

Spatial Learners Display Enhanced Oculomotor Performance

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Attention is important during navigation processes that rely on a cognitive map, as spatial relationships between environmental landmarks need to be selected, encoded, and learned. Spatial learners navigate using this process of cognitive map formation, which relies on the hippocampus. Conversely, response learners memorize a series of actions to navigate, which relies on the caudate nucleus. The present study aimed to investigate the relationship between spatial learning and oculomotor performance. We tested 23 response learners and 23 spatial learners, as determined by the 4-on-8 Virtual Maze, on an antisaccade task with a gap and emotional visual stimulus manipulation. Spatial learners displayed decreased saccadic reaction time latencies compared to response learners. Performance cost from the gap manipulation was significantly higher in response learners. These results could represent an attentional practice effect through the use of spatial strategies during navigation or a more global increase in cognitive function amongst spatial learners.

Keywords: attention; eyetracking; egocentric/allocentric; navigation; spatial memory

Subject classification codes:

Introduction

When humans navigate, they spontaneously adopt different strategies, which rely on distinct parts of the brain (Bohbot, Lerch, Thorndyraft, Iaria, & Zijdenbos, 2007; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003). People can use a spatial strategy that involves building relationships between landmarks in the environment, resulting in the formation of an internal cognitive map of the environment. This type of learning is supported by the hippocampus (Alvarez, Zola-Morgan, & Squire, 1995; Bohbot et al., 2007; Etchamendy, Konishi, Pike, Marighetto, & Bohbot, 2012; Iaria et al., 2003; Konishi & Bohbot, 2013; Konishi et al., 2013; Lerch et al., 2011; Maguire et al., 2000; McDonald & White, 1993; O'Keefe & Nadel, 1978). In contrast, the response strategy involves learning a series of stimulus-response associations without encoding more global spatial relations among multiple locations. This strategy is supported by the caudate nucleus of the striatum (Alvarez et al., 1995; McDonald & White, 1993; Packard & McGaugh, 1992, 1996). While the strength of the tendency of individuals to use a strategy can be considered as a continuum, categorical measure by using the spontaneous navigation strategy has been shown to be a strong predictor of the grey matter volume and functional activity in the hippocampus and the caudate nucleus (Bohbot et al., 2007; Etchamendy et al 2012; Iaria et al., 2003; Konishi et al. 2013; West et al., 2017). Both strategies have similar prevalence within the normal population (Bohbot et al., 2007 & 2013; Etchamendy et al 2007; West et al, 2015 & 2017).

It is now well established that spatial and response learners display significant differences in neural structure and function. Specifically, spatial learners display more gray matter and functional activity in the hippocampus, while response learners have more gray matter and functional activity in the caudate nucleus (Bohbot, Iaria, & Petrides, 2004; Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013; Konishi

et al., 2013). More recent research has found that spatial and response learners display different visual attention profiles. Drisdelle et al., (2017) tested spatial and response learners on a visual target detection task designed to elicit a robust N2pc event related potential component. The N2pc is an electrophysiological index of visual spatial attention during target selection. It was found that spatial learners displayed a larger N2pc during the treatment of target stimuli compared to response learners. This observed enhanced attentional deployment in spatial learners is thought to underlie the fact that the spatial navigation strategy is more demanding on cognitive resources and requires to more efficient deployment of attention compared to the response strategy. This study, however, is the only evidence of such a difference in the visual attention domain between spatial and response learners. We therefore wanted to further test this hypothesis by measuring oculomotor performance using eyetracking. We employed a variant of an antisaccade paradigm that allowed for the testing of three specific hypotheses:

1) Spatial learners will display overall better oculomotor performance

Based on the findings of Drisdelle et al., (2017), we predicted that spatial learners would display shorter saccadic reaction time (SRT) latencies during an oculomotor task compared to response learners. Also supporting this hypothesis is evidence demonstrating that spatial learners make more saccades towards environmental stimuli during navigation (Andersen, Dahmani, Konishi, & Bohbot, 2012). Further, spatial learners display larger amounts of medial temporal lobe gray matter (Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013) which has been associated with better visual attention performance (Chun & Phelps, 1999).

2) *Response learners will display a larger gap effect magnitude*

The gap effect represents a pattern of SRTs where the removal of a fixation point before the initiation of a saccade produces faster latencies compared to overlap trials where the fixation remains present during saccade initiation (Dorris & Munoz, 1995; Jin & Reeves, 2009). This is due to the fact that fixation cells within the superior colliculus, which allow for stable eye fixations on an object in the visual environment, release their inhibition when the fixated stimulus is removed, thereby creating shorter SRTs (Dorris & Munoz, 1995). The circuit linked to this process involves connections between the pulvinar, caudate nucleus, substantia nigra, and superior colliculus (Hikosaka & Sakamoto, 1986). Further, the caudate nucleus has an inhibitory effect on the superior colliculus by way of connections through the substantia nigra that supports target fixation (Hikosaka & Sakamoto, 1986). Because response learners display more gray matter and functional activity in the caudate nucleus (Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013; Konishi et al., 2013), we predicted that response learners would show a greater SRT difference between gap and overlap trials due to increased inhibition from the caudate nucleus onto the superior colliculus.

To test these hypotheses we used a variant of an antisaccade task from van Steenbergen et al., (2011) that also included a gap manipulation (West, Al-Aidroos, Susskind, & Pratt, 2011). Participants were asked to perform a task where they were asked to saccade towards a target stimulus (prosaccade condition) or saccade towards the opposite side of the screen (antisaccade condition). We also tested if the display of an emotional stimulus would interact with the antisaccade (Steenbergen, Band & Hommel (2011)) or gap manipulations (West et al., 2011). Before the target appeared, a stimulus from the International Affective Pictures System (IAPS; Lang, Bradley, & Cuthbert, 2008) was presented, which was either positive, negative or neutral in

valence. Participants also completed the 4 on 8 virtual maze (Bohbot et al., 2007; Iaria et al., 2003), which distinguishes between individual who use either spatial or response strategies during navigation (i.e., spatial or response learners).

Methods

Participants.

Fifty healthy right-handed participants (11 male) who were an average of 23.4 (SD = 4.11) years of age were screened into the study. The sample size was based on the previous literature using the 4 on 8 virtual maze that has achieved enough statistical power to detect differences between spatial and response learners (Drisdelle et al., 2017; Bohbot et al. 2013 etc.). An extensive online questionnaire was administered to screen for history of psychiatric or neurological disorders. The questionnaire asked about the presence or history of motion sickness, cardiovascular diseases, neurological disorders, medical conditions, psychiatric disorders and substance abuse. Participants were screened for high levels of alcohol (> 14 alcoholic beverages per week) and cigarette use (> 10 cigarettes per day). Importantly, participants were screened for habitual action video game playing. Previous evidence from our laboratory suggests that habitual action video game players are biased towards using response strategies and have unique visual attentional profiles that differ from the normal population (West et al., 2015). We therefore only included non-action video game players in our sample to control for this potential confound. Testing occurred at the University of Montreal. Participants were recruited through word of mouth or through campus advertisements. Informed consent was obtained in conformity with the local ethics committee requirements. The participants who came on site to complete the study were offered a monetary compensation equal to \$10 CAD per hours spent for the study.

Tasks

4 on 8 Virtual Maze

As outlined in previous studies (Drisdelle et al., 2017; West et al., 2015), the 4/8VM is a virtual reality task that was created using programming software from a commercial computer game (Unreal Tournament; Epic Games, Raleigh, NC) (Figure 1). The virtual reality task consists of a radial maze with eight arms branching out from the center. The enriched environment contains both distal and proximal landmarks: a tree, a rock, and mountains. At the end of each arm are stairs that lead to a pit where, if a correct pathway was chosen, an object can be picked up. The pit is positioned to make sure that it is impossible to see the objects from the center of the maze so that the participant has to enter the pathway in order to verify if it is correct.

The number of trials is up to 10 with a minimum of 5. After 3 trials, additional trials are administered until the criteria is reached, which is no errors when retrieving the objects at the end of the radial arms. In the healthy young adults, these errors are not sensitive to detecting group differences and there is no observed effect between spatial and response learners. This is because the 4 on 8 has a dual task solution. People can either use the relationship between landmarks (spatial learners) or a rigid pattern (response learners) to solve the task with a similar level of accuracy. Each trial has 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 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, which is completing a trial without making any errors within the first three trials, a maximum of five extra trials are given until participants reach criteria. If the participant failed to reach criteria following the five extra trials, the experiment was stopped and the participant was removed from the analyses. This criterion ensures that all participants have learned the task before the single probe trial is administered.

Once this criterion is reached, a single 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 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 using the spatial strategy involving learning the locations of target objects in relation to landmarks will show an increase in errors when landmarks are removed. For example, a participant using the spatial strategy would remember the position of an object relative to the tree and the mountain, which are no longer present. On the other hand, participants using the response strategy would use a sequence of open and closed pathways from a single starting position, and therefore would have a perfect score on the probe trial even when landmarks are removed. Performance on the probe trial is therefore an objective measure of strategies. This probe score is used to confirm the spontaneous navigation strategy that is reported by the participant. The probe is then followed by a final standard trial with landmarks again displayed. The spontaneous navigation strategy is obtained with a standardized interview 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. 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 (Bohbot, Del Balso, Conrad, Konishi, & Leyton, 2013; Bohbot et al., 2004; Bohbot et al., 2007; Bohbot et al., 2012; Drisdelle et al., 2017; Iaria et al., 2003; West et al., 2015). On the first trial, if participants reported using two or more landmarks 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 reported strategy was evaluated by two experimenters who were blind to each other's evaluations. If there was a discrepancy between these two ratings, a third independent experimenter rating was administered. The task took forty minutes to complete. The single probe trial at the end of the task is used to confirm the spontaneous navigation strategy. People who report using a spatial strategy should display more probe errors when the landmarks are removed (Bohbot et al., 2007; Drisdelle et al., 2017; Iaria et al., 2003; Konishi et al., 2013; West et al., 2015).

Eyetracking task procedure

We adapted the paradigm described in van Steenbergen, Band & Hommel (2011) to include a gap manipulation. Experimental displays were presented on a 24 in. LED monitor at a refresh rate of 144 Hz and a resolution of 1920×1080 pixels. Each trial began with a central fixation ring. When gaze position was maintained on the ring $0.8^\circ \times 0.8^\circ$ for 1 s, an IAPS stimulus¹ ($16^\circ \times 12^\circ$) (Lang et al., 2008) was presented for 500

¹ Following the procedure of van Steenbergen, Band & Hommel (2011), the library numbers for the IAPS stimuli used in this study are: Negative: 2120, 2205, 2520, 2590, 2691, 2730, 2750, 2800, 3015, 3030, 3053, 3100, 3170, 3180, 3181, 3400, 3500, 3530,

ms. Similar to the procedure of West et al., 2011, at this point a gap manipulation was applied where the IAPS stimulus was immediately replaced by the target stimulus (overlap condition) or the image was removed for 200 ms (gap condition) until the target stimulus, consisting of a white square subtending $1.5^\circ \times 1.5^\circ$, was then 8° to the left or right of the screen centre. We used an 8° distance in order to be far enough allow a good discrimination between saccades within the IAPS image that may be initiated after its disappearance, while it is close enough to allow a good detection from the eyetracking device.

Prosaccade and antisaccade trials were separated by blocks. Presentation of block order was counterbalanced. On prosaccade trials participants were instructed to make a saccade towards the target. On antisaccade trials, participants were instructed to make a saccade towards to side of the screen opposite the target. After a practice blocks for each saccade condition consisting of 5 trials each, 6 experimental blocks consisted of 48 trials were administered. Every one of the 96 chosen IAPS pictures (32 per category) were pictures of people. They appeared three times in randomly chosen trials (van Steenbergen, Band, & Hommel, 2011).

Eyetracking data acquisition

Saccadic eye movements were recorded by measuring pupil position and corneal reflectance using a camera-based eye tracker (SR Research EyeLink 1000) with a

3550, 6210, 6211, 6212, 6821, 6834, 6838, 9041, 9250, 9300, 9341, 9405, 9800, 9921. Neutral: 2020, 2190, 2200, 2210, 2214, 2215, 2220, 2221, 2235, 2240, 2270, 2272, 2278, 2383, 2393, 2410, 2441, 2491, 2493, 2514, 2579, 2620, 2749, 2752, 2810, 2850, 2870, 2890, 3210, 5455, 7550, 9210. Positive: 2208, 2250, 2260, 2501, 2560, 2650, 4611, 4617, 4640, 4650, 4653, 4658, 4659, 4689, 5621, 8041, 8080, 8090, 8116, 8120, 8161, 8180, 8200, 8280, 8300, 8320, 8330, 8370, 8380, 8400, 8420, 8465.

temporal resolution of 500 Hz and a RMS spatial resolution of 0.01° of visual angle. Gaze position was established using a nine-point calibration and validation scheme. The beginning and end of saccadic eye movements were determined using a $30^\circ/s$ threshold with the additional criterion that the eye exceeded an acceleration of $8000^\circ/s^2$ during the movement. These are the default saccade detection settings used by the eyelink software.

Results

4 on 8 Virtual Maze

The initial spontaneous navigational strategy was first assessed for each participant according to verbal reports. Two independent raters evaluated the strategy used by each participant and classified them as initially using either a response or spatial strategy when completing the 4/8VM. There was a 91% inter-rater concordance. When there was discrepancy between both raters' evaluation, a third rater's evaluation was employed. This resulted in 23 participants being classified as spontaneously using a response strategy and 23 participants using a spatial strategy on the 4/8VM. No participants were chosen based on prior knowledge of their preferred strategy. No significant differences of age were observed between both group ($T(44) = -.746, p = .46$). As in previous studies (Bohbot et al., 2007; Drisdelle et al., 2017; Iaria et al., 2003; West et al., 2015; West et al., 2017), spatial learners made significantly more probe trial errors ($M = 0.86$ $SD = 0.35$) compared to response learners ($M = 0.17$ $SD = 0.39$; $t(44) = 6.25, p < 0.001$; Cohen's $d = 1.63$), confirming that spatial learners relied more heavily on external landmarks when navigating.

Eyetracking data

Trials with SRT outliers (< 80 or > 500 ms) were removed from analysis (2.8 % of trials). Only correct trials were included in all analyses in order to reduce the potential effect of speed-accuracy trade-off as a parasite variable coming from the reduced accuracy in antisaccade trials. Moreover, no significant interaction of correct trials and saccade type with the spontaneous strategy over reaction time was found, reducing the possibility of speed-accuracy trade-off interference on further group comparisons ($F(1) = .516, p = 0.476$). Reaction times and accuracies were submitted to a 2 (4 on 8 strategy: spatial; response) x 3 (Emotion: negative; positive; neutral) x 2 (Antisaccade condition: prosaccade; antisaccade) x 2 (Gap condition: gap; overlap) mixed factorial ANOVA. The analysis revealed a main SRT effect of Gap condition (Gap: $M = 191.34$ ms $SD = 27.21$; Overlap: $M = 260.90$ ms, $SD = 33.28$; $F(1,44) = 870.00, p < 0.001$; partial $\eta^2 = 0.952$), Emotion (Negative: $M = 239.55$ ms $SD = 26.24$; Positive: $M = 238.20$ ms $SD = 28.64$; Neutral: $M = 231.69$ ms $SD = 27.08$; $F(2,88) = 13.93, p < 0.001$; partial $\eta^2 = 0.432$) and saccade condition (Prosaccade: 197.21 ms $SD = 27.09$ Antisaccade: $M = 275.75$ ms $SD = 35.44$; $F(1,44) = 229.91, p < 0.001$; Cohen's $d = 2.49$). Bonferonni corrected paired t-test revealed that this main effect was driven by neutral trials producing faster RTs than negative trials ($t(45) = 4.8, p < 0.001$; Cohen's $d = 0.30$) and positive trials ($t(45) = 4.2, p < 0.001$; Cohen's $d = 0.23$).

The saccade and emotion condition did not interact with any other variable and were therefore collapsed for further analyses.

Importantly, a significant Gap condition x 4 on 8 Strategy was found, $F(1,44) = 4.67, p < 0.05$; partial $\eta^2 = .096$ (Figure 2). T-tests revealed that this group difference was being driven by the overlap condition (Overlap trials: Spatial Group $M = 250.33$ ms $SD = 38.39$ vs Response Group $M = 269.47$ ms $SD = 24.50$; $t(44) = 2.1 = , p < 0.05$;

Cohen's $d = .59$). The group difference was not significant in the gap condition (Gap trials: Spatial Group $M = 185.91$ ms $SD = 30.42$ vs Response Group $M = 196.78$ $SD = 22.97$; $t(44) = 1.37$; $p = 0.18$).

An examination of the accuracy data revealed a main effect of Emotion (Negative: $M = 80.5\%$ $SD = 10.0\%$; Positive: $M = 79.1\%$ $SD = 10.7\%$; Neutral: $M = 82.1\%$ $SD = 9.8\%$; $F(2,88) = 14.39$; $p < 0.001$; partial $\eta^2 = .310$). Bonferroni corrected paired t-test revealed that this main effect was driven by neutral trials producing a higher accuracy than negative trials ($t(45) = 3.4$, $p < 0.05$; Cohen's $d = 0.16$) and positive trials ($t(45) = 4.39$, $p < 0.001$; Cohen's $d = 0.29$). A main effect of Antisaccade condition was also found (Antisaccade trials $M = 65.1\%$ $SD = 19.0\%$ vs Prosaccade trials $M = 96.0\%$ $SD = 3.3\%$; $F(1, 44) = 128.81$; $p < 0.001$; partial $\eta^2 = .745$). No other significant main effects or interactions were observed.

We then tested our hypothesis regarding the difference in magnitude of the Gap effect between spatial and response learners. To do this, we computed the change in SRT between the overall Gap and Overlap trials to establish the performance cost associated with Overlap trials. This revealed a significant difference where response learners displayed a larger Gap effect ($M = -72.69$ ms $SD = 16.69$) compared to spatial learners ($M = -64.41$ ms $SD = 16.25$; $t(44) = 1.70$, $p < 0.05$; Cohen's $d = 0.50$, one-tailed test based on our a priori hypothesis) (Figure 3).

Discussion

Our two hypotheses were supported by the data. First, spatial learners displayed decreased SRT latencies on overlap trials. It is hypothesized that this decreased SRT is observed when the superior colliculus is not disinhibited before saccade initiation, as is the case during overlap trials (Dorris & Munoz, 1995). In other words, when spatial

learners had to disengage fixation on a stimulus towards another, their SRTs were faster compared to response learners. Second, response learners experienced a larger gap effect magnitude when comparing overlap and gap trials.

These data also suggest, by the absence of interaction with the saccade condition, that there is no significant difference between groups on the specific components related to each saccade type. The antisaccade condition is putatively related to oculomotor inhibition mediated in part by the frontal eye fields, while the prosaccade condition is related to attention orienting towards a given target (Munoz and Everling, 2004). Based on these data, these processes appear to be similar in both spatial and response learners.

Data from the current study supports the conclusions of Drisdelle et al., (2017) who found that spatial learners displayed enhanced visual spatial attention as indexed by the N2pc component. Together, these data suggest that spatial learners display more efficient attentional processing. It, however, is not yet known if these observations are due to the fact that spatial learners use landmarks to navigate in their everyday life, a process that is more attentionally demanding and therefore could train the attentional system to perform at a higher level. In contrast, these data could represent a more global level of cognitive health in spatial learners. Some preliminary evidences support this second view. Both younger and older adults who are spatial learners display more grey matter in the hippocampus (Bohbot et al., 2007; Iaria et al., 2003; Konishi & Bohbot, 2013; Konishi et al., 2013). The decreased grey matter in the hippocampus is a known biomarker for neuropsychiatric illness such as depression and some dementias (Albert et al., 2011; Apostolova et al., 2006). Further, younger adults who are spatial learners use fewer addictive substances (Bohbot et al., 2013). Future studies should investigate whether the observed differences in attentional performance

between spatial and response learners are directly related to the use of the spatial strategy and cognitive map construction or is a practice effect.

Studies measuring differences between both types of learners are of importance since they allow us to better understand the impacts employing different learning strategies in peoples' daily lives. Further, because spatial learners are known to perform better on certain neuropsychiatric tests related to spatial and episodic memory (Konishi et al., 2013; Bohbot et al., 2007), training programs are currently being developed to bias one's strategy towards spatial learning (Andersen, 2010) Because of this, it is also important to understand how spatial learning might possibly impact other cognitive processes such as visual attention and motor control.

In summary, we observed that spatial learners display increased oculomotor performance, a result that is supported by a previous finding related to visual spatial attention (Drisdelle et al., 2017). In contrast, response learners experienced an increased performance cost as reflected in the magnitude of the gap effect, which is hypothesized to be related to this group's increased gray matter and activity within the caudate nucleus. Future research should establish if these observed effects are due to an individual's direct experience using the spatial or response strategy.

This work was supported by the Natural Sciences and Engineering Research Council of Canada under Grant 436140-2013.

Disclosure of interest.

The authors report no conflict of interest.

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Figure 1. 4 on 8 virtual maze

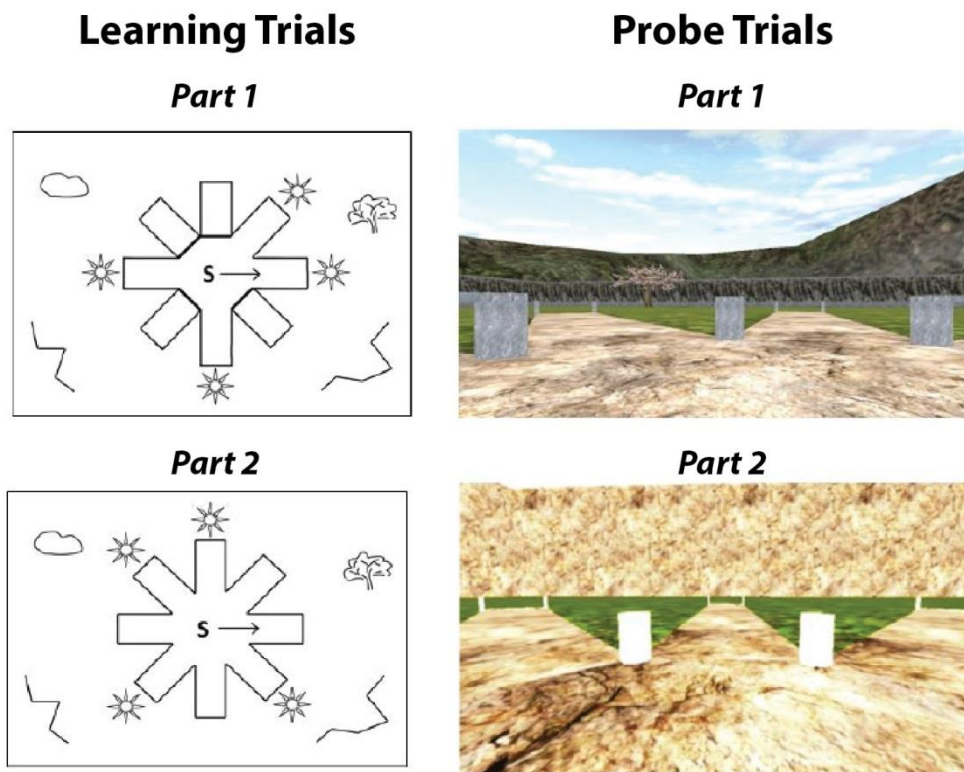


Figure 2. Gap condition by 4 on 8 strategy over response time

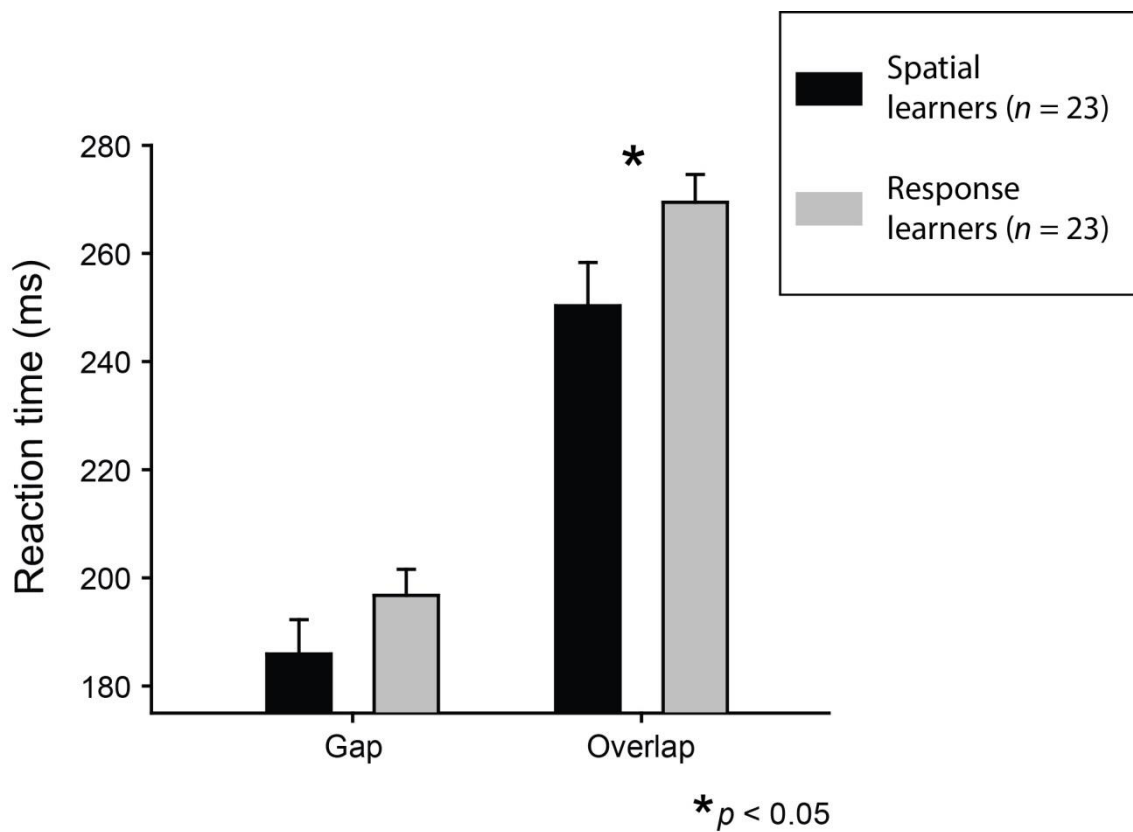


Figure 3. Gap magnitude by 4 on 8 strategy

