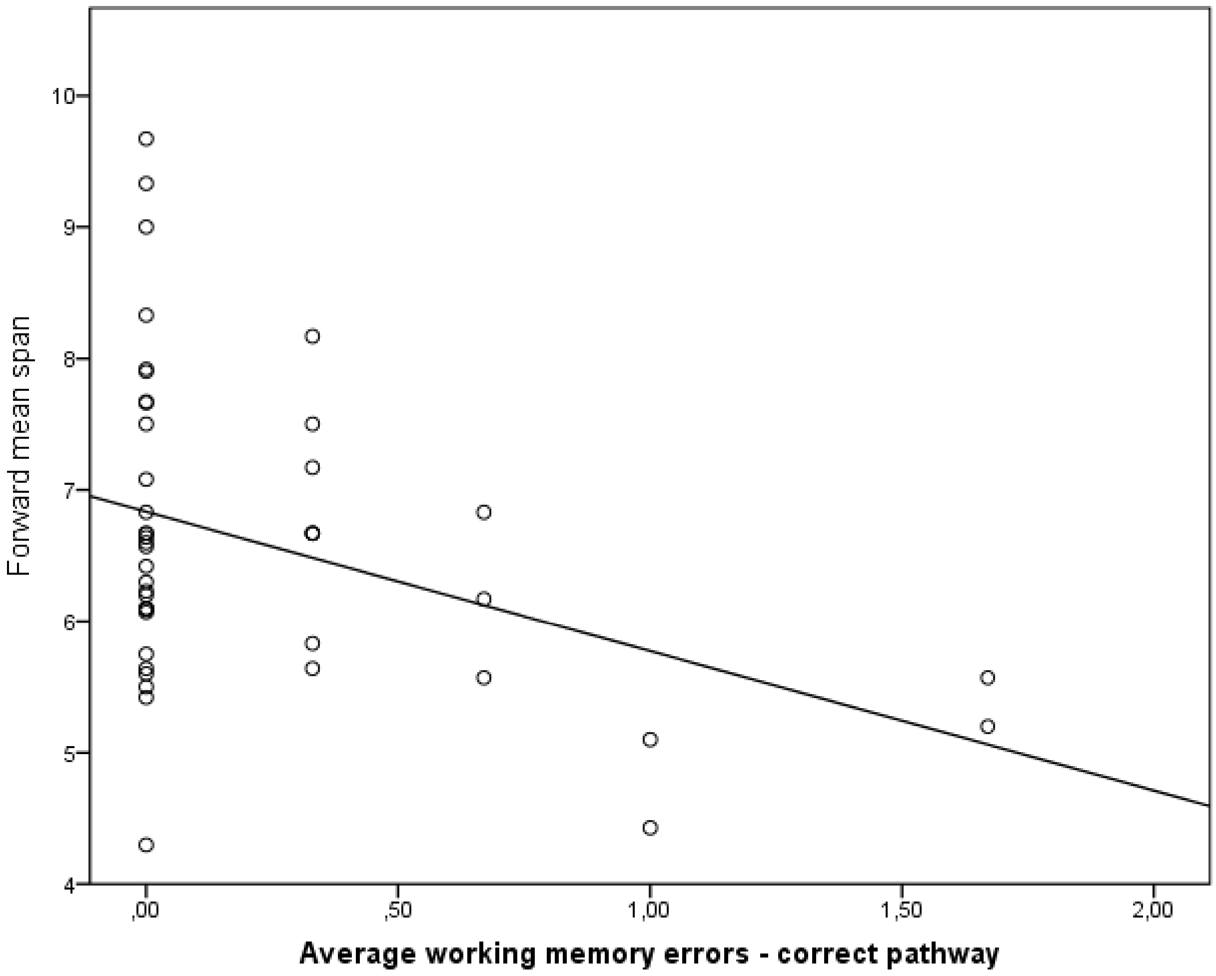


Figure 3. Significant negative correlation (R = -.392) between the forward mean span and the average number of WME for correct pathways.

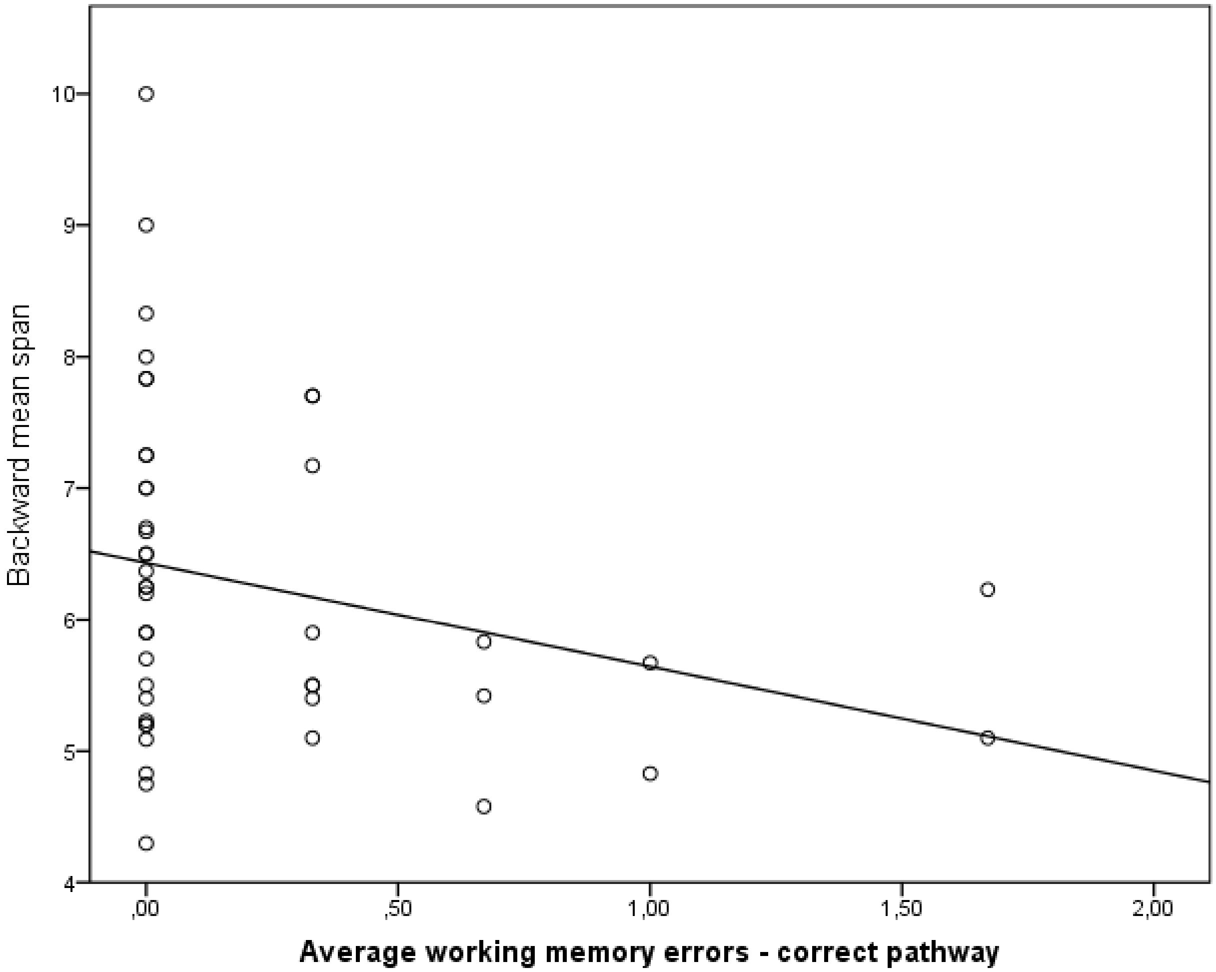


Figure 4. Non-significant negative correlation (R = -.262) between the backward mean span and the average number of WME for correct pathways.

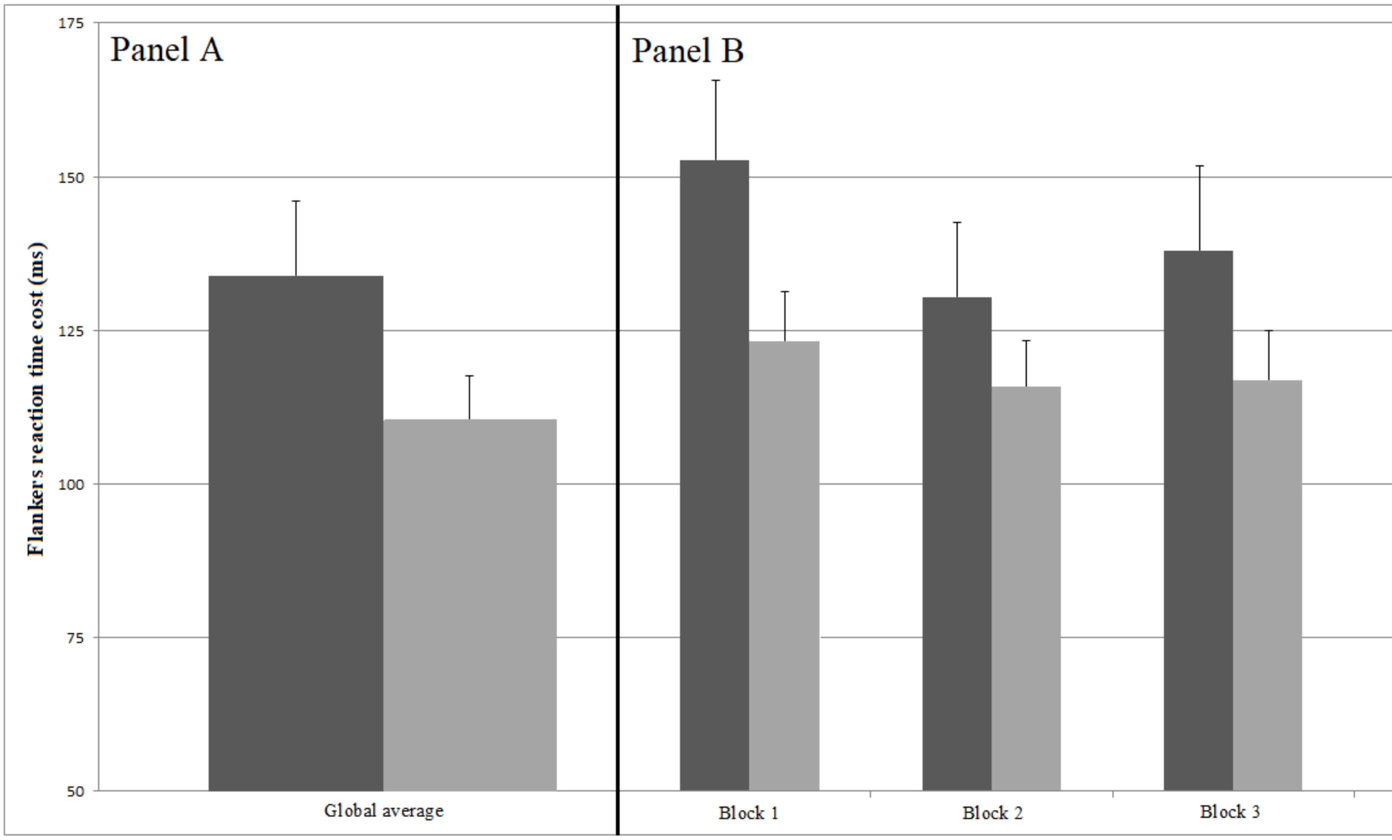


Figure 5. Flanker reaction time cost (incongruent - congruent RT) in spatial and response learners. Panel A shows global average reaction time cost. Panel B shows average reaction time cost by blocks. Error bars represent standard errors of the mean.

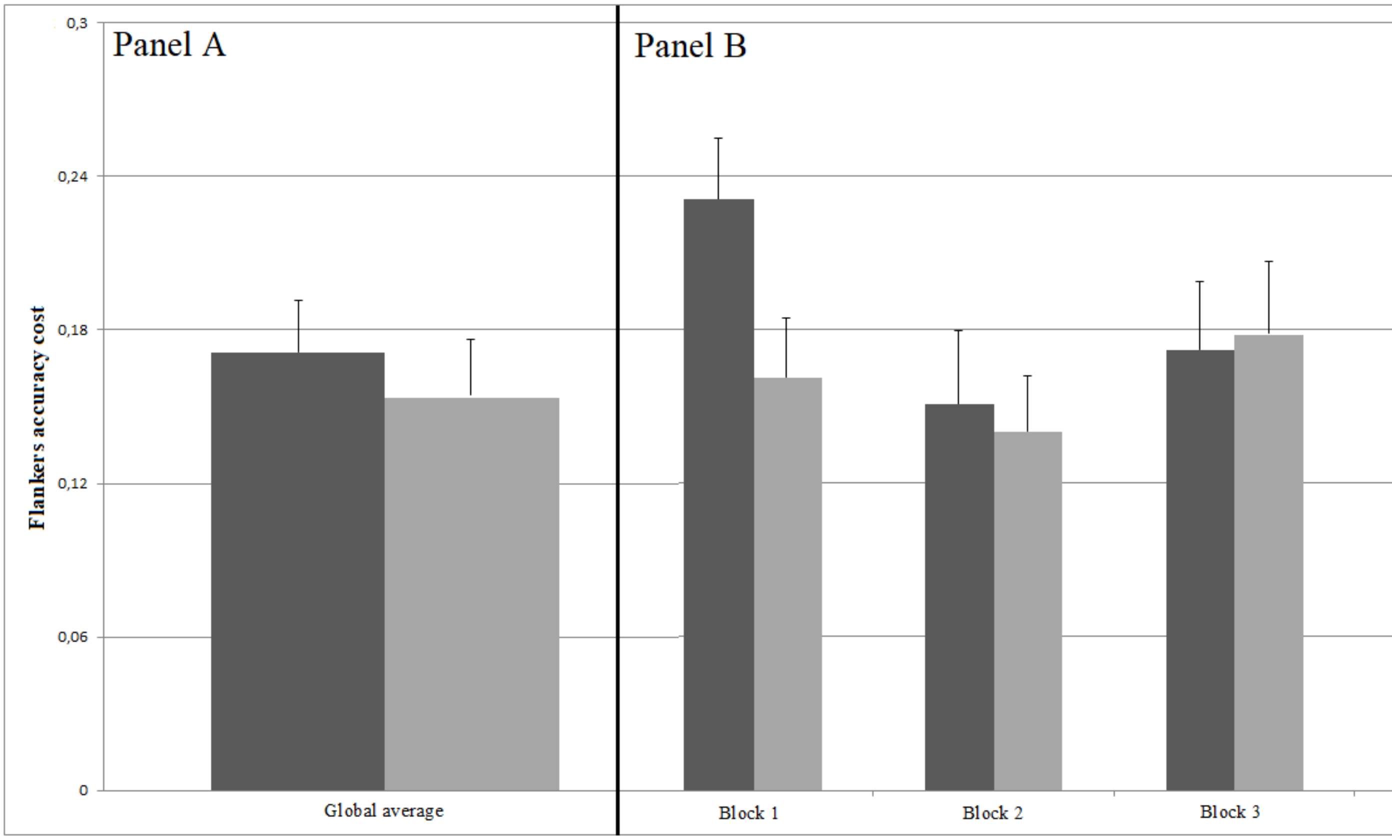


Figure 6. Flanker accuracy cost in spatial and response learners. Panel A shows global accuracy cost. Panel B shows accuracy cost (incongruent - congruent accuracy) by blocks. Error bars represent standard errors of the mean.