Olivier de Condappa[a] and Jan M. Wiener[a]
[a] Department of Psychology, Bournemouth University, Dorset, UK

Human Place and Response Learning: Navigation Strategy Selection, Pupil Size and Gaze Behavior

Corresponding author at: Oliver de Condappa, Department of Psychology, Faculty of Science and Technology, Bournemouth University, Talbot Campus, Fern Barrow, Poole, Dorset, BH12 5BB, UK. Tel: +44 1202 962209
E-mail addresses: odcondappa@bournemouth.ac.uk, jwiener@bournemouth.ac.uk

Abstract

In this study, we examined the cognitive processes and ocular behavior associated with on-going navigation strategy choice using a route learning paradigm that distinguishes between three different wayfinding strategies: an allocentric place strategy, and the egocentric associative cue and beacon response strategies. Participants approached intersections of a known route from a variety of directions, and were asked to indicate the direction in which the original route continued. Their responses in a subset of these test trials allowed the assessment of strategy choice over the course of six experimental blocks. The behavioral data revealed an initial maladaptive bias for a beacon response strategy, with shifts in favour of the optimal configuration place strategy occurring over the course of the experiment. Response time analysis suggests that the configuration strategy relied on spatial transformations applied to a viewpoint-dependent spatial representation, rather than direct access to an allocentric representation. Furthermore, pupillary measures reflected the employment of place and response strategies throughout the experiment, with increasing use of the more cognitively demanding configuration strategy associated with increases in pupil dilation. During test trials in which known intersections were approached from different directions, visual attention was directed to the landmark encoded during learning as well as the intended movement direction. Interestingly, the encoded landmark did not differ between the three navigation strategies, which is discussed in the context of initial strategy choice and the parallel acquisition of place and response knowledge.

Introduction

Spatial knowledge is typically acquired through place or response learning. In place learning, spatial knowledge is encoded relative to environmental features, while stimulus-response associations are encoded relative to the navigator in response learning (O'Keefe & Nadel, 1978; Tolman, 1948). Response learning can be further subdivided into the associative cue and beacon strategies. In the associative cue strategy, landmarks are associated with an explicit directional behavior (e.g. "turn left at the church"; Tlauka & Wilson, 1994), and in the beacon strategy, landmarks that spatially correspond with one's movement during learning activate a general behavioral action (e.g. "turn towards the church"; Waller & Lippa, 2007). Wiener, de Condappa, Harris and Wolbers (2013) recently introduced a novel route learning paradigm to examine the effects of cognitive aging on the employment of place and response strategies, which recruit the hippocampal circuit and the striatal system respectively (Iaria, Petrides, Dagher, Pike & Bohbot, 2003; Marchette, Bakker & Shelton, 2011). Two landmarks positioned at diagonally opposite corners of each intersection within a route (see Fig. 1) allowed for the use of a place, associative cue or beacon strategy during learning. Varying the approach direction to each intersection at test and asking participants to indicate the direction in which the original route proceeded allowed Wiener et al. (2013) to assess place, associative cue and beacon strategy use during the acquisition of spatial knowledge (see Fig. 1).While all three strategies resulted in successful navigation when approaching an intersection from the same direction experienced during learning, only a place strategy ensured accurate navigation when intersections were approached from an unfamiliar direction. Use of a place strategy in this environment involved encoding the spatial configuration of landmarks relative to the movement experienced through an intersection. This place strategy was referred to as the configuration strategy. Young participants increasingly adopted the optimal configuration strategy **over the course of six experimental blocks, suggesting that they recognised that only a place strategy would result in correct navigational responses in all test trials, and developed configural place knowledge accordingly. In contrast,** older adults **were unable** to adopt the **correct place** strategy**, which** was attributed to age-related hippocampal degeneration. The aim of the current study was to develop a better understanding of the cognitive processes involved in the selection and use of different navigation strategies. Specifically, we investigated the spatial decision making process underlying the configuration strategy, and participants' ocular behavior whilst employing and shifting between the configuration, associative cue and beacon navigation strategies. To do so, we employed an eye tracking variant of the task described in Wiener et al. (2013).

As discussed in Wiener et al. (2013), the spatial decision making process underlying the configuration strategy either involves (i) spatial transformations to relate the viewpoints experienced during training and test when approaching an intersection or (ii) direct access to allocentric place knowledge (O'Keefe & Nadel, 1978; Tolman, 1948). The former process is consistent with an account of place learning in which spatial knowledge is associated with views of landmarks experienced during learning (Hamilton, Driscoll & Sutherland, 2002). In the current paradigm, this process would rely on a viewpoint-dependent representation of an intersection (Shelton & McNamara, 2001; Wang & Spelke, 2002) subjected to mental rotation or perspective-taking transformations (see Hegarty & Waller, 2004), both of which have been implicated in a number of navigational tasks (Kozhevnikov, Motes, Rasch & Blajenkova, 2006). Such viewpoint-dependent place recognition should be sensitive to approach direction and would incur cognitive and time related costs that increased relative to the angular discrepancy between **the approach directions experienced during training and test** (Diwadkar & McNamara, 1997; King, Burgess, Hartley, Vargha-Khadem & O'Keefe, 2002). In contrast, direct access to a viewpoint-independent allocentric representation of an intersection should be independent of approach direction and would result in similar response times across all test trials. To distinguish between these two accounts, we analysed response times for test trials **in which the approach direction compared to training was either identical or different. Specifically, in** *same-direction* **trials, intersections were approached from the same direction experienced during training, whereas the approach direction in** *different-direction* **trials differed from training by either 90° or 180° (see Figure 3a). It should be noted, however, that participants may use different navigation strategies for different test trials. Hartley, Maguire, Spiers and Burgess (2003) found that good navigators can switch strategies depending on the demands of the navigation task, with "route following" (i.e.** *same-direction* **trials) performed most efficiently by response strategies, and "wayfinding" (i.e.** *different-direction* **trials) requiring a place strategy. Therefore, assuming that a place strategy is only employed during** *different-direction* **trials, the critical comparison to identify the spatial decision making process underlying the configuration strategy was between test trials with an angular discrepancy of 90° and 180° compared to training**.

To our knowledge, few studies relate ocular behavior during navigation to the use of different strategies. These studies primarily employed human variants of the virtual Morris Water Maze Task (MWMT), in which proximal and distal cues selectively facilitate response and place strategies respectively. Mueller, Jackson, and Skelton (2008) assessed pupil size, which corresponds with cognitive load (see Beatty, 1982), and

gaze behavior during two types of test trials that required either response or place knowledge. During visible platform trials, participants started from a variety of positions within a circular arena containing distal cues only, and were asked to navigate towards a visible target platform that changed location from trial to trial. Successful navigation in these test trials relied on a response strategy related to a proximal cue (the visible target platform). During invisible platform trials, participants were asked to navigate from a variety of start positions to a hidden platform that remained in the same location across trials. Successful navigation in these test trials required use of a place strategy that encoded the spatial relationship between distal cues and the hidden platform. Mueller et al. (2008) reported larger pupil size at the beginning of test trials that required place knowledge, reflecting the increased cognitive effort associated with place strategies compared to response strategies (Iaria et al., 2003). Furthermore, participants preferentially attended to proximal cues during response navigation and distal cues during place navigation. In another study, Livingstone-Lee and colleagues (2011) employed two virtual MWMTs to determine whether gaze behavior could be used to identify which navigation strategies participants were employing. In a maze designed to elicit response navigation, participants started from a variety of positions within a circular arena containing both proximal and distal cues, and were asked to navigate towards a hidden target platform that changed location from trial to trial. The position of one of the proximal cues varied in each trial such that it was the cue nearest the invisible platform and supported the use of a response strategy. A second maze designed to elicit place navigation contained only distal cues. Participants were again asked to navigate from a variety of start positions to a hidden platform that remained in the same location across trials. In this maze, successful navigation required place knowledge of the spatial relationship between distal cues and the hidden platform. Livingstone-Lee et al. (2011) revealed that participants primarily attended to proximal cues when employing a response strategy, and distal cues when employing a place strategy.

However, it should be noted that in these studies, response and place navigation occur when performing tasks of varying difficulty (Mueller et al., 2008) or in different environments (Livingstone-Lee et al., 2011). These test phases and wayfinding environments were intentionally designed to impose a specific navigation strategy on participants, with alternative strategies rendered ineffectual or not supported by the available cues. Therefore, it is not surprising that participants preferentially attended to cues that selectively supported the only reliable navigation strategy available. Furthermore, pupil size differences between the visible and invisible platform trials in the study by Mueller et al. (2008) could be attributed to task difficulty (Hess & Polt, 1964), rather than the respective cognitive demands of place and response navigation. In addition, only the ocular behavior at the beginning of each test trial is analysed in these studies, and not the entire spatial decision making process. In the study by Mueller et al. (2008), the observed pupil size differences are associated with the first 50ms of each test trial, while eye tracking data was only collected during the first three seconds of each test trial. Similarly, Livingstone-Lee et al. (2011) restricted the analysis of gaze behavior to the first second of each trial.

In the current study, the configuration, associative cue and beacon strategies are all supported by stable visual cues in the environment, and participants are required to perform the same task throughout the experiment. Therefore, and in contrast to studies that use variants of the MWMT, ocular behavior associated with the use of different navigation strategies occurs in the same environment under identical task demands. Furthermore, participants were free to employ a navigation strategy of their choice throughout the experiment, and participants' ocular behavior during entire test trials was recorded and analysed. Specifically, we examined how strategy choice affected pupil size **and dilation** (Marshall, Pleydell-Pearce & Dickson. 2003). **Task-evoked pupillary responses revealed that variations in pupil size reflect cognitive load, with tasks of greater complexity or difficulty associated with increases in pupil size, known as pupil dilation (Beatty, 1982; Hess & Polt, 1964; Just & Carpenter, 1993; Kahneman & Beatty, 1966). In terms of wayfinding strategies, employing a response strategy typically requires less cognitive effort than a place strategy. Accordingly, the simple stimulus-response associations involved in response strategy use result in shorter response times compared to place strategy use (Iaria et al., 2003; Wiener et al., 2013). Therefore,** if, as observed in Wiener et al. (2013), young adults increasingly adopt the more cognitively demanding configuration strategy, we expected pupil dilation to increase over the course of the experiment. Furthermore, we examined gaze behavior during configuration, associative cue and beacon strategy use. **Two factors known to influence visual attention during landmark-based wayfinding are the location of decision relevant information (i.e. the encoded landmark) and the intended movement direction (Grasso, Prévost, Ivanenko & Berthoz, 1998; Wiener, de Condappa & Höelscher. 2011; Wiener, Höelscher, Büchner & Konieczny, 2012). Unlike the landmarks in the MWMTs discussed above (Mueller et al., 2008; Livingstone-Lee et al., 2011), the environmental cues available in this paradigm can support multiple navigation strategies. This allowed us**

to analyse differences in gaze behavior when employing different strategies to gain insight into strategy-specific landmark usage during route learning and subsequent navigation.

Materials and Method

Participants

54 participants (31 females) were tested. The age range of participants was 18–43 (mean-22.02). All participants had normal or corrected-to-normal vision and received course credits or £6 for their participation.

Apparatus

Eye movements were captured using an EyeLink 1000 (SR Research Ltd.) eye tracker sampling right eye pupil position and size at 500Hz. Calibration was performed and checked for accuracy before each experimental block using a nine point grid. The experiment was presented on a 19" CRT monitor with a resolution of 1024x768 and a refresh rate of 100Hz. A standard computer keyboard was used to record responses. Participants were seated 60cm from the monitor and a desktop mounted chin rest was used to minimize head movement.

Virtual Environment

The virtual environment was constructed using WorldViz Vizard 3.0, and consisted of four-way intersections. Each intersection featured two unique landmarks located in diagonally opposite corners, allowing recognition of the intersection and identification of the approach direction (see Fig.1a). Black fog within the environment ensured only one intersection was visible from any position on the route.

Fig. 1 about here

Fig. 1 Virtual environment and navigation task. **a** A screenshot of an intersection. **b** An overview of the route, and two test trials. In *same-direction* trials, the approach direction is identical to training. Employment of any of the navigation strategies discussed results in successful navigation. In *different-direction* trials, the approach direction is different to training. In the example provided, each navigation strategy results in a different response, allowing the strategy employed to be identified

Procedure

Participants learned and were tested on a single route consisting of two left turns and two right turns. The experiment was conducted over six experimental blocks, each consisting of a training phase and a test phase. During each training phase, participants were twice passively navigated along a route. Their task was to learn the route shown. During the test phase, participants were presented with screenshots of each intersection taken from the approach direction experienced during training (*same-direction* trials), or, excluding the direction requiring reverse navigation along the original route, from the two remaining possible approach directions (*different-direction* trials) (see Fig. 1b). **Participants were informed before the experiment that they would approach intersections from various directions, and** were asked to indicate the direction of travel required to proceed along the original route by pressing the left, right or up (i.e. straight) arrow key on the keyboard provided. Both responses and response times were recorded. Prior to each test trial, a mask consisting of a scrambled image presented during test trials with blank landmarks and a centrally located fixation cross was presented for 1.5 seconds. As the route contained four turnings, each test phase consisted of four *same-direction* trials and eight *different-direction* trials presented in a random order. *Same-direction* trials test a participant's ability to recognise an intersection and repeat the movement made during training. These trials are equivalent to measures typically used to assess spatial knowledge (e.g. Wiener **et al.**, 2011), and can be solved by employing a configuration, associative cue or beacon strategy. In contrast, correctly solving *different-direction* trials required a place strategy with knowledge of the spatial relationship between landmarks at an intersection and the goal arm. **Therefore, only use of the configuration strategy would result in successful navigation in both** *same-direction* **and** *different-direction* **trials.** [1] For each experimental block, responses made in two specific *different-direction* trials (see Fig. 1b for an example of such a trial) were used to identify the navigation strategy employed by a participant. In these test trials, **use of** the associative cue and beacon strategies **result in** different, incorrect **responses**, while the configuration strategy **results in** the correct response. Therefore, participants' responses in these test trials allowed the assessment of strategy preference over the course of the experiment. **Furthermore, as participants** did not receive any feedback about the accuracy of their responses **during the experiment, their strategy choice was self-selected, and not influenced by the experimental procedure**.

Eye tracking measures

Pupil size and gaze position were measured during the entirety of the pre-trial mask and test trial. Average pupil size during test trials was compared against a baseline measure of the average pupil size during the preceding mask. The difference between these two values was calculated to determine average pupil dilation during each

test trial. Fixations occurring outside the screen or under 100ms were removed (Andersen, Dahmani, Konishi & Bohbot, 2012; Manor & Gordon, 2003; Mueller et al., 2008).

Data Analysis

Gender was included as a factor for all ANOVAs conducted in this paper, but failed to exhibit any significant main effects or interactions.

Results

Data from two participants were excluded from the final data set as their performance at *same-direction* trials did not significantly exceed chance level, suggesting an inability to learn the route **(see Wiener et al., 2013)**. The remaining fifty-two participants (29 females, age range 18 – 43, mean age 21.60) entered the behavioral analysis, with a further participant excluded from the oculomotor analysis due to technical problems with the eye tracker.

Navigation Performance

Participants chose the correct movement direction in 62% of all trials (*same-direction*: 88%, *different-direction*: 49%). An ANOVA with approach direction [same, different] and experimental block [1-6] as within-participants factors revealed that performance at *same-direction* trials was better than at *different-direction* trials [$F(1, 50) = 213.43, p < .001, \eta_p^2 = .81$], and performance improved over experimental blocks [$F(3.84, 192.17) = 23.89, p < .001, \eta_p^2 = .32$] (see Fig. 2a). A significant approach direction x experimental block interaction [$F(3.70, 184.81) = 5.32, p = .001, \eta_p^2 = .10$] suggested that performance at *same* and *different-direction* trials evolved differently over the experiment. However, planned contrasts revealed that performance improved across experimental blocks for both *same-direction* trials [$F(4.17, 212.74) = 9.78, p < .001, \eta_p^2 = .16$] and *different-direction* trials [$F(3.05, 155.31) = 19.28, p < .001, \eta_p^2 = .27$], replicating results for young participants reported by Wiener et al. (2013).

<u>**Fig**. **2** about here</u>

Fig. 2 Navigation performance and strategy choice. **a** Performance at *same-direction* and *different-direction* test trials across experimental blocks (mean±standard error). **b** Strategy choice in selected *different-direction* trials across experiment blocks

Navigation Strategy Preference

In those *different-direction* trials used to identify participants' strategy choices (see Fig. 1b), 37% of responses were consistent with configuration strategy use, 21% were consistent with associative cue use and 42% were consistent with beacon strategy use.[2] To assess strategy preference across experimental blocks (see Fig. 2b), separate ANOVAs were conducted for each strategy with experimental block as a within-participants factor and percentage of responses in line with each navigation strategy as the dependent variable. Across experimental blocks, associative cue strategy use [$F(3.59, 179.49) = 4.39, p = .003, \eta_p^2 = .08$] and beacon strategy use decreased [$F(3.71, 185.67) = 5.18, p = .001, \eta_p^2 = .09$], while configuration strategy use increased [$F(3.95, 197.53) = 16.08, p < .001, \eta_p^2 = .24$]. This demonstrates that the configuration strategy was increasingly adopted over the course of the experiment, while use of associative cue and beacon strategies decreased. Furthermore, one sampled t-tests against chance level (33%) revealed a systematic bias for the beacon strategy in the first experimental block ($M = 50.96\%, SD = 41.41; t(51) = 3.07, p = .003, r = .39$), while use of the configuration strategy was below chance level ($M = 18.27\%, SD = 32.88; t(51) = -3.30, p = .002, r = .42$) and associative cue use did not differ from chance level ($M = 30.77\%, SD = 37.25; t(51) = -.50, p = .62, r = .07$). Taken together, this demonstrates that participants initially employed a suboptimal beacon response strategy, before identifying and shifting to the optimal place strategy.

Response Time

To distinguish between two different accounts of the spatial decision making process underlying the configuration strategy, an analysis of response times at test trials with differing amounts of angular discrepancy between training and test was conducted (see Fig. 3a). The approach direction of *same-direction* trials is identical to training (0° of angular discrepancy; $M = 4.39$s), while the approach direction of *different-direction* trials differs from training by 90° ($M = 5.46$s) or 180° ($M = 6.03$s). An ANOVA with angular discrepancy [0°, 90°, 180°] as a within-participants factor revealed a significant main effect of angular discrepancy on response times [$F(1.69, 84.71) = 19.25, p < .001, \eta_p^2 = .28$] (see Fig. 3b). Bonferroni corrected pairwise comparisons revealed that response times increased as the angular discrepancy between the approach directions during training and test increased (0° vs. 90°, $p < .001$; 0° vs. 180°, $p < .001$; 90° vs. 180°, $p = .01$), suggesting that users of the configuration strategy rely on viewpoint-dependent place recognition.

Fig. 3 about here

Fig. 3 Test trial approach directions and response times. **a** Test trials with different angular discrepancies between the approach directions during training and at test. **b** Response time by angular discrepancy between training and test approach directions (mean±standard error)

Ocular Behavior

Pupil Size

Separate ANOVAs revealed that average pupil size decreased across experimental blocks during test trials [$F(1.84, 88.33) = 13.59$, $p < .001$, $\eta_p^2 = .22$] (Fig. 4a) and presentation of the mask [$F(2.69, 129.31) = 25.24$, $p < .001$, $\eta_p^2 = .35$], and average pupil size was larger during *different-direction* trials compared to *same-direction* trials [$F(1, 48) = 4.30$, $p = .044$, $\eta_p^2 = .08$] (Fig. 4b). The approach direction of the subsequent test trial did not affect average pupil size during presentation of the mask, and no interactions were observed (all $p > .05$). The decrease in pupil size across experimental blocks during test trials and presentation of the mask is consistent with effects attributed to learning (Mueller et al., 2008; Sibley, Coyne & Baldwin, 2011). Furthermore, larger pupil size during *different-direction* trials as compared to *same-direction* trials may reflect the additional cognitive effort required by users of the configuration strategy to perform spatial transformations when the approach directions during training and test are not identical.

Fig. 4 about here

Fig. 4 Pupillometry data. **a** Test trial pupil size across experimental blocks (mean±standard error). **b** Baseline pupil size across experimental blocks (mean±standard error). **c** Pupil dilation across experimental blocks (mean±standard error)

Pupil Dilation

While pupil size decreased over the course of the experiment, pupil dilation – i.e. the **task-related change** in average pupil size between the mask and test trial – increased [$F(3.27, 157.06) = 7.54$, $p < .001$, $\eta_p^2 = .14$] (Fig. 4c), although there was no significant main effect of approach direction or an interaction (both $p > .05$). This increase in pupil dilation over the course of the experiment is thought to reflect the increasing adoption of the cognitively more demanding configuration strategy. This was corroborated by a Pearson's product-moment correlation between the change in pupil dilation from block 1 to 6 and performance at *different-direction* trials, which is a measure sensitive to configuration strategy use. Analysis revealed a positive correlation [$r(51) = .39$, $p = .002$], suggesting pupil dilation is sensitive to the employment of place strategies.

Gaze Behavior

Same-Direction Trials

Fig. 5 about here

Fig. 5 Gaze behavior at *same-direction* trials. **a** Intersections where the route continued left. **b** Intersections where the route continued right

An analysis of dwell times in correct *same-direction* trials (see Fig. 5ab) revealed that participants' did not distribute gaze equally between both landmarks at an intersection, but preferentially attended to the landmark that spatially coincided with the correct response, and towards which movement occurred during learning ($M=62.74\%$, $SD=8.82$; one-sampled t-test against chance level (50%): $t(50) = 10.32$, $p < .001$, $r = .82$). This systematic gaze bias can be explained by (i) participants selectively encoding the landmark located in the direction of movement during learning (the route congruent landmark), and primarily attending to this landmark at test to inform the spatial decision making process, (ii) anticipatory gaze behavior towards the intended movement direction, or (iii) a combination of (i) and (ii). However, as the route congruent landmark and the response made by all three navigation strategies spatially coincide in *same-direction* trials, the influence of these factors on gaze behavior cannot be separated. Those *different-direction* trials used to identify strategy choice, in contrast, allowed us to separate the influence of the route congruent landmark and the chosen movement direction on gaze behavior.

Different-Direction Trials

Fig. 6 Gaze behavior at the selected *different-direction* trials used to identify navigation strategy. The route congruent landmark during training is located on the left of the featured intersection (the snake). **a** Beacon responses (chosen response was LEFT). **b** Associative cue responses (chosen response was RIGHT). **c** Configuration responses (chosen response was STRAIGHT)

In *different-direction* trials, the location of the route congruent landmark remained the same while participants' movement decisions differed depending on the strategy employed. This dissociation allowed us to assess the impact of the position of the route congruent landmark and the chosen movement direction on visual attention during spatial decision making. In the examples depicted in Fig. 6, the location of the route congruent landmark (located on the left-side of the featured intersection) and the response direction spatially correspond when employing the beacon strategy (response: left) (Fig. 6a), are diametrically opposed when using the associative cue strategy (response: right) (Fig. 6b), and are adjacent to one another for the configuration strategy (response: straight) (Fig. 6c). If participants encode the route congruent landmark, and gaze behavior is primarily influenced by the location of that landmark, participants will preferentially attend to the route congruent landmark independent of their preferred strategy and chosen movement direction (Route Congruency Model) (Fig. 7a). If, on the other hand, gaze behavior primarily reflects the intended movement direction (Direction of Response Model), the route congruent landmark will be preferentially attended to during beacon responses, visual attention during associative cue responses will be directed towards the route incongruent landmark, and attention during configuration responses will not exhibit a systematic bias for either landmark (Fig. 7b). Should both the location of the route congruent landmark and the intended movement direction influence attention, gaze behavior when employing each navigation strategy will reflect an average of the predictions made by the Route Congruency and the Direction of Response Models (The Combined Model) (Fig. 7c). The predictions for the gaze behavior of these three models were calculated using the gaze bias observed in *same-direction* trials (M=62.74) and compared to actual gaze data recorded during the test phase (dwell time percentage for route congruent landmark: configuration responses - M=60.80, SD=18.43, associative cue responses - M = 49.36, SD = 15.17, and beacon responses - M = 64.92, SD = 12.87) (Fig. 7d).[3] A Friedman's ANOVA with model [Route Congruency, Direction of Response, Combined] as a within-participants factor and the absolute difference between the participants' gaze behavior and each predictive model as the dependent variable revealed a significant main effect of model [$\chi^2(2) = 7.72$, $p = .021$], suggesting that there was a difference between the residual values of the three models. Post-hoc Wilcoxon signed rank tests with Holm-Bonferroni corrected alpha levels revealed that the Combined model fitted the participants' gaze data better than both the Direction of Response model ($Z = -2.56$, $p = .01$, $r = .25$) ($\alpha = .016˙$) and the Route Congruency model ($Z = -2.34$, $p = .019$, $r = .23$) ($\alpha = .025$), suggesting that, irrespective of strategy, participants primarily attended to the route congruent landmark and the direction of intended movement during navigation.

Fig. 7 Predictive models of gaze behavior and participant data. **a** Predicted gaze behavior of different strategy users if only the location of the route congruent landmark influences visual attention. **b** Predicted gaze behavior if only the direction of the response made influences attention. **c** Predicted gaze behavior if both the location of the route congruent landmark and the direction of response influence attention. **d** Participant Data (mean±standard error)

Discussion

We investigated navigation strategy preference during the acquisition of spatial knowledge and the oculomotor behavior associated with these choices. Knowledge of a previously learned route was tested by assessing participants' responses when approaching intersections within the route from various directions. While both place and response strategies resulted in successful navigation when approaching an intersection from the same direction experienced during learning, accurate navigation when an intersection was approached from an unfamiliar direction required the use of a configural place strategy. Participants displayed an initial bias for the suboptimal beacon response strategy, with the configuration strategy increasingly adopted over repeated training and test phases, replicating findings previously observed in young adults (Wiener et al., 2013). Response times increased as the angular discrepancy between approach directions experienced during training and test increased, suggesting that the configuration strategy relied on viewpoint-dependent spatial representations. Furthermore, increased use of the configuration strategy over the course of the experiment was associated with increased pupil dilation, reflecting the additional cognitive effort required to employ a place strategy compared to response strategies. Finally, analysis of gaze behavior revealed a strategy-independent preference for attending to (i) the landmark located in the movement direction during training and (ii) the direction of intended movement.

In this study, participants initially employed a beacon response strategy, before shifting to a configural place strategy, replicating shifts from a response strategy to a place strategy found in previous studies (Cassel, Kelche, Lecourtier & Cassel, 2012; Iglói, Zaoui, Berthoz & Rondi-Reig, 2009). While it is not surprising that participants increasingly adopted the most successful navigation strategy over the course of the experiment, our results contrast with findings that suggest hippocampus dependent place strategies develop earlier in the learning process and are acquired faster than striatal dependent response strategies (Iaria et al., 2003; Packard & McGaugh, 1996; Schmitzer-Torbet, 2007). **Instead, our findings broadly support the framework proposed by Siegel and White (1975) for the development of spatial knowledge, which states that individuals initially acquire** *landmark knowledge* **to support the identification of known places. This is followed by** *route knowledge* **– i.e. the temporal organisation of landmarks associated with behavioral actions –which is functionally equivalent to ordered landmark-based response strategy knowledge. Finally, individuals acquire** *survey knowledge* **in the form of a configural, topographic environmental representation.** Furthermore, participants' bias for a beacon response strategy in the first experimental block may reflect an initial preference for the most parsimonious navigation strategy, as in contrast to the beacon strategy, both the associative cue and configuration strategies require further spatial knowledge in addition to the encoded landmark(s). This may explain why participants initially selected the simplest, albeit suboptimal, navigation strategy – i.e. the beacon response strategy - before shifting to a more cognitively demanding and accurate place strategy. **Accordingly, few participants employed the associative cue strategy during the experiment, as it was neither the most cognitively efficient nor the most accurate navigation strategy.**

Analysis of response times allowed us to determine whether the spatial decision making process underlying the configuration strategy involved (i) spatial transformations to relate the viewpoints experienced during training and test or (ii) direct access to a viewpoint-independent allocentric representation of an intersection. Response times increased as the angular discrepancy between the approach directions during training and test increased, suggesting that participants spatially transformed their viewpoint during configuration strategy responses. Therefore, configuration strategy responses rely on viewpoint-dependent place recognition, which has been shown to be hippocampus-dependent (King et al., 2002). This finding supports an account of place learning in which spatial knowledge is associated with views of landmarks experienced during learning (Hamilton et al., 2002).

Analysis of pupillometry revealed three effects. First, average pupil size decreased over the course of the experiment, which can be explained by learning effects and/or the transfer of task relevant information from working memory to long-term memory (Mueller et al., 2008; Sibley et al., 2011). Second, average pupil size was larger during *different-direction* trials compared to *same-direction* trials, which is thought to reflect the additional cognitive effort required by users of the configuration strategy to transform viewpoints when the approach directions during training and test did not match. Finally, pupil dilation (i.e. the difference in average pupil size during the mask and subsequent test trial) increased over the course of the experiment as participants increasingly adopted the more cognitively demanding configuration strategy. Therefore pupil dilation, which is considered a reliable physiological indicator of cognitive load (Beatty, 1982), may be sensitive to shifts between response and place strategies. **However, as employing a place strategy typically results in longer response times than a response strategy (Iaria et al., 2003; Wiener et al., 2013), and as participants increasingly employed the configuration strategy over the course of the experiment, it is possible that our pupillometry**

findings may be attributed to mental fatigue, which is known to result in increased fluctuations in pupil size (Lowenstein, Feinberg & Loewenfeld, 1963; Nishiyama, Tanida, Kusumi & Hirata, 2007). However, it should also be noted that task performance typically decreases as a consequence of fatigue (Boksem, Meijman & Lorist, 2005; Mathews & Desmond, 2002). In contrast, participants' performance improved over the course of the experiment, which makes fatigue an unlikely explanation for the observed increases in pupil dilation.

The distribution of visual attention during *different-direction* trials was influenced by two factors: (i) the landmark located in the direction of movement during learning (the route congruent landmark) and (ii) the intended movement direction. Interestingly, participants exhibited a bias for the same landmark irrespective of their chosen navigation strategy, suggesting a strategy independent preference for encoding the route congruent landmark. Given that place and response learners typically attend to different environmental cues (Livingstone-Lee et al., 2011; Mueller et al., 2008), why is the same landmark encoded by the configuration, associative cue and beacon strategies in this paradigm? Firstly, the route congruent landmark naturally serves as a beacon, as the route turns in the direction of this landmark during training. As participants initially employed a beacon strategy before shifting to a configuration strategy, the continued preference for this landmark may be explained by participants **relating the** additional spatial knowledge required for the configuration strategy with the landmark **associated with their previous strategy choice (i.e. the beacon strategy). Consequently, it is not necessary to encode another landmark despite shifting navigation strategy, which would explain the continued preference for attending to the route congruent landmark at test**. Secondly, several studies suggest place and response learning occur in parallel (Cassel et al., 2012; Iglói et al., 2009; Marchette et al, 2011; Packard & McGaugh, 1996). In our paradigm, only one landmark supports the simultaneous acquisition of the configuration, associative cue and beacon strategies; the route congruent landmark. Therefore, the concurrent learning of place and response knowledge may determine the environmental cues encoded by navigators. In addition to attending to the encoded landmark, participants also attended to the chosen movement direction, reflecting an anticipatory shift of visual attention in the direction of desired movement (Grasso et al., 1998). Both the landmark encoded during learning and the intended movement direction are factors known to affect gaze behavior at different stages of landmark based navigation (Wiener et al., 2011), **with attention** initially directed towards the decision relevant information (i.e. the encoded landmark), and then shifted to the direction of intended movement. Taken together, the results from the analysis of gaze behavior suggest that visual attention during wayfinding is only a reliable means **for** identifying navigation strategy when (1) different navigation strategies are selectively supported by separate environmental cues or (2) when the available navigation strategies result in different responses. **Given that participants encoded the same landmark irrespective of navigation strategy, predicting strategy choice based on gaze behavior would depend on the shift of visual attention towards the intended movement direction, which occurs approximately 750 - 500ms before participants report their response (Wiener et al., 2011). However, such a temporal spatial analysis was beyond the scope of this study as few participants employed all three navigation strategies during the course of the experiment, and the relative use of the three strategies was not similar in any of the six experimental blocks.**

In summary, this study revealed an initial preference for a beacon response strategy, with subsequent shifts to an optimal configuration place strategy occurring over the course of the experiment. Furthermore, the configuration strategy relied on spatial transformations to relate the viewpoints experienced when approaching an intersection during training and test, rather than direct access to place knowledge. Shifts in navigation strategy to a more cognitively demanding place strategy were captured by pupil dilation, which increased as participants increasingly employed the configuration strategy. Finally, analysis of eye-tracking data revealed the influence of the encoded landmark and the direction of intended movement on visual attention. Specifically, participants primarily attended to the landmark located in the direction of movement during learning, irrespective of the strategy employed, which may reflect participants' initial preference for the beacon response strategy or the simultaneous acquisition of place and response knowledge.

References

Andersen, N. E., Dahmani, L., Konishi, K., & Bohbot, V. D. (2012). Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory, 97*(1), 81-89.

Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychological Bulletin, 91*(2), 276-292.

Boksem, M. A., Meijman, T. F., & Lorist, M. M. (2005). Effects of mental fatigue on attention: an ERP study. *Cognitive Brain Research, 25*(1), 107-116.

Cassel, R., Kelche, C., Lecourtier, L., & Cassel, J. -C. (2012). The match/mismatch of visuo-spatial cues between acquisition and retrieval contexts influences the expression of response vs. place memory in rats. *Behavioural Brain Research, 230*(2), 333-342.

Diwadkar, V. A., & McNamara, T. P. (1997). Viewpoint dependence in scene recognition. *Psychological Science, 8*(4), 302-307.

Grasso, R., Prévost, P., Ivanenko, Y. P., & Berthoz, A. (1998). Eye-head coordination for the steering of locomotion in humans: an anticipatory synergy. *Neuroscience Letters, 253*(2), 115-118.

Hamilton, D. A., Driscoll, I., & Sutherland, R.J. (2002). Human place learning in a virtual Morris water task: Some important constraints on the flexibility of place navigation. *Behavioural Brain Research, 129*, 159-170.

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less travelled: Distinct neural bases of route following and wayfinding in humans. *Neuron, 37*(5), 877-888.

Hegarty, M., & Waller, D. (2004). A dissociation between mental rotation and perspective-taking spatial abilities. *Intelligence, 32*(2), 175-191.

Hess, E. H., & Polt, J.M. (1964). Pupil size in relation to mental activity during simple problem-solving. *Science, 143,* 1190-1192

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *The Journal of Neuroscience, 23*(13), 5945-5952.

Iglói, K., Zaoui, M., Berthoz, A., & Rondi-Reig, L. (2009). Sequential egocentric strategy is acquired as early as allocentric strategy: Parallel acquisition of these two navigation strategies. *Hippocampus, 19*(12), 1199-1211.

Just, M. A., & Carpenter, P. A. (1993). The intensity dimension of thought: Pupillometric indices of sentence processing. *Canadian Journal of Experimental Psychology, 47*(2), 310-339.

Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Science*, *154*(3756), 1583-1585.

King, J. A., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2002). Human hippocampus and viewpoint dependence in spatial memory. *Hippocampus, 12*(6), 811-820.

Kozhevnikov, M., Motes, M. A., Rasch, B., & Blajenkova, O. (2006). Perspective-taking vs. mental rotation transformations and how they predict spatial navigation performance. *Applied Cognitive Psychology, 20*(3), 397-417.

Livingstone-Lee, S. A., Murchison, S., Zeman, P. M., Ghandi, M., van Gerven, D., Stewart, L., Livingstone, N. J., & Skelton, R. W. (2011). Simple gaze analysis and special design of a virtual Morris water maze provides a new method for differentiating egocentric and allocentric navigation strategy choice. *Behavioural Brain Research, 225*(1), 117-125.

Lowenstein, O., Feinberg, R., & Loewenfeld, I. E. (1963). Pupillary movements during acute and chronic fatigue. *Investigative Ophthalmology & Visual Science, 2*(2), 138-157.

Manor, B. R., & Gordon, E. (2003). Defining the temporal threshold for ocular fixation in free-viewing visuocognitive tasks. *Journal of Neuroscience Methods, 128*(1), 85-93.

Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: Differential engagement of place and response learning mechanisms predicts human navigational behavior. *The Journal of Neuroscience, 31*(43), 15264-15268.

Marshall, S. P., Pleydell-Pearce, C. W., & Dickson, B. T. (2003). Integrating psychophysiological measures of

cognitive workload and eye movements to detect strategy shifts. In *Proceedings of the 36th annual Hawaii international conference on System Sciences.* Hawaii, IEEE.

Matthews, G., & Desmond, P. A. (2002). Task-induced fatigue states and simulated driving performance. *The Quarterly Journal of Experimental Psychology: Section A, 55*(2), 659-686.

Mueller, S. C., Jackson, C. P. T., & Skelton, R. W. (2008). Sex differences in a virtual water maze: An eye tracking and pupillometry study. *Behavioural Brain Research, 193*(2), 209-215.

Nishiyama, J., Tanida, K., Kusumi, M., & Hirata, Y. (2007). *The pupil as a possible premonitor of drowsiness.* In *Proceedings of the 29th annual international conference of the IEEE Engineering in Medicine and Biology Society.* Lyon, IEEE.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, Oxford University Press.

Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of Learning and Memory, 65*(1), 65-72.

Schmitzer-Torbert, N. (2007). Place and response learning in human virtual navigation: Behavioral measures and gender differences. *Behavioral Neuroscience, 121*(2), 277-290.

Shelton, A. L., & McNamara, T. P. (2001). Systems of spatial reference in human memory. *Cognitive Psychology, 43*(4), 274-310.

Sibley, C., Coyne, J., & Baldwin, C. (2011). Pupil Dilation as an Index of Learning. In *Proceedings of the Human Factors and Ergonomics Society 55th Annual Meeting.* Las Vegas, NV. Sage.

Siegel, A. W., & White, S. H. (1975). The development of spatial representations of large-scale environments. In H. W. Reese (Ed.), *Advances in Child Development and Behaviour*, (Vol. 10, pp. 9-55). New York: Academic Press.

Tlauka, M, & Wilson, P. N. (1994). The effect of landmarks on route-learning in a computer-simulated environment. *Journal of Environmental Psychology, 14*(4), 305-313.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55*(4), 189-208.

Waller, D., & Lippa, Y. (2007). Landmarks as beacons and associative cues: Their role in route learning. *Memory and Cognition, 35*(5), 910-924.

Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences, 6*(9), 376-382.

Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive bias for extrahippocampal navigation strategies in aging humans. *The Journal of Neuroscience, 33*(14), 6012-6017.

Wiener, J. M., de Condappa, O., & Höelscher, C. (2011). Do you have to look where you go? Gaze behaviour during spatial decision making. In L. Carlson, C. Höelscher, & T. F. Shipley (Eds.) *Proceedings of the 33rd Annual Conference of the Cognitive Science Society.* Austin, TX, Cognitive Science Society.

Wiener, J. M., Höelscher, C., Büchner, S., & Konieczny, L. (2012). Gaze behaviour during space perception and spatial decision making. *Psychological Research, 76*(6), 713-729.

Footnotes

[1] Use of the configuration strategy throughout the experiment will result in 100% performance, use of the beacon strategy will result in 66.66˙% performance (only incorrect when the approach direction at test differs from training by 90°), and use of the associative cue strategy will result in 33.33˙% performance (only correct during *same-direction* trials).

[2] While a 'move towards' rule is typically associated with the beacon strategy (Waller & Lippa, 2007), we believe beacon users adopt a 'turn towards' rule in this paradigm. As each landmark at an intersection adjoins two intersection pathways, use of a 'move towards' rule at selected *same-direction* trials can be satisfied by correctly turning towards the beacon or by incorrectly continuing straight ahead, while use of a configuration, associative cue or 'turn towards' beacon strategy would result in the correct answer. A straight ahead response was made in only 5.29% of these trials, strongly suggesting beacon users employed a 'turn towards' rule.

[3] It should be noted that we assume the configuration, associative cue and beacon strategies encode the route congruent landmark during learning. If this is not the case, the predictions by all three models will be incorrect.