# THE USE OF LANDMARK-BASED WAYFINDING STRATEGIES ACROSS THE ADULT LIFESPAN

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# The Use of Landmark-based Wayfinding Strategies across the Adult Lifespan

## Olivier de Condappa

Individuals can employ different landmark-based wayfinding strategies to acquire spatial knowledge and support navigation. Allocentric strategy use is associated with a cognitive representation of a learned environment that allows flexible navigation, while egocentric strategy use is associated with uni-directional knowledge that only supports accurate navigation in tasks that involve reproducing learned behaviours. While many studies have investigated strategy use during navigation, how strategy use develops during spatial learning remains under-researched. Therefore, this thesis primarily investigated the processes underlying strategy selection. Participants' strategy preference during various navigation tasks, including a novel strategy assessment paradigm developed specifically for this research, revealed that individuals adopt the most accurate strategy available – be it allocentric or egocentric – in accordance with the demands of the concurrent navigation task. Interestingly, when allocentric knowledge was required for accurate navigation, participants initially employed a suboptimal egocentric strategy before switching to an allocentric strategy, suggesting that egocentric knowledge precedes allocentric knowledge. Finally, participants were not subject to performance-related decrements associated with the effort of switching strategies. Interestingly, during spatial learning, participants acquired spatial knowledge related to alternative strategies, and selectively encoded landmarks that were compatible with the use of multiple strategies, which may explain why switching wayfinding strategies is cognitively efficient. This thesis also investigated the effects of aging on strategy selection. Strategy preference changes across the adult lifespan, with decreasing allocentric strategy use primarily attributed to reduced hippocampal function, and impaired egocentric strategy use associated with age-related learning and memory deficits. Analysis revealed that older adults exhibited a task-independent preference for egocentric strategy use, and therefore experienced difficulty with tasks that required allocentric knowledge. However, when egocentric strategy use most efficiently supported accurate navigation, younger and older adults performed similarly, suggesting that egocentric strategy use is largely unaffected by aging. Finally, age differences in strategy preference and spatial learning were observed when the most efficient route learning strategy differed between decision points, supporting findings of increasing susceptibility to switching costs with age. In summary, young adults flexibly employ a variety of strategies to optimise navigational efficacy, while older adults' strategy choices are affected by age-related difficulties with allocentric strategy use and increased vulnerability to strategy switching costs.

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# AUTHOR'S DECLARATION

This thesis includes three articles that have previously been published. The contribution of the author to these three papers is addressed below.

**Chapter 5**

de Condappa, O., & Wiener, J. M. (2016). Human place and response learning: Navigation strategy selection, pupil size and gaze behavior. *Psychological Research, 80*(1), 82-93. doi: 10.1007/s00426-014-0642-9

The author was primarily responsible for the design of the experimental paradigm, data collection, statistical analysis and written content.

**Chapter 9**

Wiener, J. M., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: effects of cognitive aging. *Frontiers in Aging Neuroscience, 4*(7). doi: 10.3389/fnagi.2012.00007

The author contributed to the experimental paradigm, assisted with data collection, and generated some written content.

**Chapter 10**

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. doi: 0.1523/JNEUROSCI.0717-12.2013.

The author was primarily responsible for the design of the experimental paradigm, and contributed to the data analysis and written content.

# THESIS OUTLINE

The purpose of this thesis, which consists of two parts, was to investigate the spatial processes underlying the selection and use of landmark-based wayfinding strategies for different navigational tasks. Navigators employ various strategies to learn and use spatial knowledge. For example, allocentric strategies are used to acquire comprehensive knowledge of an environment, and therefore support accurate navigation in a variety of tasks. In contrast, spatial information is encoded relative to one's body during the use of egocentric strategies, which only support accurate navigation in tasks that involve reproducing learned spatial behaviours e.g. route following. In the first part of this thesis (Chapters 1 – 6), younger adults' use of different wayfinding strategies was assessed. Chapter 1 provides an overview of landmark-supported navigation, with specific emphasis on the differential use of landmarks during the employment of allocentric and egocentric strategies. In Chapter 2, the use of two different egocentric strategies – the associative cue and beacon response strategies – was examined in two separate route learning experiments. First, the efficacy of both landmark-based egocentric strategies was assessed, with the use of the more parsimonious beacon strategy expected to facilitate route learning better than associative cue strategy use. Second, the prevalence of strategy switching was investigated in an experiment in which the egocentric strategy that best supported accurate navigation differed between decision points within the same route. While in theory, alternating between associative cue and beacon strategy use would most effectively support route learning, it was also possible that the cognitive costs associated with switching between different strategies would either impair navigation, or encourage participants to adopt a less effective single strategy solution. Chapters 3, 4 and 5 present a novel navigation task – the Alternative Routes paradigm – that was developed to assess participants' preference for landmark-based allocentric and egocentric wayfinding strategies. The paradigm involves a landmark-based navigation task in which participant behaviour is used to discriminate between allocentric, associative cue and beacon strategy use. In Chapter 3, two pilot experiments were conducted to examine the suitability of the strategy assessment mechanism, while Chapter 4 presents first data from the completed paradigm, which was employed to investigate changing strategy preferences over time. Furthermore, an eye-tracking variant of the Alternative Routes paradigm was utilised to examine the ocular behaviour associated with the use of different strategies. Finally, in Chapter 6, the results of the preceding experimental chapters were summarised and discussed in a wider navigational context.

The purpose of the second half of this thesis (Chapters 7 – 11) was to investigate the effects of aging on the use of landmark-based wayfinding strategies. Research has demonstrated that a number of cognitive abilities that contribute to successful navigation decline with age. As such, older adults experience difficulty with various navigation tasks. Chapter 7 provides an overview of age-related changes in navigational abilities, with specific emphasis on age differences in allocentric and egocentric strategy use. In Chapter 8, two separate experiments examined the effects of aging on the use of egocentric strategies during route learning. First, aging is known to differentially affect associative and item memory, which are critical to associative cue and beacon strategy use respectively. Therefore, the first experiment of Chapter 8 investigated age differences in the use of both egocentric response strategies. Second, older adults are more vulnerable than younger adults to the cognitive costs associated with switching strategies. As such, navigation accuracy or strategy choice may differ between age groups when the most effective – albeit more cognitively demanding – method of learning a route is to alternate between different strategies rather than employ a single strategy. Therefore, the second experiment of Chapter 8 assessed the prevalence of strategy switching across the adult lifespan in a route learning task. Finally, Chapters 9 and 10 investigated age differences in allocentric strategy use. Research has demonstrated that age-related wayfinding deficits are more pronounced for tasks that require allocentric knowledge than egocentric knowledge. This suggests that older adults' preference for avoiding new environments may be related to an inability to return to a familiar place after initial exploration – which requires an allocentric strategy – rather than difficulties with route learning – which is typically accomplished with the use of an egocentric strategy. Therefore, Chapter 9 examined age differences in route repetition and route retracing. Age is also associated with changing strategy preferences, with older adults increasingly relying on egocentric strategies irrespective of the demands of the concurrent navigation task. However, to our knowledge, no study has examined older adults' preference for different egocentric strategies. Therefore, in Chapter 10, the Alternative Routes paradigm was employed to investigate the effects of aging on strategy preference. To conclude the second part of the thesis, the key age-related findings from Chapters 8 – 10 were discussed further in Chapter 11. Finally, the contribution of this thesis to the field of wayfinding research was addressed in Chapter 12.

# CHAPTER 1. The Use of Landmarks during Navigation

## 1.1. Introduction

In both the human and animal domain, spatial navigation – purposeful movement from one environmental location to another – is essential for everyday functioning. Successful navigation recruits a wide range of cognitive abilities, including sensory processing, memory and executive functions (see Wolbers & Hegarty, 2010 for a review), and is informed by spatial knowledge derived from internal (i.e. self-motion) and external cues (i.e. sensory stimuli in the surrounding environment). Examples of cues used to support navigation include movement-related idiothetic cues (Loomis et al., 1993; Waller, Loomis & Huan, 2004), the Earth's geomagnetic field (Cain, Boles, Wang & Lohmann, 2005; Kimchi, Etienne & Terkel, 2004), optic flow (Gramann, Müller, Eick & Schönebeck, 2005; Riecke, van Veen & Bülthoff, 2002), and various aspects of the surrounding environment (Cheng & Newcombe, 2005; Kelly, McNamara, Bodenheimer, Carr & Rieser, 2008; Kolarik, Cirstea, Pardhan & Moore, 2014; Nardi, Newcombe & Shipley, 2011; Porter et al., 2007; Stankiewicz & Kalia, 2007). Human navigators primarily rely on selected visual cues within an environment – known as landmarks – to inform spatial behaviour. Specifically, landmarks are used to identify places, self-orient, designate targets, guide navigation, provide a frame of reference, and support the acquisition and use of spatial information (see Chan, Baumann, Bellgrove & Mattingley, 2012 for a review). Landmarks are typically incorporated into two qualitatively different types of spatial representation: a cognitive map and route knowledge. A cognitive map is a complex mental representation of an environment that develops from knowledge of the spatial relationships between landmarks (O’Keefe & Nadel, 1978; Tolman, 1948), and allows navigators to plan and traverse new paths between known locations e.g. novel detours and short-cuts. Route knowledge, in contrast, consists of behavioural responses associated with landmarks, and allows known routes to be traversed (Waller & Lippa, 2007). Navigators utilise a variety of heuristics or mnemonics – known as wayfinding strategies – to identify, interpret, acquire, organise and retrieve landmark-based spatial information. Strategy choice is therefore an important determinant of a navigator’s spatial knowledge and behaviour. In the following chapters, the spatial processes underlying the selection and use of landmark-based wayfinding strategies were investigated.

## 1.2. Landmark Properties

Landmarks have been defined in many ways within spatial cognition literature. However, there is general agreement that landmarks are distinct features of an environment that are utilised by navigators as points of reference –for identifying places, determining one’s position and organising spatial knowledge – or to inform spatial behaviour (Caduff & Timpf, 2008; Lynch, 1960; Stankiewicz & Kalia, 2007). Different types of landmarks are available to navigators in the surrounding environment. For example, both geometric (e.g. structures and arrays) and non-geometric visual cues (e.g. colour, texture, pattern) can be used to inform spatial behaviour (Gillner, Weiß & Mallot, 2008; Kelly et al., 2008; Schmitzer-Torbert, 2007; Stankiewicz & Kalia, 2007; Tommasi, Chiandetti, Pecchia, Sovrano & Vallortigara, 2012). However, in human navigation, landmark-based spatial knowledge is predominantly derived from objects – physical entities within an environment that are independent of its structure. In most environments, many objects are available to support navigation. However, when learning novel environments, few objects or cues are incorporated into spatial knowledge, suggesting that navigators selectively encode landmarks (e.g. Aginsky, Harris, Rensink & Beusmans, 1998; Hamid, Stankiewicz & Hayhoe, 2010). Research has shown that the process of selecting navigationally informative landmarks depends on several key object properties (Burnett, 2000; Sorrows & Hirtle, 1999).

First, objects must be visually salient i.e. perceptually distinct, to function as landmarks, as easily detectable objects are more navigationally informative than landmarks that are difficult to see (see Caduff & Timpf, 2008 for a review). For example, Chamizo, Rodrigo, Peris and Grau (2006) found that the performance of rats searching for a hidden target improved when the size or brightness of the only available landmark increased (also see Lopez, de Vasconcelos & Cassel, 2008). In addition, Miller and Carlson (2011) found that irrespective of navigational relevance, larger and more uniquely coloured objects were better recognised by participants after a route learning task. Taken together, these findings suggest that object saliency is an important factor in landmark selection.

Secondly, in order to provide unambiguous navigation support, landmarks must be unique. Landmarks that cannot be easily distinguished from one another are more likely to be identified incorrectly than unique landmarks, and are therefore less reliable and informative navigation aids. For example, Wiener, de Condappa and Hölscher (2011) found that when wayfinding decision points contained both a unique and repeated object, participants primarily attended to the unique object during navigation. This finding suggests that participants utilised the unique object as a landmark, as the repeated object could not be used to provide decision point-specific navigation support. Furthermore, Kelly (2010) found that Clark's nutcracker birds learned the geometry of a rectangular array of four objects when the objects were unique, but not when the objects were identical, suggesting that unique cues facilitate the acquisition of spatial knowledge, while common cues do not.

Stability and permanence are also important landmark properties, as only landmarks that remain in a fixed position can provide reliable spatial information about the surrounding environment across multiple visits. For example, triangle completion tasks, in which participants are guided along two sides of an unmarked triangular path and asked to determine the correct turning angle and travel distance required to return directly to the original starting position, are completed less accurately when the position of the surrounding cues change during the task, compared to when they remained fixed (Foo, Warren, Duchon & Tarr, 2005; Riecke et al., 2002). Mallot and Gillner (2000) also found that recombining groups of landmarks associated with different movement directions significantly reduced navigation accuracy. Furthermore, a study conducted by Waller and Lippa (2007) revealed that switching the position of two landmarks at a known decision point delayed participants' navigational responses, suggesting that changes in landmark position impaired the spatial decision making process. It should also be noted that participants' wayfinding performance can be affected by changes in the availability of environmental cues between learning and subsequent navigation. For example, occluding or removing objects from a learned environment often renders specific landmark-based wayfinding strategies ineffective (e.g. Hurlebaus, Basten, Mallot & Wiener, 2008; Iaria, Petrides, Daghar, Pike & Bohbot, 2003). Therefore, in order to provide reliable spatial support over time, object stability and permanence are important landmark properties.

Finally, the position of an object within an environment is an important factor in landmark selection. For example, objects located at decision points – environmental locations that require navigators to make a spatial choice – are more likely to be utilised as landmarks than objects at non-decision points. Indeed, several studies have found that compared to objects located at non-decision points, objects at decision points are i) recognised more accurately, ii) recognised faster, and iii) more likely to be associated with travel direction (Han, Byrne, Kahana & Becker, 2012; Janzen, 2006; Miller & Carlson, 2011; Schinazi & Epstein, 2010). Furthermore, after learning a route in a driving simulator, Aginsky et al. (1997) found that participants were more sensitive to changes made to the appearance of buildings located at decision points than at non-decision points. In addition, objects at decision points also occur more frequently in both route descriptions and map drawings than objects at non-decision points (Denis, Pazzaglia, Cornoldi, & Bertolo, 1999; Michon & Denis, 2001; Miller & Carlson, 2011). Finally, recognition tasks conducted after learning an environment revealed that activity in the parahippocampal gyrus increased for objects at decision points (i.e. landmarks), but not for non-decision point objects (Janzen, Jansen & van Turennout, 2008; Janzen & van Turennout, 2004; Janzen, Wagensveld & van Turennout, 2007; Janzen & Weststeijn, 2007). These studies suggest that objects that differ in navigational relevance due to their position in an environment are processed differently. Taken together, these findings suggest that objects at decision points are more likely to be incorporated into spatial knowledge.

In summary, landmark-based navigation depends on the appropriate selection of environmental objects to support the acquisition and use of spatial knowledge. Research has demonstrated that several navigational tasks are performed better when the landmarks utilised by navigators are salient, unique, stable and located at decision points.

## 1.3. Landmark Supported Navigation

To demonstrate that the use of landmarks facilitates navigation, several studies have examined participants' spatial behaviour in both the presence and absence of landmarks. For example, the acquisition and use of route knowledge is affected by the availability of potential landmarks. Waller and Lippa (2007) found that compared to learning a route in a landmark-rich environment, route learning without the support of landmarks (i.e. by remembering a sequence of movement responses) was associated with less accurate navigation, and poorer route knowledge after five decision points. Furthermore, in a study by Evans, Skorpanich, Gärling, Bryant and Bresolin (1984), participants viewed a video of a route through a model environment that contained either i) no landmarks, ii) only proximal landmarks (intramaze cues that are only visible in the immediate location), and iii) only distal landmarks ( extramaze cues that are visible over large spatial areas). When asked to place photographs of the environment relative to one another on a blank piece of paper, participants that learned the route in the presence of landmarks positioned the photographs more accurately than participants that learned the environment in the absence of landmarks. Finally, Ruddle, Volkova, Mohler and Bülthoff (2011) asked participants to repeat and retrace a route through a virtual environment in which object cues were either present or absent. Analysis revealed that participants made fewer errors when proximal landmarks were used to support route learning. Taken together, these findings suggest that route learning is facilitated by the use of landmarks.

Landmarks can also be utilised to develop more complex spatial knowledge, such as a cognitive representation of an environment. For example, in a study conducted by Jansen-Osmann and Fuchs (2006), participants explored a virtual environment that either contained or was devoid of objects. In a subsequent navigation task, landmark use was associated with faster learning of a novel short-cut between two points. Furthermore, O'Laughlin and Brubaker (1998) asked participants to draw an aerial map of a single story home that was either furnished (with landmarks) or unfurnished (without landmarks). Participants that viewed the home containing landmarks reproduced the floor plan more accurately than participants that viewed the home without landmarks. The results of these studies suggest that landmarks can be used to facilitate the development of a cognitive map.

Finally, internal cues derived from self-motion can be used to support navigation. Specifically, motion-related vestibular, proprioceptive and perceptual cues support path integration, in which navigators update their orientation and location in an environment based on perceived linear and/or rotational movement (Etienne & Jeffrey, 2004; Mittelstaedt & Mittelstaedt, 1980). However, studies have shown that path integration tasks, which normally take place in featureless environments, are completed more accurately when the surrounding environment contains object cues. For example, Foo et al. (2005) asked participants to complete a virtual reality triangle completion task in either an object-rich or featureless environment. Compared to participants in the object-rich environment, participants in the featureless environment underestimated the turning angle required to take the novel short-cut, and did not travel far enough to complete the triangular path. Consequently, the error between the target destination and participants' final position was three times greater in the featureless environment. Similarly, Riecke et al. (2002) found that participants performed triangle completion tasks more accurately when they relied on landmarks rather than optic flow. Taken together, these studies suggest that the errors that typically accumulate during motion-informed path integration are significantly reduced when landmarks are used to support navigation.

In summary, navigators complete a variety of different tasks more accurately when objects that can function as landmarks are available in the surrounding environment. As a result, navigation is more likely to be influenced by spatial knowledge derived from object landmarks than from other cues (e.g. Foo et al., 2005; Kelly & Spetch, 2004).

## 1.4. Landmark-based Wayfinding Strategies

Navigators can employ two different types of strategies to acquire landmark-based spatial knowledge: an allocentric place strategy, and an egocentric response strategy. Allocentric place strategy use involves encoding the spatial relationships between landmarks and/or locations, resulting in a cognitive map that supports flexible navigation within an environment (O'Keefe & Nadel, 1978; Tolman, 1948). Therefore, allocentric strategy use depends on an extrinsic, environment-centred frame of reference that is associated with viewpoint-independent spatial knowledge (Klatzky, 1998). In contrast, the behavioural responses associated with successful navigation are encoded relative to one’s body during egocentric response strategy use, resulting in route knowledge (e.g. ‘Turn right/move straight on at decision point X’. As such, egocentric strategy use relies on an intrinsic frame of reference, with spatial knowledge organised with respect to the individual (Klatzky, 1998). Egocentric knowledge is therefore viewpoint-dependent, and only supports accurate navigation when the position and orientation of the navigator in the environment is identical to learning (Hartley, Maguire, Spiers & Burgess, 2003). To date, research has identified three different egocentric response strategies that can be employed to learn novel routes. Sequential response strategy use involves encoding a series of body movements in temporal order (e.g. ‘Turn left, then turn right…’; Iglói, Zaoui, Berthoz & Rondi-Reig, 2009), and is the only available knowledge-based wayfinding strategy in landmark-free environments. However, the use of a sequential response strategy in both landmark-rich and landmark-free environments does not effectively support the acquisition of long routes (e.g. Waller & Lippa, 2007), and depends on a fixed starting position and orientation i.e. changes in start location and/or facing direction do not affect the fixed series of movement responses executed during sequential response strategy use, therefore resulting in inaccurate navigation. In contrast, the use of landmark-based egocentric strategies allows navigators to learn longer routes, and acquire location-specific spatial knowledge. Two different landmark-based egocentric strategies utilise environmental objects differently to support the acquisition of spatial knowledge at individual decision points. Associative cue-based learning involves relating a directional response with an encoded landmark located at a wayfinding decision point (e.g. 'Turn left at the church'; Tlauka & Wilson, 1994). Recognition of the encoded landmark during subsequent navigation facilitates the recall of the corresponding route knowledge, which is then used to inform spatial behaviour. In contrast, objects that spatially correspond with a goal location are encoded during beacon strategy use. Subsequent recognition of encoded landmarks triggers a universal behavioural response that results in movement relative to the position of the landmark (e.g. 'Turn/move towards the petrol station'; Waller & Lippa, 2007). Both associative cue and beacon-based knowledge consists of simple stimulus-response pairings, with landmarks serving as a cue for navigation behaviour. However, associative cue strategy use relies on the association between two items of spatial knowledge – landmark identity and an explicit directional response – to support navigation at wayfinding decision points. In contrast, beacon strategy use depends solely on the knowledge of landmark identity, as a fixed behavioural response is performed throughout beacon-based navigation. Therefore, beacon strategy use is more parsimonious than associative cue strategy use, and consequently better supports spatial learning and navigation in tasks that can be completed with route knowledge (Waller & Lippa, 2007). To conclude, landmark use differs according to the wayfinding strategy employed. Allocentric strategy use involves encoding landmarks relative to other environmental features, resulting in a comprehensive spatial representation of an environment. In contrast, stimulus-response associations are encoded relative to the navigator during egocentric strategy use, resulting in uni-directional route knowledge.

Allocentric and egocentric strategies are employed by good navigators for different navigational purposes (Etchamendy & Bohbot, 2007; Hartley et al., 2003). For example, tasks that involve determining novel paths to known destinations require allocentric knowledge of the surrounding environment. In contrast, tasks that involve reproducing known or experienced spatial behaviours (e.g. following a well-known route) can be completed accurately with the use of either an allocentric or egocentric strategy. However, navigators typically employ an egocentric strategy in such tasks, as it is less cognitively demanding than an allocentric strategy. Therefore, landmark-based allocentric and egocentric strategies are primarily used to facilitate different types of spatial learning and navigation.

## 1.5. Wayfinding Strategy Assessment Paradigms

### *The Morris Water Maze Task*

Several experimental paradigms have been designed to determine the wayfinding strategy employed by participants. The most widely used paradigm is the Morris Water Maze (Morris, 1981), which was developed to examine the spatial memory of rodents, and has since been implemented in virtual environments to test human participants (Astur, Ortiz & Sutherland, 1998; Sandstrom, Kaufman & Huettel, 1998). In its most common format, the Morris Water Maze Task (MWMT) consists of a circular pool containing opaque water and a hidden submerged target platform (see Figure 1). Typically, the circular pool does not contain any proximal cues, although distal cues are present in the surrounding environment. During training, successful navigation to the target platform from a variety of start positions requires allocentric knowledge of the spatial relationship between distal cues and the goal location. Allocentric strategy use is then determined by search patterns during a probe trial in which the target platform has been removed. Search primarily conducted in the target platform’s prior location is thought to indicate the use of an allocentric strategy, while random search suggests a lack of allocentric learning (e.g. Astur, Taylor, Mamelak, Philpott & Sutherland, 2002; Driscoll, Hamilton, Yeo, Brooks & Sutherland, 2005; Skelton, Ross, Nerad & Livingstone, 2006). Furthermore, variations to the traditional experimental protocol and MWMT environment have provided insight into how the use of visual landmarks varies according to strategy preference, with distal and proximal cues supporting allocentric and egocentric strategy use respectively (Mueller, Jackson & Skelton, 2008; Livingstone-Lee et al., 2011). However, the criteria utilised to determine participants’ strategy preference in the MWMT has been criticised, as behaviour that is assumed to reflect allocentric strategy use can also be attributed to beacon-based navigation (Hamilton, Johnson, Redhead & Verney, 2009). Specifically, search in the correct quadrant of the circular enclosure can be informed by both allocentric knowledge of the platform’s precise location, and the use of a single distal cue to guide movement in the direction of the target platform.

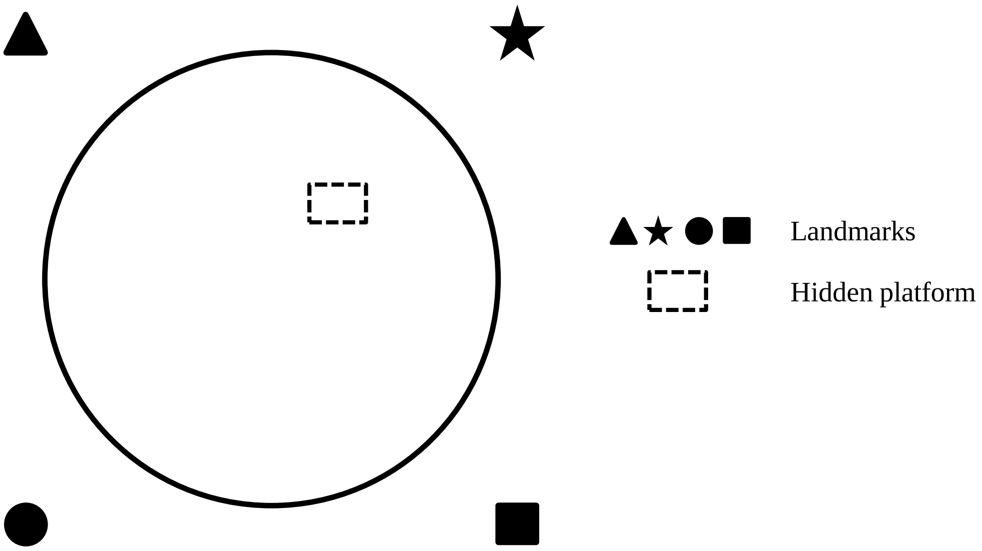


**Figure 1.** An overview of a Morris Water Maze environment. During training, participants must navigate to the hidden platform from a variety of start positions within the circular arena. Participants' strategy preference is then determined by navigation behaviour during probe trials in which the hidden platform is removed.

### *The T- Maze, Y-Maze and Cross Maze Tasks*

The T-maze (Blodgett & McCutchan, 1947; Levy, Astur & Frick, 2005), Y-maze (Bowers & Alexander, 1967; Rodgers, Sindone & Moffat, 2012) and Cross maze (Tolman, Ritchie & Kalish, 1946b; Packard & McGaugh, 1996) were originally developed to investigate navigation behaviour in rodents, and have since been adapted to study human spatial memory. All three paradigms are used to assess strategy preference in a similar fashion to one another. The T-maze consists of a T shaped environment, while the Y- and Cross maze feature three or four arms radiating from a central junction respectively (see Figure 2 for an example of a Cross Maze). Training in these paradigms involves navigation from a fixed starting position (the base of the stem in a T-maze, and at the end of a radial arm in the Y- and Cross maze) to a goal arm located to either the left or right of the maze junction. Use of an allocentric strategy in these mazes involves knowledge of the spatial relationship between the goal arm and distal environmental cues, while egocentric strategy use requires a simple 'Turn left/right' motor response. Strategy preference is assessed by probe trials in which the starting position is different to that in training. In the case of the T-maze, the maze itself is rotated 180° relative to the external environment, while in the Y- and Cross maze, the starting position shifts to a different radial arm (neither the original start or goal arm in the Y-maze, and the radial arm directly opposite the original starting arm in the Cross maze). Navigation to the position of the goal suggests allocentric strategy use, while executing the same turning response learned during training is indicative of egocentric strategy use. However, it should be noted that, similar to the MWMT, responses thought to reflect allocentric strategy use in these paradigms also correspond with beacon-based navigation (Blodgett, McCutchan & Mathews, 1949; Skinner et al., 2003). Specifically, accurate navigation can be informed by both allocentric knowledge of the goal arm's location, and the use of a landmark that spatially coincides with the correct arm to direct movement.

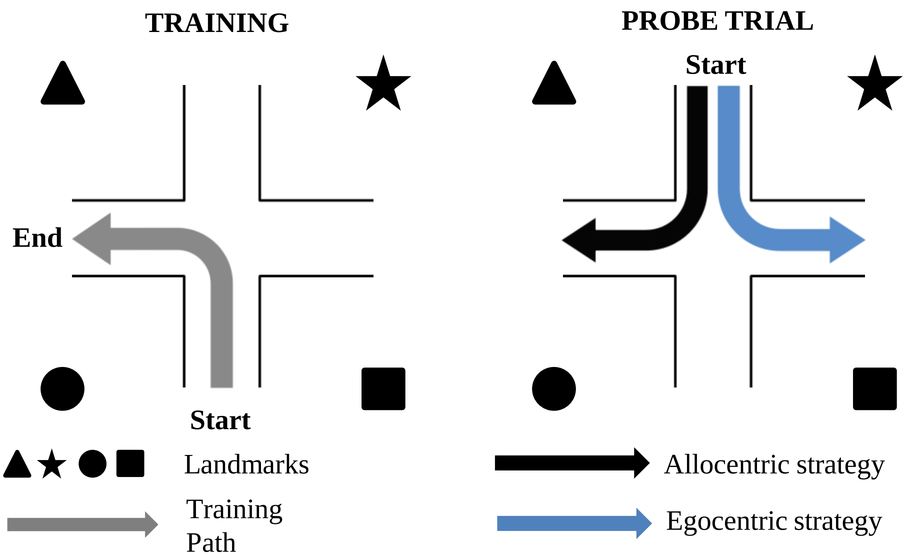


**Figure 2.** An example of a Cross Maze task. Left: An overview of the training procedure. Participants learn to navigate from a fixed starting position to a goal arm. Right: An overview of a probe trial. Allocentric and egocentric strategy use are associated with different responses.

### *The Radial Arm Maze Task*

The Radial Arm Maze (RAM) was initially used to examine spatial working memory in rodents i.e. the strategies employed to explore or search environments (Olton & Samuelson, 1976), but has recently been modified to discriminate between allocentric and egocentric strategy use in humans (Iaria, Petrides, Dagher, Pike & Bohbot, 2003; Bohbot, Iaria & Petrides, 2004; Etchamendy, Konishi, Pike, Marighetto & Bohbot, 2012). The most commonly used variant of the virtual RAM involves eight identical arms radiating outwards from a circular centre platform, with extramaze distal cues located in the surrounding environment (see Figure 3). During training, participants learn to navigate to radial arms containing hidden rewards, which involves either i) knowledge of the spatial relationship between distal cues and the goal arms i.e. an allocentric place strategy, or ii) knowledge of the goal arms relative to one another, a fixed starting position or a single external landmark i.e. an egocentric response strategy (Etchamendy & Bohbot, 2007). Participants' strategy preference is then determined by performance in a single probe trial in which all available distal cues are obscured from view. As allocentric knowledge consists of the spatial relationships between landmarks and other environmental features, the absence of distal cues is particularly detrimental to the use of an allocentric strategy. Therefore, allocentric strategy users are more likely to make navigational errors during probe trials than egocentric strategy users. Furthermore, shifts in wayfinding strategy from an allocentric strategy to an egocentric strategy have been reported in RAM tasks (Iaria et al., 2003; Bohbot et al., 2004; Etchamendy & Bohbot, 2007), although it should be noted that these findings are based on post-experiment participant reports, and not behavioural data.

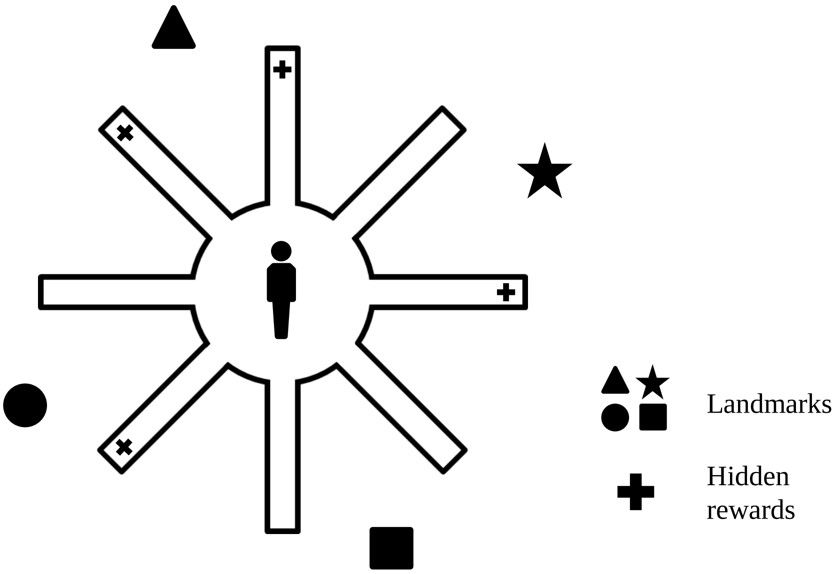


**Figure 3.** An overview of a Radial Arm Maze environment. During training, participants learn to navigate to radial arms containing hidden rewards. Participants' strategy preference is then determined by navigation behaviour during probe trials in which all landmarks are occluded from view.

### *The Starmaze Paradigm*

The Starmaze paradigm (Rondi-Reig, Petit, Tobin, Tonegawa & Berthoz, 2006) consists of ten identical alleys, five of which form a central pentagon, with the remaining five alleys radiating from the vertices of the pentagon (see Figure 4). During training, participants learn to navigate from a fixed starting position in one of the radial alleys to a goal located in a separate radial alley. To successfully learn the route, participants can employ i) an allocentric strategy to learn the location of the goal arm relative to the surrounding distal cues, ii) an egocentric sequential response strategy to learn the correct series of movement responses required to navigate to the goal arm (Iglói et al., 2009), or iii), if proximal cues are available, an egocentric beacon response strategy to learn which environmental cues spatially coincide with movement along the route (Rondi-Reig et al., 2006). Probe trials in which participants start from a novel location are used to determine strategy preference, with direct navigation to the goal location suggesting use of an allocentric place strategy. In contrast, egocentric strategy use involves the same fixed behavioural actions learned during training, resulting in incorrect navigation. Interestingly, analysis of participant behaviour in the Starmaze paradigm can also identify switches between wayfinding strategies during probe trials. Specifically, indirect navigation to the goal location corresponds with initial use of an egocentric strategy followed by a shift to an allocentric strategy (Iglói et al., 2009). Furthermore, repeated training and probe test trials allow the assessment of strategy preference over time, although the provision of positive feedback irrespective of navigation accuracy during probe trials may artificially influence participants' strategy choice.

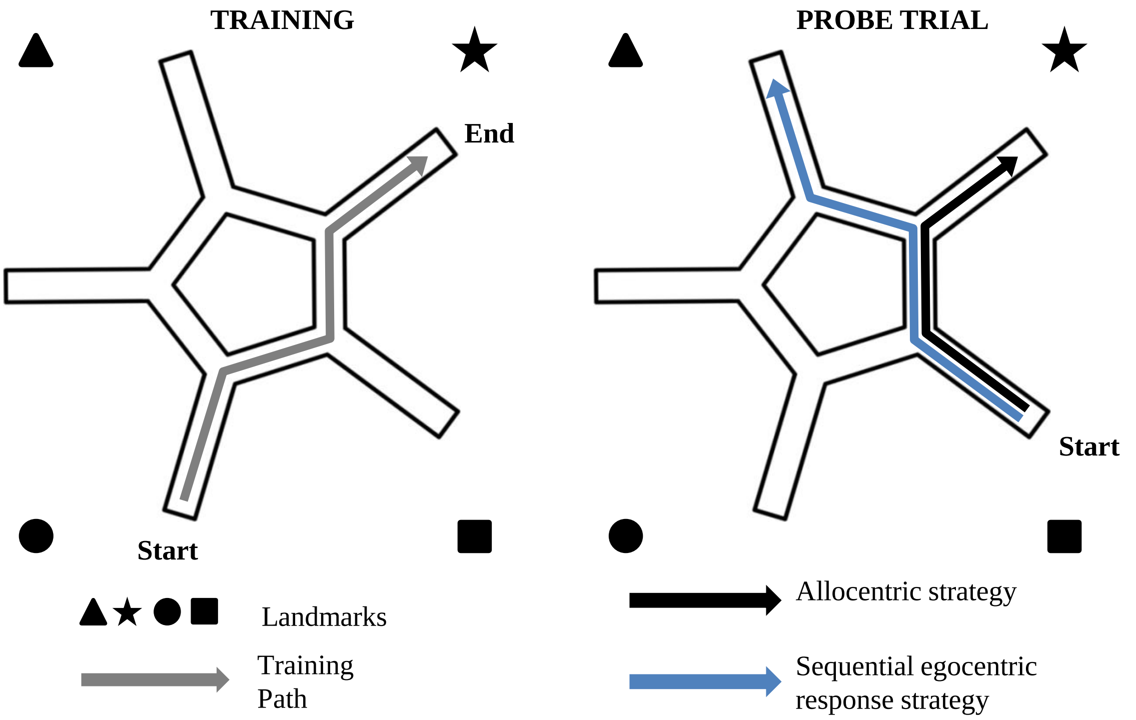


**Figure 4.** An example of a Starmaze task. Left: An overview of the training procedure. Participants learn to navigate from a fixed starting position to a goal arm. Right: An overview of a probe trial. Allocentric and sequential egocentric response strategy use are associated with different responses.

### *The Dual Strategy Paradigm*

Finally, in the Dual Strategy Paradigm (DSP), participants are passively transported along a circuitous path in a grid-like virtual maze, and asked to learn the location of twelve unique objects (see Figure 5; Furman, Clements-Stephens, Marchette & Shelton, 2014; Marchette, Bakker & Shelton, 2011). During a subsequent test phase, participants are instructed to navigate to target objects from a variety of route locations. Participants' strategy preference is determined in a subset of test trials that can be completed by either following the original route, or taking a novel short-cut. Navigating along the learned path suggests that participants' spatial behaviour is informed by egocentric route knowledge, while the use of novel short-cuts suggests that participants acquired allocentric knowledge of the environment. Interestingly, the DSP differs from the paradigms discussed previously, as both allocentric and egocentric strategy use support accurate – albeit different – navigation. Therefore, a persistent bias for a specific strategy may reflect a preference for either more efficient learning (i.e. egocentric strategy use) or more efficient navigation (i.e. allocentric strategy use).

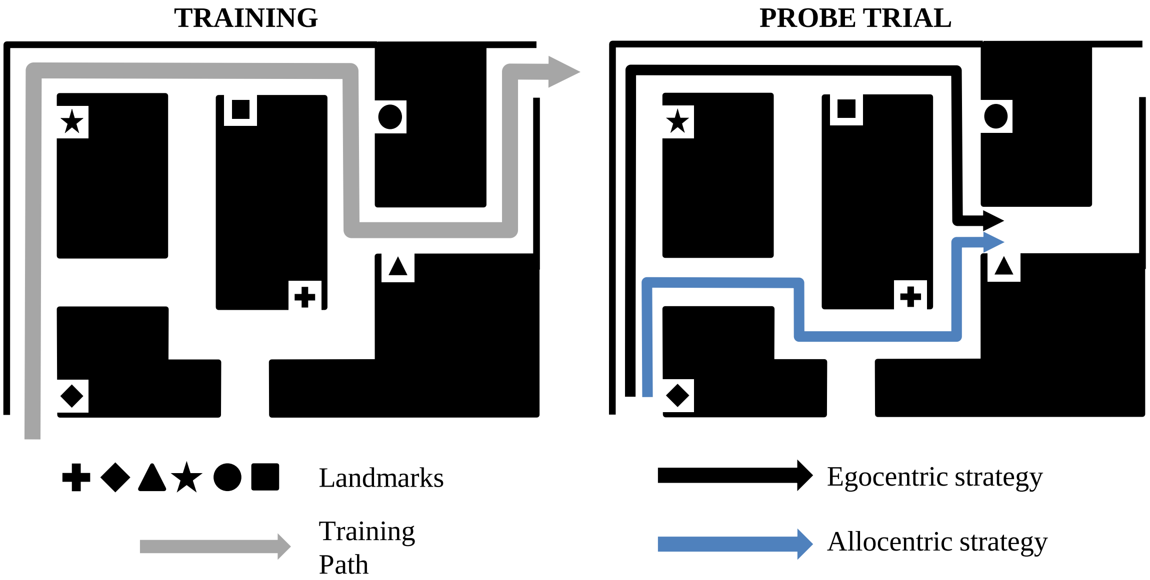


**Figure 5.** An overview of the Dual Strategy Paradigm. Left: A section of the training procedure. Participants are passively transported along a route through the environment. Right: An overview of a probe trial. Participants must navigate from a known location (the diamond in the example above) to a target landmark (the triangle). Use of a novel short-cut is indicative of allocentric strategy use, while following the original route suggests egocentric strategy use.

In summary, a variety of different paradigms are utilised to identify participants' wayfinding strategy choice. However, there are limitations associated with the criteria and mechanisms employed to assess strategy preference in many of these paradigms. First, in some paradigms, behaviour that is typically attributed to allocentric strategy use also corresponds with the use of an egocentric beacon strategy. Second, specific types of egocentric strategy use are rarely differentiated, and finally, the tasks participants perform are not typically representative of real-world navigation. As such, the findings associated with these paradigms must be interpreted conservatively.

### 1.6. The Neural Basis of Wayfinding Strategies

Research has shown that allocentric and egocentric strategy use depend on different neural networks (see Burgess, 2008; Chrastil, 2013 for a review). Hippocampal place cells, which respond differentially when a specific environmental location is occupied, have been strongly implicated in the formation and use of cognitive maps – first, in freely moving rats (O'Keefe & Dostrovsky, 1971), and more recently in humans (Ekstrom et al., 2003). Specifically, different patterns of hippocampal place cell activity across discrete areas of an environment are thought to correspond with an allocentric spatial representation (Wilson & McNaughton, 1993). As such, allocentric strategy use is thought to depend on the hippocampus and surrounding structures (see Burgess, Maguire & O'Keefe, 2002 for a review). In contrast, egocentric strategy use relies on the striatal circuits, which are involved in learning and enacting stimulus-response associations (Devan, Hong & McDonald, 2011; Hiebert et al., 2014; Packard & Knowlton, 2002).

Several studies have reported differences in the neural correlates of allocentric and egocentric strategy use during navigation. For example, Iaria et al. (2003) found that self-reported allocentric and egocentric strategy use in a virtual RAM task correlated with activity in the right hippocampus and caudate nucleus respectively. Similarly, Bohbot, Lerch, Thorndycraft, Iaria and Zijdenbos (2007) found that in a virtual RAM task, allocentric strategy use correlated with gray matter density in the hippocampus, while use of an egocentric strategy correlated with gray matter density in the caudate nucleus. Marchette et al. (2011) employed a DSP and found that participants' ratio of allocentric and egocentric strategy use positively correlated with the proportion of activity in the bilateral hippocampus and caudate during learning (also see McIntyre, Marriott and Gold, 2003). Furthermore, Hartley et al. (2003) found that accurate navigation in a task that required allocentric knowledge was associated with hippocampal activity, while successful navigation of a learned route, which typically involves egocentric response strategy use, activated the caudate nucleus. Finally, Hirshhorn, Grady, Rosenbaum, Winocur and Moscovitch (2011) tested participants’ knowledge of Toronto within three months of moving to the city, and after one year of residency. Interestingly, the involvement of the right hippocampus during a number of spatial tasks decreased over time, while activity in the caudate, among other regions, increased. The authors suggest that this finding may reflect a change from an allocentric strategy to a habit based (i.e. egocentric) strategy. Taken together, these studies suggest that allocentric strategy use depends on the hippocampus, while the stratum, especially the caudate nucleus, is involved in egocentric strategy use.

Further support for hippocampal involvement in the use of allocentric strategies can be found in studies that explicitly assess strategy choice. For example, Parslow et al. (2004) asked participants to complete both an allocentric and egocentric version of a virtual MWMT. In the allocentric version of the task, participants started from a variety of positions in a circular arena containing stable distal cues, and were asked to navigate to the location of a target pole. During probe trials, accurate navigation to the learned location of the pole, which was removed from the environment, involved knowledge of the spatial relationship between distal cues and the pole i.e. allocentric knowledge. In the egocentric version of the task, participants navigated to the target pole from a fixed start position. However, as the array of cues was rotated for the probe trial, accurate navigation in the absence of the target pole depended on egocentric knowledge. Parslow et al. (2004) found that hippocampal and parahippocampal activity increased during learning of the allocentric task, but not the egocentric task. In a similar study conducted by Shipman and Astur (2008), participants completed both an allocentric and egocentric version of a virtual MWMT. Right hippocampal activity was observed during the early stages of allocentric strategy use, but not egocentric strategy use, which may reflect an initial period of orienting oneself and determining the goal location. In addition, Cornwell, Johnson, Holroyd, Carver and Grillon (2008) found that hippocampal theta oscillations, which are implicated in memory formation, peaked in the anterior left hippocampus and the parahippocampal cortices during a virtual MWMT. Furthermore, navigation performance, which corresponds with allocentric strategy use, was positively correlated with theta activity in the left posterior hippocampus/parahippocampal region during the early stages of wayfinding. Finally, in a study by Jordan, Schadow, Wuestenberg, Heinze and Jäncke (2004), participants were shown an overview of a maze and asked to determine the shortest route between a defined start and end position. In a subsequent test phase, participants were asked to navigate between the designated start and end locations in a virtual first person analog of the maze, with post-experimental written descriptions used to identify strategy preference. Compared to egocentric strategy use, allocentric strategy use during navigation was associated with increased activity in the left parahippocampal gyrus, the left hippocampus, the thalamus, and the right cerebellum.

Several studies have also demonstrated that the hippocampal region is associated with the development of allocentric knowledge. In a study conducted by Iaria, Chen, Guariglia, Ptito and Petrides (2007), participants freely explored a virtual city until they could correctly indicate the location of the available landmarks on an overview of the environment, demonstrating the development of an accurate cognitive map. During a subsequent test phase, participants were asked to navigate between different pairs of landmarks via the shortest route. Analysis revealed that the hippocampal and retrosplenial regions were equally involved in both the formation and use of cognitive maps, with left anterior and right posterior hippocampal activity observed during the learning and test phases respectively. In a similar experiment, Iaria, Lanyon, Fox, Giaschi and Barton (2008) also found that participants with better structural integrity of the right hippocampus formed and used cognitive maps most effectively. In addition, Moffat, Elkins and Resnick (2006) encouraged participants to develop a cognitive map of a virtual environment by informing them of two subsequent test tasks that required allocentric spatial knowledge: reproducing an aerial map of the environment, and determining the shortest route to a target object. Moffat et al. (2006) reported significant activity in the hippocampus and surrounding structures during learning. In a study by Grön, Wunderlich, Spitzer, Tomczak and Riepe (2000), participants were asked to navigate through an unfamiliar maze containing several landmarks. Analysis of participants' neural activity during the task, which required allocentric processing, revealed significant activity in the right hippocampus and parahippocampal region. Furthermore, Wolbers and Büchel (2005) used participants' improving knowledge of the spatial relationship between landmarks in a virtual town to assess the development of a survey representation, and found that the acquisition of new survey knowledge was associated with activity in the hippocampus.

The hippocampus has also been shown to contribute significantly to the development and use of cognitive maps associated with real world environments. For example, Maguire et al. (2000) found that compared to an age-matched control group, taxi drivers with extensive wayfinding knowledge of London had a significantly larger posterior hippocampal region. Furthermore, the time spent training and working as a taxi driver was positively correlated with right posterior hippocampal volume (see also Woollett & Maguire, 2011). In addition, Schinazi, Nardi, Newcombe, Shipley and Epstein (2013) asked participants to perform a variety of spatial tasks as they became increasingly familiar with a novel college campus, and found that performance in a pointing task that required allocentric knowledge was positively correlated with right hippocampal volume.

In summary, research has demonstrated that the acquisition and use of allocentric and egocentric knowledge depends on the hippocampal and striatal regions respectively.

## 1.7. The Development of Spatial Knowledge

Individuals are thought to acquire the knowledge required for allocentric and egocentric strategy use either sequentially, or in parallel. The most influential framework regarding the acquisition of spatial knowledge was proposed by Siegel and White (1975), and suggests that individuals' spatial representations develop sequentially in three stages. Individuals first acquire *landmark knowledge* to facilitate the recognition of known locations, then *route knowledge*, which consists of the temporal order of landmarks and the paths between them. Finally, individuals develop *survey knowledge* i.e. a cognitive map. Therefore, Siegel and White (1975) suggest that increasing egocentric knowledge is the precursor to allocentric knowledge. In support of this framework, Appleyard (1970) found that when asked to produce a sketch map of a city, newcomers included more routes and paths than long-time residents. In addition, Golledge and Spector (1978) revealed that participants' cognitive maps were more accurate for places they visited often than those they visited infrequently. Furthermore, Thorndyke and Hayes-Roth (1982) tested participants' knowledge of their work place by asking them to estimate the direction, Euclidian distance and walking distance to a number of target destinations. Thorndyke and Hayes-Roth (1982) found that participants with greater pre-experimental knowledge of the test environment performed more accurately, suggesting that increased navigation experience is related to the development of cognitive maps. Taken together, these studies suggest that individuals first acquire egocentric knowledge of an environment, before developing allocentric knowledge (but see Blajenkova, Motes & Kozhevnikov, 2005; Huynh & Doherty, 2007; Ishikawa & Montello, 2006).

In contrast, it is possible that allocentric and egocentric spatial knowledge are acquired simultaneously. For example, Iglói et al. (2009) conducted a Starmaze task and found i) that some participants were able to switch from an egocentric strategy to an allocentric strategy during an initial probe trial, and ii) that participants executed immediate bidirectional shifts between egocentric and allocentric strategies without additional experience of the environment. Similarly, Marchette et al. (2011) found that after learning a route through a virtual environment, participants often used both allocentric and egocentric strategies during subsequent navigation. Finally, Hirtle and Hudson (1991) found that after learning a landmark-rich route twice, some participants could accurately judge the Euclidean distance, route distance and the spatial relationship between landmarks, thus demonstrating the use of a cognitive map. Overall, these studies suggest that cognitive maps may develop concurrently with landmark and route knowledge (also see Cassel, Kelche, Lecourtier & Cassel, 2012; Devlin, 1976).

Finally, it has also been argued that cognitive maps are developed earlier in the learning process than landmark and route knowledge, as the hippocampus supports the rapid learning of allocentric knowledge, while the striatum is involved in the slower acquisition of stimulus-response associations (i.e. egocentric knowledge) (Bast, Wilson, Witter & Morris, 2009; Packard & Knowlton, 2002). For example, Schmitzer-Torbert (2007) assessed participants' strategy preference in a multiple T-maze task during either the early or later stages of training, and found that allocentric strategy use was prevalent during initial learning, while egocentric strategy use was more common later in training. Furthermore, Chang and Gold (2003) measured the release of acetylcholine (ACh), which is indicative of neural activity, in both the hippocampus and striatum of rats during a Cross Maze task. Probe trials administered throughout training revealed that rats initially employed an allocentric strategy, before increasingly adopting an egocentric response strategy. Correspondingly, ACh levels increased in the hippocampus at the beginning of training, and in the striatum later in training. Similarly, Packard and McGaugh (1996) administered probe trials after 8 and 16 days of training in a Cross Maze, and found that rats initially relied on an allocentric place strategy, before shifting to an egocentric response strategy. Taken together, these findings suggest that allocentric knowledge is acquired faster than egocentric knowledge.

In summary, findings regarding the development of spatial knowledge have proved inconclusive. The dominant framework of spatial microgenesis (Siegel & White, 1975) suggests that individuals first acquire knowledge sufficient for egocentric strategy use, before developing a cognitive map of an environment. However, it has also been argued that i) both types of knowledge are acquired in parallel, and ii) allocentric knowledge precedes egocentric knowledge.

### 1.8. Conclusions

To conclude, environmental objects can be used to facilitate the acquisition of spatial knowledge and inform subsequent navigation. Research has shown that individuals select landmarks based on several key object properties, including saliency, distinctiveness, permanence and position, and incorporate them into spatial knowledge using two different types of wayfinding strategies: hippocampal-dependent allocentric strategies, and striatal-dependent egocentric strategies. Several paradigms allow researchers to assess participants' strategy choices, and help provide a better understanding of the spatial decision making processes involved in different navigation tasks. However, to date, little consensus has been reached regarding the development of spatial knowledge while learning new environments.

# CHAPTER 2. Egocentric Response Strategies: Associative Cue and Beacon-based Navigation

## 2.1. Overview

This chapter presents two experiments that examine the use of two different egocentric response strategies for the purposes of learning a route. Associative cue strategy use relies on cued recall to successfully navigate learned routes, with encoded landmarks facilitating the retrieval of stored route knowledge (Tlauka & Wilson, 1994). In contrast, beacon-based learning depends on item memory, with subsequent navigation involving movement towards the encoded landmark (Waller & Lippa, 2007). Previous research has revealed that beacon strategy use supports faster learning and more accurate navigation than associative cue strategy use. Therefore, the purpose of Experiment 1 was to further investigate the differences between associative cue and beacon-based navigation in a novel route learning task.

The wayfinding strategies available to navigators often vary across environmental locations. For example, if the availability of cues differs at decision points within an environment, navigators may be able to utilise landmark-based wayfinding strategies at some decision points, but not at others. Therefore, alternating between wayfinding strategies is commonplace during real-world navigation. In other cognitive domains, it has been found that switching between different strategies incurs cognitive costs that result in increased error rates and response times (Kiesel et al., 2010). However, to date, no research has investigated how switching between strategies while traversing a route affects navigation performance. Therefore, the aim of Experiment 2 was to examine whether alternating between associative cue and beacon-based navigation affects the efficacy of either strategy.

## 2.2. Introduction

Landmarks are salient environmental features that can be used to support the acquisition of spatial knowledge, with landmark-rich routes typically learned better than landmark-free routes (Jansen-Osmann & Fuchs, 2006; Ruddle, Volkova, Mohler & Bülthoff, 2011; Waller & Lippa, 2007). Employing an egocentric response strategy, which involves encoding route knowledge relative to one’s body, is the most efficient landmark-based method of learning a route (Hartley, Maguire, Spiers & Burgess, 2003). Landmarks are utilised differently during the use of the most common egocentric strategies – the associative cue and beacon response strategies (Waller & Lippa, 2007). Associative cue strategy use involves relating an explicit behavioural action with a landmark located at a wayfinding decision point, forming a stimulus-response pair (e.g. ‘Turn left at the supermarket’). Subsequent navigation involves cued recall, with recognition of the encoded landmark triggering retrieval of the stored response. In contrast, navigators selectively encode landmarks that spatially coincide with the direction of the route during beacon strategy use. During subsequent navigation, recognition of an encoded landmark activates a general behavioural action that results in movement along the learned route (e.g. ‘Turn/move towards the supermarket’). As explicit directional responses are not encoded for each decision point, the route knowledge required to employ a beacon strategy is functionally equivalent to item memory (Waller & Lippa, 2007).

Waller and Lippa (2007) conducted a series of experiments examining the function of associative cue and beacon landmarks. In their paradigm, participants navigated through a linear arrangement of rooms, with two doors located at the far side of each room. One of these two doors allowed access to the next room in sequence, with two landmarks positioned either horizontally between both doors or adjacent to each door to facilitate associative cue or beacon strategy use respectively (see Figure 6). Waller and Lippa (2007) found that beacon strategy use supported faster route learning and more accurate navigation than associative cue strategy use, which was attributed to differences in the route knowledge required to employ each strategy. While a single landmark must be encoded at each decision point to employ either egocentric strategy, associative cue-based learning requires additional memory resources to relate an explicit directional response with each individual landmark. In contrast, decision point-specific directional knowledge is not required to employ a beacon strategy, as the same behavioural response is triggered when beacon landmarks are encountered during navigation. Therefore, beacon strategy use is more parsimonious than associative cue strategy use, and supported route learning better. Waller and Lippa (2007) also found that after learning a route, beacon strategy users recalled more landmarks than associative cue users, suggesting that the relative efficiency of the beacon strategy allowed users to devote more cognitive resources to encoding landmarks. Finally, in rooms that supported beacon-based learning, participants’ spatial behaviour corresponded with beacon strategy use even when the position of landmarks at learned decision points were switched i.e. participants navigated towards the new position of the beacon landmark. Interestingly, a post-experiment questionnaire revealed that participants were aware of the landmark switch, suggesting that they encoded and retrieved strategy-irrelevant knowledge of landmark position during learning and subsequent navigation respectively. This was reflected by an increase in navigational response times when the position of landmarks was switched compared to when landmark position remained stable, suggesting that participants processed the discrepancy in landmark position. Therefore, despite recognising the landmark switch, participants relied on the spatial decision making process underlying the beacon strategy to guide navigation, rather than knowledge of prior landmark location.

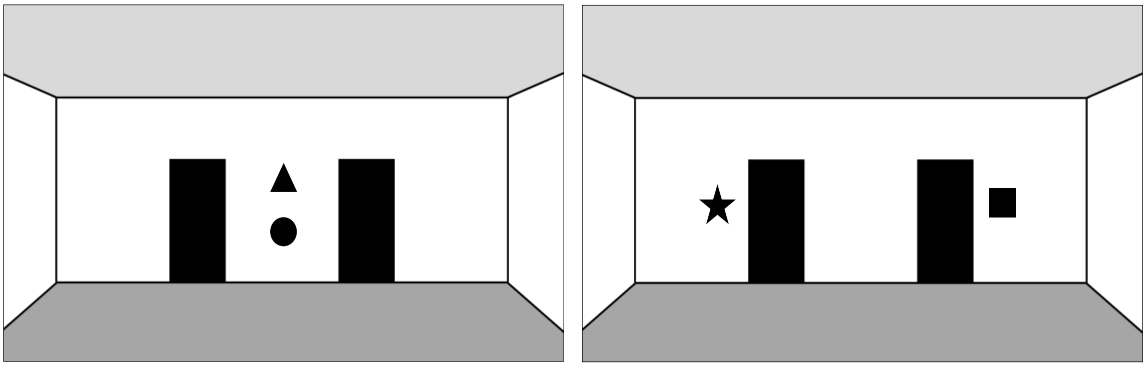


**Figure 6.** An example of decision points used by Waller and Lippa (2007) to elicit different types of egocentric strategy use. Left: An Associative Cue room. Participants must associate a movement direction with a single landmark to learn which door allows access to the next room. Right: A Beacon room. The most efficient method of learning to navigate through the room is to encode the landmark that spatially coincides with route movement, and turn towards the encoded landmark during subsequent navigation.

The purpose of this chapter was to further investigate the properties of associative cue and beacon-based learning. Specifically, we examined whether beacon strategy use supported route learning better than associative cue strategy use in an experimental paradigm in which decision points were tested in a random order. In Waller and Lippa's experiments, participants navigated through rooms in the same order experienced during learning, allowing the use of a sequential response strategy in which a series of memorised movement responses are executed to support route navigation. Indeed, the removal of landmarks from a learned route did not reduce performance to chance level in routes designed to elicit either associative cue or beacon strategy use, suggesting that participants were not necessarily relying on landmark-based route knowledge. In the experiments presented in this chapter, participants' decision point-specific route knowledge was tested in random order, deterring the use of a sequential response strategy, and encouraging the use of a landmark-based route learning strategy. Specifically, the arrangement of landmarks at wayfinding decision points was manipulated to encourage either associative cue or beacon strategy use (see Figure 7). Associative cue and beacon-based learning were assessed in two experiments: a between-groups experiment (Experiment 1) in which the wayfinding environment encouraged the use of either an associative cue or beacon response strategy to learn an entire route, and a within-groups experiment (Experiment 2) in which different decision points within the same route encouraged the use of different route learning strategies. Given that less cognitive effort is required to encode and recall beacon-based knowledge than associative cue-based knowledge, we expected to replicate the findings of Waller and Lippa (2007) in Experiment 1, with beacon strategy use supporting more accurate navigation and better learning than associative cue strategy use. Furthermore, we assessed the spatial knowledge acquired by participants during the use of each strategy. Previously, Waller and Lippa (2007) found that beacon-based route learners navigated above chance level in the absence of landmarks, and noticed changes in landmark location, suggesting that beacon strategy users acquired strategy-irrelevant knowledge of i) the sequence of turns required to proceed along the route, and ii) the position of landmarks within the environment. Therefore, we assessed participants' decision point-specific knowledge of turning (i.e. route) direction and landmark position to determine whether navigators only encode information necessary for their concurrent strategy.

In Experiment 2, participants learned a route in which decision points either required associative cue strategy use, or encouraged the use of a beacon strategy. The primary purpose of this experimental design was to investigate whether participants learned the route by i) employing a single wayfinding strategy, or ii) switching between two different strategies. As an associative cue strategy is available at any decision point featuring a landmark, participants can employ an associative cue strategy to learn the entire route, rather than utilise a second, more efficient strategy (i.e. a beacon strategy) at specific decision points. Participants may prefer to employ a single strategy throughout the route due to the cognitive costs associated with employing and switching between two different strategies. These costs, which are similar to alternation or mixing costs found in task switching literature (see Kiesel et al., 2010; Monsell, 2003 for reviews), include lower accuracy and increased response latencies, and may explain why participants continue to use a single strategy despite the availability of a more efficient or accurate alternative strategy (Bröder & Schiffer, 2006; Luwel, Lemaire & Verschaffel, 2005; Schillemans, Luwel, Bulté, Onghena & Verschaffel, 2009). However, it should be noted that strategy shifts during navigation are common, with some studies suggesting that different wayfinding strategies are acquired in parallel (Cassel, Kelche, Lecourtier & Cassel, 2012; Iglói, Zaoui, Berthoz & Rondi-Reig, 2009; Marchette, Bakker & Shelton, 2011; Packard & McGaugh, 1996). Interestingly, in a study that employed a similar within-participants design, Waller and Lippa (2007) found that participants switched between an associative cue and beacon response strategy when learning a route with decision points that encouraged the use of different wayfinding strategies. Specifically, the performance advantage for beacon over associative cue-based learning was also evident when both strategies were employed within the same route, suggesting that the costs associated with alternating strategies are outweighed by the benefits of employing a superior strategy at selected decision points. Therefore, we expected that optimal navigation performance would involve the use of both an associative cue and beacon response strategy to learn a single route, with participants learning decision points that facilitate beacon strategy use better than those that encourage associative cue strategy use. If, as expected, participants employ two wayfinding strategies to learn a single route, the second aim of Experiment 2 was to investigate whether switching strategies affected associative cue or beacon-based learning and navigation. In their paper, Waller and Lippa (2007) did not compare the efficacy of either strategy when employed separately or in conjunction to learn a route. Therefore, to determine the costs of switching between strategies during navigation, we compared strategy-specific navigation performance in Experiments 1 and 2. Due to the additional cognitive effort required to employ two wayfinding strategies compared to one, we expected associative cue and beacon strategy use to be less accurate and efficient in Experiment 2.

## 2.3. Experiment 1

The primary purpose of Experiment 1 was to replicate and extend the research of Waller and Lippa (2007) using a navigation paradigm that better controlled for the use of a sequential response strategy. Specifically, the aim of this experiment was to: i) compare associative cue and beacon-based route learning, ii) assess whether the turning direction required to accurately navigate through a decision point is associated with landmarks during associative cue as well as beacon strategy use, and iii) determine whether the position of landmarks in an environment is learned when employing an associative cue or beacon strategy.

### 2.3.1. Method

**Participants.** Forty-four participants (mean age = 20.20, *SD* = 2.39) from Bournemouth University participated in the study in return for course credit or payment of £6. Twenty-two participants were assigned to the Associative Cue experimental group (13 females) and 22 participants were assigned to the Beacon experimental group (12 females).

**Figure 7.** Decision points designed to encourage different types of egocentric strategy use. Left: An Associative Cue intersection. Participants must associate a movement direction with a single landmark to learn the route through the intersection. Right: A Beacon intersection. The most efficient method of learning the route is to encode the landmark that spatially coincides with route movement, and turn towards the encoded landmark during subsequent navigation.

**Materials and Apparatus.** The route learning task was presented in a virtual environment rendered in Vizard 3.0 (WorldViz). The route contained 18 intersections, each featuring two unique landmarks. Landmarks were either suspended from the centre of the ceiling in a vertical arrangement (Associative Cue condition) or located on each side of an intersection (Beacon condition) (See Figure 7). The experiment was presented on a 22” LCD monitor with a resolution of 1680x1050 and a screen refresh rate of 120Hz. A standard computer keyboard was used to record responses.

**Procedure.** Participants were randomly assigned to the Associative Cue or Beacon condition, and completed four tasks designed to assess route and environmental knowledge in the following order (see Figure 8).

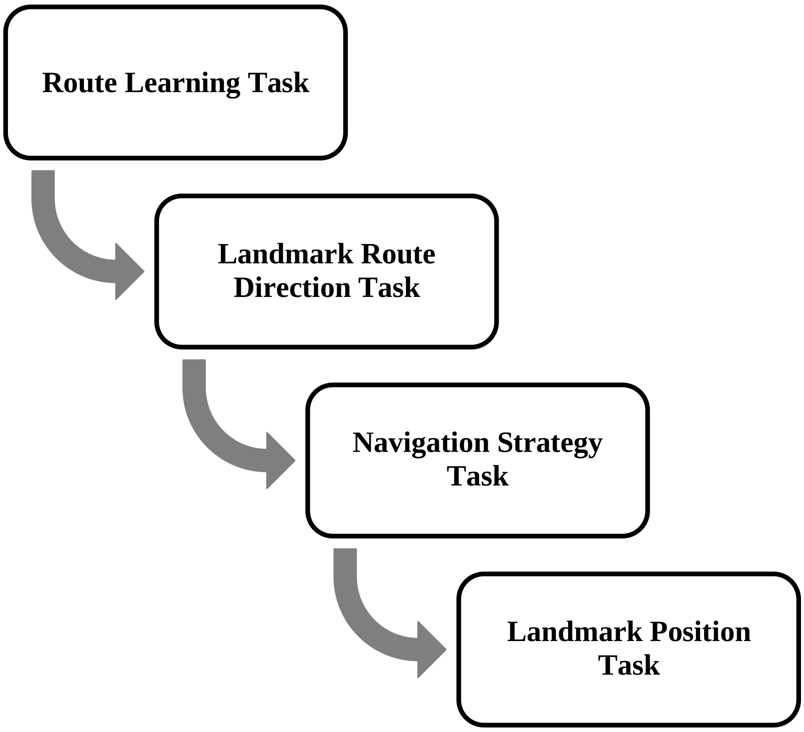


**Figure 8.** Task order. Participants first completed the *Route Learning Task*, which consisted of six experimental blocks. This was followed by the *Landmark Route Direction Task*, the *Navigation Strategy Task*, and finally, the *Landmark Position Task*.

***Route Learning Task.*** Participants completed six experimental blocks, each consisting of a training phase and a test phase. During each training phase, participants were passively navigated along a route consisting of 18 intersections with nine left turns and nine right turns. Participants were asked to learn the route shown. In the Associative Cue condition, two landmarks were suspended from the ceiling in the centre of each intersection (see Figure 7). To successfully learn the route through each intersection, participants had to associate the correct movement direction (left/right) with one or both of the centrally located landmarks. In the Beacon condition, landmarks were located at either side of each intersection (see Figure 7).While participants could also employ an associative cue strategy in the Beacon condition, the most efficient route learning strategy available involved encoding the landmark that spatially corresponded with movement through an intersection, and employing a general ‘Turn towards…’ rule upon recognising the encoded landmark during subsequent navigation i.e. a beacon response strategy. To assess route knowledge during the test phase, participants were tested on each intersection individually and in random order. In each test trial, participants were passively transported towards a single intersection, with movement ending at the centre of the junction. Participants were asked to indicate the direction of travel required to proceed along the original route by pressing the left or right arrow key on the keyboard provided. Responses made more than two seconds after movement stopped were not recorded.

***Landmark Route Direction Task.*** Following the final block of the *Route Learning Task*, participants were presented with each landmark in a random order, and instructed to indicate the direction of movement required to proceed along the original route when approaching the intersection featuring the presented landmark. The purpose of this task was to establish whether participants associated explicit directional knowledge with landmarks in both experimental conditions. While such knowledge is necessary to employ an associative cue strategy, beacon-based navigation involves the use of a ‘Turn towards landmark X’ rule to support navigation, and therefore does not require explicit directional route knowledge.

***Navigation Strategy Task.*** While an associative cue strategy is the only wayfinding strategy available to participants in the Associative Cue condition, participants in the Beacon condition can employ either a beacon or associative cue strategy. To identify which strategy participants employed in the Beacon condition, participants completed a *Navigation Strategy Task* consisting of a single test phase from the *Route Learning Task*. The position of the landmarks at three intersections were switched, with the landmarks at all other intersections remaining in the same position (i.e. stable). Responses made at these probe intersections were used to identify the strategy employed. In comparison to navigation at the same intersection in the final block of the *Route Learning Task* (block 6), a different movement response at probe intersections in the *Navigation Strategy Task* is indicative of beacon strategy use, as the beacon landmark changes location from one side of the intersection to the other between tasks. In contrast, the same movement response at probe intersections is indicative of associative cue strategy use, as landmark location does not influence the associative cue spatial decision making process (Waller & Lippa, 2007). Furthermore, response times were compared between probe intersections in the *Navigation Strategy Task* (block 7) and the corresponding intersections in block 6 of the *Route Learning Task* to determine whether landmark position was evaluated during participants’ spatial decision making process. Similar response times would suggest that, irrespective of the strategy employed, participants did not assess landmark position. In contrast, increased response times in the *Navigation Strategy Task* would suggest that participants noticed the landmark switch, resulting in a longer spatial decision making process. In a similar task, Waller and Lippa (2007) demonstrated that changes in landmark location were associated with increased response times during beacon-based navigation, suggesting that participants reflected upon changes in landmark position. To ensure that participants in both conditions followed an identical experimental protocol, participants in the Associative Cue condition also completed a variant of the *Navigation Strategy Task* in which the position of the vertically arranged landmarks were switched at selected intersections.

***Landmark Position Task.*** Participants were presented with images of each stable landmark (i.e. landmarks at probe intersections in the *Navigation Strategy Task* were not used in this task) in a random order, and instructed to indicate its position at the intersection containing the presented landmark. Participants in the Associative Cue condition were asked if the landmark was the uppermost or lowermost landmark, and participants in the Beacon condition were asked if the landmark was located on the left or right side of the intersection. The purpose of this task was to establish whether participants acquired positional knowledge about the landmarks present in the Associative Cue and Beacon conditions. While the position of a landmark in relation to the route through an intersection is important for the selection of beacon landmarks, neither associative cue or beacon strategy use depends on explicit positional knowledge about landmarks at an intersection to support spatial navigation.

Participants received instructions prior to each task, and were therefore unaware of the nature of any following tasks. Responses and response times were recorded for each task, and participants did not receive any feedback about their performance.

### Analysis

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

### 2.3.2. Results

***Route Learning Task.*** Participants in the Associative Cue condition chose the correct movement direction in 75.3% of test trials, while participants in the Beacon condition answered 84.1% of test trials correctly. An ANOVA with experimental block [1-6] as a within-participants factor and condition [Associative Cue, Beacon] as a between-participants factor revealed that navigation accuracy improved over the course of the experiment from 58.5% in the first block to 89.1% in the sixth block (main effect of experimental block: $F(2.47, 103.83) = 55.00$, $p < .001$, $\eta_p^2 = .57$), and that participants in the Beacon condition performed better than participants in the Associative Cue condition [$F(1, 42) = 4.42$, $p = .042$, $\eta_p^2 = .01$] (see Figure 9). A significant block x condition interaction [$F(2.47, 103.83) = 4.66$, $p = .007$, $\eta_p^2 = .10$] suggested that participants in the Associative Cue and Beacon conditions learned the route differently over the course of the experiment. Post-hoc analysis revealed that participants reached ceiling level performance in the fourth experimental block in the Associative Cue condition and the third experimental block in the Beacon condition, demonstrating a learning advantage for beacon strategy use over associative cue strategy use.

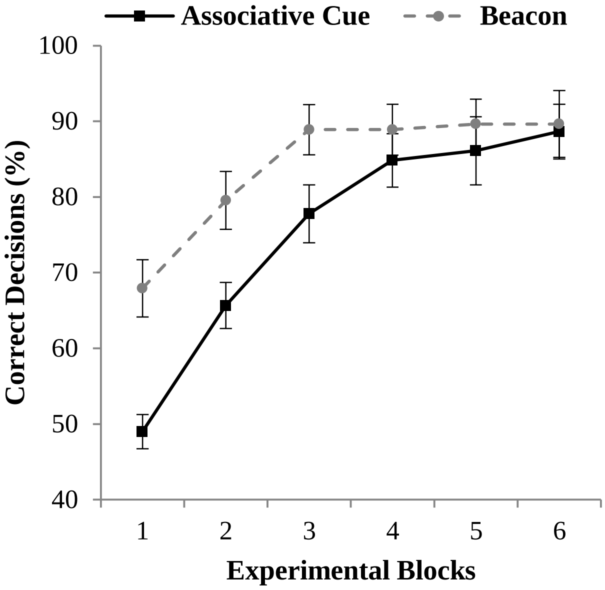


**Figure 9.** Navigation accuracy across experimental blocks by condition (mean±standard error).

***Landmark Route Direction Task.*** The percentage of trials in which participants correctly chose the route direction associated with a landmark was used as the dependent variable in the following analysis. One sampled *t*-tests against chance level (50%) revealed that participants in both the Associative Cue ($M = 82.52\%$, $SD = 14.13$; $t(21) = 10.79$, $p < .001$, $r = .92$) and Beacon condition ($M = 75.15\%$, $SD = 16.70$; $t(21) = 7.06$, $p < .001$, $r = .84$) associated directional route knowledge with landmarks. While associating a specific movement response with an encoded landmark is necessary to employ an associative cue strategy, such explicit directional knowledge is not required for a beacon response strategy. Therefore, this result suggests that participants in the Beacon condition either i) employed a beacon strategy, but acquired strategy-irrelevant directional route knowledge or ii) employed an associative cue strategy despite the availability of the more cognitively efficient beacon response strategy. During beacon-based learning, navigators encode the landmark that spatially coincides with route movement (the Route Congruent Landmark). If participants primarily employed a beacon strategy in the Beacon Condition, it is more likely that they associated explicit directional knowledge with the Route Congruent landmark than with the landmark that did not correspond with the learned path (i.e. the Route Incongruent Landmark). Accordingly, a paired samples t-test revealed that participants in the Beacon condition preferentially associated directional route knowledge with the beacon landmark (Route Congruent Landmark – *M* = 93.15%, *SD* = 10.51), rather than with the Route Incongruent landmark (*M* = 57.14%, *SD* = 32.27) (*t*(21) = 4.90, *p* < .001, *r* = .73). It should also be noted that as associative cue strategy use does not involve defined landmark selection criteria – i.e. either landmark at an intersection can serve as an associative cue – a similar comparison between strategy-relevant and irrelevant landmarks was not performed for the Associative Cue condition.

***Navigation Strategy Task.*** To determine whether participants employed a beacon response strategy in the Beacon condition, we compared the movement decisions made by participants in the three probe trials (block 7) to the corresponding intersection in the final block of the *Route Learning Task* (block 6). Participants changed their response in 86.4% of probe trials, suggesting that participants relied on beacon-based navigation in the Beacon condition (*M* = 86.36%, *SD* = 19.68; one-sampled *t*-test against chance level (50%): *t*(21) = 8.67, p < .001, *r* = .88). Furthermore, response times at probe intersections in the *Navigation Strategy Task* (block 7: *M* = 4.08s, *SD* = 1.81) and the same intersection in final block of *Route Learning Task* (block 6: *M* = 4.03s, *SD* = 1.97) did not significantly differ (*p* > .05), suggesting that participants did not evaluate landmark position during navigation.

***Landmark Position Task.*** The percentage of trials in which participants correctly identified the position of a landmark at a decision point was used as the dependent variable in the following analysis. One sampled *t*-tests against chance level (50%) revealed that participants in both the Associative Cue (*M* = 91.97%, *SD* = 8.01; *t*(21) = 24.57, *p* < .001, *r* = .98) and Beacon condition (*M* = 90.76%, *SD* = 12.68; *t*(21) = 15.08, *p* < .001, *r* = .96) acquired knowledge of landmark position. It is conceivable that participants in the Associative Cue condition selected landmarks to encode by their position in the environment (e.g. the lowermost landmark at each intersection), resulting in general positional knowledge of different landmark groups (strategy-relevant and irrelevant), rather than explicit positional knowledge of each individual landmark. In contrast, the lateral position of the beacon landmark (Route Congruent) and the strategy-irrelevant landmark (Route Incongruent) varies between intersections in the Beacon condition. Therefore, participants' knowledge of the position of both Route Congruent (*M* = 94.55%, *SD* = 10.21; *t*(21) = 20.46, *p* < .001, *r* = .98) and Route Incongruent landmarks (*M* = 86.97%, *SD* = 16.78; *t*(21) = 10.34, *p* < .001, *r* = .91) suggests that positional information about each individual landmark was explicitly encoded during route learning in the Beacon condition. Furthermore, a paired samples *t*-test revealed that participants' knowledge of landmark position was more precise for Route Congruent landmarks than Route Incongruent landmarks ($t(21) = 3.14$, $p < .005$, $r = .56$).

### 2.3.3. Discussion

Experiment 1 revealed that route learning is supported better by the use of a beacon response strategy than an associative cue strategy, replicating the findings reported by Waller and Lippa (2007). Participants in the Beacon Condition not only navigated more accurately than participants in the Associative Cue condition in the *Route Learning Task*, but also reached ceiling level performance earlier. Interestingly, despite employing a strategy that relies solely on the observed position of an encoded landmark to inform movement decisions, participants in the Beacon Condition associated explicit knowledge of route direction with the beacon landmark. Such information is not required to employ a beacon response strategy, suggesting that participants acquired strategy-irrelevant spatial knowledge. However, it should be noted that explicit directional knowledge is required to employ an associative cue strategy. Therefore, participants in the Beacon Condition acquired route knowledge relevant to both the beacon and associative cue strategies. Finally, participants in the Beacon Condition also acquired knowledge regarding the position of landmarks in the environment. Although the position of an encoded landmark is utilised to inform beacon-based navigation, neither beacon nor associative cue strategy use requires explicit knowledge of landmark position, again suggesting that participants acquired spatial knowledge that was not essential to their preferred wayfinding strategy. Taken together, the acquisition of strategy-irrelevant route and environmental knowledge during beacon-based learning provides an interesting perspective on participants' performance in the *Navigation Strategy Task*. When the position of landmarks were switched at known intersections, participants turned towards the beacon landmark (now located on the opposite side of the intersection) despite possessing conflicting knowledge regarding the landmark's original position and the direction in which the route originally proceeded. Indeed, response time analysis suggests that the spatial decision making process employed by participants in the Beacon Condition was not influenced by knowledge of route direction or landmark position. As such, it appears that beacon-based navigation relies solely on strategy-relevant route knowledge, rather than any supplementary spatial knowledge acquired during learning.

## 2.4. Experiment 2

A within-participants design was adopted in Experiment 2, with each participant learning a route that encouraged associative cue and beacon-based learning at different decision points (see Figure 7). The purpose of Experiment 2 was i) to determine whether participants learned a single route by switching between the associative cue and beacon response strategies depending on the environmental support available at each decision point, ii) to assess the route and environmental knowledge acquired by participants when alternating between two strategies to learn the same route, and iii) to compare the results of Experiments 1 and 2 in order to identify any differences in navigation performance and spatial knowledge that result from learning a route by employing a single wayfinding strategy or switching between two different strategies.

### 2.4.1. Method

**Participants.** Twenty-two participants (11 females, mean age = 20.23, *SD* = 2.67) from Bournemouth University participated in the study in return for course credit or payment of £6.

**Materials, Apparatus and Procedure.** The materials, apparatus and procedure for Experiment 2 were similar to those for Experiment 1 with minor modifications made to the virtual environment and the *Navigation Strategy Task* to support a within-participants experimental design. First, all participants learned the same 18 intersection route, which contained nine Associative Cue intersections and nine Beacon intersections (see Figure 7) distributed in a random order along the route. Second, in the *Navigation Strategy Task,* landmarks were switched at two Associative Cue and two Beacon intersections. While an associative cue strategy was required to support learning at Associative Cue intersections, participants were able to employ either a beacon or associative cue strategy at Beacon intersections. Therefore, the purpose of the *Navigation Strategy Task* was to determine participants' strategy choice at Beacon intersections. Response differences between probe Beacon intersections in the *Navigation Strategy Task* and the corresponding intersection in block 6 of the *Route Learning Task* would not only be indicative of beacon strategy use, but would also suggest that participants alternated between associative cue and beacon-based navigation. In contrast, a preference for an associative cue strategy would suggest that participants chose to employ a single strategy to learn the entire route i.e. an associative cue strategy, rather than incur accuracy and response time costs associated with switching to a different – albeit more efficient – strategy at Beacon intersections i.e. a beacon strategy.

### 2.4.2. Results

***Route Learning Task.*** Participants chose the correct movement direction in 79% of all trials (Associative Cue intersections: 75.2%, Beacon intersections: 82.7%). An ANOVA with experimental block [1-6] and intersection type [Associative Cue, Beacon] as within-participants factors revealed that performance improved over the course of the experiment from 56.3% in the first block to 88.1% in the sixth block (main effect of experimental block: $F(2.52, 52.82) = 27.97$, $p < .001$, $\eta_p^2 = .57$), and that participants performed better at Beacon intersections compared to Associative Cue intersections [$F(1, 21) = 13.11$, $p = .002$, $\eta_p^2 = .38$] (see Figure 10). A marginally significant block x condition interaction [$F(5, 105) = 2.31$, $p = .049$, $\eta_p^2 = .01$] suggested that participants' performance at the Associative Cue and Beacon intersections evolved differently over the course of the experiment. Post-hoc analysis revealed that ceiling level performance was reached in the third experimental block for Associative Cue intersections, and the second experimental block for Beacon intersections, demonstrating an advantage for learning Beacon intersections as compared to Associative Cue intersections. Taken together, these results, which are similar to those reported in Experiment 1, suggest that participants used different strategies at different types of intersection.

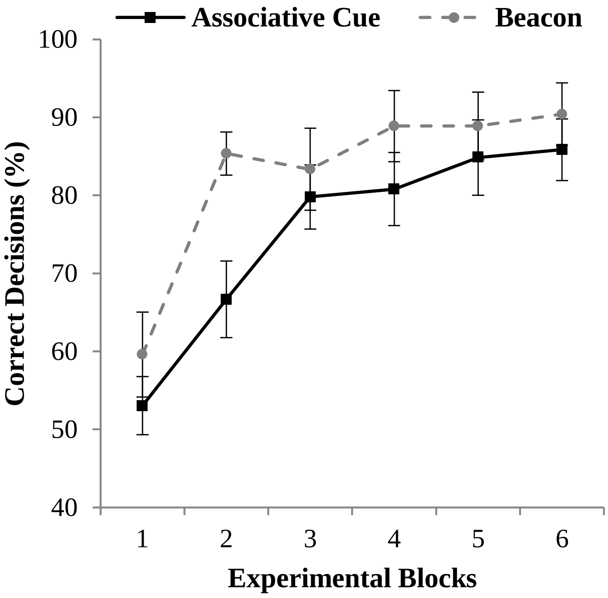


**Figure 10.** Navigation accuracy across experimental blocks by intersection type (mean±standard error).

***Landmark Route Direction Task.*** The percentage of trials in which participants correctly chose the route direction associated with a landmark was used as the dependent variable in this analysis. One sampled *t*-tests against chance level (50%) revealed that participants associated directional knowledge with landmarks at both Associative Cue ($M = 75.97\%$, $SD = 17.74$; $t(21) = 6.87$, $p < .001$, $r = .83$) and Beacon intersections ($M = 77.88\%$, $SD = 15.75$; $t(21) = 8.30$, $p < .001$, $r = .88$). As in Experiment 1, associating explicit directional knowledge with landmarks at Beacon intersections suggest that participants either acquired strategy-irrelevant route knowledge during beacon-based learning, or employed an associative cue strategy throughout the route. However, this knowledge was preferentially associated with Route Congruent landmarks ($M = 86.88\%$, $SD = 10.51$) rather than Route Incongruent Landmarks ($M = 68.88\%$, *SD* = 25.49) at Beacon intersections (*t*(21) = 2. 62, *p* = .016, *r* = .50), suggesting that participants acquired strategy-irrelevant spatial knowledge during beacon strategy use.

***Navigation Strategy Task.*** Compared to navigation in block 6 of the *Route Learning Task*, participants changed their movement response in 65.9% of Beacon probe trials in the *Navigation Strategy Task* (block 7), suggesting that participants employed a beacon strategy at Beacon intersections (*M* = 65.91%, *SD* = 35. 81; one-sampled *t*-test against chance level (50%): *t*(21) = 2.08, p = .05, *r* = .41), and therefore alternated between associative cue and beacon strategy use during route navigation. Furthermore, response times at these intersections (block 6: *M* = 4.21s, *SD* = 2.16, block 7: *M* = 4.51s, *SD* = 1.60) were not significantly different, suggesting that participants did not evaluate landmark position when navigating through Beacon intersections.

***Landmark Position Task.*** The percentage of trials in which participants correctly identified landmark position was used as the dependent variable in the following analysis. One sampled *t*-tests against chance level (50%) revealed that participants acquired knowledge about the position of landmarks at both Associative Cue (*M* = 75.97%, *SD* = 21.43; *t*(21) = 5.68, *p* < .001, *r* = .78) and Beacon intersections (*M* = 87.99%, *SD* = 11.54; *t*(21) = 15.45, *p* < .001, *r* = .96). At Beacon intersections, participants acquired positional knowledge of both the Route Congruent (*M* = 93.51%, *SD* = 13.02; *t*(21) = 15.67, *p* < .001, *r* = .96) and Route Incongruent landmark (*M* = 82.47%, *SD* = 16.46; *t*(21) = 9.25, *p* < .001, *r* = .90), suggesting that the position of each individual landmark at Beacon intersections was explicitly encoded during learning. Furthermore, participants' knowledge of landmark position was better for Route Congruent landmarks than for Route Incongruent landmarks (*t*(21) = 2.77, *p* < .011, *r* = .52).

#### 2.4.2.1. Between-Participants and Within-Participants Analysis.

Analyses were conducted to examine whether learning a route by employing a single strategy or alternating between two different strategies affects participants' navigation performance and spatial knowledge. In the following analyses, all references to the associative cue strategy relate to the Associative Cue condition in Experiment 1, and Associative Cue intersections in Experiment 2, while all references to the beacon strategy relate to the Beacon condition in Experiment 1, and Beacon intersections in Experiment 2.

***Route Learning Task.*** Separate ANOVAs for associative cue and beacon performance were conducted to examine how navigation accuracy was affected by switching between two different strategies compared to using only a single strategy. An ANOVA with experimental block [1-6] as a within-participants factor, Experiment [1, 2] as a between-participants factor and associative cue performance as the dependent variable revealed a main effect of experimental block [*F*(3.05, 128.08) = 53.16, $p < .001$, $\eta_p^2 = .56$], but no significant main effect of Experiment or an interaction. Similarly, an ANOVA with beacon performance as the dependent variable revealed a main effect of experimental block [*F*(2.53, 106.19) = 31.36, $p < .001$, $\eta_p^2 = .43$], but no other main effects or interactions. Taken together, these findings suggest that alternating between two different strategies while learning a single route does not affect the efficacy of either an associative cue or beacon response strategy.

***Landmark Route Direction Task.*** Independent samples *t*-tests did not reveal any significant differences in *Landmark Route Direction Task* performance between Experiments 1 and 2 (all $p > .05$). This finding suggests that learning a route by switching between two different strategies does not affect the route knowledge associated with landmarks during associative cue or beacon-based learning.

***Navigation Strategy Task.*** An independent samples *t*-test revealed that compared to navigation in block 6 of the *Route Learning Task*, participants in Experiment 1 changed their response at beacon strategy probe trials more frequently than participants in Experiment 2 [*t*(32.62) = 2.35, $p = .03$, $r = .38$], suggesting that beacon strategy use was more prevalent in Experiment 1 than in Experiment 2. Given that beacon strategy use was above chance level in both experiments, this finding suggests that participants were less likely to employ the most effective strategy at decision points when strategy switching was required compared to when it was not.

***Landmark Position Task.*** Independent samples *t*-tests revealed that only participants' positional knowledge of landmarks when employing an associative cue strategy decreased when alternating between two different wayfinding strategies compared to using only a single strategy [*t*(32.62) = 2.35, $p = .025$, $r = .54$]. This result suggests that the additional cognitive effort required to alternate between different strategies selectively impaired the learning of landmark position during associative cue strategy use.

***Response Time.*** To determine whether alternating between strategies or employing a single strategy to learn a route affected response times, separate independent samples *t*-tests were conducted for each strategy to compare response times in Experiment 1 and Experiment 2. Response times during associative cue (Experiment 1: *M* = 4.51s, *SD* = 1.35; Experiment 2: *M* = 5.02s, *SD* = 1.40) and beacon-based navigation (Experiment 1: *M* = 4.40s, *SD* = 1.75; Experiment 2: *M* = 4.58s, *SD* = 1.65) did not differ across experiments (both $p > .05$), suggesting that the spatial decision making process associated with each strategy was not affected by strategy switching during navigation.

### 2.4.3. Discussion

Experiment 2 revealed that instead of employing a single wayfinding strategy to learn an entire route, participants elected to use the associative cue and beacon response strategies at different decision points, replicating the findings of Waller and Lippa (2007). In the *Route Learning Task*, participants performed better at Beacon intersections than Associative Cue intersections, suggesting that different strategies were used to navigate through each type of intersection. As a similar advantage for beacon over associative cue-based learning was observed in Experiment 1, we concluded that participants were switching between the associative cue and beacon strategies during navigation. This finding was further corroborated by the *Navigation Strategy Task*, which determined the strategy employed by participants at decision points that were intended to encourage beacon-based learning. Given that an associative cue strategy was required to successfully navigate through Associative Cue intersections, participants' behaviour at probe Beacon intersections not only corresponded with beacon strategy use, but also confirmed that participants alternated between strategies during navigation.

While it was possible to use an associative cue strategy to learn the entire route, participants chose to employ the associative cue and beacon response strategies at different intersections. Given that in other cognitive tasks e.g. mental arithmetic and perceptual discrimination (Jersild, 1927; Rubin & Meiran, 2005), switching between different strategies is known to reduce accuracy and increase response times in comparison to using a single strategy, why did participants employ two strategies to learn a single route? Firstly, in comparison to using a single strategy to learn a route (Experiment 1), analysis revealed no accuracy or response time costs associated with alternating between an associative cue and beacon strategy during navigation (see the Between-Participants and Within-Participants Analysis), which suggests that navigation may be resistant to the switching costs known to affect other cognitive tasks. Indeed, it is possible that the purpose of acquiring spatial knowledge related to alternative strategies (see Experiment 1) was to facilitate potential strategy switches. Secondly, while an associative cue strategy could be employed at every intersection, beacon-based learning was only possible at selected intersections. By alternating between route learning strategies, participants essentially chose to employ a beacon strategy over an associative cue strategy at these intersections. Therefore, participants may have decided that the benefit of employing a more effective strategy at these decision points was greater than any potential switching costs. However, it should be noted that beacon strategy use was more prevalent in the Beacon condition of Experiment 1 than at Beacon intersections in Experiment 2. This finding suggests that participants' strategy choice at intersections that supported beacon strategy use changed between experiments. Therefore, participants' were less likely to employ the optimal strategy at a decision point if strategy switching is involved.

Finally, alternating between strategies did not affect the strategy-irrelevant spatial knowledge (i.e. route direction and landmark position) associated with landmarks during beacon-based learning. In contrast, alternating between different strategies selectively reduced strategy-irrelevant knowledge of landmark position during associative cue strategy use, while strategy-dependent landmark-based knowledge of route direction was not affected. Taken together, these findings suggests that i) the strategy that requires greater cognitive effort is more vulnerable to switching costs, and ii) switching costs affect strategy-irrelevant learning more than strategy-relevant learning.

## 2.5. General Discussion

In this chapter, we investigated the effectiveness of two landmark-based route learning strategies: the associative cue and beacon response strategies. Both a between-groups and within-groups experiment revealed that when employed separately or in combination to learn a route, beacon strategy use facilitated learning and navigation better than associative cue strategy use, replicating the findings of Waller & Lippa (2007). Furthermore, when the most effective wayfinding strategy differed between decision points, participants primarily chose to alternate between different strategies rather than use a single strategy to learn the entire route (Experiment 2). This result suggests that navigators are prepared to expend the additional cognitive effort required to switch strategies in order to optimise route learning. However, despite this finding, it should be noted that compared to when a single strategy was sufficient to optimise route learning (Experiment 1), participants' use of the most effective strategy at decision points was less prevalent when strategy switching was required (Experiment 2). Therefore, the costs associated with alternating strategies affect navigators' strategy choice. Interestingly, analysis conducted to compare participant behaviour from the between and within-group experiments found that repeatedly switching between strategies did not affect the efficacy of either associative cue or beacon-based navigation, suggesting that switching costs did not affect subsequent navigation performance. Finally, when employing a beacon strategy, participants acquired strategy-irrelevant route and environmental knowledge during learning. Specifically, knowledge of route direction and the position of objects at decision points was acquired during beacon-based learning, although this information was not used during subsequent navigation.

A comparison of associative cue and beacon-based learning revealed an accuracy and learning advantage for beacon strategy use, which can be attributed to the different memory demands of each strategy. While the recognition of an encoded landmark triggers the recall of a specific directional response during associative cue use, landmark recognition activates a general behavioural response during beacon strategy use. As such, associative cue and beacon-based navigation rely on cued recall and item memory respectively. Therefore, compared to associative cue strategy use, beacon strategy use is more parsimonious and less cognitively demanding, resulting in superior route learning performance (Waller & Lippa, 2007).

The performance advantage for beacon over associative cue-based learning was evident both when each strategy was used individually to learn a route (Experiment 1), and when the two strategies were used to learn different decision points within the same route (Experiment 2). Interestingly, associative cue and beacon-based navigation accuracy did not differ between experiments. Given that the additional cognitive effort required to alternate between tasks rather than perform a single task often results in increased error rates and response times (e.g. Jersild, 1927; Spector & Biedermann, 1976), our results suggest that alternating between different landmark-based route learning strategies does not incur switching costs that affect navigation accuracy, which may reflect the fact that navigation is a ubiquitous task in which strategy switching is commonplace (e.g. Cassel et al., 2012; Iglói et al., 2009). However, additional measures of spatial learning revealed that participants' strategy choice and environmental knowledge were affected by the costs associated with switching strategies. For example, participants' were less likely to employ the most effective route learning strategy at a decision point when switching strategies was involved. Furthermore, switching strategies was associated with impaired knowledge of landmark position during associative cue-based route learning. These differences, however, were not sufficient to directly affect landmark-based route navigation.

Finally, strategy-irrelevant spatial knowledge was acquired during beacon-based learning. Firstly, explicit route directional knowledge similar to the stored behavioural response required for an associative cue strategy was associated with the beacon landmark during beacon-based learning. Therefore, sufficient knowledge to employ an associative cue strategy was acquired during beacon strategy use. While some studies suggest that spatial knowledge associated with different wayfinding strategies can be acquired in parallel (Cassel et al., 2012; Iglói et al., 2009; Marchette et al., 2011; Packard & McGaugh, 1996), Wang, Mou and Sun (2014) recently found that during route learning, participants initially acquire beacon-based knowledge (when available) before developing associative cue knowledge with increasing experience of the environment. However, it was beyond the scope of this study to determine how and when participants' route knowledge developed. Secondly, participants acquired knowledge about the position of both landmarks at a decision point during beacon-based learning. Given that such information is not required to employ either an associative cue or beacon strategy, why did participants acquire knowledge of landmark position? First, object location may be encoded automatically due to the importance of spatial knowledge for many everyday tasks, including navigation (Hasher & Zacks, 1979; Pouliot & Gagnon, 2005). Alternatively, it is possible that participants acquired more detailed knowledge of the wayfinding environment as their experience of the route increased (Montello, 1998). Finally, participants may have developed a cognitive map of the environment, of which knowledge of landmark position is an important component (O'Keefe & Nadel, 1978; Tolman, 1948). Interestingly, when the position of both landmarks was switched at beacon decision points, participants chose to turn towards the relocated beacon landmark despite possessing conflicting knowledge of prior landmark position and route direction. Given that such knowledge was not acquired to support participants' chosen route learning strategy, it is possible that this information was not recalled during the spatial decision making process associated with beacon-based navigation. Alternatively, participants may have been cognisant of the conflict between their spatial knowledge and the outcome of their preferred wayfinding strategy, and elected to navigate in accordance with the beacon response strategy. Indeed, Waller and Lippa (2007) found that such a conflict interfered with beacon strategy use and resulted in longer navigational response times. However, in this study, response times did not differ between test trials in which the position of the landmarks at beacon decision points remained stable or were switched. This finding suggests that participants relied solely on strategy-relevant route knowledge during beacon-based navigation, and did not recall any strategy-irrelevant knowledge acquired during learning.

## 2.6. Summary

Over two experiments, participants learned routes containing decision points designed to elicit either associative cue or beacon strategy use. Both experiments revealed that compared to associative cue strategy use, beacon strategy use facilitated better route learning and more accurate navigation, which was attributed to differences in the knowledge and spatial decision making process associated with each strategy. Furthermore, using each strategy separately or in conjunction to learn a single route did not affect the efficacy of either associative cue or beacon-based learning, which suggests that i) employing the most efficient strategy for each decision point may be the most effective method of learning a route, and ii) navigation may be less vulnerable to the cognitive costs typically associated with alternating between different strategies. However, despite the potential advantages of alternating between different strategies during navigation, optimal wayfinding strategy use was less prevalent when strategy switching was required compared to when a single strategy was sufficient. Finally, strategy-irrelevant knowledge regarding route direction and landmark position was acquired during beacon-based learning, but did not influence the spatial decision making process employed during subsequent navigation.

# CHAPTER 3. Developing a Novel Strategy Assessment Paradigm

## 3.1. Overview

Researchers employ several different wayfinding paradigms to identify participants' strategy preferences. However, few paradigms discriminate between different egocentric strategies, or assess participants' strategy preference at different stages during the acquisition of spatial knowledge. The following chapter presents pilot data from two experiments that informed the design of a novel strategy assessment paradigm that i) distinguishes between allocentric, associative cue and beacon strategy use, and ii) allows participants' strategy choice to be assessed over time.

## 3.2. Introduction

Wayfinding strategy use is typically assessed with the use of several different paradigms (cf. T-maze; Blodgett & McCutchan, 1947; cf. Morris Water Maze; Morris, 1981; cf. Radial Arm Maze; Olton & Samuelson, 1976; cf. Y-maze; Rodgers, Sindone & Moffat, 2012; cf. Starmaze; Rondi-Reig, Petit, Tobin, Tonegawa & Berthoz, 2006; cf. Cross maze; Tolman, Ritchie & Kalish, 1946b). These paradigms typically differentiate between allocentric and egocentric strategy use, which rely on environmental and body-based frames of reference respectively. However, as discussed in Chapter 1, assessing strategy preference unambiguously is still a difficult task. For example, allocentric and egocentric beacon strategy use are not separable in many paradigms, and few paradigms discriminate between the use of different egocentric response strategies. Therefore, one of the primary purposes of this thesis was to develop a method for assessing participants' strategy preferences accurately.

The paradigm developed for this thesis is conceptually similar to the Cross Maze task (Tolman et al., 1946b), which was developed to investigate strategy use in rodents. During training, rodents learn to navigate from a fixed starting position to a rewarded goal arm through a single four-way intersection surrounded by distal cues (see Figure 11). Navigation in a probe trial in which rodents were released from a novel starting position (the arm directly opposite the original start location) is then used to determine strategy preference. Typically, correctly navigating to the previously rewarded arm is indicative of allocentric strategy use, while repeating the same behavioural response executed during learning suggests the use of a memory-based response strategy (e.g. turning left). However, research has demonstrated that navigation normally attributed to allocentric strategy use also corresponds with the use of an egocentric directional response strategy (Blodgett, McCutchan & Mathews, 1949; Skinner et al., 2003), which is functionally equivalent to a beacon strategy. Directional response learning involves encoding a landmark that is located in the same relative direction as the target arm.

Subsequent navigation involves moving towards the encoded landmark to reduce the distance between oneself and a target destination, and results in accurate navigation during Cross Maze task probe trials (Blodgett et al., 1949; Skinner et al., 2003). As such, allocentric and directional response strategy use can result in the same response during probe trials, and are therefore not dissociable in the Cross Maze task (see Figure 11).

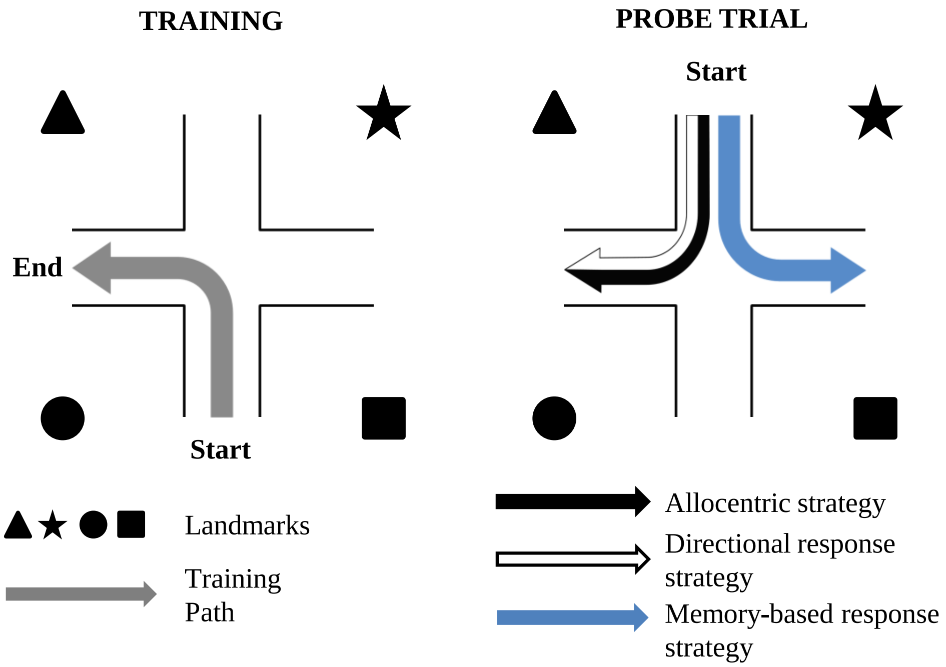


**Figure 11.** The use of different strategies in a Cross Maze task. Left: An overview of the training procedure. Participants learn to navigate from a fixed starting position to a goal arm. Right: An overview of a probe trial. Note that allocentric strategy use and a landmark-based directional response (i.e. beacon strategy use) cannot be distinguished from one another.

While the paradigm developed in this thesis also involves navigation through a four-way intersection, differences in cue location and the start position of probe trials eliminates any ambiguity related to strategy preference (see Figure 12). First, local cues positioned in diagonally opposite corners of each decision point do not reliably support directional learning. As each cue adjoins two arms, in certain test trials, landmark-based directional navigation can result in movement towards either adjacent arm. Therefore, directional response strategy use is unreliable, and unlikely to be employed in this navigation task. Second, participant behaviour in selected test trials can be used to differentiate between three different wayfinding strategies: an allocentric strategy, and the egocentric associative cue and beacon response strategies (see Figure 12). In these probe trials, participants approach the central junction from a direction that differs from learning by 90 degrees, and are asked to navigate to the target destination. Interestingly, in many strategy assessment paradigms, changes in start position only occur during probe trials. Therefore, probe trials differ from prior experimental navigation to such an extent that participants' strategy choice is only assessed on one occasion. In contrast, the starting position of test trials will vary throughout the experiments discussed in this chapter, allowing multiple assessments of strategy preference over time.

The following experiments investigated whether the paradigm developed for the purposes of this thesis accurately assesses participants' strategy preferences. Therefore, the pilot data presented in this chapter is purely exploratory, and will be used to inform the design of a complete working paradigm that will be presented in the following chapter.

## 3.3. Experiment 1

The purpose of this experiment was to examine whether the novel strategy assessment mechanism described above identified participants' strategy preferences accurately and reliably.

### 3.3.1. Method

**Participants.** Twenty-five participants (19 females, mean age = 19.68, *SD* = 1.28) from Bournemouth University participated in the study in return for course credit.

**Materials and Apparatus.** Vizard 3.0 (WorldViz) was used to render the virtual environment in which the navigation task was presented. Each of forty separate intersections featured two unique landmarks located in diagonally opposite corners which could be used to support three different landmark-based wayfinding strategies: an allocentric strategy, and the egocentric associative cue and beacon response strategies (see Figure 12). The task was presented on a 22" LCD monitor with a resolution of 1680x1050 pixels and a screen refresh rate of 120Hz. A standard computer keyboard was used to record participants' responses.

**Procedure.** The forty intersections generated for this experiment were presented in a random order. For each intersection, participants first completed a training phase followed by a single test trial. During training, participants were twice passively transported through a single intersection from a fixed starting position to an arm located on either the left or right-hand side of the central junction. To learn the location of the goal arm, participants could either i) encode the spatial relationship between the available cues and the goal arm (i.e. allocentric learning), ii) associate the turning movement experienced during training with an available cue (i.e. associative cue-based learning), or iii) identify and encode the landmark that spatially corresponds with the path of the route through a decision point (i.e. beacon-based learning) (see Figure 12). In the subsequent test trial, participants were transported towards the central junction and asked to navigate to the goal arm. The test trial start position varied across different intersections, with participants navigated towards the central junction from either the same arm as training, or, excluding the goal arm, from the two remaining radial arms. As egocentric strategy use involves performing a fixed behavioural response irrespective of one’s position in an environment, associative cue and beacon-based navigation are often inaccurate when a known location is approached from an unfamiliar direction. In contrast, allocentric knowledge is conceptualised as a cognitive map that supports flexible navigation in an environment. Therefore, only allocentric strategy use supported accurate navigation in all test trials. A subset of ten test trials, hereafter known as strategy probe trials, was used to determine participants’ strategy preference. In these trials, allocentric strategy use supported accurate navigation, while associative cue and beacon-based navigation resulted in different, incorrect responses (see Figure 12). Therefore, participants’ responses in probe trials were used to identify strategy choice.

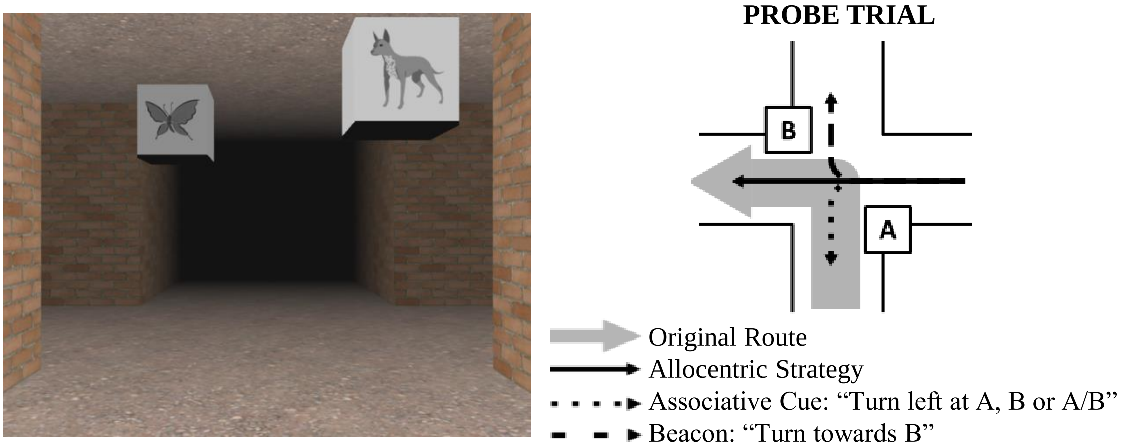


**Figure 12.** An intersection and a strategy assessment probe trial. Left: A screenshot of a single intersection. The location of the landmarks can be used to unambiguously identify the approach direction. During training, the path through the intersection turned either left or right. Right: An overview of a probe trial. The approach direction is different to that experienced during training. In the example provided, the use of each navigation strategy results in a different response, allowing the strategy employed to be identified.

Prior to the experiment, participants were informed that they would approach learned intersections from a variety of directions, and were asked to indicate the direction of travel required to navigate to the goal arm by pressing the left, right or up (i.e. straight) arrow key on the keyboard provided.

**Analysis.** In order to gain a better understanding of the trends emerging from the data, participants’ performance in the forty test trials was condensed into five experimental blocks consisting of eight trials. Similarly, the ten strategy probe trials were analysed in five sets of two trials.

### 3.3.2. Results

When the approach direction during training and at test is identical, use of any of the strategies discussed above supports accurate navigation. Therefore, chance level performance or worse in these trials suggests an inability to learn routes. Chi-squared tests revealed that all participants performed significantly above chance level (33.33%) in these test trials, and were therefore capable route learners.

**Performance.** Participants chose the correct movement direction in 57.7% of all trials. An ANOVA with experimental block [1-5] as a within-participants factor revealed that participants' performance improved over the course of the experiment from 49.2% in the first block to 65.8% in the fifth block ($F(4, 96) = 5.04$, $p = .001$, $\eta_p^2 = .17$; see Figure 13).

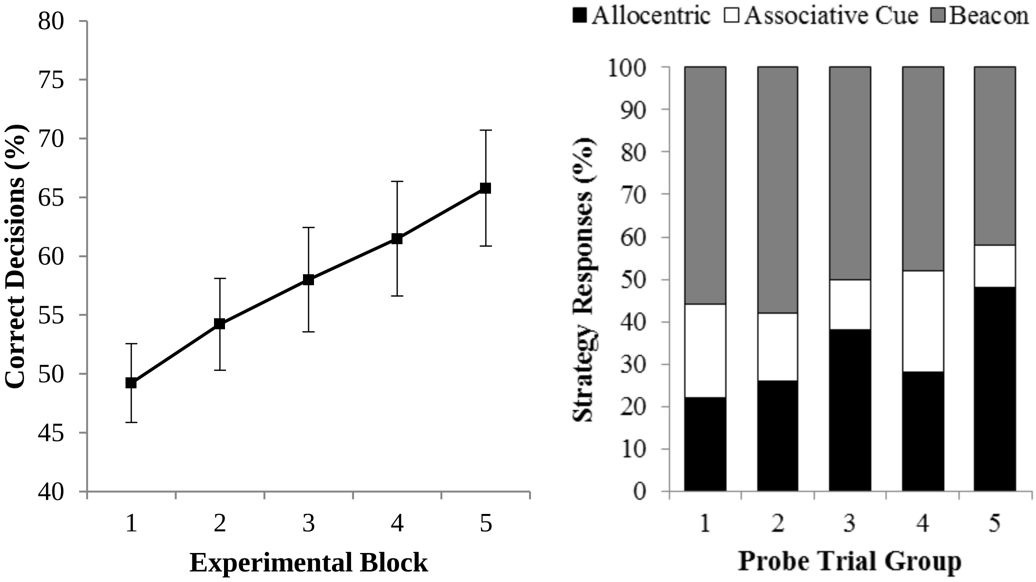


**Figure 13.** Performance and strategy preference. Left: Navigation accuracy across experimental blocks (mean±standard error). Right: Percentage of responses corresponding with each wayfinding strategy in probe trials over the course of the experiment.

**Strategy Preference.** Participant behaviour in strategy probe trials was assessed to determine strategy preference over the course of the experiment. 32.2% of participants' responses in probe trials corresponded with allocentric strategy use, 16.7% were consistent with associative cue use, and 51% were indicative of beacon strategy use. To examine changes in strategy preference throughout the experiment, three strategy-specific ANOVAs were conducted with probe trial set [1-5] as a within-participants factor, and the percentage of responses corresponding with the employment of each strategy as the dependent variable. Analysis revealed that neither associative cue [$F(4, 96) = 2.332$, $p = .06$, $\eta_p^2 = .09$] or beacon strategy use [$F(4, 96) = 1.02$, $p = .40$, $\eta_p^2 = .04$] changed over the course of the experiment, while allocentric strategy use increased (main effect of probe trial set: $F(4, 96) = 3.46$, $p = .01$, $\eta_p^2 = .13$; see Figure 13). Furthermore, strategy preference in the first probe trial set was analysed to determine participants' initial strategy choice. One sampled *t*-tests against chance level (33.33%) revealed a systematic bias for a beacon response strategy in the first probe trial set ($M = 56\%$, $SD = 41.63$; $t(24) = 2.72$, $p = .012$, $r = .49$), while both allocentric ($M = 22\%$, $SD = 32.53$; $t(24) = -1.74$, $p = .094$, $r = .33$) and associative cue use strategy use ($M = 22\%$, $SD = 32.53$; $t(24) = -1.74$, $p = .094$, $r = .33$) did not significantly differ from chance level. Taken together, these findings suggest that participants initially employed a beacon response strategy, before increasingly adopting an allocentric strategy.

### 3.3.3. Discussion

The results of Experiment 1 provide initial evidence that the paradigm presented in this thesis may be suitable for assessing participants' strategy preferences. First, performance increased over the course of the experiment, suggesting that participants learned how to solve the navigation task. Second, the analysis revealed that participants initially employed a suboptimal beacon response strategy to support route acquisition, which may reflect a preference for the simplest available strategy during the early stages of spatial learning. Thereafter, participants increasingly adopted the correct allocentric strategy, replicating findings that demonstrate that individuals adapt their strategy choice according to the demands of the concurrent navigation task (Iaria, Petrides, Daghar, Pike & Bohbot, 2003; Cassel, Kelche, Lecourtier & Cassel, 2012; Iglói, Zaoui, Berthoz & Rondi-Reig, 2009; Marchette, Bakker & Shelton, 2011).

However, as the participants were tested on the forty intersections in a random order, the ten probe trials were not equally distributed throughout the experiment i.e. the interval between each set of strategy probe trials was not standardised. Therefore, the strategy preference data discussed above may not accurately represent the development of participants' strategy use over the course of the experiment. For this reason, a second study was conducted to assess changes in participants' strategy preference more reliably.

## 3.4. Experiment 2

In order to properly assess participants' strategy preferences over time, a second study was conducted with strategy probe trials occurring at regular intervals throughout the experiment.

### 3.4.1. Method

**Participants.** Twenty-eight participants (23 females, mean age = 20.14, *SD* = 3.49) from Bournemouth University participated in the study in return for course credit.

**Materials, Apparatus, Procedure and Analysis.** The materials, apparatus, procedure and analysis for Experiment 2 were identical to those for Experiment 1 except that the order of intersections was pseudorandomised. Specifically, every four test trials included a single strategy probe trial to ensure that participant's strategy preference was assessed systematically over the five experimental blocks.

### 3.4.2. Results

All participants performed above chance level (33.33%) when the starting position of a test trial was identical to training, and were therefore able route learners.

**Performance.** Participants navigated correctly in 59.9% of all trials. An ANOVA with experimental block [1-5] as a within-participants factor revealed that participants' performance improved over the course of the experiment from 53.5% in the first block to 65.6% in the fifth block ($F(4, 108) = 3.87$, $p = .006$, $\eta_p^2 = .13$; see Figure 14).

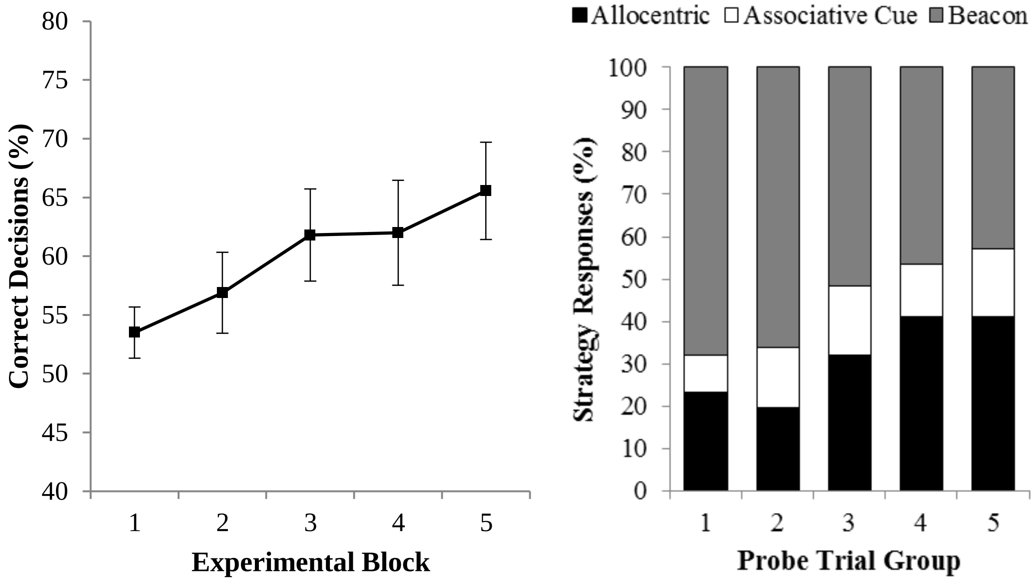


**Figure 14.** Performance and strategy preference. Left: Navigation accuracy across experimental blocks (mean±standard error). Right: Percentage of responses corresponding with each wayfinding strategy in probe trials over the course of the experiment.

**Strategy Preference.** In the strategy probe trials used to assess strategy choice, 30.9% of participants' responses were consistent with the use of an allocentric strategy, 13.7% corresponded with associative cue use, and 55.4% were indicative of beacon strategy use. Separate ANOVAs revealed that over the course of the experiment, associative cue use did not change [$F(4, 108) = 0.61$, $p = .66$, $\eta_p^2 = .02$], beacon strategy use decreased [$F(2.75, 74.12) =$

5.07, $p = .004$, $\eta_p^2 = .16$], and allocentric strategy use increased [$F(2.75, 74.25) = 4.57$, $p = .007$, $\eta_p^2 = .15$] (see Figure 14). Furthermore, a one sampled *t*-test against chance level (33.33%) revealed that participants exhibited a bias for a beacon response strategy in the first experimental block ($M = 67.86\%$, $SD = 39.00$; $t(27) = 4.68$, $p < .001$, $r = .67$). In contrast, allocentric strategy use did not significantly differ from chance level ($M = 23.21\%$, $SD = 34.65$; $t(27) = -1.54$, $p = .134$, $r = .28$) and associative cue strategy use was below chance level ($M = 8.93\%$, $SD = 23.78$; $t(27) = -5.43$, $p < .001$, $r = .72$). Taken together, these results suggest that participants initially employed a beacon strategy to support spatial learning, before increasingly adopting an allocentric strategy.

### 3.4.3. Discussion

The findings of Experiment 2 largely replicated the results of Experiment 1. Participants' performance improved over the course of the experiment, again suggesting that participants were increasingly able to solve the navigation task. This finding was further supported by increasing use of the optimal allocentric strategy, and decreasing use of the suboptimal beacon response strategy. Taken together, these findings suggest that the novel paradigm introduced in this chapter may be suitable for accurately assessing strategy preference.

## 3.5. General Discussion

This chapter introduces a novel method for determining the landmark-based wayfinding strategy employed by participants during navigation. Participants complete a task that involves navigating to a known target location from both familiar and unfamiliar approach directions. While only the use of an allocentric strategy supports accurate navigation irrespective of approach direction, both an associative cue and beacon response strategy are also available to navigators. In selected trials, different responses correspond with allocentric, associative cue and beacon strategy use. Therefore, participants' strategy choice can be determined by their behaviour in these strategy probe trials. Two pilot experiments revealed that i) participants learned to successfully perform the navigation task, and ii) the probe trials accurately and reliably assessed participants' strategy preference.

Importantly for a novel paradigm, participants' performance improved over the course of both experiments, suggesting that the navigation task was not overly demanding. Indeed, given that navigating to a known location from a novel approach direction is a common task, participants' spatial behaviour in this paradigm is more applicable to real-world navigation than many other strategy assessment paradigms. For example, the Morris Water Maze Task (Morris, 1981) involves locating a hidden platform in a circular body of water, and cannot be considered an analog of a typical navigational task. Similarly, the selective concealment of distal cues during probe trials in the Radial Arm Maze task (e.g. Iaria et al., 2003) is not a common navigational circumstance. Therefore, the basis of the task presented in this chapter may provide a more accurate reflection of participants' navigation abilities.

In addition, the strategy probe trials employed in both experiments proved to be an accurate mechanic for assessing participants' strategy choice. Participants' improved accuracy was reflected in increasing use of the optimal allocentric strategy, and decreasing use of a beacon response strategy. Initially, participants' exhibited a maladaptive bias for a beacon strategy, which may reflect a preference for the simplest available wayfinding strategy during the early stages of spatial learning. Subsequently, participants adopted an allocentric strategy, which supported accurate navigation in all test trials. Therefore, participants' strategy preferences shifted in response to the demands of the concurrent navigation task, replicating the findings of other studies investigating changes in strategy choice (e.g. Cassel et al., 2012; Iglói et al., 2009). Furthermore, as the starting position of test trials varies relative to training throughout the experiment, the task demands associated with strategy probe trials do not differ from other test trials. Therefore, multiple probe trials can be administered in an experiment to assess strategy preference over time without affecting the experimental protocol. Finally, while the novel paradigm presented in this chapter is conceptually similar to the Cross Maze task (Tolman et al., 1946b), differences between the two paradigms affect the accuracy with which participants' strategy choice is assessed. First, changes in cue placement allow allocentric and directional (i.e. beacon) response strategy use to be differentiated, and second, changing the start position of both probe and standard test trials allows the use of three different wayfinding strategies to be assessed over time.

However, it should be noted that this chapter presents the findings from exploratory pilot studies. Further amendments are required to build a working strategy assessment paradigm. First, it is possible that participants thought to be using an associative cue strategy were in fact simply replicating the turning movements observed during learning. Therefore, the completed paradigm will involve learning a multiple intersection path, and a test phase in which participants must navigate through intersections in a random order. Such amendments should preclude the use of a memory-based response strategy. Furthermore, to properly investigate strategy preference over time, participants' strategy choice should be assessed on multiple occasions in the same environment. Therefore, the completed paradigm will involve repeated training and test phases in a single environment.

In conclusion, this chapter presents preliminary data from a novel method of strategy assessment that accurately distinguishes between the use of three landmark-based wayfinding strategies: an allocentric place strategy, and the egocentric associative cue and beacon response strategies. While the experiments reported here test the paradigm in its basic form, several areas of development have been identified, and will subsequently be addressed. If successful, the completed paradigm should allow researchers to investigate strategy use over time with greater accuracy and detail.

## 3.6. Summary

In summary, this chapter tested an initial concept for a novel strategy assessment paradigm that distinguishes between allocentric, associative cue and beacon strategy use, and identifies changes in strategy preference over time. The results of two pilot studies suggest that the strategy assessment mechanism is accurate, and embedded in a task that can be successfully learned by participants. The findings of these two experiments have subsequently informed the development of a complete, working strategy assessment paradigm that is presented in the following chapter.

# CHAPTER 4. Allocentric and Egocentric Strategy Use in a Novel Wayfinding Task

## 4.1. Overview

While Chapter 2 demonstrated that participants are willing to repeatedly switch between two different wayfinding strategies in order to optimise route learning, more permanent shifts in strategy preference either coincide with developing spatial knowledge, or are made in response to task demands. However, as discussed in Chapters 1 and 3, the paradigms typically employed to assess strategy use often have issues with reliability and validity. Therefore, we introduce a novel wayfinding paradigm based on a task presented in the previous chapter that allows the accurate and comprehensive assessment of participants' strategy preference over time. In this paradigm, participants complete a common navigation task – re-joining a known route from an unfamiliar direction – in a virtual environment containing local landmarks. Responses made in a subset of test trials are used to assess participants' use of three different wayfinding strategies: an allocentric place strategy, and the egocentric associative cue and beacon response strategies. Furthermore, to monitor strategy preference over time, participants' strategy choice is assessed on multiple occasions throughout the task, which can only be completed successfully with the use of an allocentric strategy. The remainder of this chapter provides an overview of the novel strategy assessment paradigm, and presents the experimental data from its first use.

## 4.2. Introduction

Visual landmarks, which are salient features of an observed environment, can be used to inform a variety of spatial behaviours. In particular, individuals often rely on landmarks to facilitate the acquisition of spatial knowledge, recognise environmental locations, and support navigation and orientation (Jansen-Osmann & Fuchs, 2006; Ruddle, Volkova, Mohler & Bülthoff, 2011; Steck & Mallot, 2000). As such, in Siegel and White's (1975) influential framework for the development of spatial knowledge, landmark knowledge is considered an essential precursor to a cognitive map of an environment. Landmarks are typically divided into two categories; global and local. Global landmarks are distant reference points that retain the same orientation or configuration when viewed from multiple locations along a route. Therefore, global landmarks (e.g. The Eiffel Tower) are visible from many areas of the surrounding environment and provide global spatial information. Local landmarks, in contrast, are situated at specific locations within an environment, and are only visible when in close proximity. Therefore, local landmarks only support navigation in the immediate vicinity. Landmarks are typically incorporated into spatial knowledge through the use of two different wayfinding strategies. Allocentric strategy use involves encoding the spatial relationship between different environmental features e.g. landmarks and/or environmental locations (O'Keefe & Nadel, 1978; Tolman, 1948), resulting in a viewpoint-independent spatial representation that can be used to perform a wide variety of navigation tasks. In contrast, egocentric strategy use involves encoding spatial knowledge relative to oneself. As such, landmark-based egocentric strategy use results in stimulus-response associations between an encoded landmark and a body-centred behavioural action. Egocentric knowledge is therefore viewpoint-dependent, and only accurately supports wayfinding when subsequent navigation is identical to learning (e.g. when repeating a learned route). Landmark-based egocentric strategies can be further subdivided into the associative cue and beacon strategies. Employing an associative cue strategy involves relating an observed landmark with an explicit directional behaviour, forming a stimulus-response pair (Tlauka & Wilson, 1994). Perception of the encoded landmark during subsequent navigation serves as a cue to retrieve and execute the stored response (e.g. ‘Turn left at the church’). Beacon strategy use, on the other hand, relies on landmarks that spatially coincide with one’s movement during learning (Waller & Lippa, 2007), with perception of the encoded landmark during navigation triggering a general behavioural action (e.g. ‘Turn towards the church’). Unlike associative cue strategy use, beacon strategy use does not require explicit directional knowledge, and is therefore considered the most parsimonious landmark-based egocentric strategy. In addition to using contrasting frames of reference, allocentric and egocentric strategy use selectively activate different neural structures. Allocentric strategy use relies on the hippocampal circuit, while egocentric response strategies are associated with the striatal system, specifically the caudate nucleus (Antonova et al., 2011; Doeller, King & Burgess, 2008; Etchamendy & Bohbot, 2007; Hartley, Maguire, Spiers & Burgess, 2003; Iaria, Petrides, Dagher, Pike & Bohbot, 2003). Indeed, Marchette, Bakker and Shelton (2011) found that in a task that could be completed with the use of either an allocentric or egocentric strategy, participants' ratio of allocentric and egocentric navigation was positively correlated with the proportion of bilateral hippocampal and caudate activity during learning. Furthermore, Bohbot, Lerch, Thorndycraft, Iaria and Zijdenbos (2007) reported that allocentric and egocentric strategy use were correlated with gray matter density in the hippocampus and caudate nucleus respectively.

Several paradigms employed in wayfinding research distinguish between allocentric and egocentric strategy use by examining participants' navigation behaviour in environments that contain landmarks (see Paul, Magda & Abel, 2009; Knierim & Hamilton, 2011 for a review). However, many of these paradigms do not assess strategy preference accurately. For example, in the Morris Water Maze (Morris, 1981), T-Maze (Blodgett & McCutchan, 1947) and Cross Maze tasks (Tolman, Ritchie & Kalish, 1946b), the use of a beacon-based response strategy can account for spatial behaviour that is typically attributed to allocentric strategy use (Blodgett, McCutchan & Mathews, 1949; Hamilton, Johnson, Redhead & Verney, 2009; Skinner et al., 2003). Furthermore, as some tasks only explicitly assess allocentric learning, a lack of accurate or efficient navigation is often interpreted as egocentric response strategy use, rather than unsuccessful allocentric strategy use. Many wayfinding paradigms also use distal (global) and proximal (local) landmarks to facilitate allocentric and egocentric learning respectively. Therefore, landmarks that selectively support different wayfinding strategies often vary in location, visibility, size, number and familiarity, which are important landmark properties that may influence strategy choice. Furthermore, in some tasks, landmarks present during learning or exploratory wayfinding are concealed (cf. Radial Arm Maze; Iaria et al., 2003) or manipulated (Mallot & Gilner, 2000) during test or probe trials, inhibiting navigation supported by these landmarks, and rendering specific wayfinding strategies artificially ineffective. Such significant changes made to an environment during probe trials also prevent the assessment of changing strategy preference over time, which provides insight into task-related development of spatial knowledge.

In this study, we employed a novel wayfinding paradigm to distinguish between allocentric, associative cue and beacon strategy use, which to our knowledge, is only the second wayfinding paradigm to differentiate between multiple egocentric response strategies (cf. Starmaze paradigm; Rondi-Reig, Petit, Tobin, Tonegawa & Berthoz, 2006). Participants were asked to learn a route through a virtual environment, which in contrast to other wayfinding paradigms, featured stable, permanent local landmarks positioned in diagonally opposite corners of each decision point (see Figure 15). Participants could utilise these landmarks to support allocentric, associative cue or beacon strategy use. While allocentric learning relies on distal cues in most landmark-based navigation paradigms, allocentric strategy use in this experiment involved encoding the spatial configuration of local landmarks at each route location. We refer to this allocentric strategy as the configuration strategy. After learning the route, participants approached decision points from either the same direction experienced during learning, or from a different direction, and were asked to indicate the direction of travel required to proceed along the original route (see Figure 16). When a route location was encountered from the same direction as learning, use of any of the three strategies discussed above resulted in successful navigation. However, when a route location was approached from a direction that differed from training, the use of an egocentric strategy often resulted in incorrect navigation as a consequence of performing a fixed behavioural action irrespective of one’s position within the environment. Instead, successful navigation in these situations depends on the use of an allocentric strategy, which allows navigators to establish their position in an environment before making a response. In a subset of these test trials, hereafter known as strategy probe trials, associative cue and beacon-based navigation resulted in different, incorrect responses, while configuration strategy use supported accurate navigation (see Figure 16). Therefore, participants’ responses in these trials were used to assess strategy preference.

Assessing participants' strategy preference after repeated training phases allowed us to examine changes in strategy choice over time. Many paradigms provide participants with feedback in the form of targets, rewards or pleasing/noxious tones, thus reinforcing existing strategy use or initiating strategy change (e.g. Y-maze task; Rodgers, Sindone & Moffat, 2012). In contrast, participants in this study received no feedback related to response accuracy. Therefore, their strategy preference was self-selected, and not influenced by the experimental protocol. Findings regarding initial strategy choice have proved inconclusive, with studies reporting either a preference for an egocentric strategy (Cassel, Kelche, Lecourtier & Cassel, 2012; Iglói, Zaoui, Berthoz & Rondi-Reig, 2009; Levy, Astur & Frick, 2005; Packard & McGaugh, 1996) or no preference at all (Bohbot, Iaria & Petrides, 2004; Iaria et al., 2003; Schmitzer-Torbet, 2007). Thereafter, shifts in wayfinding strategy are often made in response to task demands, and occur in the direction of the optimal strategy. Specifically, navigators identify and adopt a strategy that supports accurate navigation and efficient spatial decision making. Such shifts in strategy have been observed between navigation tasks (Etchamendy & Bohbot, 2007; Hartley et al., 2003), within navigation tasks (Iaria et al., 2003; Marchette et al., 2011) and during test/probe trials (Cassel, et al., 2012; Iglói et al., 2009). As only allocentric strategy use supports successful navigation in all test situations, we predicted that participants' use of the configuration strategy would increase over the course of the experiment, while egocentric strategy use declined.

Finally, shifts in wayfinding strategy from egocentric strategies to an allocentric strategy are expected to affect response time. As associative cue and beacon strategy use does not involve encoding one's position in an environment during learning, the approach direction during subsequent navigation does not affect the time taken to perceive an encoded landmark, retrieve stored route knowledge (in the case of associative cue use only), and execute a behavioural response. In contrast, configuration strategy use is informed by processing the spatial relationship between different environmental features to determine one's position and orientation before making a movement response. This involves greater cognitive effort compared to response strategy use, and is associated with increased response times (Iaria et al., 2003; Zaehle et al., 2007). Therefore, we predicted that response time will increase relative to configuration strategy use.

## 4.3. Method

**Participants.** Forty participants (20 females, mean age = 21.78, *SD* = 5.26) took part in the experiment. Individuals received either course credit or £5 for their participation.

**Apparatus.** Vizard 3.0 (WorldViz) was used to construct the virtual environment, which consisted of inter-connected four-way intersections. Each intersection featured two unique landmarks located in diagonally opposite corners that could be used to recognise route locations and determine one's position in the environment (see Figure 15). Furthermore, black fog within the environment only allowed participants to view one intersection at a time. The task was presented on a 22” LCD monitor with a resolution of 1680x1050 pixels and a screen refresh rate of 120Hz. A standard computer keyboard was used to record responses.

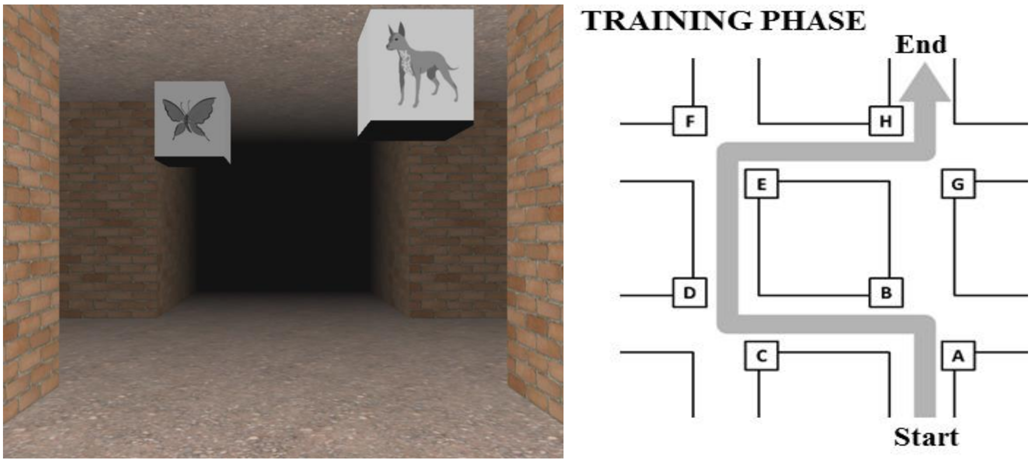


**Figure 15.** An overview of the navigation task. Left: A screenshot of an intersection within the route. The location of the landmarks can be used to unambiguously identify the approach direction. Right: An overview of the training route.

**Procedure.** Participants learned and were tested on a single route that consisted of two left turns and two right turns at four-way intersections. Participants completed six experimental blocks, each of which included a training phase and a subsequent test phase. During training, participants were twice passively navigated along the route. Their task during this phase of the experiment was to learn the route shown. During the test phase, participants were passively transported towards each decision point within the route, with movement ending at the centre of the intersection. Each intersection was approached from either the direction experienced during training (***same-direction*** trials), or, excluding the direction in which the route originally proceeded, from the two remaining possible approach directions (***different-direction*** trials) (see Figure 16). Prior to the experiment, participants were informed that they would approach route locations from a variety of 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. As each route contained four decision points, each test phase was comprised of 12 test trials (four ***same-direction*** trials, eight ***different-direction*** trials) presented in a randomised order. ***Same-direction*** trials test a participant’s ability to recognise an intersection and repeat the movement experienced during training. These trials are equivalent to measures typically used to assess uni-directional route knowledge (e.g. Wiener, De Condappa & Höelscher, 2010), and could be solved by employing a configuration, associative cue or beacon strategy. In contrast, accurate navigation in ***different-direction*** trials required the use of an allocentric place strategy with knowledge of the spatial relationship between the landmarks at an intersection and the goal arm. For each experimental block, responses made in two selected ***different-direction*** trials (see Figure 16) were used to determine the wayfinding strategy employed by a participant. In these strategy probe trials, associative cue and beacon-based navigation result in different, incorrect responses, while configuration strategy use results in successful navigation. Therefore, participants' responses in these test trials allowed the assessment of strategy preference over the course of the experiment.

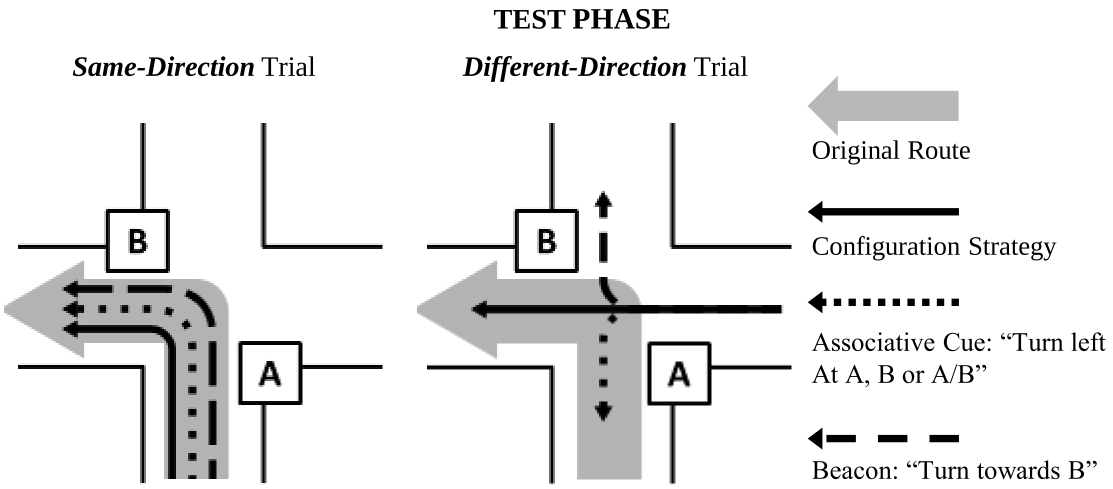


**Figure 16.** Trial types during the test phase. Left: In ***same-direction*** trials, the approach direction is identical to that experienced during training. Employment of any of the navigation strategies discussed supports accurate navigation. Middle: In ***different-direction*** trials, the approach direction is different to that experienced during training. In the example provided, the use of each navigation strategy results in a different response, allowing participants strategy choice to be determined. Right: Key

**Analysis.** Gender was included as a between-participants factor in all ANOVAs conducted. However, only significant main effects or interactions involving gender are reported.

## 4.4. Results

Seven participants were excluded from the experiment as chi-squared test revealed that their performance at ***same-direction*** trials did not significantly exceed chance level (33.33%). As ***same-direction*** trials can be solved correctly by employing any of the strategies discussed above (see Figure 16), chance level performance or worse suggests an inability to learn the route. The remaining thirty-three participants (17 females, mean age = 21.66, *SD* = 5.44) entered the final analysis.

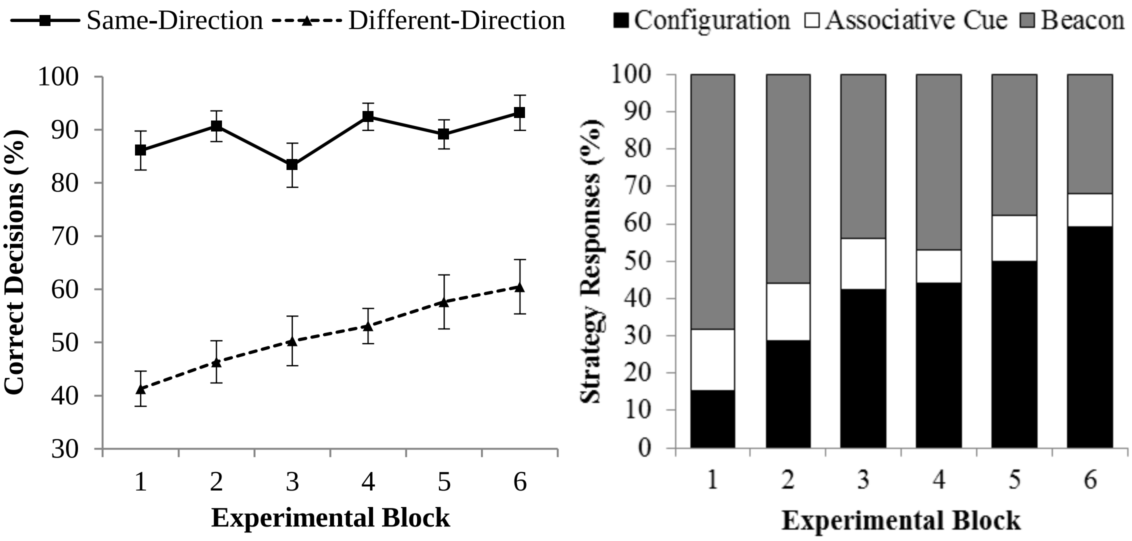


**Figure 17.** Performance and strategy preference. Left: Navigation accuracy at ***same-direction*** and ***different-direction*** test trials across experimental blocks (mean±standard error). Right: Percentage of responses corresponding with each wayfinding strategy in strategy assessment probe trials over the course of the experiment.

**Performance.** Participants chose the correct movement direction in 64.1% of all trials (***same-direction***: 89.1%, ***different-direction***: 51.5%). An ANOVA with approach direction [same, different] and experimental block [1-6] as within-participants factors and gender [male, female] as a between participants factor revealed that performance at ***same-direction*** trials was better than at ***different-direction*** trials (main effect of approach direction: *F*(1, 31) = 112.81, *p* < .001, $\eta_p^2$ = .78) and performance improved over experimental blocks from 56.2% in the first block to 71.6% in the fifth block [*F*(3.374, 104.61) = 4.40, *p* = .004, $\eta_p^2$ = .12] (see Figure 17). However, no main effect of gender was observed (*p* > .05). Significant approach direction x experimental block [*F*(5, 155) = 2.77, *p* = .02, $\eta_p^2$ = .08] and approach direction x gender [*F*(1, 31) = 4.62, *p* = .04, $\eta_p^2$ = .13] interactions suggest that the difference between participants' performance in ***same*** and ***different-direction*** trials changed over the course of the experiment, and that males and females performed differently at ***same*** and ***different-direction*** trials. Post-hoc analysis revealed that across experimental blocks, participants’ performance improved for ***different-direction*** trials [*F*(3.39, 108.41) = 5.87, *p* = .001, $\eta_p^2$ = .16], but not for ***same-direction*** trials (*p* > .05). As participants could use either a configuration, associative cue or beacon strategy to navigate accurately in ***same-direction*** trials, successful employment of any wayfinding strategy in each experimental block may explain why performance in these test trials did not change over the course of the experiment. In contrast, as only allocentric strategy use supports accurate navigation in all ***different-direction*** trials, the increase in performance found in these test trials may reflect the increasing adoption of the optimal configuration strategy over the course of the experiment. Finally, planned contrasts did not reveal any performance-related gender differences at ***same*** or ***different-direction*** trials. However, the raw data does suggest that females (92.3%) perform better than males (85.8%) at ***same-direction*** trials, while males (56.1%) outperform females (47.2%) at ***different-direction*** trials.

**Strategy Preference.** Previous descriptions of beacon-based wayfinding strategies have conceptualised the general behavioural action associated with the perception of an encoded landmark as a ‘Move towards landmark X’ rule, which reduces the distance between the navigator and the encoded landmark (O'Keefe & Nadel, 1978). However, this definition applies to the use of distal cues as beacons, with beacon landmarks remaining navigationally relevant over multiple decision points. In such instances, the perception and activation of a subsequent beacon can occur either upon arrival at, or in the process of moving towards, the current beacon landmark. However, similar to Waller and Lippa (2007), we conceptualise the general behavioural action adopted during beacon strategy use in this paradigm as a ‘Turn towards landmark X’ rule for several reasons. Firstly, the current paradigm featured proximal cues, which could only be used to support navigation at one intersection (i.e. a single decision point). Furthermore, black fog within the environment restricted participants' view to the immediate route location, thus preventing landmarks from other intersections from becoming navigationally relevant before movement through the current intersection concluded. Taken together, these two aspects of the environment precluded the use of landmarks as distal cues that support navigation over multiple decision points, making a ‘move towards’ beacon strategy less likely. Secondly, 90° turns are executed at each intersection during learning, increasing the likelihood of beacon strategy use involving a ‘turn towards’ rule rather than a ‘move towards’ rule. Finally, each individual landmark adjoins two of the four arms radiating from the central junction of each intersection. When the beacon landmark is located at the far-side of an intersection during test (e.g. the butterfly in Figure 15), the use of a ‘move towards’ rule can be satisfied by either a turn in the direction of the beacon, or by continuing straight ahead. This ambiguity means that either response has a 50% chance of being selected when employing this rule. In contrast, the use of an explicit ‘turn towards’ rule can only be resolved by a single navigational behaviour i.e. turning towards the beacon landmark. To determine whether beacon strategy use was associated with a ‘move towards’ or a ‘turn towards’ rule, we examined those ***same-direction*** trials in which the use of a ‘move towards’ beacon strategy would produce an incorrect straight ahead response in 50% of trials. For example, as the path through the intersection in Figure 15 continued left, the butterfly landmark would be encoded during beacon-based learning. In subsequent ***same-direction*** test trials, the use of a ‘move towards’ rule during beacon-based navigation could result in either a left turn or a straight ahead response. In contrast, the use of a configuration, associative cue or ‘turn towards’ beacon strategy would result in accurate navigation (a left turn). Over the course of the experiment, only 8.12% of these ***same-direction*** trials were answered with a straight ahead response, strongly suggesting that beacon strategy use was associated with a ‘turn towards’ beacon rule that generates an explicit response, rather than an ambiguous ‘move towards’ rule.

In the probe trials used to determine participants' strategy preference (see Figure 16), 40% of responses were consistent with configuration strategy use, 12.6% corresponded with associative cue use, and 47.4% were consistent with beacon strategy use. To assess strategy preference over the course of the experiment, separate ANOVAs were conducted for each strategy with experimental block [1-6] as a within-participants factor and the percentage of responses corresponding with the employment of each strategy as the dependent variable. Over the course of the experiment, associative cue strategy use did not change [$F(2.94, 91.04) = 0.87$, $p = .46$, $\eta_p^2 = .03$], beacon strategy use decreased [$F(5, 155) = 6.91$, $p < .001$, $\eta_p^2 = .18$], and configuration strategy use increased [$F(3.60, 111.75) = 10.86$, $p < .001$, $\eta_p^2 = .26$] (see Figure 17). This analysis demonstrates that participants increasingly adopted the configuration strategy over the course of the experiment, with beacon strategy use decreasing. Furthermore, one sampled *t*-tests against chance level (33.33%) revealed a systematic bias for a beacon strategy in the first experimental block ($M = 68.18\%$, $SD = 37.12$; $t(32) = 5.39$, $p < .001$, $r = .69$), while configuration ($M = 15.15\%$, $SD = 31.83$; $t(32) = -3.28$, $p = .003$, $r = .50$) and associative cue use ($M = 16.67\%$, $SD = 29.76$; $t(32) = -3.22$, $p = .003$, $r = .49$) were both significantly below chance level. Taken together, these findings suggest that participants initially employed a suboptimal beacon response strategy, before identifying and shifting to the correct allocentric place strategy.

**Response Time.** Over the course of the experiment, participants' average response time was 5.96s (***same-direction***: 5.68s, ***different-direction***: 6.10s). An ANOVA with approach direction [same, different] and experimental block [1-6] as within-participants factors revealed that participants took longer to respond in ***different-direction*** trials than in ***same-direction*** trials (main effect of approach direction: $F(1, 31) = 22.54$, $p < .001$, $\eta_p^2 = .42$), although no main effect of experimental block was observed ($p > .05$). A significant approach direction x experimental block interaction [$F(5, 155) = 4.65$, $p = .001$, $\eta_p^2 = .13$] suggests that the difference between response times in ***same*** and ***different-direction*** trials changed over the course of the experiment (see Figure 18). No other interactions were observed (all $p > .05$). Planned contrasts revealed that over six experimental blocks, participants' response times decreased in ***same-direction*** trials

[$F(2.62, 83.76) = 4.36$, $p = .009$, $\eta_p^2 = .12$], but did not change significantly in ***different-direction*** trials ($p > .05$). Taken together, these results suggest that participants' response times in ***same*** and ***different-direction*** trials evolved differently over the course of the experiment.

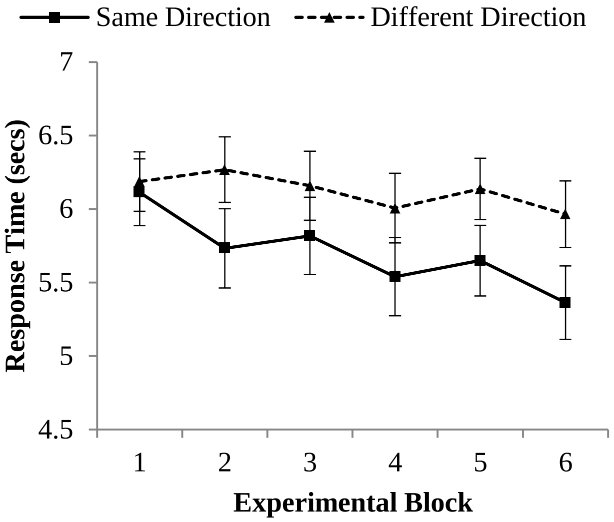


**Figure 18:** Response times at ***same*** and ***different-direction*** trials across experimental blocks (mean±standard error).

While egocentric strategy use relies on simple stimulus-response associations, allocentric strategy use involves assessing the spatial relationship between different environmental features before determining a movement response. As such, allocentric navigation involves a more complex spatial decision making process than egocentric navigation, and often results in longer response times (e.g. Iaria et al., 2003). Therefore, we expected the increasing use of the configuration strategy to result in increased response times in ***same*** and ***different-direction*** trials. To examine whether strategy choice affected response times, a one tailed Pearson's product-moment correlation was conducted between performance at the strategy assessment probe trials (See Figure 16), and response times at ***same*** and ***different-direction*** test trials. Performance at probe trials provides an index of each participant's preference for allocentric and egocentric navigation over the course of the experiment, as only configuration strategy use results in accurate navigation. A moderate positive correlation was found between strategy preference and response times in ***different-direction*** trials [$r(33) = .403$, $p = .02$], but not in ***same-direction*** trials ($p > .05$).Taken together, these findings suggest that participants' chosen wayfinding strategy only affects response time in ***different-direction*** trials.

## 4.5. Discussion

This chapter presents a novel wayfinding paradigm that allowed us to assess participants' wayfinding strategy choices during the acquisition of spatial knowledge. In contrast to existing wayfinding paradigms that typically distinguish between allocentric and egocentric learning, this paradigm – which will be referred to as the Alternative Routes paradigm for the remainder of this thesis – additionally discriminates between associative cue and beacon response strategy use. Participants' knowledge of a previously learned route was tested by examining navigation accuracy when known decision points were approached from various directions. Participants could employ either an allocentric or egocentric strategy to correctly follow the route when intersections were approached from the same direction experienced during learning. However, only allocentric strategy use consistently resulted in accurate navigation when an intersection was approached from a direction different to training. Participants initially exhibited a maladaptive bias for a beacon response strategy, with the optimal configuration strategy increasingly adopted over the course of six experimental blocks. Furthermore, configuration strategy use was positively correlated with response times, reflecting the additional cognitive effort required to employ an allocentric place strategy compared to an egocentric response strategy.

Participants' initial preference for a beacon response strategy provides novel insight into the early stages of spatial learning. Considering that configuration strategy use supports successful navigation in all test situations, and local landmarks are typically conceptualised as associative cues (O'Keefe & Nadel, 1978; Siegel & White, 1975), participants' bias for beacon-based navigation in the first experimental block suggests that initial strategy choice may be influenced by the relative cognitive demands of the available wayfinding strategies. Beacon strategy use involves performing a universal behavioural action upon recognition of a single encoded landmark at each decision point. In contrast, associative cue use involves additionally relating explicit directional knowledge with each encoded landmark, while allocentric strategy use requires spatial knowledge of multiple environmental features to both establish one's position and orientation, and determine a movement response. Therefore, participants initially employed the least cognitively demanding, albeit suboptimal wayfinding strategy – the beacon strategy – before switching to the more cognitively demanding and accurate configuration strategy. These findings correspond with the assumption that humans are cognitive misers. Specifically, research in the field of reasoning and rational thought has found that individuals' primary consideration when first performing a task is to preserve cognitive resources, rather than accuracy (Stanovich, 2009).

Taken together, participants' changing strategy preferences support Siegel and White's (1975) theoretical framework for the development of spatial knowledge, which contends that individuals initially acquire *landmark knowledge* to facilitate place recognition, followed by knowledge of the routes between consecutive landmarks i.e. *route knowledge*, and finally, *survey knowledge* i.e. a cognitive map. In this study, participants relied on landmark knowledge to employ a beacon strategy in the first experimental block, before subsequently developing a cognitive map to support configuration strategy use. Given that participants approached route locations from different directions, beacon strategy use, which involves performing a fixed behavioural action irrespective of one's position in an environment, did not support accurate navigation in all test trials. Therefore, participants may have recognised the need for a spatial representation of the environment that allowed flexible navigation through each intersection, and developed viewpoint-independent survey knowledge accordingly.

Given that use of the more cognitively demanding configuration strategy increased over the course of the experiment, we expected a corresponding increase in the time participants' took to make a movement response. Instead, response times decreased when intersections were approached from the same direction as training (***same-direction*** trials), and did not vary when intersections were approached from a different direction (***different-direction*** trials). Furthermore, correlational analyses revealed that participants' frequency of configuration strategy use was related to average response time in ***different-direction*** trials, but not in ***same-direction*** trials. Taken together, these findings suggest that participants' strategy preference evolved differently at ***same*** and ***different-direction*** test trials. Interestingly, Hartley et al. (2003) found that good navigators select the most appropriate wayfinding strategy according to the navigational requirements of the concurrent task, with egocentric strategies employed during tasks that involve repeating a learned route (i.e. ***same-direction*** trials), and allocentric strategies utilised for tasks that require flexible navigation (i.e. ***different-direction*** trials). Given that egocentric beacon strategy use was prevalent during the early stages of spatial learning, participants most likely employed the same strategy in ***same-direction*** trials throughout the experiment. As such, participants' response times in ***same-direction*** trials are consistent with practice effects (e.g. Olesen, Westerberg & Klingberg, 2004; Rabbit & Banerji, 1989). In contrast, the absence of response time-related practice effects in ***different-direction*** trials can be explained by participants' switching to the more cognitively demanding configuration strategy over the course of the experiment. In addition, these findings also suggest that participants acquired both egocentric and allocentric spatial knowledge, and chose the most efficient strategy for ***same-direction*** trials (i.e. an egocentric response strategy) and the most accurate strategy for ***different-direction*** trials (i.e. the configuration strategy).

In summary, we present a novel wayfinding paradigm that allowed the assessment of participants' strategy preference over time. Specifically, the navigation task employed in this study distinguished between three different wayfinding strategies: a configural allocentric strategy, and the egocentric associative cue and beacon response strategies. Participants exhibited an initial maladaptive bias for a beacon response strategy before increasingly adopting the optimal configuration strategy over the course of the experiment. This finding suggests that participants initially employed the simplest wayfinding strategy available, before identifying and switching to a more accurate strategy. Finally, response time analysis suggests that participants employed different strategies when known intersections were approached from either a direction identical or different to training, reflecting the differing navigational demands associated with these tasks. First data suggests that the paradigm introduced in this chapter accurately determined participants' initial strategy preference and identified any further shifts in wayfinding strategy that occurred over the course of the experiment. As only an allocentric place strategy supported successful navigation throughout the experiment, performance in the navigation task was sensitive to allocentric learning and provided insight into the development of spatial knowledge. Furthermore, in contrast to the unusual tasks performed in alternative wayfinding paradigms, such as learning the location of a hidden platform in a circular arena (Morris Water Maze Task), the task performed by participants in this paradigm (i.e. re-joining a known route from various approach directions) is more applicable to real-world navigation. Taken together, the Alternative Routes paradigm can be used to investigate several aspects of wayfinding strategy use, and may provide novel insight into navigational differences between different participant groups (see Chapter 10 for an application of this paradigm to study the effects of cognitive aging on wayfinding strategy selection).

## 4.6. Summary

This chapter presented the first data collected with a novel strategy assessment task that discriminates between the use of three different wayfinding strategies: an allocentric place strategy, and the associative cue and beacon response strategies. Analysis revealed that participants exhibited an initial maladaptive preference for a beacon response strategy, before increasingly adopting the optimal allocentric strategy. Furthermore, response time corresponded with allocentric strategy use, reflecting the additional cognitive effort required to employ an allocentric strategy compared to an egocentric strategy. Taken together, these findings suggest that the Alternative Routes paradigm accurately assesses strategy choice, and is sensitive to changes in strategy preference over time.

# CHAPTER 5. Ocular Behaviour Associated with Allocentric and Egocentric Strategy Use

## 5.1. Overview

This chapter provides an overview of an accepted manuscript that provides further insight into the spatial processes involved in the use of the allocentric, associative cue and beacon strategies (see Appendix A). First, eye-tracking technology was used in conjunction with the Alternative Routes paradigm presented in Chapter 4 to provide an insight into how environmental cues are used to support different strategies. The secondary aim of this paper was to examine whether variations in pupil size, which are indicative of cognitive load, are sensitive to shifts between wayfinding strategies that differ in cognitive complexity. Finally, an additional analysis that was not possible in Chapter 4 was conducted to determine whether allocentric strategy use in the Alternative Routes paradigm involved direct access to a cognitive map, or spatial transformations applied to viewpoint-dependent environmental representations.

## 5.2. Paper I

de Condappa, O., & Wiener, J. M. (2016). Human place and response learning: Navigation strategy selection, pupil size and gaze behavior. *Psychological Research, 80*(1), 82-93. doi: 10.1007/s00426-014-0642-9

## 5.3. Paper Abstract

In this study, we examined the cognitive processes and ocular behaviour 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 behavioural 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.

## 5.4. Theoretical Background

Several studies suggest that distal and local cues are utilised to support the acquisition and subsequent use of egocentric and allocentric knowledge respectively (e.g. Hurlebaus, Basten, Mallot & Wiener, 2008). However, landmark use has typically been assessed by subjective post-experiment questionnaires (e.g. Andersen, Dahmani, Konishi & Bohbot, 2012) or wayfinding behaviour in virtual environments that have changed significantly between learning and test (e.g. Iaria, Petrides, Daghar, Pike &Bohbot, 2003). In contrast, the use of eye-tracking technology allows landmark preference to be measured during wayfinding in stable environments that better corresponds with real-world navigation. In addition to providing support for the differential use of distal and local cues during allocentric and egocentric navigation (e.g. Livingstone-Lee et al., 2011; Mueller, Jackson & Skelton, 2008), eye-tracking studies have also found that allocentric strategy users attended to landmarks more than egocentric strategy users during initial learning (Andersen et al., 2012), and that successful navigators use distal cues to inform their initial movement trajectory before relying on local cues to guide finer navigation (Hamilton, Johnson, Redhead & Verney, 2009). However, as the environments in these studies often contain landmarks that selectively support specific wayfinding strategies – i.e. navigators must rely on different groups of landmarks to support allocentric and egocentric strategy use – the findings discussed above provide little insight into landmark selection associated with the use of different strategies. Therefore, the primary aim of this study was to assess strategy-dependent landmark selection and encoding processes in an environment featuring landmarks that could be used to support multiple wayfinding strategies. As such, we employed an eye-tracking variant of the Alternative Routes paradigm to assess gaze behaviour related to the use of different wayfinding strategies.

A second ocular behaviour that may vary according to strategy use is pupil size, which is a known physiological indicator of cognitive effort (see Beatty, 1982). Specifically, pupil size is correlated with cognitive effort, with tasks of increasing complexity associated with pupil dilation. As employing an allocentric place strategy requires more cognitive effort than an egocentric response strategy (Hartley, Maguire, Spiers & Burgess, 2003), the use of different wayfinding strategies may evoke different pupillary responses. Indeed, Mueller et al. (2008) found that compared to trials that could be solved using an egocentric response strategy, pupil size was larger at the beginning of trials that required allocentric knowledge. Therefore, the secondary purpose of this study was to investigate whether shifts in strategy preference – which have been found in previous implementations of the Alternative Routes paradigm (see Chapter 3 and 4) – are reflected in changes in pupil size.

Finally, while simple stimulus-response associations form the basis of landmark-based egocentric route knowledge, there are two differing accounts of the spatial representations associated with allocentric strategy use. Typically, allocentric knowledge is conceptualised as a cognitive map that is viewpoint invariant (O'Keefe & Nadel, 1978). However, allocentric learning can also involve encoding a viewpoint-dependent spatial representation that is compared to subsequent views of the same location to support navigation (Wang & Spelke, 2002). Therefore, the final aim of this study was to identify the spatial representation associated with allocentric configuration strategy use in the Alternative Routes paradigm.

## 5.5. Hypotheses

In this experiment, participants completed an eye-tracking variant of the Alternative Routes paradigm (see Chapter 4). Participants learned a short route through a virtual environment containing four-way intersections. Two local landmarks were located in diagonally opposite corners of each intersection to facilitate route recognition, and support the use of three wayfinding strategies: a configuration-based allocentric strategy, and the associative cue and beacon response strategies. Strategy choice and landmark preference were assessed in test trials in which participants approached intersections from various directions and were asked to navigate along the original route. Given that the eye-tracking and behavioural variants of this task are functionally equivalent, we expected to replicate the strategy choice findings reported in Chapter 4, with participants initially exhibiting a bias for the suboptimal beacon strategy, before switching to an allocentric place strategy that supports successful navigation in all test trials.

While our investigation into the strategy-related landmark preference is primarily exploratory, empirical research does provide some insight into landmark selection and encoding. Firstly, in order to minimise the amount of information required to learn and retrieve spatial knowledge, participants that employ an egocentric strategy are likely to encode a single landmark at each intersection (Hamid, Stankiewicz & Hayhoe, 2010). While associative cue strategy use is not associated with defined selection criteria when choosing between multiple landmarks at a decision point, successful beacon strategy use depends on landmarks that spatially correspond with the direction of movement during learning (Waller & Lippa, 2007). This suggests that participants will not attend to the same landmark at each intersection during associative cue-based navigation, but will selectively attend to landmarks that are congruent with route movement during beacon strategy use. In contrast, participants are likely to attend to both landmarks at an intersection during configuration strategy use, as i) the configural knowledge required to employ an allocentric place strategy is derived from object-to-object spatial relationships (Wang, 2012), and ii) because allocentric learners utilise more landmarks during navigation than egocentric learners (Andersen et al., 2012).

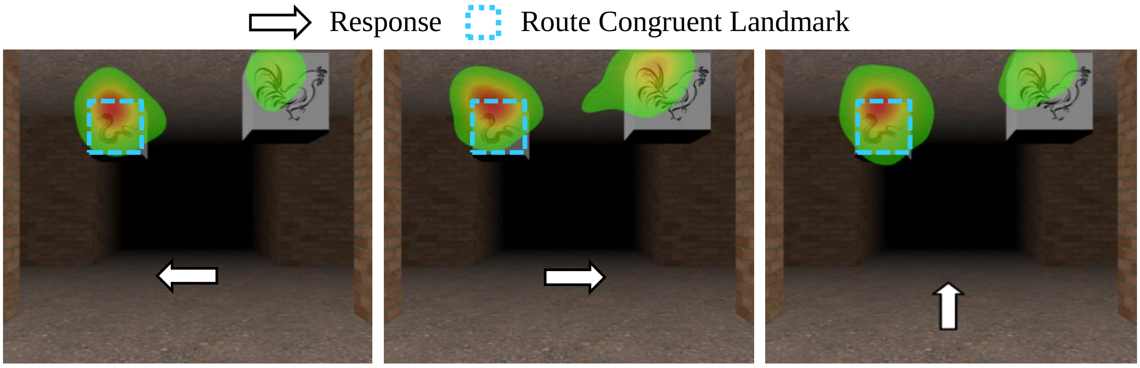
Furthermore, we expected differences in the cognitive effort required to employ allocentric and egocentric strategies to be reflected in participants' pupil size during navigation. Specifically, we expected shifts from an egocentric strategy to the more cognitively demanding configuration strategy to be accompanied by a corresponding increase in pupil dilation during navigation.

Finally, to determine the spatial representation utilised during allocentric strategy use, we analysed participants' response times when route locations were approached from different directions. If configuration strategy use depends on a viewpoint-independent cognitive map that allows direct access to spatial knowledge irrespective of one's position in an environment, then the approach direction at test will not influence the time taken to make a response. Alternatively, configuration strategy use may involve comparing the view of an intersection at test to a viewpoint-dependent representation encoded during learning. Should this be the case, the time required to perform this spatial computation will increase relative to the angular discrepancy between the approach directions experienced during training and test, resulting in variations in response time between test trials with different start positions.

## 5.6. Main Findings

Participants initially employed a beacon response strategy to learn the route, before increasingly adopting the optimal configural place strategy, replicating the findings reported in Chapter 4. The use of a beacon response strategy during initial learning suggests that participants relied on the simplest – albeit suboptimal – available wayfinding strategy to support the early stages of knowledge acquisition, before subsequently identifying and employing the correct configuration strategy for the remainder of the experiment.

Interestingly, analysis of gaze behaviour during test trials revealed that participants utilised the same environmental cue to support configuration, associative cue and beacon strategy use. Specifically, participants exhibited a strategy-independent bias for attending to landmarks that spatially coincided with the direction of the route during learning (the Route Congruent Landmark; see Figure 19). At the beginning of the experiment, participants may have selectively encoded this landmark, which naturally serves as a beacon, to support the use of the prevailing beacon response strategy. Despite subsequently adopting an allocentric place strategy, participants may have continued to utilise the landmark associated with their previous strategy choice rather than expend additional cognitive effort to unnecessarily encode another environmental cue. Alternatively, the landmark selectively encoded by participants irrespective of strategy choice was the only environmental cue that supports a configuration, associative cue and beacon strategy. Therefore, participants may have encoded this landmark as it facilitates the simultaneous acquisition of all three wayfinding strategies. Furthermore, the observed shifts in strategy were also accompanied by changes in task-evoked pupillary responses, with increasing use of the more cognitively demanding configuration strategy associated with increased pupil dilation during test trials. This finding suggests that pupil dilation may be sensitive to shifts between allocentric and egocentric strategy use.



**Beacon strategy use** **Associative Cue strategy use** **Configuration strategy use**

**Figure 19.** Gaze behaviour associated with the use of different strategies. The Route Congruent Landmark during training is located on the left of the featured intersection (the snake). Irrespective of the strategy employed, participants primarily attended to the Route Congruent Landmark to inform subsequent navigation. Therefore, participants exhibited a strategy-independent preference for encoding the same landmark during learning.

Finally, response times increased relative to the angular discrepancy between the approach directions experienced during training and test, suggesting that configuration strategy use depends on a viewpoint-dependent spatial representation rather than direct access to an allocentric cognitive map. Specifically, configuration strategy use involved determining the correct movement direction after resolving any spatial differences between the viewpoint encoded during learning and the viewpoint at test.

## 5.7. Summary

The paper discussed in this chapter replicates the key findings reported in Chapter 4, providing support for the reliability of the Alternative Routes paradigm. Specifically, participants again initially employed a beacon response strategy, before increasingly adopting the optimal configuration strategy over time. In addition, analysis of gaze behaviour revealed that participants attended to the same landmark during configuration, associative cue and beacon strategy use, which suggests that participants facilitate shifts in wayfinding strategy by i) utilising the landmark associated with a previous strategy choice to support a new wayfinding strategy, or ii) acquiring multiple landmark-based wayfinding strategies in parallel. Furthermore, pupil dilation captured the shift from egocentric strategy use to the use of a more cognitively demanding allocentric strategy. Therefore, in the absence of other behavioural measures, variations in pupil size during navigation may prove useful in identifying individuals who switch wayfinding strategies. Finally, it was revealed that use of the configuration strategy involved view-dependent allocentric navigation, rather than the use of a cognitive map.

# CHAPTER 6. Discussion: Chapters 1-5

## 6.1. Overview

The purpose of the first part of this thesis (Chapters 1-5) was to investigate the selection and use of landmark-based wayfinding strategies. Landmarks are environmental features that are utilised by individuals to acquire spatial knowledge and inform subsequent navigation. Interestingly, landmark use varies according to the strategy employed to support navigation. For example, allocentric strategy use, which depends on the hippocampus, involves processing the spatial relationship between environmental cues. As such, allocentric strategy users develop a cognitive map of a learned environment that supports flexible navigation e.g. taking detours and novel short-cuts (O'Keefe & Nadel, 1978; Tolman, 1948). In contrast, the striatal circuits are implicated in the use of egocentric response strategies, which involve encoding spatial knowledge relative to the navigator's body (Hartley, Maguire, Spiers & Burgess, 2003; Iaria, Petrides, Dagher, Pike & Bohbot, 2003; Waller & Lippa, 2007). Therefore, egocentric strategy use supports navigation tasks that involve reproducing learned behaviours, such as route repetition. The following discussion will address task-dependent selection and use of landmark-based wayfinding strategies in relation to the findings of the preceding four experimental chapters.

## 6.2. Key Findings

The key findings regarding the selection and use of landmark-based wayfinding strategies were:

1. Beacon strategy use facilitates route learning better than associative cue strategy use.
2. Alternating between associative cue and beacon strategy use during navigation does not affect the efficacy of either egocentric strategy.
3. Egocentric strategy use precedes allocentric strategy use.
4. Learning associated with different wayfinding strategies may occur in parallel.
5. Shifts between allocentric and egocentric strategy use can be determined by changes in the pupillary response to navigation.

## 6.3. Discussion of Key Findings

Individuals typically use egocentric response strategies to efficiently perform tasks that involve uni-directional navigation, such as route repetition. Previously, Waller and Lippa (2007) compared the efficacy of two egocentric route learning strategies – the landmark-based associative cue and beacon response strategies – and found that beacon strategy use supported better learning and more accurate navigation than associative cue strategy use. The first experiment of Chapter 2 also revealed a learning and accuracy advantage for beacon strategy use over associative cue strategy use, replicating the results reported by Waller and Lippa

(2007). These findings are thought to reflect differences in the relative memory demands of each strategy. Specifically, associative cue and beacon-based navigation depend on cued recall and item recognition respectively. As such, beacon strategy use requires less cognitive effort than associative cue strategy use, and therefore supports the acquisition and use of route knowledge better. Indeed, the simplicity and accuracy associated with beacon strategy use may explain why it emerges earlier in the lifespan than other landmark-based wayfinding strategies (Learmonth, Newcombe, Sheridan & Jones, 2008; Lee, Shusterman & Spelke, 2006; Lee & Spelke, 2010).

The strategies available to navigators during real-world route learning often vary between decision points due to differences in landmark availability, position, proximity, uniqueness and number. Therefore, it is often possible, and sometimes necessary, to employ a variety of strategies to learn a single route. While it may seem advantageous to employ the optimal route learning strategy at each decision point, switching strategies is cognitively demanding, and is associated with efficacy-related decrements in a variety of cognitive domains (see Kiesel et al., 2010; Monsell, 2003 for reviews). The purpose of Experiment 2 in Chapter 2 was to examine participants' strategy choice and navigation performance in a route learning task that could be completed by i) adopting the optimal strategy – either an associative cue or beacon strategy – at each decision point, or ii) avoiding switching costs and employing an associative cue strategy throughout the route. Analysis revealed that participants alternated between associative cue and beacon strategy use during route navigation without incurring significant switching costs. That is, whether employed separately or in conjunction with one another to learn a route, the efficacy of associative cue and beacon strategy use did not change. These findings suggest that alternating between different egocentric response strategies to optimise route learning and navigation performance is a process that is largely resistant to the switching costs known to affect other cognitive tasks.

To date, there has been little agreement regarding the temporal development of spatial knowledge. While the dominant framework in spatial microgenesis suggests that individuals acquire egocentric knowledge before allocentric knowledge (Siegel & White, 1975), it has also been argued that i) allocentric knowledge develops earlier than egocentric knowledge (Packard & McGaugh, 1996), and ii) both types of knowledge are learned in parallel (Iglói, Zaoui, Berthoz & Rondi-Reig, 2009). In Chapters 3, 4 and 5, participants completed variants of a novel navigation task – the Alternative Routes paradigm – that was employed to assess participants' strategy preference over time. During the task, participants were required to continue along a learned route that was approached from various directions. When decision points were approached from the same direction as learning, participants could employ either an allocentric or egocentric strategy to support accurate navigation. In contrast, only the use of an allocentric strategy allowed participants to continue along the original route when decision points were approached from a direction that differed from learning. In four separate experiments, participants initially employed a beacon response strategy, before increasingly adopting an allocentric strategy. It should also be noted that participants were informed prior to the experiment that they would approach known decision points from a variety of different directions. Therefore, despite being aware of the demands of the navigation task, participants' initial maladaptive bias for a beacon response strategy suggests that egocentric knowledge is developed earlier in the spatial learning process than allocentric knowledge. Taken together, participants' changing strategy preferences in Chapters 3, 4 and 5 are consistent with the framework proposed by Siegel and White (1975), which suggests that individuals first acquire egocentric knowledge of landmarks and the routes between them, before finally developing allocentric knowledge.

However, there is some evidence to suggest that navigators acquire different strategies in parallel. For example, an analysis of participants' gaze behaviour in the Alternative Routes paradigm revealed that the same landmark was used to support allocentric, associative cue and beacon-based navigation (Chapter 5). Specifically, participants exhibited a strategy-independent preference for encoding the landmark that spatially corresponded with the path of the route through each intersection. While this landmark naturally serves as a beacon, participants could use either cue at a decision point to support associative cue and allocentric strategy use. Therefore, participants' strategy-independent preference for encoding a universal landmark suggests that landmark selection may be related to the parallel acquisition of multiple strategies. Furthermore, during both associative cue and beacon-based learning, participants acquired spatial knowledge that was not required to employ their chosen strategy, but could be used to support an alternative wayfinding strategy (Chapter 2). First, participants associated explicit directional knowledge with individual landmarks during beacon-based learning. While such knowledge is not necessary to employ a beacon response strategy, it is required for associative cue-based navigation. Second, participants acquired strategy-irrelevant knowledge of landmark position during both associative cue and beacon-based learning. Interesting, such knowledge is required to employ an allocentric strategy, which involves processing the spatial relationships between different environmental cues. Taken together, these findings provide additional evidence suggesting that navigators develop different strategies in parallel (e.g. Iglói et al., 2009; Marchette, Bakker & Shelton, 2011), and may explain why participants switched strategies efficiently in Chapter 2.

Finally, researchers typically identify participants' strategy preference by analysing wayfinding behaviour (e.g. Cornwell, Johnson, Holroyd, Carver & Grillon, 2008), or administering post-experimental questionnaires (e.g. Etchamendy & Bohbot, 2007). Some studies also suggest that response time differences between allocentric and egocentric strategy use can be used to identify participants' strategy choice (e.g. Iaria et al., 2003; Wiener, de Condappa, Harris & Wolbers, 2012). Specifically, allocentric strategy use is more cognitively demanding than egocentric strategy use, and is therefore associated with increased response times. Similarly, task-related variations in pupil size are also sensitive to cognitive load (see Beatty, 1982), with pupil dilation increasing relative to task complexity. In Chapter 5, analysis of fluctuations in pupil size during navigation revealed that pupil dilation increased with increasing use of an allocentric strategy. This finding suggests that pupil dilation is sensitive to shifts in wayfinding strategy, and may prove to be a reliable physiological indicator of strategy preference.

## 6.4. Conclusions

Good navigators identify and subsequently employ wayfinding strategies that support accurate navigation in the concurrent task. In order to optimise wayfinding efficacy, navigators must often change strategies. Permanent shifts in strategy choice are typically made in response to task demands, and involve the adoption of a more successful wayfinding strategy. In contrast, navigators alternate between multiple strategies when the optimal wayfinding strategy differs between decision points, with strategy switches corresponding with differences in strategy preference between successive environmental locations. Interestingly, there is some evidence to suggest that navigators prepare for potential strategy switches by acquiring knowledge required for different strategies in parallel, and selectively encoding environmental cues that support the use of multiple wayfinding strategies. These findings, along with the ubiquity of strategy switching during navigation, may explain why navigators do not incur switching costs known to affect other cognitive tasks. Taken together, it is apparent that adaptive strategy selection is an important ability for good navigators.

# CHAPTER 7. Aging and Wayfinding

## 7.1. Introduction

Age-related cognitive decline has been observed in a variety of domains, including memory, attention, processing speed and executive functions (Albinet, Boucard, Bouquet & Audiffren, 2012; Craik & Rose, 2012; Bopp & Verhaeghen, 2005; McDowd & Shaw, 2000; Old & Naveh-Benjamin, 2008; Park et al., 2002; Reuter-Lorenz & Sylvester, 2005; Salthouse, 1996; West, 1996; Zacks, Hasher & Li, 2000). Age is also associated with impaired spatial cognition, with deficits observed in visuospatial perception, mental imagery, spatial learning and memory, and navigation (Burgess, 2008; Klencklen, Després & Dufour, 2012). This chapter will review the effects of normal aging on navigation and wayfinding strategy use, and discuss the neurobiological basis of age-related differences.

## 7.2. General Wayfinding

Studies investigating the driving habits of older adults provide insight into the effects of aging on everyday navigation tasks. Older adults self-report a decline in several wayfinding abilities and skills, and often avoid unfamiliar environments in order to minimise the risk of getting lost (Burns, 1999; Bryden, Charlton, Oxley & Lowndes, 2010, 2013). Burns (1999) surveyed the wayfinding abilities and driving habits of adults between 21 and 85 years old, and found that in comparison to adults under the age of 60, adults 60 years and older reported greater difficulties with wayfinding, rated their wayfinding skills as poorer, and avoided unfamiliar places and routes. Bryden et al. (2010, 2013) administered a questionnaire to adult drivers aged 65 years and older regarding self-perceived cognition, and wayfinding abilities and practices. Wayfinding difficulties were more likely to be reported by participants that were older, and rated their memory, planning and attention abilities as poorer. Furthermore, 14% of participants avoided unfamiliar locations regularly, and reported increased stress and reduced confidence when driving in unfamiliar areas. Indeed, 60 – 80% of participants reported difficulties wayfinding in various unfamiliar situations, while fewer than 10% rated their wayfinding ability as poor in known locations, supporting findings that suggest that age-related wayfinding deficits are more pronounced in novel environments than in familiar surroundings (Devlin, 2001). While these studies highlight older adults' self-perceived wayfinding deficits, empirical research has identified a variety of wayfinding tasks and processes that are affected by normal cognitive aging. Therefore, the remainder of this chapter will examine the effects of aging on several wayfinding abilities, and provide a sensory and physiological basis for age-related wayfinding differences.

### 7.3. Sensorimotor Deficits and Path Integration

Movement during navigation relies on sensorimotor functions that provide self-motion cues, which allow individuals to update their orientation and position in an environment based on perceived movement (Etienne & Jeffrey, 2004; Mittelstaedt & Mittelstaedt, 1980). These functions, which involve processing vestibular information (linear and rotational movement detected by sensory receptors located in the inner ear), proprioceptive feedback (body position derived from limb, muscle and joint feedback) and optic flow (the displacement of visual information during perceived movement), deteriorate with age (Agrawal, Carey, Della Santina, Schubert & Minor, 2009; Goble, Coxon, Wenderoth, Van Impe & Swinnen, 2009; Lich & Bremmer, 2014). Sensorimotor deficits are particularly evident in path integration tasks, which typically take place in featureless environments, and therefore rely on self-motion cues. Path integration involves the use of linear and/or rotational movement to discern one's position relative to a starting location or orientation (Etienne & Jeffrey, 2004; Mittelstaedt & Mittelstaedt, 1980). Path integration is often tested using the Triangle Completion (TC) Task, in which participants move along two sides of a triangular route and are asked to return to their point of origin via a single, linear path. Accurate navigation requires the integration of knowledge about the distance travelled along both sides of the triangle and the angular rotation of the intermediary turn. These different types of knowledge can also be assessed separately in Distance Reproduction (DR) Tasks, in which participants are asked to return to a start location after moving a set distance, and Rotation Reproduction (RR) Tasks, in which participants experience and then reproduce rotational movements. Several studies have used these tasks to investigate age-related deficits in sensorimotor abilities (Adamo, Briceño, Sindone, Alexander & Moffat, 2012; Allen, Kirasic, Rashotte & Haun, 2004; Harris & Wolbers, 2012; Mahmood, Adamo, Briceño & Moffat, 2009).

Research conducted in real-world environments has found that age differences in path integration are influenced by the number of available self-motion cues. For example, Allen et al. (2004) blindfolded participants, thus inhibiting the influence of optic flow on path integration, and compared TC performance during active movement (guided walking) or passive conveyance (via wheelchair). While younger and older adults performed similarly in the guided walking condition, in which both vestibular information and proprioceptive feedback was available, age-related deficits were found when participants were conveyed by wheelchair and only vestibular information was available. Similarly, Adamo et al. (2012) found that while distance and rotational errors did not differ between younger and older adults when both vestibular information and proprioceptive feedback was available during a TC task, age differences were found when vestibular information or optic flow were the only source of self-motion information. Taken together, these studies suggest that older adults require more sources of sensorimotor information than younger adults to support accurate path integration. In many virtual environment setups, however, accurate path integration depends entirely on the use of optic flow to determine the speed and direction of self-motion. As such, age-related deficits in virtual path integration tasks are indicative of impaired processing of optical flow in older adults. For example, Mahmood et al. (2009) found that in a virtual environment, older adults were less accurate than younger adults at TC and DR, and that older adults' TC performance deficit was attributable to the rotational component of the task. Harris and Wolbers (2012) also examined aging and path integration in virtual environments, and found age-related deficits in TC, DR and RR, as well as a tendency for older adults to underestimate the amount of movement and/or rotation required to correctly solve each task. Taken together, these studies demonstrate age-related deficits in tasks that rely on self-motion cues.

As a consequence of age-related decline in sensorimotor functions, processing self-motion cues requires a greater proportion of older adults' attentional resources compared to younger adults' (Li & Lindenberger, 2002; Woollacott & Shumway-Cook, 2002). In addition, concurrent performance of sensorimotor and cognitive tasks results in competition for processing resources, with deficits in the performance of either task being more pronounced for older adults (Beurskens & Bock, 2012, 2013). Therefore, wayfinding difficulties experienced by older adults may be explained by a lack of cognitive resources devoted to processing navigationally relevant information. For example, Lövdén, Schellenbach, Grossman-Hutter, Krüger and Lindenberger (2005) asked younger and older participants to learn a route through a virtual environment while walking on a treadmill. Movement through the environment was synchronised with the speed of the treadmill, thus providing participants with the self-motion cues associated with walking in a physical environment. Lövdén et al. (2005) found that age differences in wayfinding performance were significantly reduced, but not entirely eliminated, when participants were allowed to hold onto a handrail for walking support, suggesting that the sensorimotor demands associated with physical movement contribute to age-related deficits in the acquisition and use of spatial knowledge.

## 7.4. Landmark Use

Older adults' wayfinding difficulties in environments featuring visual cues have been attributed to age differences in the use of landmarks to support the acquisition of spatial knowledge. For example, Head and Isom (2010) asked participants to repeatedly navigate along a marked path through a landmark-rich virtual environment. Analysis revealed that younger and older adults followed the designated route a similar number of times over five minutes, suggesting that assisted route navigation did not differ between the age groups. However, when partial or complete removal of the markings increased participants' reliance on landmark-based route knowledge, older adults traversed the route fewer times than younger adults, suggesting age-related impairments in landmark use. The following paragraphs will discuss the effects of aging on several wayfinding processes that are critical for using landmarks to learn and recall spatial knowledge.

Age differences have been reported in the assessment and selection of landmarks, suggesting that younger and older adults evaluate the spatial significance of environmental cues differently. For example, Driscoll, Hamilton, Yeo, Brooks and Sutherland (2005) conducted a study in which participants were asked to locate a fixed, hidden platform in a virtual Morris Water Maze Task (MWMT) (see Chapter 1 for an overview of the MWMT). Driscoll et al. (2005) found that the fixed spatial relationship between the position of the platform and the location of distal cues was less likely to be noticed by older adults (60 years old and over) than younger adults (aged 20 – 39) and middle aged adults (aged 40 – 59). Similarly, Moffat and Resnick (2002) found that in a virtual MWMT, older adults were less likely than younger adults to consider informative distal cues as navigationally relevant. Furthermore, in a virtual environment study conducted by Schuck et al. (2013), participants were required to learn the location of an object within a circular enclosure containing a single intramaze cue, and surrounded by distal cues. In specific test trials, the intramaze cue and the circular boundary were displaced relative to one another. Errors in participants' recall of prior object location revealed that older adults relied on the intramaze cue to determine object location, while younger adults relied on the boundary of the circular enclosure. In another study, Lipman (1991) asked participants why selected scenes from a learned environment were navigationally important. While younger adults attached importance to the presence of critical route events (i.e. turns), older adults were more likely to consider the visual distinctiveness of landmarks as important. Taken together, these studies suggest that younger and older adults evaluate and subsequently encode environmental cues differently.

Older adults' differential use of landmarks may also be associated with age-related decline in landmark memory. Studies have reported either age equivalency (Campbell, Hepner & Miller, 2014; Head & Isom, 2010; Moffat & Resnick, 2002) or age-related deficits (Evans, Brennan, Skorpanich & Held, 1984; Jansen, Schmelter & Heil, 2010; Lipman, 1991) for landmark recall, which involves remembering visual cues from an experienced environment. Similarly, older adults have performed as well as (Wilkniss, Jones, Korol, Gold & Manning, 1997), or worse (Liu, Levy, Barton & Iaria, 2011; Rosenbaum, Winocur, Binns & Moscovitch, 2012) than younger adults in landmark recognition tasks, which require participants to identify whether stimuli were present in an environment or not. Interestingly, age-related deficits in landmark recognition may be related to wider age differences in scene recognition. While younger and older adults' recognition of experienced scenes is typically equivalent, older adults are more likely to indicate that they have previously encountered novel scenes (foils). For example, Head and Isom (2010) found that despite recognising scenes from an explored environment as well as younger adults, older adults were less accurate at identifying foils. Furthermore, Kirasic (1991) found that in both familiar and newly experienced environments, older adults’ recognition of experienced scenes was poorer than younger adults. Cushman, Stein and Duffy (2008) also found that among eight wayfinding subtests administered to participants following route learning, performance in a scene recognition task best distinguished between younger and older adults. These findings may explain why older adults’ recognition of objects and buildings within a virtual environment was equivalent to that of younger adults, but age-related deficits were found in identifying foils (Zakzanis, Quintin, Graham & Mraz, 2009).

Age differences have also been found in the spatial knowledge associated with landmarks. For example, Liu et al. (2011) tested participants’ ability to remember which direction a route continued at decision points containing a single landmark. Age was negatively correlated with task performance, suggesting that older adults have difficulty associating route knowledge with landmarks. Furthermore, Head and Isom (2010) found that after controlling for experience within a route learning environment, older participants were able to recall landmarks as well as younger participants, but had less accurate knowledge of the directional information associated with each landmark.

Older adults' knowledge of the spatial relationships between landmarks is also impaired compared to younger adults. For example, Evans et al. (1984) asked participants to recall buildings from a highly familiar downtown area. In addition to recalling fewer buildings than younger adults, older adults were less likely to recall buildings in an order reflecting the spatial arrangement of the environment, suggesting age-related deficits in the organisation of landmark memory. Lipman (1991) also found that after learning two partially overlapping routes, older adults were less likely than younger adults to recall landmarks in a sequential order. Instead, older adults tended to recall landmarks according to distinctiveness, or with no apparent order or categorical organisation. Furthermore, Wilkniss et al. (1997) found that older adults identified which objects were present along a learned route as well as younger adults, but were impaired at sequentially ordering landmarks. Similarly, Head and Isom (2010) reported that older adults' knowledge of the temporal order of landmarks within a route was poorer than younger adults', despite age-equivalent landmark recall. Conversely, Rosenbaum et al. (2012) did not find any age differences in a task that required participants to sequentially order a set of landmarks located on a route through downtown Toronto. The authors suggest older adults' extensive experience and familiarity with the city may have resulted in an age-resistant long-term spatial representation of the environment. Indeed, a subsequent task involving route learning in a novel environment revealed significant age differences.

In summary, aging is associated with a number of impairments that affect landmark supported wayfinding. These include age differences in landmark evaluation and memory, as well as age-related deficits in the spatial and temporal knowledge associated with landmarks.

## 7.5. Route Planning, Learning and Navigation

Age-related deficits in route learning have been demonstrated in a variety of contexts, with normal cognitive aging associated with impaired route planning, acquisition and navigation. Salthouse and Siedlecki (2007) investigated the effects of aging on route selection in two separate tasks. In The Mazes task, older adults took longer than younger adults to determine the optimal path through an overview of a maze. In the Zoo Trip task, participants were given a map of a zoo with thirteen exhibits, and asked to plan the most efficient route between six target exhibits. Compared to younger adults, older adults chose less efficient routes and were more likely to accidentally omit or revisit exhibits. In addition, Sjölinder, Höök, Nilsson and Andersson (2005) found that after exploring a virtual supermarket, older adults took less efficient routes between target items. Taken together, these results suggest that deficits in route selection and planning may significantly contribute to the navigation difficulties experienced by older adults.

Age-related difficulties have also been reported during the acquisition of route knowledge. For example, Moffat, Zonderman and Resnick (2001) asked participants to determine the shortest route from a fixed starting position to a hidden goal location. An analysis of participants' errors revealed that compared to younger adults, older adults were more likely to visit off-route locations multiple times, suggesting that older adults failed to learn from prior navigational experience. Jansen et al. (2010) also found that the number of trials needed to learn a route increased with age when comparing younger (20 – 30 years), middle aged (40 – 50) and older (60 – 70) age groups. In another study, Lipman (1991) presented participants with ordered images depicting two partially overlapping routes. When asked what they remembered about the routes, older adults reported more non-spatial information than younger adults, suggesting that age-related impairments in route learning may be associated with the allocation of attention to route-irrelevant information.

Several studies in both real-world and virtual environments have revealed age-related deficits in repeating previously traversed routes. For example, Wilkniss et al. (1997) found that after guiding participants along a route through a hospital building, older adults' route following performance was poorer than younger adults’ when asked to navigate unaided along the learned route. An analysis of navigation errors revealed that older adults made more errors irrespective of the number of movement options at each decision point (two or more) or the correct response (turn or maintain course). Similarly, Rosenbaum et al. (2012) found age-related deficits in both immediate and delayed recall of a novel route that spanned three floors of a building. In another study, Cushman et al. (2008) passively transported participants along a route in both a real-world and virtual hospital, and found that older adults performed worse than younger adults when asked which direction the route continued at ten different decision points. Furthermore, Zakzanis et al. (2009) found that after being shown a route through a virtual city, older adults took longer to re-navigate the route and made more wrong turns compared to younger adults.

While older adults' route learning difficulties are more pronounced in complex environments, age-related deficits are also apparent in simple navigation tasks. For example, Meulenbroek, Petersson, Voermans, Weber and Fernández (2004) designed a simple route following task to minimize age differences in an fMRI study, with participants required to learn a route through a virtual home containing only five decision points. Despite the simplicity of the route learning task, older adults did not perform as well as younger adults when asked to select the correct movement direction at each decision point from two response options. Liu et al. (2011) also found age differences in a simple task that required participants to compare two virtual routes containing three turns. Compared to younger (18 – 30 years of age) and middle aged adults (31-45), older adults (46 – 67) were less able to determine whether the two routes were identical.

In summary, age-related deficits in route planning, learning and navigation may why explain older adults avoid unfamiliar areas, and report reduced confidence and increased stress in new surroundings.

### 7.6. Spatial Memory

Age differences in encoding and retrieving knowledge of the spatial relationship between environmental cues and/or locations are well established in wayfinding research, with studies employing a variety of wayfinding and map-based tasks to examine the effects of normal aging on the formation and use of cognitive maps (O’Keefe & Nadel, 1978; Tolman, 1948). For example, the ability to take novel short-cuts between environmental locations suggests the use of an accurate cognitive map. Head and Isom (2010) found that after free exploration of a landmark-rich virtual environment, older adults travelled further compared to younger adults when asked to navigate between two landmarks. Similarly, after exploring a virtual town containing several landmarks, Etchamendy, Konishi, Pike, Marighetto and Bohbot (2012) asked participants to navigate between two landmarks using the most direct route. Older adults travelled significantly greater distances than younger adults to reach the target landmark. Furthermore, in a study conducted by Moffat, Elkins and Resnick (2006), participants learned a virtual environment containing several rooms, hallways and objects. Compared to younger adults, older adults made more errors when asked to navigate to a designated object by the shortest available route. Finally, Moffat et al. (2001) found that when trying to find the shortest route between a start location and goal, younger and older adults deviated from the correct path at a similar number of decision points. However, older adults committed more spatial memory errors –deviating from the correct path at the same decision point on multiple occasions – than younger adults. Overall, the inefficient navigation exhibited by older adults in these tasks suggests that aging is associated with impaired environmental knowledge.

Successful acquisition and recall of cognitive maps can also be determined by participants' ability to accurately reproduce key spatial characteristics of a wayfinding environment on an aerial map. For example, Uttl and Graf (1993) asked participants to indicate the location of given exhibits on a floor plan of a museum room, and found that performance was similar in four equal age groups between 15 and 54 years of age, but began to decline in older participants. Furthermore, when provided with an overview of an explored environment, older adults were less accurate than younger adults at both identifying locations that contained landmarks, and naming landmarks at designated positions (Head and Isom, 2010). Moffat and Resnick (2002) also assessed participants' allocentric knowledge of a MWMT environment in two separate cognitive mapping tasks, and found age-equivalent knowledge of proximal cues, but age-related impairments in the knowledge of outer room geometry. Finally, Jansen et al. (2010) found age-related deficits in a task that required participants to draw a geometric overview of an environment through which both younger and older adults learned a route to criterion. Therefore, despite age-equivalent route knowledge, older adults' environmental knowledge was impaired. Taken together, these findings suggest that older adults construct and recall cognitive maps with less accuracy than younger adults.

While these findings demonstrate age-related deficits in the knowledge associated with cognitive maps, some studies have explicitly investigated age differences in the formation and the use of cognitive maps separately. For example, Iaria, Palermo, Committerri and Barton (2009) asked participants to explore and learn a virtual environment. The formation of an accurate cognitive map was then tested by assessing participants' placement of landmarks on an aerial map of the environment. Subsequently, participants were asked to navigate between two landmarks via the shortest possible route, which required use of the cognitive map formed during learning. Iaria et al. (2009) found that compared to younger adults, older adults required more experience within the environment to correctly place landmarks on an overview map, and took longer and made more errors when navigating to a target location. Liu et al. (2011) also assessed participants’ ability to construct and utilise cognitive maps. Compared to younger and middle aged adults, older adults required significantly more first-person experience of a virtual environment to consistently place landmarks accurately on an aerial map of the environment. Furthermore, having formed an accurate cognitive map, older adults were less able to determine whether passive navigation between two landmarks was achieved by the shortest route or not. Taken together, these studies suggest that aging separately affects the formation and the subsequent use of cognitive maps.

Interestingly, age-related deficits in environmental knowledge are less pronounced in familiar surroundings, suggesting that spatial representations of frequently experienced environments may be less susceptible to the effects of aging. For example, Campbell et al. (2014) found age-equivalent performance in two separate tasks that required participants to provide directions between familiar landmarks, and indicate the location of sixteen landmarks on a map of the Sydney Central Business District. Rosenbaum et al. (2012) asked participants familiar with downtown Toronto to indicate the correct direction and distance between a marked location and an unmarked landmark on a blank map featuring only downtown city limits. Age differences were not found for distance estimates, although interestingly, older adults' direction estimates were more accurate than younger adults'. Conversely, in a similar task performed in a newly learned virtual supermarket, Sjölinder et al. (2005) found that older adults were less accurate than younger adults at estimating the direction and distance to a target item. Furthermore, Kirasic (1991) found that older adults performed complex spatial tasks better in familiar environments than in novel environments, while younger adults’ task performance did not differ between environments. However, it should be noted that age-related wayfinding deficits have also been reported in highly familiar environments. For example, Evans et al. (1984) found that older adults were less accurate than younger adults at placing highly familiar buildings on a blank map containing a single well-known landmark. Furthermore, Campbell et al. (2014) found that when presented with a street-level photograph of a familiar landmark, older adults were less accurate than younger adults at both indicating the relative location of a second landmark, and determining the cardinal facing direction of the given photograph. Overall, these findings suggest that age-related deficits in the formation and use of cognitive maps may be partially attenuated by environmental familiarity.

Finally, several studies suggest that translating information and knowledge between different perspectives may contribute to age differences in the formation and use of cognitive maps. In a study conducted by Yamamoto and DeGirolamo (2012), participants learned virtual environments either through exploratory navigation or from a map-like aerial perspective, and were then asked to indicate the location of landmarks on a blank map. Age-related deficits were only found when environments were learned through exploration, suggesting a specific age-related impairment in incorporating first-person navigational experience into a spatial representation. Wilkniss et al. (1997) provided participants with an overview of a hospital floor with a clearly marked route to learn. Participants first demonstrated that they had memorised the route by successfully reproducing the route on a blank map, before physically navigating the route with a blank map for support. Compared to younger adults, older adults required more attempts to reproduce the route on a blank map, and made more course maintenance errors during navigation (incorrectly turning when the correct route continued straight ahead). These results suggest that older adults are impaired in both learning a two-dimensional aerial representation of a route, and utilising this knowledge in a physical, three-dimensional environment. Similarly, Carelli et al. (2011) and Morganti and Riva (2014) asked participants to indicate the optimal path through an overview of a maze, before navigating through a virtual analog of the same maze. Despite being allowed to use the self-completed overhead maze as a navigational aid, older adults completed fewer virtual mazes than younger adults within a set time limit, suggesting age-related deficits in transferring survey knowledge into route knowledge.

In conclusion, empirical research has revealed age-related impairments in both the construction and subsequent use of cognitive maps. Specifically, increasing age has been associated with less accurate and complete cognitive maps, and an inability to use cognitive maps to perform complex spatial tasks.

## 7.7. Wayfinding Strategies

Younger and older adults exhibit biases for different wayfinding strategies when performing a range of navigational tasks. For example, some studies have found age-related deficits during initial exploration of an environment, suggesting that older adults employ less efficient search strategies than younger adults. In participants’ first experience of a MWMT environment, Moffat, Kennedy, Rodrigue and Raz (2007) and Moffat and Resnick (2002) found that older adults travelled longer distances than younger adults to find a hidden platform. As participants had no prior experience of the MWMT environment, older adults’ poorer performance could not be explained by age-related deficits in environmental learning. Instead, the authors of these studies suggest that older adults’ ineffective search behaviour may reflect age differences in strategy choice, planning, or perseverative activity (continuing to search an area that has been sufficiently explored).

However, the majority of literature examining age differences in strategy choice has primarily focused on the use of allocentric and egocentric strategies to acquire spatial knowledge. For example, several studies have employed virtual MWMTs to investigate age differences in allocentric and egocentric learning (Driscoll et al., 2003; Driscoll et al., 2005; Moffat et al., 2007; Moffat & Resnick, 2002; Yuan, Daugherty & Raz, 2014). Allocentric knowledge is required to learn the position of a hidden platform relative to environmental cues, with participants' behaviour during training and probe trials used to assess strategy preference. Specifically, a lack of allocentric learning is demonstrated by inefficient navigation to the hidden platform during training, and random search patterns during probe trials in which the hidden platform is removed. These studies found that age was associated with increased path length and response latencies during training, and reduced search time in the correct quadrant during removed platform probe trials. Several additional findings also reveal age differences in MWMT performance. Firstly, Moffat and Resnick (2002) found that older adults were less likely than younger adults to encode a subset of cues that were available to support allocentric learning. Secondly, Yuan et al. (2004) found that age-related deficits in MWMT performance resulted from older adults performing more turns (10 – 90°) and course reversals (over 90°) than younger adults during learning. Finally, a post-experiment questionnaire administered by Driscoll et al. (2005) revealed that allocentric strategy use decreased with age. Taken together, these findings suggest that age is associated with maladaptive strategy preferences.

Real world analogs of MWMT have also revealed age-related deficits in allocentric learning. For example, Gazova et al. (2013) found age-equivalent performance in an egocentric task that required participants to locate a hidden goal that maintained a fixed spatial relationship with respect to the start position. In contrast, older adults did not perform as well as younger adults in an allocentric task that required knowledge of the spatial relationship between a hidden goal and two distal cues, suggesting that aging is associated with difficulties in allocentric learning, but not egocentric learning. In another study, Newman and Kaszniak (2000) asked participants to learn the position of a target pole within a tent containing six environmental cues positioned against the tent walls. The pole was then removed from the tent, and participants were asked to indicate the previous position of the pole in two different test situations that required allocentric knowledge. First, two cues were removed from the tent, and second, participants experienced the environment from a different start position. Newman and Kaszniak (2000) found that older adults were less accurate than younger adults at replacing the pole within the tent in the absence of two environmental cues and across a variety of start positions (both novel and familiar). Antonova et al. (2008) also employed a similar MWMT variant to the one used by Newman and Kaszniak (2000) in which participants learned the position of a pole within a virtual environment containing visual cues. During test trials in which the pole was absent, older adults were less accurate at recalling the position of the pole within the environment. As allocentric knowledge is required for accurate performance in the tasks employed by Antonova et al. (2008) and Newman and Kaszniak (2000), older adults' impaired performance is indicative of allocentric learning deficits. Interestingly, as the target pole is clearly visible during learning in both studies, participants were not required to search for the target, as is the case in many MWMTs. Therefore, any deficits in MWMT performance could be attributed solely to impaired allocentric learning, rather than inefficient search strategies during initial exploration of the MWMT environment (e.g. Moffat et al., 2007; Moffat & Resnick, 2002).

A number of other experimental paradigms have also been used to investigate wayfinding strategy choice across different age groups. Rodgers, Sindone and Moffat (2012) found age differences in a Y-maze strategy assessment task that differentiated between allocentric and egocentric strategy use. Older participants preferentially employed an egocentric strategy (82%), while both strategies were used similarly by younger participants (egocentric – 46%, allocentric – 54%). Etchamendy et al. (2012) assessed strategy preference using a Concurrent Spatial Discrimination Learning Task (CSDLT) conducted in a virtual environment that consisted of 12 identical arms radiating out from a circular central junction. Participants initially studied six separate pairs of neighbouring arms from the radial maze, with one arm from each pair containing a reward. Subsequently, participants were presented with four different pairings of adjacent arms (e.g. a rewarded arm initially paired with its empty clockwise neighbour would later be presented with its empty anti-clockwise neighbour), and asked to indicate which arm contained a reward. To correctly solve this task, participants required knowledge of the spatial relationship between radial arms and distal cues in the surrounding environment. An identical left/right decision during both training and test was indicative of a fixed stimulus-response strategy, while successfully identifying the rewarded arm irrespective of which neighbouring arm was visible suggested allocentric strategy use. Despite learning the original pairings to the same criterion, older adults’ task performance was poorer than younger adults’, suggesting that older adults employed an egocentric response strategy to learn the initial pairings, while younger adults employed an allocentric place strategy. Interestingly, a similar study did not report age differences in strategy choice (Konishi et al., 2013), although age was associated with an increase in the number of training phases required to learn the original pairings, suggesting that older adults were less efficient at acquiring allocentric knowledge. Finally, Bohbot et al. (2012) asked participants to complete a task in an 8 arm radial maze that involved remembering which four arms contained a hidden reward. A post-experiment questionnaire revealed that allocentric strategy use, which involved knowledge of the spatial relationship between radial arms and extramaze cues, decreased across the lifespan, which suggests an age-related shift in strategy preference from allocentric strategies to egocentric strategies.

Taken together, these studies demonstrate that younger adults' strategy choice varies according to the requirements of the navigation task, while older adults preferentially employ egocentric response strategies over allocentric place strategies irrespective of task demands.

## 7.8. Wayfinding and Age-related Neurological Differences

While older adults’ wayfinding difficulties have often been discussed in the context of age-related decline in a variety of cognitive domains (e.g. Moffat et al., 2007; Moffat et al., 2001; Salthouse & Siedlecki, 2007), differences in spatial memory and strategy choice have primarily been associated with age-related neurological changes. Specifically, the successful formation and use of cognitive maps and the employment of allocentric place strategies are thought to critically depend on the hippocampus and surrounding structures (Burgess, 2008; Iaria, Petrides, Dagher, Pike & Bohbot, 2003; Moffat & Resnick, 2002; O’Keefe & Nadel, 1978), which are particularly vulnerable to structural and physiological changes with increasing age (Raz & Rodrigue, 2006; Rosenzweig & Barnes, 2003). In contrast, the striatal circuits, which are recruited for route navigation and employment of egocentric response strategies (Bohbot, Lerch, Thorndycraft, Iaria & Zijdenbos, 2007; Hartley, Maguire, Spiers & Burgess, 2003; Iaria et al., 2003) are affected by aging to a lesser extent (Raz, 2000; Raz et al., 2003). Therefore, age-related wayfinding deficits appear to be more pronounced in hippocampal-dependent tasks than striatal-dependent tasks. To conclude this chapter, the effects of age-related neurological changes on several navigational tasks will be reviewed in detail.

### 7.8.1. Neural Activity

Several studies have identified age differences in neural activity during navigation, suggesting that age-related neural changes may contribute to older adults’ wayfinding deficits. For example, prior to experiencing a virtual environment, Moffat et al. (2006) informed participants about subsequent mapping and navigation tasks to encourage allocentric learning. During encoding, older adults showed less activity than younger adults in the hippocampus, parahippocampal gyrus, retrosplenial cortex and circumscribed regions of the parietal lobe, and more activity in the frontal lobe. Furthermore, of several structures that were positively correlated with navigation accuracy in either age group, only the parahippocampal gyrus, cuneus and inferior temporal gyrus were correlated with performance in both younger and older adults. In addition to finding age-related deficits in MWMT performance, Antonova et al. (2009) found that only younger adults showed significant activation of the hippocampus and parahippocampal gyrus when both learning and recalling the location of a target object. Meulenbroek et al. (2004) also found that while learning a simple route, older adults showed weaker activity than younger adults in the posterior fusiform/parahippocampal and supramarginal regions. Furthermore, older adults showed more activity in the perisylvian region and the anterior cingulate cortex during encoding, suggesting an age-related deficit in suppressing task-irrelevant information. Finally, during the first learning phase of a CSDLT, Konishi et al. (2013) found that significant activity recorded in the right hippocampus of younger adults was absent in older adults. Interestingly, older adults also took longer to learn the initial arm pairings, although age differences were not observed in subsequent wayfinding performance. Furthermore, older adults that employed an allocentric strategy showed activity in the hippocampus during learning, while older adults that employed a response strategy showed significant activity in the left caudate nucleus. Taken together, these studies suggest that the involvement of the hippocampus and surrounding structures during navigation differs between younger and older adults, and may provide a neural basis for age-related decrements in wayfinding.

Interestingly, it could be argued that age differences in neural activity may reflect changing learning preferences across the lifespan, rather than age-related neurophysiological changes. Specifically, as hippocampal-dependent learning is typically more complex than striatal-dependent learning, age-related deficits in allocentric learning and cognitive map formation may reflect older adults' preference for simpler, less demanding wayfinding strategies over task accuracy. Such an account would explain why younger adults typically adopt the most effective strategy according to task demands, while older adults exhibit a task-independent preference for egocentric response strategies. Accordingly, in paradigms that require a cognitive map (e.g. MWMT and CSDLT), younger and older adults adopt allocentric and egocentric strategies respectively. As these strategies recruit different neural networks, it is not surprising that age differences in neural activity are found during such tasks. However, it should be noted that Konishi et al. (2013) found age differences in hippocampal activity despite younger and older adults exhibiting similar strategy preferences, suggesting that age is associated with the recruitment of different neural networks for wayfinding, rather than differences in strategy choice.

### 7.8.2. Brain Volumetry

Age differences in neural activity may be related to a number of neurological changes that occur over the lifespan. For example, aging may differentially affect navigation tasks that recruit the hippocampus and striatum due to volumetric changes that occur with increasing age. Studies have reported that hippocampal shrinkage accelerates in older adults (Du et al., 2006; Fjell et al., 2005; Kennedy et al., 2009; Liu et al., 2003; Raz et al., 2005; but see Sullivan, Marsh & Pfefferbaum, 2005), while striatal volume decreases linearly with age (Koikkalainen et al., 2007; Raz et al., 2003). As such, it is not surprising that performance in hippocampus-dependent spatial tasks declines with age, while striatal-dependent navigation tasks are less affected. For example, Driscoll et al. (2003) found that older adults' poorer performance in a MWMT compared to younger adults was accompanied by an age-related decline in both hippocampal volume and markers of neural integrity. Head and Isom (2010) also found that in older adults, hippocampal volume was associated with wayfinding behaviour in a task that required allocentric knowledge, while navigation performance in an egocentric route learning task was associated with the volume of the caudate nucleus. Furthermore, Konishi and Bohbot (2013) determined older adults' strategy preference in a CSDLT, and found that gray matter volume in the right hippocampus was positively correlated with allocentric strategy use and negatively correlated with egocentric strategy use.

However, some volumetric studies suggest that the neurological underpinnings of age-related wayfinding differences lie outside the hippocampus. For example, in a study conducted with both younger and older adults, Yuan et al. (2014) found that MWMT performance was associated with orbitofrontal cortex volume, but not hippocampal volume. Similarly, Moffat et al. (2007) found that across younger and older participants, MWMT performance was associated with the volume of the caudate nucleus, and prefrontal gray and white matter, but not the hippocampus. However, when each age group was analysed separately, Moffat et al. (2007) found that virtual MWMT performance was associated with hippocampal volume only among younger adults, but not older adults. Therefore, it is possible that older adults' preference for a striatal-dependent response strategy attenuated the association between navigation performance and hippocampal volume.

Interestingly, frequently performing navigation tasks that require allocentric knowledge has been found to protect the hippocampus from age-related volume loss. Lövdén et al. (2012) asked participants walking on treadmills to locate target enclosures in a virtual zoo surrounded by distal landmarks. Participants completed training sessions every other day, with novel zoo environments of varying complexity used both within and between training sessions to encourage allocentric learning throughout the four month study. fMRI and diffusion tensor imaging measurements revealed that both younger and older participants' hippocampal volume remained stable over the course of the experiment and the following four months, while hippocampal volume decreased for age-matched control groups.

In summary, several studies suggest that the vulnerability of the hippocampus to age-related volume loss contributes to older adults' difficulties with the formation and use of cognitive maps, and the employment of allocentric place strategies.

### 7.8.3. Hippocampal Place Cells

In addition to structural change, the hippocampus is also susceptible to age-related physiological changes that may contribute to age differences in wayfinding ability. However, as the procedures to investigate these changes are particularly invasive, research has primarily been conducted with mammalian species. For example, rodent studies have provided the basis for investigating age differences in the characteristics of hippocampal place cells, which are pyramidal neurons that respond selectively when a mammal is in a specific region of a learned environment, known as a place field (Ekstrom et al., 2003; Muller, Kubie & Rancke, 1987; O'Keefe & Dostrovsky, 1971). As place cell activity is relatively unaffected by one's orientation, place fields are thought to correspond with an allocentric representation of a known environment i.e. a cognitive map. Therefore, age differences in the properties of place cells provide insight into age-related wayfinding difficulties. For example, when comparing hippocampal place cell activity between familiar and novel environments, the differences observed in the spatial firing patterns of young rats were reduced or absent in aged rats (Wilson, Ikonen, Gallagher, Eichenbaum & Tanila, 2005; Wilson et al., 2003). These findings suggest that as a consequence of place cell rigidity – which is when the same spatial representation is applied across different environments – aged rats did not generate new a spatial representation (i.e. re-map) in response to environmental changes. Furthermore, Wilson et al. (2004) found that aged rats required more experience of a novel environment than young rats to develop new spatial representations. Similarly, Barnes, Suster, Shen and McNaughton (1997) compared place cell activity between the first and second exposure to a novel environment, and found highly similar place field maps for young rats, and completely different place field arrangements in a subset of aged rats, suggesting that failure to retrieve the correct cognitive map may contribute to age-related deficits in learning new environments. Wilson et al. (2004) also found that in contrast to young and aged rats that performed well in a MWMT, the place fields of MWMT impaired aged rats failed to rotate relative to the displacement of several cues located on the arena walls. A further experiment revealed that aged rats' place fields did not rotate initially, but occasionally rotated correctly thereafter. These findings suggest that age-related deficits in learning new environments may be related to delayed and unstable anchoring of place fields to external cues. Furthermore, even in learned environments, aged rats are less likely than younger rats to re-map in response to a number of cue-related manipulations, including counter-rotating, reconfiguring and removing cues (Tanila, Shapiro & Eichenbaum, 1997a; Tanila, Shapiro, Gallagher & Eichenbaum, 1997).

Research has also demonstrated that the alignment of hippocampal maps with the external environment slows with age. For example, Rosenzweig, Redish, McNaughton and Barnes (2003) found that within a linear track, aged rats were impaired at learning the location of a goal area that maintained a fixed spatial relationship with external cues, but not with the start location, which varied between trials. Interestingly, when rats began traversing the track, their place fields were aligned with the release box at the starting position, whereas towards the end of the journey, their place fields realigned with the external room. This realignment occurred later in aged rats compared to younger rats, and was correlated with learning of the goal area, suggesting that age-related delays in hippocampal map realignment may be associated with age-impaired spatial memory. Finally, in a study conducted by Oler and Markus (2000), rats initially retrieved rewards from a figure eight maze that was subsequently converted to plus maze. Compared to middle-aged rats, the place fields of aged rats were less affected by environmental and task-related differences (the figure eight maze required running laps in either direction, while the plus maze involved visiting different arms by returning to the central junction), suggesting an age-related impairment in responding to changes in environment and task demands.

Taken together, these findings suggest that the effects of aging on the characteristics of hippocampal place cells contribute to a variety of age-related navigation deficits.

### 7.9. Conclusions

In summary, age-related deficits have been identified in a number of wayfinding and navigation abilities. These include sensorimotor deficits, as well as impaired acquisition, integration, and recall of navigationally relevant information. Age-related wayfinding deficits appear to be more pronounced in complex spatial tasks that require allocentric knowledge or processing. Such tasks rely on the hippocampal circuit, which is subject to age-associated structural and physiological changes that have been related to impaired navigational abilities in older adults. For example, age-associated reduction in hippocampal volume has been found to accompany poorer performance in a variety of spatial tasks in several mammalian species, including humans. Furthermore, the characteristics of place cells in the rodent hippocampus change with age, resulting in impaired learning of new environments and the incorrect retrieval and use of cognitive maps.

# CHAPTER 8. Egocentric Route Learning Strategies and Aging

## 8.1. Overview

Learning and following routes are everyday tasks that older adults experience increasing difficulty with as they age. Consequently, older adults often restrict their daily activities to known areas and purposefully avoid unfamiliar environments (Burns, 1999). However, as age-related deficits are more pronounced in tasks that require greater cognitive effort, it is possible that older adults' route learning impairments may vary according to the cognitive demands of different wayfinding strategies. For example, beacon strategy use, which depends solely on the recognition of encoded landmarks, is more parsimonious than associative cue strategy use, which involves recognition-triggered recall of explicit spatial knowledge. Therefore, the purpose of the first experiment presented in this chapter was to investigate the effects of aging on the use of two route learning strategies that differ in cognitive complexity: the egocentric associative cue and beacon response strategies.

Chapter 2 revealed that in general, younger adults were able to alternate between associative cue and beacon-based navigation without incurring switching costs. However, this wayfinding ability may decline with age for a number of reasons. First, older adults are more susceptible to switching costs than younger adults, and second, age is associated with a reduced strategy repertoire (Hodzik & Lemaire, 2011; Kray & Lindenberger, 2000; Wasylyshyn, Verhaeghen & Sliwinski, 2011). Therefore, the aim of the second experiment reported in this chapter was to examine older adults' ability to alternate between associative cue and beacon strategy use while navigating along a route.

As the purpose of this chapter was to investigate the effects of aging on the same navigational abilities examined in Chapter 2, we employed the same tasks described in Chapter 2 to collect data from older adults, and utilised participants' data from Chapter 2 as the younger adult group.

## 8.2. Introduction

Normal cognitive aging is associated with deficits in a number of navigation tasks (see Chapter 7). Consequently, older adults are less confident in their wayfinding abilities and often avoid unfamiliar or novel environments (Burns, 1999; Bryden, Charlton, Oxley & Lowndes, 2010, 2013). While complex navigation tasks such as the development and use of cognitive maps are particularly susceptible to the effects of aging (e.g. Iaria, Palermo, Committeri & Barton, 2009), age-related deficits have also been found in simple, ubiquitous navigation tasks. For example, age differences have been reported in route learning, which involves acquiring sufficient knowledge to repeat a specific path between two points within an environment. In relation to the acquisition of route knowledge, aging is associated with less efficient learning (Jansen, Schmelter & Heil, 2010), recurring navigation errors (Moffat, Zonderman & Resnick, 2001) and impaired evaluation of environmental information (Lipman, 1991). Furthermore, several studies have revealed that compared to younger adults, older adults make more errors during subsequent navigation of learned routes (Cushman, Stein & Duffy, 2008; Meulenbroek, Petersson, Voermans, Weber & Fernández, 2004; Rosenbaum, Winocur, Binns & Moscovitch, 2012; Wilkniss, Jones, Korol, Gold & Manning, 1997; Zakzanis, Quintin, Graham & Mraz, 2009).

The difficulties older adults experience with tasks that require a cognitive map have been attributed to age-related deficits in the use of allocentric place strategies (e.g. Driscoll, Hamilton, Yeo, Brooks & Sutherland, 2005; Newman & Kaszniak, 2000). Allocentric strategy use involves processing the spatial relationship between multiple cues, and supports flexible navigation in familiar environments e.g. planning and traversing new paths between known locations. However, age differences in allocentric strategy use do not account for older adults' difficulties with route learning and navigation, which are tasks typically completed with the use of egocentric response strategies (Hartley, Maguire, Spiers & Burgess, 2003). Egocentric strategy use involves encoding spatial information relative to one's body, resulting in uni-directional spatial knowledge that supports the navigation of learned paths. Therefore, age-related deficits in route learning and navigation suggest that aging also affects older adults' use of egocentric response strategies. However, to our knowledge, no study has explicitly examined how the use of different egocentric strategies changes with age. Therefore, the purpose of this chapter was to investigate the use of egocentric strategies across the adult lifespan.

In object-rich environments, two different landmark-based egocentric response strategies can be employed to successfully learn a route. Associative cue-based learning involves relating an explicit directional behaviour with a landmark located at a wayfinding decision point, forming a stimulus-response pair (e.g. 'Turn left at the supermarket'; Tlauka & Wilson, 1994). Recognition of the encoded landmark during subsequent route navigation triggers the retrieval and execution of the stored response, resulting in accurate navigation at a decision point. In contrast, beacon-based learning involves encoding landmarks that spatially correspond with movement through a decision point. Subsequent perception of an encoded landmark activates a fixed behavioural action that is performed relative to the landmark's position (e.g. 'Move/turn towards the church'; Waller & Lippa, 2007). Interestingly, in a route learning task completed by younger adults, Waller and Lippa (2007) found an accuracy and learning advantage when participants employed a beacon strategy compared to an associative cue strategy, which was attributed to differences in the route knowledge required to employ each strategy. Associative cue-based navigation is functionally equivalent to cued recall, and requires at least two items of spatial knowledge to support navigation at each decision point: the identity of a landmark and an explicit directional response. In contrast, the same behavioural action is executed each time an encoded landmark is recognised during beacon-based navigation (e.g. ‘Turn towards …’). Therefore, beacon strategy use is equivalent to item recognition, as only knowledge of the beacon landmark is required to support navigation at each decision point. As such, beacon strategy use is less cognitively demanding than associative cue strategy use, and therefore better facilitates route learning.

The primary aim of this study was to investigate the effects of aging on associative cue and beacon response strategy use (Experiment 1). As beacon-based learning is more efficient than associative cue-based learning, we predicted an age-independent navigation accuracy and route learning advantage for beacon strategy use over associative cue strategy use, replicating the findings reported by Waller and Lippa (2007). Furthermore, we expected the differences between associative cue and beacon-based learning to be more pronounced in older adults than in younger adults, as aging is known to differentially affect associative memory –which is required to employ an associative cue strategy – and item memory – which is involved in beacon strategy use (Bastin et al., 2013; Old & Naveh-Benjamin, 2008). Specifically, age-related decrements are greater in cued recall tasks than in item recognition tasks (Craik & McDowd, 1987; Ratcliff, Thapar & McKoon, 2011), which may reflect i) the increased difficulty older adults experience with more cognitively demanding tasks (Salthouse, 1992), or ii) age-related deficits in associative binding and retrieval (Naveh-Benjamin, 2000).

The secondary aim of this study was to investigate age differences in strategy choice and switching (Experiment 2). Specifically, we asked participants to complete a route learning task that could be solved either entirely with the use of an associative cue strategy, or by selectively employing an associative cue or beacon strategy at different decision points. Compared to using an associative cue strategy to learn the entire route, the advantage gained by employing the more effective beacon strategy at selected decision points may motivate participants to alternate between different strategies within the same route. However, compared to employing a single strategy, alternating between different strategies requires more cognitive effort, and typically incurs switching costs that affect task accuracy and response times (see Kiesel et al., 2010; Monsell, 2003 for reviews). In Chapter 2, we found that young adults elected to employ different strategies at different decision points, and did not incur any switching costs. Specifically, the efficacy of associative cue and beacon-based learning did not decrease as a result of being used in conjunction to learn a single route, and the accuracy and learning advantage for beacon strategy use over associative cue strategy use was still evident. However, it is possible that older adults may perform this task differently to younger adults due to age-related variations in strategy choice (see Lemaire, 2010 for a review). For example, aging is associated with the use of fewer strategies to complete tasks (Hodzik & Lemaire, 2011), suggesting that in contrast to younger adults' selective use of two route learning strategies, older adults may instead rely on a single strategy. Furthermore, as older adults are more susceptible to switching costs than younger adults (Kray & Lindenberger, 2000; Wasylyshyn, Verhaeghen & Sliwinski, 2011), they may elect to employ an associative cue strategy throughout the route rather than incur performance-related decrements associated with strategy switching. Taken together, these age differences suggest that in contrast to younger adults, older adults may employ a single wayfinding strategy to learn an entire route.

Finally, we examined age differences in the route and environmental knowledge associated with landmarks during route learning. Given that older adults experience difficulty with cued recall, we expected to find age-related deficits in the explicit directional knowledge paired with landmarks during associative cue strategy use. Interestingly, our previous study involving younger adults revealed that during beacon-based learning, participants associated directional route knowledge with landmarks, and learned the position of objects at decision points. Given that such knowledge is not required for beacon-based navigation, participants either encoded strategy-irrelevant spatial knowledge intentionally or automatically. However, it was beyond the scope of the experiments conducted in Chapter 2 to differentiate between these two alternatives. In this chapter, analysis of older adults' route and environmental knowledge may provide insight into how strategy-irrelevant spatial knowledge is acquired. Acquiring such knowledge intentionally would involve associative learning, which is known to deteriorate with age. Therefore, we would expect older adults to have poorer strategy-irrelevant knowledge than younger adults. However, if age-related deficits in associative cue strategy use (i.e. intentional associative learning) were not accompanied by age differences in strategy-irrelevant knowledge, we could infer that such information was encoded automatically, as unlike intentional processes, automatic processes are typically not influenced by aging (Hasher & Zacks, 1979).

## 8.3. Experiment 1

The primary goals of Experiment 1 were to investigate the effects of aging on i) the efficacy of associative cue and beacon-based route learning, and ii) the route and environmental knowledge acquired during associative cue and beacon strategy use.

### 8.3.1. Method

**Participants.** Eighty participants [44 young adults (25 females, mean age = 20.20, *SD* = 2.39) and 36 older adults (19 females, mean age = 74.11, *SD* = 5.63)] took part in the study. Data collected in the first experiment of Chapter 2 was used for the younger adult group. All participants were screened for mild cognitive impairment (MCI) using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005). No participants were excluded according to a recommended cut-off score for MCI of 23 (Luis, Keegan & Mullan, 2009).

**Materials and Apparatus.** The route learning task was presented in a virtual environment rendered in Vizard 3.0 (WorldViz). The route in each condition consisted of 18 intersections (nine left turns, nine right turns), each of which contained two unique landmarks. In the Associative Cue condition, landmarks were suspended from the centre of the ceiling in a vertical arrangement, while in the Beacon condition, landmarks were positioned on either side of an intersection (See Figure 20). The experiment was presented on a 22” LCD monitor with a resolution of 1680x1050 and a screen refresh rate of 120Hz. A standard computer keyboard was used to record responses.

**Figure 20.** Decision points designed to encourage different types of egocentric strategy use. Left: An Associative Cue intersection. Participants must associate a movement direction with a single landmark to learn the route through the intersection. Right: A Beacon intersection. The most efficient method of learning the route is to encode the landmark that spatially coincides with route movement, and turn towards the encoded landmark during subsequent navigation.

**Procedure**. Participants were assigned randomly to either the Associative Cue or Beacon condition, and completed four tasks that assessed route and environmental knowledge in the following order (see Figure 21).

***Route Learning Task.*** Participants completed six experimental blocks, each of which consisted of a separate training and test phase. During each training phase, participants were passively transported along a route that they were asked to learn. In the Associative Cue condition, two landmarks were suspended from the centre of each intersection (See Figure 20). Successfully learning the route through each intersection involved associating an explicit directional response with a specific landmark (e.g. ‘Turn right at the teddy bear’ in Figure 20) i.e. associative cue-based learning. In the Beacon condition, landmarks were attached to each side of an intersection. While participants could rely on an associative cue strategy to support route learning, the most efficient wayfinding strategy available involved encoding the landmark that spatially coincided with route movement, and executing a general behavioural action relative to its observed position during subsequent navigation (e.g. ‘Turn towards the clothes peg’ in Figure 20) i.e. beacon strategy use. Following each training phase, participants’ completed a test phase that involved navigating through each route intersection in a random order. Participants were passively transported to the centre of each intersection, and asked to indicate the direction in which the route proceeded by pressing the left or right arrow key on the keyboard provided. Any responses made more than two seconds after movement terminated were not recorded.

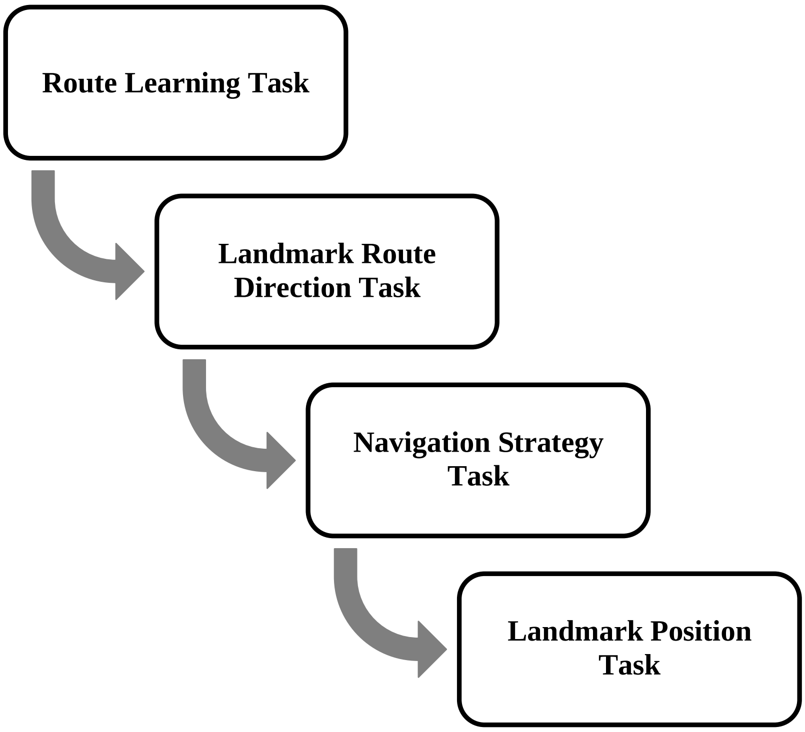


**Figure 21.** Task order. Participants first completed the *Route Learning Task*, which consisted of six experimental blocks. This was followed by the *Landmark Route Direction Task*, the *Navigation Strategy Task*, and finally, the *Landmark Position Task*.

***Landmark Route Direction Task.*** The purpose of this task was to assess the directional route knowledge associated with landmarks during learning. Each individual landmark from the learned route was presented to participants in a random order. Participants were asked to indicate whether the route continued left or right at the intersection containing the presented landmark. Participants made their responses by pressing the left or right arrow keys on the keyboard provided.

***Navigation Strategy Task.*** The purpose of this task was to determine the strategy employed by participants in the Beacon condition. The *Navigation Strategy Task* consisted of a single test phase from the *Route Learning Task,* and featured three probe intersections in which the positions of the two unique landmarks were switched. The positions of the landmarks at the remaining fifteen intersections were unchanged (stable intersections). Responses at the probe intersections were used to determine the route learning strategy employed by participants in the Beacon condition. Compared to navigation at the same intersection in the final block of the *Route Learning Task* (block 6), a different movement response at probe intersections in the *Navigation Strategy Task* (block 7) corresponds with beacon strategy use, as only beacon-based navigation would be affected by differences in landmark position between tasks. In contrast, identical responses at probe intersections in the *Navigation Strategy Task* and the same intersection in block 6 of the *Route Learning Task* is indicative of associative cue strategy use, as the location of an encoded landmark does not affect the content of the explicit directional response retrieved during associative cue-based navigation. To ensure that participants in both conditions followed an identical experimental procedure, participants in the Associative Cue condition completed an associative cue variant of the *Navigation Strategy Task* in which the position of the vertically arranged landmarks were switched at selected intersections.

***Landmark Position Task.*** The purpose of this task was to assess the environmental knowledge acquired by participants during learning. Participants were presented with each individual landmark from the route in a random order, and asked to indicate its position within the respective intersection. Participants in the Associative Cue condition were asked whether the presented landmark was the uppermost or lowermost landmark at an intersection, while participants in the Beacon condition indicated whether the presented landmark was located on the left or right side of an intersection. Participants made their responses by pressing the corresponding arrow key on the keyboard provided. It is important to note that landmarks at probe intersections in the *Navigation Strategy Task* were excluded from this task, as their environmental position varied across the preceding tasks.

Responses were recorded for each task, and participants did not receive any feedback about the accuracy of their responses.

### 8.3.2. Results

Two older adults were excluded from the experiment due to difficulty comprehending the tasks and failure to report movement decisions within the time window. The remaining thirty-four older participants (17 females, mean age = 74.03, *SD* = 5.68) entered the final analysis.

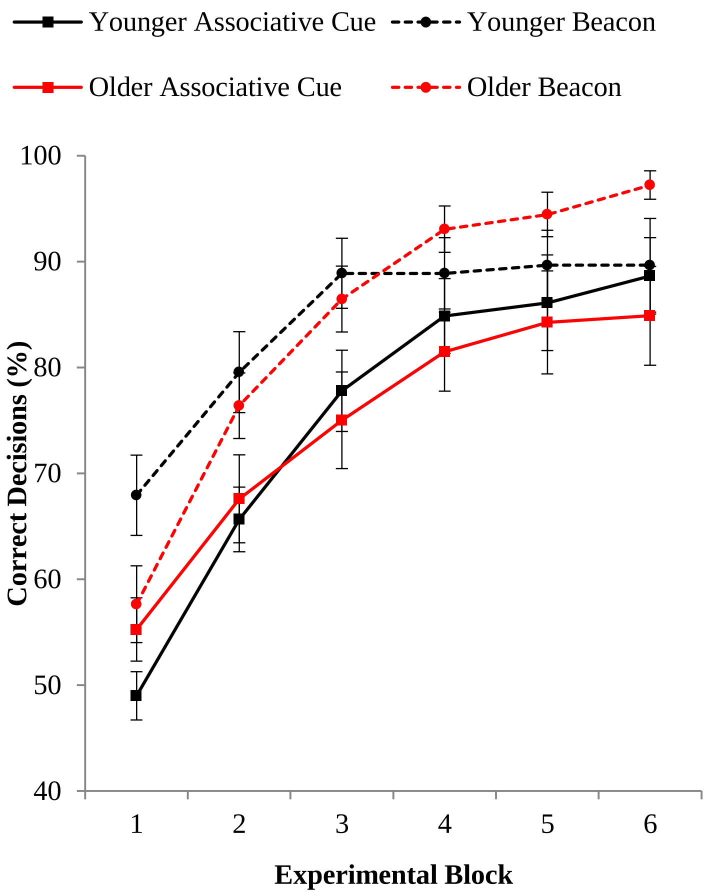


**Figure 22.** Younger and older adults' navigation accuracy across blocks by condition (mean±standard error).

***Route Learning Task.*** Participants chose the correct movement direction in 75% of test trials in the Associative Cue condition (younger: 75.3%, older: 74.7%), and 84.1% of test trials in the Beacon condition (younger: 84.1%, older: 84.2%). An ANOVA with experimental block [1-6] as a within-participants factor, and condition [Associative Cue, Beacon] and age [Younger, Older] as between-participants factors revealed that navigation accuracy improved over the course of the experiment from 57.6% in the first block to 89.8% in the sixth block (main effect of block: $F(2.90, 214.66) = 126.63$, $p < .001$, $\eta_p^2 = .63$), and that participants in the Beacon condition performed better than participants in the Associative Cue condition (main effect of condition: $F(1, 74) = 8.85$, $p = .004$, $\eta_p^2 = .11$). Interestingly, no main effect of age was found ($p = .94$; see Figure 22), suggesting that younger and older adults performed similarly. Furthermore, no significant two-way interactions were found (all $p > .05$), although the three-way block x condition x age interaction was significant [$F(2.90, 214.66) = 5.23$, $p = .002$, $\eta_p^2 = .07$]. To interpret this interaction, separate ANOVAs were conducted for each participant group with experimental block as a within-participant factor and condition as a between-participant factor. While a significant block x condition interaction [$F(2.47, 103.83) = 4.66$, $p = .007$, $\eta_p^2 = .10$] revealed that younger adults reached ceiling level performance earlier in the Beacon condition than in the Associative Cue condition (see Chapter 2 for a more detailed analysis), no such interaction was found for older adults ($p = .368$), suggesting that the advantage for beacon-based learning over associative cue-based learning is age-dependent.

***Landmark Route Direction Task.*** The percentage of trials in which participants correctly chose the route direction associated with a landmark was used as the dependent variable in the following analysis. One sampled *t*-tests against chance level (50%) revealed that younger and older adults associated directional route knowledge with individual landmarks in both the Associative Cue (younger: 82.5%, older: 76.4%) and Beacon conditions (younger: 75.1%, older: 73%) (all $p < .001$). Furthermore, an ANOVA with condition [Associative Cue, Beacon] and age group [Younger, Older] as between-participants variables and performance as the dependent variable did not reveal any main effects or an interaction (all $p > .05$). Taken together, these findings suggest that irrespective of age or condition, participants associated explicit directional knowledge with landmarks during route learning.

***Navigation Strategy Task.*** The dependent variable used in the following analysis was the percentage of responses made in the three probe trials that differed from navigation in block 6 of the *Route Learning Task.* One sampled *t*-tests against chance level (50%) revealed that both younger (86.4%) and older (76%) adults responded differently when the position of landmarks at probe intersections had been switched (both $p < .01$), suggesting that participants in both age groups employed a beacon response strategy in the Beacon condition. Furthermore, an independent samples *t*-test found that younger and older adults' behaviour in probe trials did not differ significantly, suggesting that beacon strategy use was similarly prevalent in both age groups ($p > .05$). Taken together, these results suggest that younger and older adults did not differ in their preference for a beacon strategy in the Beacon condition.

***Landmark Position Task.*** The percentage of trials in which participants correctly identified the position of a landmark at a decision point was used as the dependent variable in the following analysis. One sampled *t*-tests against chance level (50%) revealed that younger and older adults acquired knowledge of landmark position in both the Associative Cue (younger: 92%, older: 88.1%) and Beacon conditions (younger: 90.6%, older: 91.2%) (all $p < .001$). Furthermore, an ANOVA with condition [Associative Cue, Beacon] and age group [Younger, Older] as between-participants variables and performance as the dependent variable did not reveal any main effects or an interaction (all $p > .05$). Taken together, these findings suggest that irrespective of age, participants acquired knowledge of landmark position to a similar extent in both the Associative cue and Beacon conditions.

### 8.3.3. Discussion

The purpose of this experiment was to investigate the effects of aging on the efficacy of associative cue and beacon-based route learning. Associative cue and beacon response strategy use depend on associative and item memory respectively. As associative memory is more vulnerable to the effects of aging than item memory (Old & Naveh-Benjamin, 2008), we expected age-related deficits to be more pronounced during associative cue strategy use than beacon strategy use. Interestingly, the results of the *Route Learning Task* revealed that aging has little effect on the use of either egocentric response strategy. Wayfinding accuracy during both associative cue and beacon-based navigation did not differ between age groups, with beacon strategy use supporting route navigation better than associative cue use (Waller & Lippa, 2007). However, the learning advantage for beacon strategy use over associative cue strategy use observed in the younger adult group was not found in the older adult group, suggesting that aging eliminates the learning differences between associative cue and beacon strategy use. Taken together, these results suggest that egocentric strategy use may be resistant to age-related memory deficits, which contrasts with several studies that report route learning difficulties in older adults (Cushman et al., 2008; Meulenbroek et al., 2004; Wilkniss et al., 1997; Zakzanis et al., 2009).

Analysis also revealed that both younger and older adults associated explicit directional information with landmarks during associative cue and beacon-based learning. While such knowledge is required to successfully employ an associative cue strategy, beacon strategy use relies only on landmark knowledge. Therefore, participants acquired sufficient knowledge to employ both egocentric strategies during beacon-based learning, which may be related to the parallel or sequential acquisition of spatial knowledge required for different wayfinding strategies (Iglói, Zaoui, Berthoz & Rondi-Reig, 2009; Packard & McGaugh, 1996; Wang, Mou & Sun, 2014). Finally, participants in both age groups acquired strategy-irrelevant knowledge of landmark position during associative cue and beacon strategy use. As landmark location does not inform the spatial decision making process involved in either associative cue or beacon-based navigation, it is possible that such knowledge was acquired either i) automatically during wayfinding (Pouliot & Gagnon, 2005), ii) as a result of increasing experience with the route learning environment (Montello, 1998), or iii) in order to support a wayfinding strategy that depends on knowledge of landmark position i.e. an allocentric strategy. Taken together, these results reveal that, irrespective of age, participants acquired strategy-relevant and irrelevant spatial knowledge during associative cue and beacon-based learning. Finally, as we did not find age-related decrements in associative learning during route acquisition (i.e. associative cue strategy use), we were unable to determine whether participants intentionally or automatically encoded strategy-irrelevant spatial knowledge.

## 8.4. Experiment 2

Research has revealed that normal cognitive aging is associated with the use of fewer strategies to complete tasks, and a reluctance to expend the cognitive effort required to switch between different strategies (Hodzik & Lemaire, 2011; Kray & Lindenberger, 2000; Wasylyshyn et al., 2011). Therefore, the aim of Experiment 2 was to examine age differences in wayfinding strategy choice and switching. Specifically, we asked participants to complete a route learning task that could be solved by i) exclusively employing an associative cue strategy, or ii) alternating between associative cue and beacon-based learning at different decision points.

### 8.4.1. Method

**Participants.** Forty-one participants [22 young adults (11 females, mean age = 20.23, *SD* = 2.67) and 19 older adults (8 females, mean age = 72.16, *SD* = 6.79)] took part in the study. Data collected in the second experiment of Chapter 2 was used for the younger adult group. No participants were excluded according to a recommended MoCA cut-off score for MCI of 23.

**Materials, Apparatus and Procedure.** The materials, apparatus and procedure for Experiment 2 were similar to those for Experiment 1 with minor modifications made to the virtual environment in the *Route Learning* and *Navigation Strategy Tasks* to allow the use of different wayfinding strategies at different decision points. First, all participants were asked to learn the same 18 intersection route, which consisted of nine Associative Cue intersections and nine Beacon intersections (see Figure 20) distributed in a random order along the route. Second, in the *Navigation Strategy Task*, landmarks were switched at two Associative Cue and two Beacon intersections. While only an associative cue strategy was available to support learning at Associative Cue intersections, participants were able to learn the route at Beacon intersections by employing either a beacon or associative cue strategy. Therefore, participants could either employ a single wayfinding strategy at all decision points i.e. an associative cue strategy, or alternate between associative cue and beacon strategy use throughout the route. In order to determine how participants learned the route, strategy choice at probe Beacon intersections was assessed in the *Navigation Strategy Task*. Specifically, behaviour that corresponds with beacon strategy use also suggests that participants alternated between different route learning strategies, while associative cue-based navigation at probe Beacon intersections is consistent with use of a single strategy to learn the entire route.

### 8.4.2. Results

Two older adults were excluded from the experiment as they failed to report their movement decisions within the allotted time period. The remaining seventeen older participants (7 females, mean age = 71.65, *SD* = 6.50) entered the final analysis.

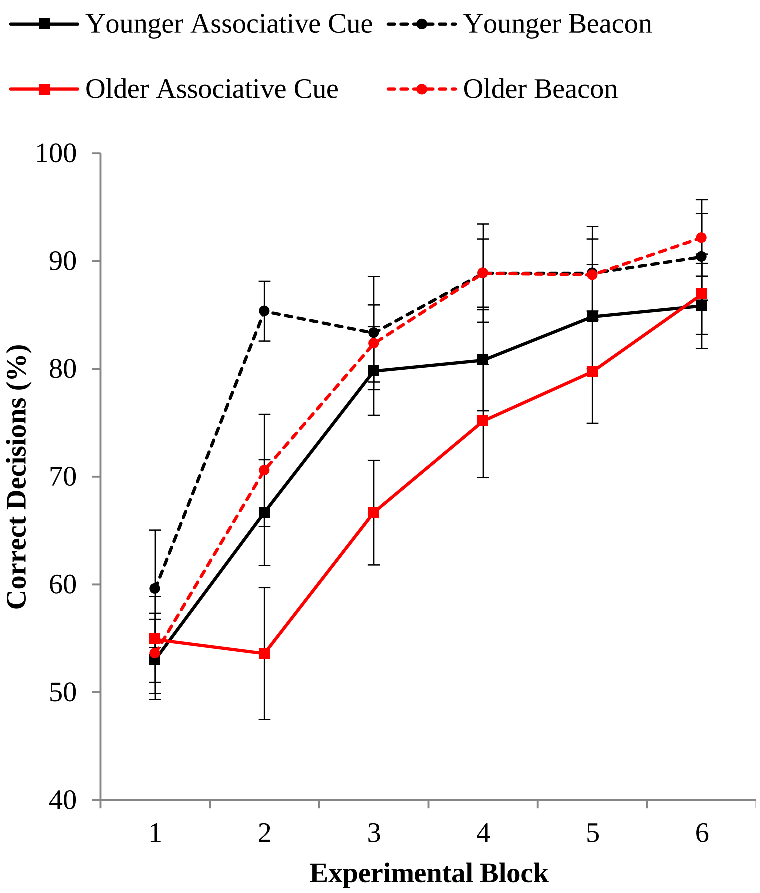


**Figure 23.** Younger and older adults' navigation accuracy over blocks by intersection type (mean±standard error).

***Route Learning Task.*** Participants correctly identified the direction in which the route originally continued at 72.3% of Associative Cue intersection test trials (younger: 75.2%, older: 69.5%), and 81.1% of Beacon intersection test trials (younger: 82.7%, older: 79.4%). A 6 x 2 x 2 ANOVA with experimental block [1-6] and intersection type [Associative Cue, Beacon] as within-participants factors, and age [Younger, Older] as a between-participants factor revealed that performance improved over the course of the experiment from 55.4% in the first block to 88.7% in the sixth block (main effect of block: $F(3.21, 118.85) = 61.04$, $p < .001$, $\eta_p^2 = .62$), and participants performed better at Beacon intersections than Associative Cue intersections (main effect of intersection type: $F(1, 37) = 24.84$, $p < .001$, $\eta_p^2 = .40$) (see Figure 23). However, no main effect of age was found ($p = .35$). Furthermore, the block x intersection type [$F(4.07, 150.73) = 3.97$, $p = .004$, $\eta_p^2 = .01$] and block x age [$F(3.21, 118.85) = 2.75$, $p = .042$, $\eta_p^2 = .07$]

interactions were significant, suggesting that participants' performance over the course of the experiment differed between age groups and intersection types. All other interactions were non-significant ($p > .05$). Post-hoc analysis revealed that participants’ performance reached ceiling level performance in block 5 at Associative Cue intersections and in block 4 at Beacon intersections, demonstrating a learning advantage for beacon strategy use over associative cue strategy use. Furthermore, younger and older adults reached ceiling level performance in the third and fifth blocks respectively, suggesting that age is associated with less efficient learning.

***Landmark Route Direction Task.*** The percentage of trials in which participants correctly chose the route direction associated with a landmark was used as the dependent variable in this analysis. One sampled *t*-tests against chance level (50%) revealed that younger and older adults associated directional route knowledge with individual landmarks at both Associative Cue (younger: 76%, older: 73.4%) and Beacon intersections (younger: 77.9%, older: 83.6%) (all $p < .001$). Furthermore, an ANOVA with and age group [Younger, Older] as a between-participants variable, intersection type [Associative Cue, Beacon] as a within-participants variable and performance as the dependent variable revealed a main effect of intersection type [$F(1, 37) = 7.45$, $p =.01$, $\eta_p^2 = .17$], but no significant main effect of age or an interaction (both $p > .05$). Taken together, these results suggest that participants were more likely to associate knowledge of route direction with landmarks at Beacon intersection than at Associative Cue intersections.

***Navigation Strategy Task.*** The percentage of participants' responses at Beacon intersection probe trials that differed from navigation in block 6 of the *Route Learning Task* was used as the dependent variable in the following analysis. Separate one-sampled *t*-tests against chance level (50%) revealed that younger adults’ responded differently in probe trials ($M = 65.9\%$, $SD = 35.81$; $p = .05$), while older adults' did not exhibit a bias for either changing or repeating the response made in block 6 of the *Route Learning Task* ($M = 50\%$, $SD = 46.77$; $p > .05$). Given that stable and changing responses are indicative of associative cue and beacon strategy use respectively, this finding suggests that younger adults primarily alternated between associative cue and beacon strategy use during navigation. Older adults, in contrast, did not exhibit a specific preference for either alternating between different strategies or employing a single strategy (i.e. an associative cue strategy) throughout the route. Interestingly, an independent samples *t*-test revealed that the prevalence of beacon strategy use at Beacon intersections did not differ between age groups ($p > .05$), suggesting that younger and older adults’ strategy repertoires did not differ. Therefore, age-related variations in strategy choice during navigation cannot be attributed to age differences in strategy repertoires.

***Landmark Position Task.*** The percentage of trials in which participants correctly identified the position of a landmark was used as the dependent variable in the following analysis. One sampled *t*-tests against chance level (50%) revealed that younger adults acquired knowledge landmark position at both Associative Cue (76%) and Beacon intersections (88%) (both $p < .001$). In contrast, older adults' knowledge of landmark position exceeded chance level at Beacon intersections (85.3%) ($p < .001$), but not at Associative Cue intersections (56.7%) ($p = .479$). An ANOVA with age group [Younger, Older] as a between-participants variable, intersection type [Associative Cue, Beacon] as a within-participants variable, and performance as the dependent variable revealed a main effect of intersection type [$F(1, 37) = 29.46$, $p <.001$, $\eta_p^2 = .44$] and an age x intersection type interaction [$F(1, 37) = 4.90$, $p =.03$, $\eta_p^2 = .12$], but no main effect of age ($p =.106$). These findings suggest that participants acquired better knowledge of landmark position at Beacon intersections than Associative Cue intersections, and that younger and older adults' knowledge of landmark position differed between intersection types. However, post-hoc analysis did not reveal any age differences in participants' knowledge of landmark position at either Associative Cue or Beacon intersections (both $p > .05$).

### 8.4.3. Discussion

Experiment 2 investigated the effects of aging on the prevalence of strategy switching during route learning. Both younger and older adults completed a route learning task in which participants could either i) employ an associative cue strategy to learn the entire route, or ii) switch between an associative cue and beacon strategy throughout the route. While alternating between different strategies allows participants to employ the most effective strategy at each decision point, switching strategies is associated with cognitive costs that negatively affect accuracy and response times. As such, participants may prefer to conserve cognitive resources and employ a single strategy to learn the route. Previously, younger adults completed the task by alternating between associative cue and beacon-based navigation (see Chapter 2), suggesting that the benefits of employing a more effective route learning strategy at selected decision points (i.e. a beacon strategy rather than an associative cue strategy) outweighed the cognitive costs associated with switching strategies. However, as aging is associated with reduced strategy repertoires and increased vulnerability to switching costs (Hodzik & Lemaire, 2011; Kray & Lindenberger, 2000; Wasylyshyn et al., 2011), we predicted that older adults were less likely to alternate strategies than younger adults. Analysis of the *Route Learning Task* revealed that regardless of the optimal strategy available at an intersection (either an associative cue or beacon strategy), navigation accuracy did not differ between age groups. Furthermore, both younger and older participants learned the route more effectively at decision points designed to elicit beacon strategy use than at intersections that required the use of an associative cue strategy. Taken together, these findings suggest that i) both younger and older adults alternated between different strategies to complete the task, and ii) age was not associated with more pronounced switching costs.

However, a number of interesting findings may be indicative of both age differences in strategy choice and age-dependent switching costs. For example, analysis of participants' strategy preferences in the *Navigation Strategy Task* revealed that in contrast to younger adults, older adults did not exhibit a specific bias for either alternating between strategies or employing a single strategy to learn the route. Interestingly, the prevalence of beacon strategy use did not differ significantly between age groups, suggesting that both younger and older adults were similarly able to employ a beacon strategy. Given that aging did not affect navigation accuracy at decision points that required the use of an associative cue strategy, these findings suggest that older adults' strategy choices cannot be explained by an age difference in strategy repertoires. Indeed, as there were no notable age differences in strategy choice in Experiment 1, the age-related variations in strategy preference found in this experiment are task-dependent. That is, the cognitive demands associated with the most effective approach to learning the route (i.e. alternating strategies) may have differentially influenced younger and older adults' strategy preference.

In addition, there is some evidence to suggest that switching costs increased with age. For example, in the *Route Learning Task*, younger adults reached ceiling level performance earlier than older adults at both Associative Cue and Beacon intersections. In contrast to age differences at Beacon intersections, age-related deficits in learning efficiency at Associative Cue intersections cannot be attributed to differences in strategy choice, as no other landmark-based wayfinding strategy is available to support learning at Associative Cue intersections. Given that there were no learning differences between younger and older adults in the Associative Cue condition in Experiment 1, this age-related learning deficit is task-dependent. That is, as participants in Experiment 1 employed a single strategy to learn the route, age differences in reaching ceiling level performance in this experiment are most likely associated with strategy switching. Therefore, alternating between different wayfinding strategies incurs age-related switching costs that affect older adults' ability to learn routes efficiently. Finally, both age-groups associated directional route knowledge with individual landmarks at Associative Cue and Beacon intersections. However, while both younger and older adults learned the position of landmarks during beacon strategy use, only younger adults acquired strategy-irrelevant knowledge of landmark location during associative cue-based learning. As older adults also learned the position of landmarks during associative cue strategy use in Experiment 1, these findings can again be attributed to switching costs, which have a greater effect on i) older adults, ii) the more cognitively demanding route learning strategy, and iii) strategy-irrelevant learning.

## 8.5. General Discussion

Several studies investigating the effects of aging on route learning have reported age-related deficits in both the acquisition and subsequent use of route knowledge (Cushman et al., 2008; Jansen et al., 2010; Lipman, 1991; Moffat et al., 2001; Meulenbroek et al., 2004; Rosenbaum et al., 2012; Wilkniss et al., 1997; Zakzanis et al., 2009). These findings suggest that older adults experience difficulty with employing route learning strategies effectively. Therefore, the primary purpose of this chapter was to investigate the effects of aging on the use of landmark-based egocentric strategies for route learning. Specifically, the efficacy of associative cue and beacon strategy use was assessed across the adult lifespan in two separate route learning tasks. Analysis of participants’ navigation performance in both tasks revealed few age differences, suggesting that associative cue and beacon-based route learning does not change significantly with age. This finding conflicts with studies that report increased route learning difficulties with age, and suggests that the spatial processes involved in associative cue and beacon strategy use are not subject to well-established age-related cognitive deficits. In Experiment 1, analysis revealed that the efficacy of associative cue and beacon-based learning was largely unaffected by normal cognitive aging, with only the learning advantage for beacon strategy use over associative cue use eliminated with age. Furthermore, strategy irrelevant spatial knowledge was acquired by both younger and older adults during associative cue and beacon-based learning. Specifically, participants learned the position of landmarks irrespective of the strategy employed, and associated explicit route direction knowledge with individual landmarks during beacon-based learning. Given that we expected age-related difficulties with associative learning to impair specific elements of older adults' route and environmental knowledge, the results of Experiment 1 suggest that learning in this paradigm was not affected by age-related deficits in associative memory. Experiment 2 revealed that navigation accuracy did not differ between age groups when performing a route learning task that could be best completed by alternating between associative cue and beacon-based navigation at different decision points. While this finding suggests that younger and older adults performed the task similarly, age differences found in other measures of spatial learning may be related to the cognitive costs associated with switching strategies. First, younger adults primarily adopted the optimal strategy at each decision point, and therefore switched strategies during navigation. In contrast, older adults did not exhibit a preference for either the optimal approach of alternating strategies, or the less effective – albeit adequate – approach of employing an associative cue strategy throughout the route. Older adults' strategy preference may have varied as age is associated with increased vulnerability to switching costs. Therefore, some older adults may have chosen to employ a single wayfinding strategy throughout the route rather than incur accuracy and response time costs related to strategy switching. Second, older adults reached ceiling level performance later than younger adults, and failed to acquire knowledge of landmark position during associative cue-based learning. Given that no underlying age differences in spatial learning were found when participants employed a single wayfinding strategy to learn a route (Experiment 1), these results suggest that older adults were more susceptible to switching costs than younger adults.

Associative cue and beacon-based learning rely on associative and item memory respectively. As such, beacon strategy use is less demanding than associative cue strategy use, and supports faster route learning and more accurate navigation (Waller & Lippa, 2007). Given that associative memory is more vulnerable to the effects of aging than item memory (Bastin et al., 2013; Old & Naveh-Benjamin, 2008), we expected age-related route learning deficits to be more pronounced during associative cue strategy use than beacon strategy use. However, Experiment 1 revealed that aging did not have a pronounced effect on the use of either egocentric strategy. Indeed, only the advantage for beacon over associative cue-based learning observed in the younger participant group was found to be age-dependent. Taken together, these results suggest that landmark-based route learning may be largely resistant to the deleterious effects of aging. This finding contrasts with many studies that report an age-related decline in route learning ability, which may be explained by differences in testing protocol. In many studies, participants are asked to navigate through decision points in the same order experienced during learning (e.g. Cushman et al., 2008; Moffat et al., 2001; Meulenbroek et al., 2004; Rosenbaum et al., 2012; Wilkniss et al., 1997; Zakzanis et al., 2009). Participants are therefore able to employ a sequential response strategy, which involves memorising and subsequently executing a number of spatial behaviours in a specific temporal order (e.g. ‘Turn left, turn right, go straight on…’). Successful sequential response strategy use depends on temporal memory, which deteriorates with age (Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995). Therefore, age differences in these route learning studies may reflect age-related difficulties with sequential response strategy use. In contrast, participants in Experiment 1 and 2 were asked to navigate through decision points in a random order during each test phase, preventing the use of a sequential response strategy. As such, participants relied on landmark-based wayfinding strategies to learn the route. Therefore, differences between the findings reported in this chapter and previous research may be explained by differences in wayfinding strategy use. It is also possible that both the screening procedures and environments utilised in different studies may contribute to contrasting findings in age-related route learning research. For example, differences in pre-experimental screening for cognitive impairments may have resulted in older adult groups that vary in route learning capacity. Alternatively, the presence of navigationally irrelevant stimuli (i.e. distractors) in other studies may have impaired older adults' route learning performance. In this experiment, the only distinct features of the route learning environment were the landmarks at each intersection. In contrast, there are many navigationally irrelevant stimuli (e.g. people, vehicles, non-decision point objects) in experiments conducted in both real-world environments and life-like virtual environments (e.g. Cushman et al., 2008; Meulenbroek et al., 2004; Rosenbaum et al., 2012; Wilkniss et al., 1997; Zakzanis et al., 2009). As such, it is possible that age-related difficulties with ignoring distracters (Hasher, Zacks & May, 1999) may also account for older adults' route learning deficits in other studies.

Aging is associated with reduced strategy repertories and increased vulnerability to switching costs (Hodzik & Lemaire, 2011; Kray & Lindenberger, 2000; Wasylyshyn et al., 2011). As both of these factors contribute to age-related variations in strategy choice (see Lemaire, 2010), we expected younger and older adults' strategy preference during route learning to differ when it was more advantageous to alternate between associative cue and beacon-based navigation than to exclusively employ an associative cue strategy. Experiment 2 revealed that younger adults primarily chose to switch strategies while navigating along the route, while older adults did not exhibit a significant preference for either alternating between two strategies or exclusively employing a single wayfinding strategy. Given that participants' strategy repertoires did not change with age, this finding suggests that the cognitive demands associated with the optimal route learning approach (i.e. switching strategies) affected younger and older adults’ strategy choices differently. Furthermore, strategy-related age differences that were found in Experiment 2, but not when participants employed a single wayfinding strategy in Experiment 1, suggest that strategy switching differentially affects younger and older adults. For example, younger adults reached ceiling level performance earlier than older adults, suggesting that strategy switching selectively impaired older adults' ability to learn the route efficiently. Furthermore, during associative cue-based learning, both younger and older adults related directional route knowledge with landmarks, but only younger adults acquired knowledge of landmark position. In contrast, there were no age differences in associating the same spatial knowledge with landmarks during beacon-based learning. Given that associative learning is required to relate both types of spatial information with individual landmarks, it is surprising that only older adults’ knowledge of landmark position during associative cue use is selectively affected by strategy switching. However, it should be noted that associative cue-based learning is more demanding than beacon based-learning, and explicit directional knowledge is essential for associative cue-based navigation, while landmark position is not. Therefore, alternating between different wayfinding strategies incurred switching costs that i) increased with age, ii) affected the more demanding strategy to a greater extent, and iii) first affected strategy-irrelevant processes. Interestingly, while both age-related variations in strategy choice and age-dependent switching costs were found in Experiment 2, older adults’ navigation accuracy did not differ significantly from younger adults’. These age differences may not have influenced navigation accuracy as i) the differences between associative cue and beacon-based navigation accuracy are not substantial enough to reflect subtle differences in strategy preference, and ii) some of the spatial processes subject to age-related switching costs do not inform navigation.

In summary, we conducted two experiments that investigated the effects of aging on the use of landmark-based route learning strategies. In Experiment 1, the only age difference found during associative cue and beacon strategy use concerned the learning efficiency of each egocentric response strategy relative to one another. Therefore, the absence of substantial age differences in Experiment 1 suggests that acquiring and subsequently using route knowledge are resistant to age-related memory deficits. However, Experiment 2 revealed that the demands associated with switching strategies affect younger and older adults’ strategy preferences differently. Specifically, younger adults primarily employed the more complex – and effective – approach of switching strategies between decision points, while older adults did not exhibit a preference for either alternating strategies or employing a single strategy to learn a route. As the cognitive costs associated with strategy switching increase over the lifespan, older adults may find the use of a single strategy more effective than employing different – albeit optimal – strategies at different decision points. Indeed, alternating between two strategies during navigation incurred age-related switching costs that affected older adults’ acquisition of route and environmental knowledge. Most significantly, older adults did not learn the route as quickly as younger adults. In addition, age-related switching costs specifically affected the use of the most demanding strategy, and the acquisition of strategy-irrelevant knowledge.

## 8.6. Summary

In Experiment 1, older adults’ use of the associative cue and beacon response strategies was largely comparable to that of younger adults’. Indeed, an age-related absence of the learning advantage for beacon strategy use over associative cue strategy use was the only difference found between the age groups, suggesting that aging does not influence the use of landmark-based egocentric strategies. Experiment 2, however, found that when alternating between strategies was advantageous to route learning, younger adults’ primarily switched strategies while older adults did not exhibit a preference for either alternating strategies or exclusively employing a single strategy. This finding suggests that the cognitive costs associated with switching between two strategies affects younger and older adults’ strategy choices differently. Interestingly, Harris and Wolbers (2014) recently demonstrated that age-related switching deficits also affect shifts between egocentric and allocentric strategies. In their study, participants learned two routes through a virtual environment, and pointed to unseen landmarks, demonstrating accurate egocentric and allocentric knowledge respectively. However, when asked to navigate between the two routes, older adults were less likely to take novel short-cuts, supporting our findings of an age difference related to strategy switching.

# CHAPTER 9. The Effects of Aging on Route Repetition and Retracing

## 9.1. Overview

Chapter 8 revealed that aging did not impair the use of landmark-based egocentric response strategies for the purposes of learning a route. However, after reaching a target destination, everyday wayfinding often involves a return journey to either the initial start position, or an intermediary location. Successfully retracing a route in the opposite direction requires allocentric processing, as the knowledge acquired during egocentric strategy use is only useful for uni-directional navigation. However, as discussed in Chapter 7, aging is associated with impaired allocentric processing. Therefore, the purpose of the paper summarised in this chapter was to investigate age differences in route repetition and route retracing (see Appendix B).

## 9.2. Paper II

Wiener, J. M., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: effects of cognitive aging. *Frontiers in Aging Neuroscience, 4*(7).

## 9.3. Paper Abstract

Retracing a recently travelled route is a frequent navigation task when learning novel routes or exploring unfamiliar environments. In the present study we utilized virtual environments technology to investigate age-related differences in repeating and retracing a learned route. In the training phase of the experiment participants were guided along a route consisting of multiple intersections each featuring one unique landmark. In the subsequent test phase, they were guided along short sections of the route and asked to indicate overall travel direction (repetition or retracing), the direction required to continue along the route, and the next landmark they would encounter. Results demonstrate age-related deficits in all three tasks. More specifically, in contrast to younger participants, the older participants had greater problems during route retracing than during route repetition. While route repetition can be solved with egocentric response or route strategies, successfully retracing a route requires allocentric processing. The age-related deficits in route retracing are discussed in the context of impaired allocentric processing and shift from allocentric to egocentric navigation strategies as a consequence of age-related hippocampal degeneration.

## 9.4. Theoretical Background

Navigating a novel route is often followed by a return journey which involves retracing the learned route in the opposite direction. Compared to repeating a learned route, route retracing is considered a more complex task for two primary reasons. Firstly, the direction in which a route is learned is integrated into spatial knowledge, with landmark recognition facilitated better by primes that immediately preceded a target object on a learned route (i.e. the order of presentation was identical to learning), than primes that immediately followed a target object (i.e. the presentation order was contrary to learning) (Janzen, 2006; Schinazi & Epstein, 2010). Secondly, route repetition and route retracing involve different spatial decision making processes. While uni-directional egocentric knowledge is sufficient for route repetition, additional allocentric knowledge is required to retrace a route. Specifically, route retracing requires a spatial representation that allows individuals to identify the direction in which a route is being traversed and navigate through route locations accordingly. As it is a more complex task, navigation errors are more frequent during route retracing than repetition. For example, Ruddle, Volkova, Mohler and Bülthoff (2010) found that in comparison to repeating a route, participants made more errors during route retracing in both landmark-free and landmark-rich environments. Increased familiarity with a route in the return direction is also associated with improved route retracing performance. For example, looking back during route learning in anticipation of a return journey has been found to improve subsequent retracing performance (Cornell, Heth & Rowat, 1992; Heth, Cornell & Flood, 2002), suggesting that viewing previously traversed terrain prepares participants for route retracing. Furthermore, it is possible to acquire equivalent knowledge of a route in both directions. Ishikawa and Montello (1996) repeatedly navigated participants along a real-world route either in a single direction (uni-directional group) or in both the outward and return direction (bidirectional group). A number of experimental tasks, which involved route repetition for the uni-directional group and route retracing for the bidirectional group, revealed that route knowledge did not differ significantly between the two experimental groups, suggesting that the bi-directional group acquired route retracing knowledge as well as the uni-directional group acquired knowledge for route repetition. However, as participants in these studies had previously viewed or travelled along the learned route in the opposite direction, it is possible that they relied on a separate viewpoint-dependent representation for route retracing, rather than allocentric spatial knowledge.

While the studies discussed above examine route retracing in young adults, to our knowledge, only a single study has investigated older adults' performance of this task. In a study conducted by Liu, Levy, Barton and Iaria (2011), participants completed two separate tasks in a landmark-free virtual environment that assessed route repetition and route retracing knowledge. In the route repetition task, participants viewed two routes consisting of three turns, and were asked to determine whether they were identical. In the route retracing task, participants were passively transported along a short route at the end of which they turned 180 degrees, and completed a second route of identical length. Participants were asked whether the second route traversed the first route in the opposite direction. Liu et al. (2011) reported age-related impairments in both tasks, with deficits in identifying route retracing emerging earlier in the adult lifespan, supporting findings that suggest that age-related wayfinding deficits are more pronounced in tasks that rely on allocentric knowledge. Such tasks critically depend on the hippocampus, which is particularly sensitive to age-related neurodegeneration and has been implicated in route retracing (van Asselen et al., 2006). However, it should be noted that as Liu et al. (2011) were investigating age differences in a wide range of wayfinding abilities, the scope of the route repetition and retracing tasks was relatively limited. Therefore, the aim of the current paper was to examine the effects of aging on these navigation tasks in greater depth. Specifically, we employed a novel, landmark-based route learning paradigm to assess age differences in the spatial decision making processes associated with route repetition and retracing.

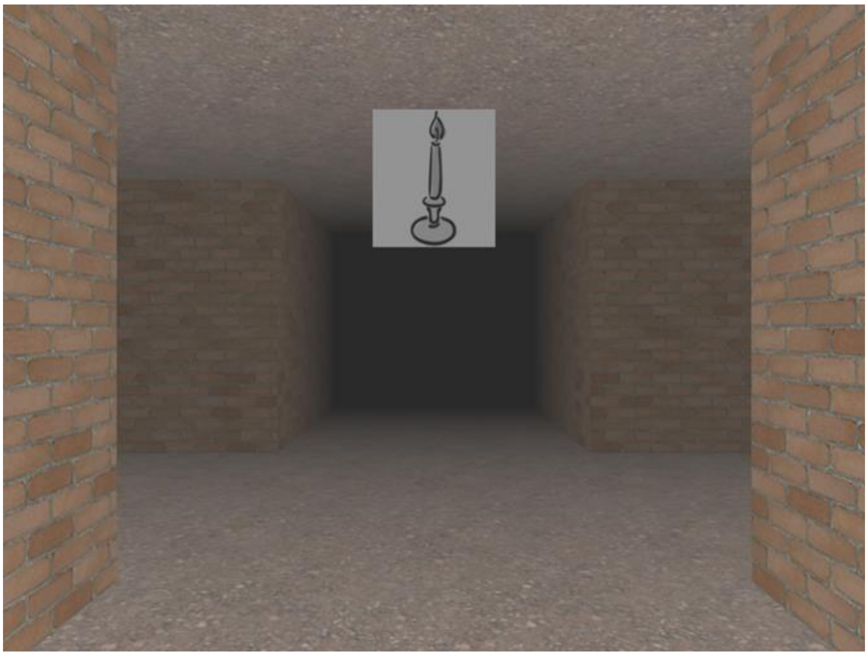


**Figure 24.** An example of an intersection within the route. The route proceeded to the left, right or continued straight ahead at each intersection.

## 9.5. Hypotheses

In this experiment, participants learned a route through a virtual environment containing eleven intersections. To support route learning, each intersection featured a single, centrally located landmark (see Figure 24). During the test phase, participants were passively transported along a section of the route and asked to identify whether the route was traversed in the same direction as learning (route repetition) or in the opposite direction (route retracing). Participants were then asked to i) indicate the direction of movement required to continue repeating or retracing the route, and ii) identify the landmark located at the next intersection. While viewpoint-dependent egocentric knowledge is sufficient to solve route repetition trials, viewpoint-independent allocentric knowledge is required for route retracing trials. As tasks that can be solved with egocentric knowledge are less susceptible to the effects of aging than tasks that require allocentric knowledge, we expected age-related deficits to be more pronounced in retracing trials.

## 9.6. Main Findings

While both age groups were similarly able to identify the overall travel direction when the route was repeated, older adults were significantly poorer than younger adults at recognising route retracing. Further analysis revealed that participants determined the direction of travel by comparing the temporal sequence of landmarks experienced during training and test. The additional complexity involved in recalling a learned sequence in reverse order has previously been associated with age-related impairments in non-spatial tasks (e.g. digit span), which may explain why older adults experienced difficulty identifying route retracing. Furthermore, in both route repetition and route retracing trials in which the travel direction was correctly identified, age-related deficits were found for both indicating the movement direction required to remain on the route, and identifying the landmark at the subsequent intersection. Interestingly, while younger participants' performance in these tasks improved over the course of the experiment irrespective of travel direction (repetition or retrace), a specific learning impairment was observed in older adults when asked to indicate the movement direction required to continue retracing the route. While employing an egocentric strategy is most effective for this task during route repetition, accurate navigation during route retracing depends on a spatial representation that allows navigators to determine both the direction in which a route is being travelled and the corresponding movement response. Therefore, age-related deficits in allocentric processing may explain older adults' impaired spatial decision making during route retracing. In summary, this study revealed that age-related deficits in route retracing were more pronounced than in route repetition. In particular, older adults were less able to identify route retracing, which may be explained by age-related difficulties in processing a learned sequence of landmarks or route locations in reverse order. Furthermore, while younger adults learned to navigate accurately during route retracing trials, older adults' performance remained close to chance level throughout the experiment, suggesting that age-related deficits in allocentric processing impaired older adults' ability to traverse a learned route in the opposite direction.

## 9.7. Summary

The paper discussed in this chapter revealed age-related deficits in both route repetition and route retracing. However, older adult's wayfinding difficulties were more pronounced and widespread during route retracing than route repetition, suggesting that tasks that rely on allocentric processing are affected by aging more than tasks that can be solved using egocentric knowledge.

Interestingly, age-related deficits in navigation accuracy during route repetition contrasts with the results of both experiments in Chapter 8. However, methodological differences between these experiments may account for this discrepancy. Specifically, the test phase in this study assessed three different types of route knowledge (route direction, navigation accuracy and landmark order), while only navigation accuracy was tested in the primary test phase in Chapter 8. Furthermore, while only uni-directional knowledge was tested in Chapter 8, participants' knowledge of the return journey was also assessed in this chapter. Therefore, the additional cognitive complexity associated with this study may explain why age-related deficits in navigation accuracy were found during route repetition.

# CHAPTER 10. The Effects of Aging on Allocentric and Egocentric Strategy Use

## 10.1. Overview

Age is associated with a decline in hippocampal function that is known to affect older adults' ability to process spatial information allocentrically (Antonova et al., 2009; Moffat, Elkins & Resnick, 2006). As a result, older adults experience greater difficulty with hippocampal-dependent tasks than tasks that rely on extrahippocampal structures (see Chapter 7). Age-related declines in allocentric processing are also known to affect older adults' strategy choice, with several studies reporting an age-related bias for egocentric response strategies over allocentric place strategies irrespective of task demands (Moffat & Resnick, 2002; Rodgers, Sindone & Moffat, 2012). Therefore, the primary purpose of the paper summarised in this chapter was to use the Alternative Routes paradigm (see Chapter 4) to investigate the effects of aging on allocentric and egocentric strategy use. Furthermore, replicating the findings of studies that previously examined aging and strategy choice would provide further validation for the Alternative Routes paradigm.

## 10.2. Paper III

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.

## 10.3. Paper Abstract

Efficient spatial navigation requires not only accurate spatial knowledge but also the selection of appropriate strategies. Using a novel paradigm that allowed us to distinguish between beacon, associative cue, and place strategies, we investigated the effects of cognitive aging on the selection and adoption of navigation strategies in humans. Participants were required to re-join a previously learned route encountered from an unfamiliar direction. Successful performance required the use of an allocentric place strategy, which was increasingly observed in young participants over six experimental sessions. In contrast, older participants, who were able to recall the route when approaching intersections from the same direction as during encoding, failed to use the correct place strategy when approaching intersections from novel directions. Instead, they continuously used a beacon strategy and showed no evidence of changing their behaviour across the six sessions. Given that this bias was already apparent in the first experimental session, the inability to adopt the correct place strategy is not related to an inability to switch from a firmly established response strategy to an allocentric place strategy. Rather, and in line with previous research, age-related deficits in allocentric processing result in

shifts in preferred navigation strategies and an overall bias for response strategies. The specific preference for a beacon strategy is discussed in the context of a possible dissociation between beacon-based and associative-cue-based response learning in the striatum, with the latter being more sensitive to age-related changes.

## 10.4. Theoretical Background

Normal cognitive aging affects many aspects of spatial navigation, including the use of various wayfinding strategies. Typically, allocentric strategies are used to support flexible navigation between known environmental locations, while egocentric strategies are employed to traverse familiar routes (Hartley, Maguire, Spiers & Burgess, 2003). Several studies investigating strategy preference across the lifespan have reported age-related impairments in allocentric strategy use, and an increased reliance on egocentric response strategies with age (Moffat & Resnick, 2002; Rodgers et al., 2012). These age-related shifts in strategy preference have been associated with the differential effects of aging on the hippocampus and striatum, which support allocentric and egocentric strategy use respectively. In contrast to the striatal circuits, the hippocampus and surrounding structures are particularly vulnerable to age-related neurodegeneration (Raz, 2000; Raz & Rodrigue, 2006; Raz et al., 2003; Rosenzweig & Barnes, 2003). As such, age-related wayfinding deficits are more pronounced in tasks that require allocentric knowledge (e.g. taking novel short-cuts), than in tasks that can be completed with egocentric knowledge (e.g. repeating a learned route). The primary purpose of the paper summarised in this chapter was to employ the Alternative Routes paradigm to investigate the effects of aging on strategy preference. Age differences in allocentric and egocentric strategy use have primarily been established using a variety of different wayfinding paradigms e.g. virtual and real world analogs of the Morris Water Maze Task (e.g. Driscoll, Hamilton, Yeo, Brooks and Sutherland, 2005; Newman & Kaszniak, 2000), the Y-Maze task (e.g. Rodgers et al., 2012), the Radial Arm Maze task (e.g. Bohbot et al., 2012) and the Concurrent Spatial Discrimination Learning Task (e.g. Etchamendy, Konishi, Pike, Marighetto & Bohbot, 2012). Therefore, replicating the findings of these studies would provide further support for the validity of the Alternative Routes paradigm.

Interestingly, age-related neurological processes may also affect older adults' preference for two different egocentric strategies: the associative cue and beacon response strategies. Associative cue and beacon strategy use depend on landmarks to support the acquisition and use of route knowledge, and are thought to rely on different regions of the striatum. The dorsal and dorsolateral striatum have been implicated in associative cue-based learning (Featherstone & McDonald, 2004, 2005), which involves pairing an encoded landmark with an explicit motor response, while the ventral and dorsomedial striatum are thought to support beacon-based learning (Devan & White, 1999), which relies on the spatial correspondence between an encoded landmark and a learned route to guide subsequent navigation. Given that the dorsal striatum is more susceptible to age-related neurodegenerative processes than the ventral striatum (Kim et al., 2011; Kuwabara et al., 2012; Tupala et al., 2003), older adults may exhibit a selective preference for beacon strategy use over associative cue strategy use. However, to our knowledge, no study has explicitly investigated the effects of aging on different egocentric strategies, and no paradigm distinguishes between associative cue and beacon strategy use. Therefore, the secondary aim of this paper was to examine older adults' use of the associative cue and beacon response strategies.

## 10.5. Hypotheses

In this study, we employed the Alternative Routes paradigm (see Chapters 3, 4 and 5) to examine age differences in strategy preference. Participants learned a short route through a virtual environment containing two landmarks at each decision point. During test, participants approached each route intersection from a variety of directions and were asked navigate along the original route, with responses in subset of test trials distinguishing between allocentric, associative cue and beacon strategy use. As only allocentric knowledge supported successful navigation in all test trials, we expected younger adults to increasingly adopt an allocentric strategy over the course of six experimental blocks (see Chapters 3, 4 and 5). In contrast, we expected older adults, who are known to experience difficulty with allocentric learning, to rely on a suboptimal egocentric response strategy throughout the experiment. Furthermore, due to the differential effects of aging on the neural systems thought to underlie associative cue and beacon-based learning, we predicted that older adults would preferentially employ a beacon strategy over an associative cue strategy.

## 10.6. Main Findings

Analysis revealed that in test trials that involved repeating the learned route, both younger and older adults' performance improved over the course of the experiment. However, in test trials that required navigation that differed from learning, younger adults' performance improved throughout the experiment, while older adults' performance remained poor. Taken together, these results suggest that normal cognitive aging affects performance in tasks that require allocentric knowledge, but not tasks that can be completed with egocentric knowledge. This finding was further supported by analysis of participants' strategy preference. Over the course of six experimental blocks, younger adults increasingly adopted the correct allocentric strategy, replicating previous findings (see Chapters 3, 4 and 5). In contrast, allocentric strategy use remained low among older adults, who preferentially employed a suboptimal beacon response strategy throughout the experiment. Given that employing an allocentric strategy would result in more accurate navigation, older adults' lack of allocentric learning supports previous findings that demonstrate an age-related deficit in allocentric processing. Furthermore, older adults exhibited an egocentric strategy bias for beacon-based learning rather than associative cue-based learning, which may be related to the differential effects of aging on the dorsal and ventral striatum. Specifically, the dopamine system in the dorsal striatum, which is implicated in associative learning, appears to be more vulnerable to age-related decline than the dopamine system in the ventral striatum, which is thought to be involved in beacon strategy use (Kim et al., 2011; Kuwabara et al., 2012; Tupala et al., 2003).

## 10.7. Summary

Over time, younger adults increasingly adopted an allocentric place strategy to support more accurate navigation. In contrast, older adults preferentially employed a suboptimal egocentric strategy throughout the experiment, and showed no evidence of adapting their strategy choice in response to the demands of the navigation task. This finding replicates previous studies that report reduced allocentric strategy use in older adults, and provides further support for the validity of the Alternative Routes paradigm presented in this thesis. Furthermore, older adults exhibited a specific preference for a beacon strategy rather than an associative cue strategy, which may be related to the differential effects of aging on the striatal areas thought to support the use of each strategy.

# CHAPTER 11. Discussion: Chapters 7-10

## 11.1. Overview

While younger adults are adept at choosing an appropriate strategy based on their wayfinding needs, older adults often employ egocentric response strategies irrespective of task demands (Bohbot et al., 2012; Etchamendy, Konishi, Pike, Marighetto & Bohbot, 2012; Rodgers, Sindone & Moffat, 2012). This change in strategy preference across the adult lifespan has primarily been attributed to an age-related decline in hippocampal function that affects older adults' ability to acquire and utilise allocentric spatial knowledge (Moffat, 2009; Raz & Rodrigue, 2006; Rosenzweig & Barnes, 2003). In contrast, egocentric strategy use is relatively unaffected by age as the striatal circuits are less vulnerable to age-related structural and physiological change (Raz, 2000; Raz et al., 2003). Therefore, the purpose of the second part of this thesis was to investigate the effects of aging on landmark-based strategy choice and efficacy. The following discussion will address the key findings of the preceding three experimental chapters.

## 11.2. Key Findings

The key findings related to the effects of aging on the use of wayfinding strategies were:

1. Aging has little effect on route learning supported by the use of either an associative cue or beacon strategy.
2. Older adults are more vulnerable than younger adults to switching costs associated with alternating between different strategies during route learning and navigation.
3. Age is associated with impaired acquisition of allocentric knowledge.
4. Older adults exhibit a task-independent preference for egocentric strategy use.

## 11.3. Discussion of Key Findings

Several studies have reported age-related deficits in the acquisition and subsequent use of landmark-based route knowledge (e.g. Jansen, Schmelter & Heil, 2010; Lipman, 1991; Wilkniss, Jones, Korol, Gold & Manning, 1997). These deficits, which include age-related impairments in recognising landmarks and associating spatial knowledge with environmental cues (Head & Isom, 2010; Liu, Levy, Barton & Iaria, 2011; Rosenbaum, Winocur, Binns & Moscovitch, 2012), suggest that older adults have difficulty employing landmark-based route learning strategies. However, the first experiment of Chapter 8 found that aging had no effect on associative cue and beacon strategy use. Specifically, route learning and navigation accuracy did not differ between younger and older adults when employing either strategy. Furthermore, the knowledge associated with landmarks during both associative cue and beacon-based learning did not differ between age groups, suggesting that the acquisition of spatial knowledge is not affected by age-related deficits in associative memory (see Old & Naveh-Benjamin, 2008 for a review). These results, which suggest that the spatial processes involved in route learning are largely resistant to the effects of aging, contrast with findings of age-related route learning deficits in other studies (Cushman, Stein & Duffy, 2008; Moffat, Zonderman & Resnick, 2001; Meulenbroek, Petersson, Voermans, Weber & Fernández, 2004; Rosenbaum et al., 2012; Wilkniss et al., 1997; Zakzanis, Quintin, Graham & Mraz, 2009). However, compared to these studies, the absence of age differences in Chapter 8 may be attributed to i) the experimental procedure preventing the use of a sequential response strategy (e.g. 'Turn left, then right, then left...'), ii) stricter and/or more comprehensive screening for mild cognitive impairment, or iii) fewer distracters within the route learning environment.

Chapter 2 revealed that younger adults were able to alternate between different strategies during navigation without incurring significant switching costs. However, empirical research in other cognitive domains has demonstrated that older adults are more vulnerable to switching costs than younger adults, and are therefore less inclined to change strategies (Kray & Lindenberger, 2000; Wasylyshyn, Verhaeghen & Sliwinski, 2011). The second experiment in Chapter 8 investigated age differences in the prevalence and cost of strategy switching. Analysis revealed that the cognitive costs associated with alternating between associative cue and beacon strategy use affected younger and older adults differently. For example, while younger adults preferentially alternated between different strategies in order optimise navigation accuracy, older adults did not exhibit a preference either for employing the optimal strategy at each decision point, or using a single strategy throughout the route. This finding suggests that the risk of incurring age-related switching costs discouraged some older adults from alternating between different strategies. Furthermore, age differences that were not found when participants employed a single strategy to learn a route (Chapter 8, Experiment 1) were also indicative of age-dependent switching costs. First, older adults reached ceiling level performance later than younger adults, which suggests that switching strategies impairs older adults' ability to acquire route knowledge efficiently. Second, older adults' knowledge of landmark position during associative cue strategy use was poorer than younger adults', suggesting that age-related switching costs first affect i) the most cognitively demanding wayfinding strategy, and ii) strategy-irrelevant spatial processes. Taken together, these results suggest alternating between different wayfinding strategies incurs age-dependent switching costs that affect various aspects of older adults' spatial behaviour.

Older adults often avoid unfamiliar areas as they feel less confident and more anxious in new surroundings (Burns, 1999; Bryden, Charlton, Oxley & Lowndes, 2010, 2013). While these findings suggest that older adults experience significant wayfinding difficulties in novel environments, Chapter 8 revealed that older adults are able to learn new routes as well as younger adults. Therefore, older adults’ reluctance to explore unfamiliar areas may reflect age-related difficulties with more complex navigation tasks. For example, being able to return to a familiar location is critical to learning a new environment (Miller & Eilam, 2011), and often involves retracing a route in the opposite direction. Interestingly, retracing a route accurately requires viewpoint-independent allocentric knowledge, as navigators must be able to recognise decision points from different perspectives, and determine the correct movement direction. In contrast, uni-directional egocentric knowledge is sufficient to repeat a learned route. Given that aging affects allocentric processing more than egocentric processing, it is possible that an inability to retrace a successfully learned route may deter older adults from visiting new environments. The effects of aging on route repetition and retracing were investigated in Chapter 9, which revealed that age-related navigation deficits were more pronounced when retracing a route than repeating a route. Furthermore, older adults exhibited a specific impairment for learning which direction to move in order to continue retracing a route. Specifically, younger adults' knowledge of such information improved over time, while older adults' remained poor. Taken together, these results suggest that age-related impairments in learning allocentric spatial knowledge contribute to older adults’ self-imposed wayfinding restrictions.

Finally, research has shown that strategy preferences change with age. While younger adults’ strategy choice varies in response to the concurrent navigation task, older adults preferentially employ egocentric response strategies irrespective of task demands (Bohbot et al., 2012; Etchamendy et al., 2012; Rodgers et al., 2012). While decreasing allocentric strategy use over the lifespan has been related to the loss of hippocampal function with age, older adults’ preference for egocentric strategies has received little attention. Chapter 10 assessed age differences in strategy choice using the Alternative Routes paradigm, and found that younger adults increasingly adopted an allocentric strategy over the course of the experiment to support accurate navigation. In contrast, older adults exhibited a maladaptive bias for a beacon response strategy that did not change over time. These results provide additional support for previous research that has demonstrated increasing use of egocentric response strategies with age, and age-related impairments in allocentric learning (e.g. Antonova et al., 2008; Gazova et al., 2013; Newman & Kaszniak, 2000). Interestingly, the findings reported in Chapter 10 provide further insight into older adults’ preference for egocentric response strategies, which was limited to the use of a beacon strategy. It is possible that older adults selectively employed a beacon response strategy over an associative cue strategy because i) beacon strategy use supports learning and navigation better, ii) beacon strategy use is less cognitively demanding, or iii) the effects of aging are more pronounced on the neural systems that support associative cue strategy use than beacon strategy use.

## 11.4. Conclusions

Normal cognitive aging is associated with changes in strategy use that affect older adults' ability to perform numerous navigation tasks. First, older adults experience difficulty with the use of allocentric place strategies, which support tasks that require flexible or novel navigation. Instead, older adults preferentially employ egocentric response strategies, which allow learned spatial behaviours to be repeated. As a result of these age differences in strategy use, older adults' navigational accuracy in tasks that rely on allocentric knowledge is reduced. Second, tasks that can be performed optimally by alternating between strategies are approached differently by younger and older adults when less cognitively demanding alternatives are available. These differences, which are independent of age-related impairments in allocentric strategy use, likely reflect the increased vulnerability of older adults to switching costs. In summary, the effective and appropriate use of wayfinding strategies declines across the adult lifespan due to age-related deficits in allocentric strategy use, and older adults' vulnerability to switching costs associated with changing strategies.

# CHAPTER 12. General Discussion

## 12.1. Overview

The purpose of this thesis was to investigate the selection and use of landmark-based wayfinding strategies across the adult lifespan. As such, Chapters 1 – 6 investigated strategy use during different navigational tasks, while Chapters 7 – 11 examined the effects of aging on strategy preference and efficacy. For a more detailed discussion of both parts of the thesis, see Chapters 6 and 11. The remainder of this chapter will summarise the key findings of the research presented in this thesis, discuss the contributions to the field of research, and provide recommendations for additional research.

## 12.2. Summary of Key Findings

The key findings regarding the selection and use of wayfinding strategies were:

1. Beacon strategy use facilitates route learning better than associative cue strategy use.
2. Alternating between associative cue and beacon strategy use during navigation does not affect the efficacy of either egocentric strategy.
3. Egocentric strategy use precedes allocentric strategy use.
4. Learning associated with different wayfinding strategies may occur in parallel.
5. Shifts between allocentric and egocentric strategy use can be determined by changes in the pupillary response to navigation.

The key findings related to the effects of aging on the use of wayfinding strategies were:

1. Aging has little effect on route learning supported by the use of either an associative cue or beacon strategy.
2. Older adults are more vulnerable than younger adults to switching costs associated with alternating between different strategies during route learning and navigation.
3. Age is associated with impaired acquisition of allocentric knowledge.
4. Older adults exhibit a task-independent preference for egocentric strategy use.

## 12.3. Further Contributions to Research Field

The novel wayfinding paradigm presented in this thesis (Chapters 3, 4, 5 and 10) provides a more detailed and valid assessment of strategy choice than many other existing paradigms. First, the Alternative Routes paradigm can be employed to distinguish between the use of three different landmark-based wayfinding strategies. Specifically, participants' navigational behaviour can be used to explicitly differentiate between the employment of an allocentric place strategy, and two landmark-based egocentric strategies: the associative cue and beacon response strategies. In contrast, only one other paradigm – to our knowledge – can be used to discriminate between different types of egocentric strategy use (cf. Starmaze paradigm; Rondi-Reig, Petit, Tobin, Tonegawa & Berthoz, 2006). Second, the task completed by participants – re-joining a learned route – corresponds better with real world navigation than the tasks performed by participants in other strategy assessment paradigms. For example, the Morris Water Maze Task involves searching for a hidden platform in a circular enclosure (Morris, 1981), while participants must navigate with previously visible landmarks obscured from view during the Radial Arm Maze Task (e.g. Iaria et al., 2003). As such, the Alternative Routes paradigm provides a more valid assessment of participants' strategy use. Third, the Alternative Routes paradigm allows strategy preference to be assessed over time, providing insight into the acquisition of wayfinding strategies, and the development of spatial knowledge. Furthermore, as the use of different strategies is informed by the same visual scene, the Alternative Routes paradigm can be employed to examine strategy-dependent behavioural and neurological differences (e.g. gaze behaviour and neural activity) without the need to control for perceptual differences in the part of the environment used to support different strategies. Finally, age differences in strategy preference (Chapter 10) suggest that participants’ behaviour in the Alternative Routes paradigm may correspond with the integrity of different neural regions. Firstly, it is well established that allocentric strategy use is indicative of normal hippocampal function (see Burgess, Maguire & O'Keefe, 2002). Secondly, research suggests that the types of learning involved in associative cue and beacon strategy use depend on the ventral and dorsal striatum respectively (Devan & White, 1999; Featherstone & McDonald, 2004, 2005). Therefore, in addition to impaired hippocampal function, it is possible that a stable maladaptive bias for either egocentric strategy reflects reduced involvement of different areas within the striatum. However, further research regarding the relative contribution of the ventral and dorsal striatum to wayfinding is required first. In summary, the Alternative Routes paradigm improves upon many of the paradigms currently used in wayfinding research, and may prove suitable to investigate the effects of neurological changes and differences on wayfinding strategy use.

While egocentric and allocentric strategy use are typically differentiated by spatial behaviour and/or subjective post-experimental questionnaires, navigators' ocular behaviour may also provide insight into strategy preference. However, to date, few studies relate ocular metrics with concurrent strategy use (Andersen, Dahmani, Konishi & Bohbot, 2012; Hamilton, Johnson, Redhead & Verney, 2009; Livingstone-Lee et al., 2011; Mueller, Jackson & Skelton, 2008). In Chapter 5, analysis of participants' ocular behaviour while completing the Alternative Routes task revealed that changes in pupil size during navigation are a reliable physiological indicator of changes in strategy preference. Specifically, Chapter 5 revealed that variations in pupil dilation correspond with shifts in strategy choice, with pupil size increasing more during allocentric strategy use than egocentric strategy use. Compared to traditional determinants of strategy choice, there are several advantages to using pupil dilation to assess strategy preference. First, pupil dilation is an online measure of strategy choice, and can therefore be used to assess strategy preference throughout the entire wayfinding process. For example, it is extremely difficult to objectively assess strategy use during the acquisition of spatial knowledge. However, analysis of pupil size during learning can be used to monitor the development of egocentric and allocentric strategies. Specifically, changes in pupil dilation over time or between environmental locations may be indicative of strategy switches. Secondly, most strategy assessment paradigms involve unusual navigation tasks in which egocentric and allocentric strategy use are differentiated by participants' spatial behaviour. However, as pupil dilation is a physiological response, it can be used to assess strategy preference i) in the absence of behavioural differences between egocentric and allocentric strategy use, and ii) in a much wider variety of realistic navigation tasks. Finally, in tasks that require allocentric knowledge, poor navigation is often attributed to egocentric strategy use. However, inaccurate and/or indirect navigation may also reflect strategy shifts during navigation (e.g. Cassel, Kelche, Lecourtier & Cassel, 2012; Iglói et al., 2009), or difficulties associated with allocentric strategy use. Given that pupil size varies according to strategy use, pupil dilation could be used to differentiate between these alternatives. In summary, pupil dilation is a promising determinant of strategy preference that may help elucidate the spatial processes involved in the acquisition and use of wayfinding strategies.

## 12.4. Future Directions

While this thesis provides novel insight into the use of landmark-based wayfinding strategies across the adult lifespan, additional research is required to further our understanding of several findings. First, further research is needed to determine whether navigators acquire spatial knowledge that does not correspond with their chosen strategy because i) certain aspects of the environment are encoded automatically (Hasher & Zacks, 1979; Pouliot & Gagnon, 2005), or ii) such knowledge facilitates potential shifts in wayfinding strategy. Second, the relationship between strategy choice and pupil size has only been examined in three published studies to date (de Condappa & Wiener, 2016; Mueller, Jackson & Skelton, 2008; Livingstone-Lee et al., 2011). Therefore, pupil size needs to be assessed in other wayfinding contexts to determine whether pupil dilation is a reliable physiological indicator of strategy preference. Third, the potential contribution of the ventral and dorsal striatum to associative cue and beacon-based navigation respectively also requires further investigation (see Chapter 10). While this will likely involve the use of fMRI technology, the navigation paradigms introduced in Chapters 2 and 4 may prove useful in examining the neural correlates associated with the use of both egocentric response strategies. Fourth, the Alternative Routes paradigm has been employed in a behavioural, ocular and aging context. While these studies demonstrate that the paradigm can be used to accurately assess strategy preference, wider use of the paradigm is required to verify its sensitivity to hippocampal function. To this end, researchers can employ the paradigm to study clinical populations, and a physical maze can be easily constructed for use in animal studies. Finally, few navigation studies explicitly investigate age-related impairments in strategy switching. Instead, older adults' preference for egocentric response strategies in tasks that require allocentric knowledge is often attributed to age-related difficulties with allocentric strategy use (Bohbot et al., 2012; Etchamendy et al., 2012; Rodgers et al., 2012). However, the results of Chapter 8 suggest that the cognitive costs associated with switching strategies influence younger and older adults' spatial behaviours differently. Therefore, further research is required to investigate age differences in wayfinding strategy switching (e.g. Harris & Wolbers, 2014).

## 12.5. Conclusions

In summary, good navigators identify and adopt the most accurate wayfinding strategy according to the demands of the concurrent spatial task. In order to optimise navigation accuracy, individuals often switch strategies – both permanently and repeatedly – within the same task. While the mental effort associated with changing strategies results in performance-related decrements in a variety of cognitive tasks, similar costs were not observed when switching between different wayfinding strategies. Indeed, navigators may facilitate potential strategy switches by i) acquiring spatial knowledge relevant to different strategies in parallel, and ii) selectively encoding landmarks that support the use of multiple strategies. Strategy use, however, changes significantly with age. First, older adults experience increasing difficulty with the use of allocentric strategies, which are necessary for complex tasks that involve flexible navigation e.g. taking novel short-cuts and detours. Second, age-dependent switching costs influence age differences in strategy preference, route learning efficiency and spatial learning. For example, older adults that alternate between different route learning strategies incur switching costs that affect learning efficiency and the acquisition of strategy-irrelevant spatial knowledge. Finally, this thesis makes two novel contributions to the field of strategy assessment. First, we present a new strategy assessment task – the Alternative Routes paradigm – that differentiates between the use of an allocentric strategy, and the associative cue and beacon response strategies. Thus far, this novel paradigm has been employed in a behavioural, ocular and aging context in this thesis. Second, we demonstrate that pupil size may be a reliable physiological indicator of changing strategy preference. Specifically, changes in the pupillary response to navigation correspond with shifts between egocentric and allocentric strategy use.

# CHAPTER 13. References

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# CHAPTER 14. Appendices

## 14.1. Appendix A

de Condappa, O., & Wiener, J. M. (2016). Human place and response learning: Navigation strategy selection, pupil size and gaze behavior. *Psychological Research, 80*(1), 82-93. doi: 10.1007/s00426-014-0642-9

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ORIGINAL ARTICLE

# Human place and response learning: navigation strategy selection, pupil size and gaze behavior

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**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 favor 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. 1a) 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. 1b).While all three strategies resulted

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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 et al. (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 analyzed 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 50 ms of each test trial, while eye-tracking data were only collected during the first 3 s 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 analyzed. 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

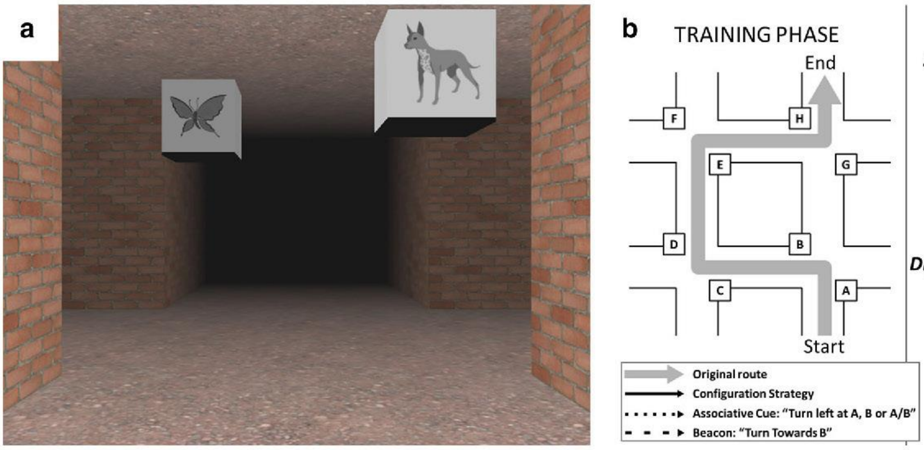

**Fig. 1** Virtual environment and navigation task. **a** A screenshot of an intersection. **b** An overview of the route, and two test trials. In same-direction trials, the approach direction is identical to training. Employment of any of the navigation strategies discussed results in successful navigation.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

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 recognized 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 (1) spatial transformations to relate the viewpoints experienced during training and test when approaching an intersection or (2) 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 analyzed 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 Fig. 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 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 analyze differences in gaze behavior when employing different strategies to gain insight into strategy-specific landmark usage during route learning and subsequent navigation.

## Materials and methods

### 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 500 Hz. 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 1,024 × 768 and a refresh rate of 100 Hz. A standard computer keyboard was used to record responses. Participants were seated 60 cm 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.

### 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 s. 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 recognize 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

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[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).

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 100 ms 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 [$F(1, 50) = 213.43$, $p < 0.001$, $\eta_p^2 = 0.81$], and performance improved over experimental blocks [$F(3.84, 192.17) = 23.89$, $p < 0.001$, $\eta_p^2 = 0.32$] (see Fig. 2a). A significant approach direction x experimental block interaction [$F(3.70, 184.81) = 5.32$, $p = 0.001$, $\eta_p^2 = 0.10$] 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 [$F(4.17, 212.74) = 9.78$, $p < 0.001$, $\eta_p^2 = 0.16$] and different-direction trials [$F(3.05, 155.31) = 19.28$, $p < 0.001$, $\eta_p^2 = 0.27$], replicating results for young participants reported by Wiener et al. (2013).

### 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 [$F(3.59, 179.49) = 4.39$, $p = 0.003$, $\eta_p^2 = 0.08$] and beacon strategy use decreased [$F(3.71, 185.67) = 5.18$, $p = 0.001$, $\eta_p^2 = 0.09$], while configuration strategy use increased [$F(3.95, 197.53) = 16.08$, $p < 0.001$, $\eta_p^2 = 0.24$]. 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 ($M = 50.96$ %, $SD = 41.41$; $t(51) = 3.07$, $p = 0.003$, $r = 0.39$), while use of the configuration strategy was below chance level ($M = 18.27$ %, $SD = 32.88$; $t(51) = -3.30$, $p = 0.002$, $r = 0.42$) and associative cue use did not differ from chance level ($M = 30.77$ %, $SD = 37.25$; $t(51) = -0.50$, $p = 0.62$, $r = 0.07$). 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

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[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.

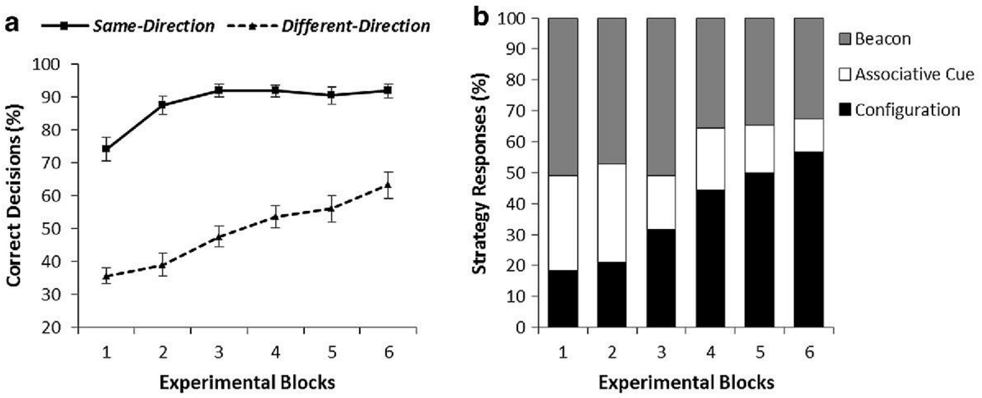


**Fig. 2** Navigation performance and strategy choice. **a** Performance at same-direction and different-direction test trials across experimental blocks (mean ± standard error). **b** Strategy choice in selected different-direction trials across experiment blocks

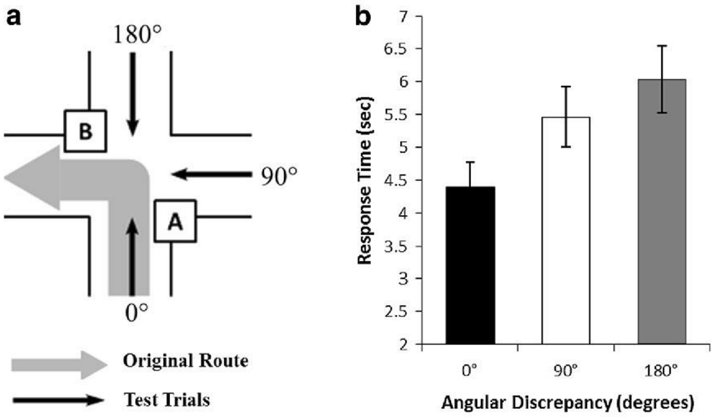


**Fig. 3** Test trial approach directions and response times. **a** Test trials with different angular discrepancies between the approach directions during training and at test. **b** Response time by angular discrepancy between training and test approach directions (mean ± standard error)

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 [$F(1.69, 84.71) = 19.25$, $p < 0.001$, $\eta_p^2 = 0.28$] (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°, $p < 0.001$; 0° vs. 180°, $p < 0.001$; 90° vs. 180°, $p = 0.01$), suggesting that users of the configuration strategy rely on viewpoint-dependent place recognition.

## Ocular behavior

### *Pupil size*

Separate ANOVAs revealed that average pupil size decreased across experimental blocks during test trials [$F(1.84, 88.33) = 13.59$, $p < 0.001$, $\eta_p^2 = 0.22$] (Fig. 4a) and presentation of the mask [$F(2.69, 129.31) = 25.24$, $p < 0.001$, $\eta_p^2 = 0.35$], and average pupil size was larger during different-direction trials compared to same-direction trials [$F(1, 48) = 4.30$, $p = 0.044$, $\eta_p^2 = 0.08$] (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 $p > 0.05$). 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.

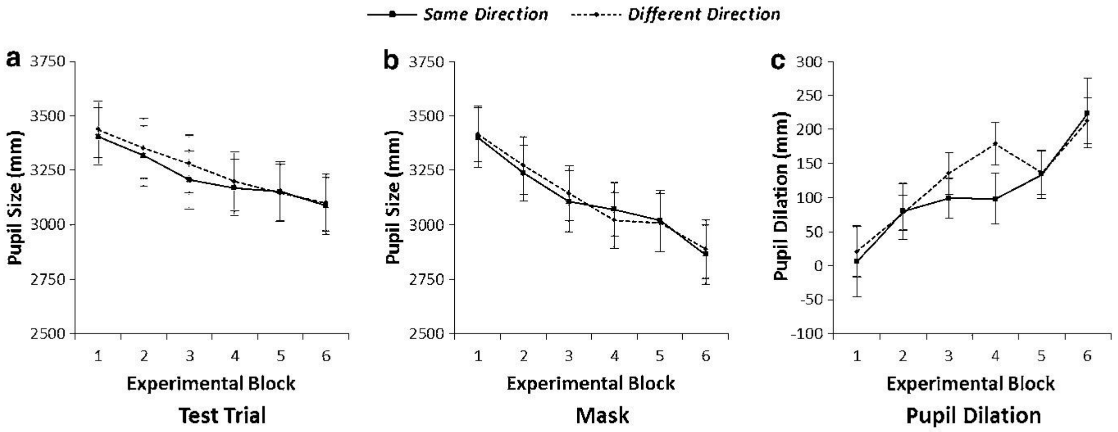


**Fig. 4** Pupillometry data. **a** Test trial pupil size across experimental blocks (mean ± standard error). **b** Baseline pupil size across experimental blocks (mean ± standard error). **c** Pupil dilation across experimental blocks (mean ± standard error)

### *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 [$F(3.27, 157.06) = 7.54$, $p < 0.001$, $\eta_p^2 = 0.14$] (Fig. 4c), although there was no significant main effect of approach direction or an interaction (both $p > 0.05$). 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 [$r(51) = 0.39$, $p = 0.002$], suggesting pupil dilation is sensitive to the employment of place strategies.

## Gaze behavior

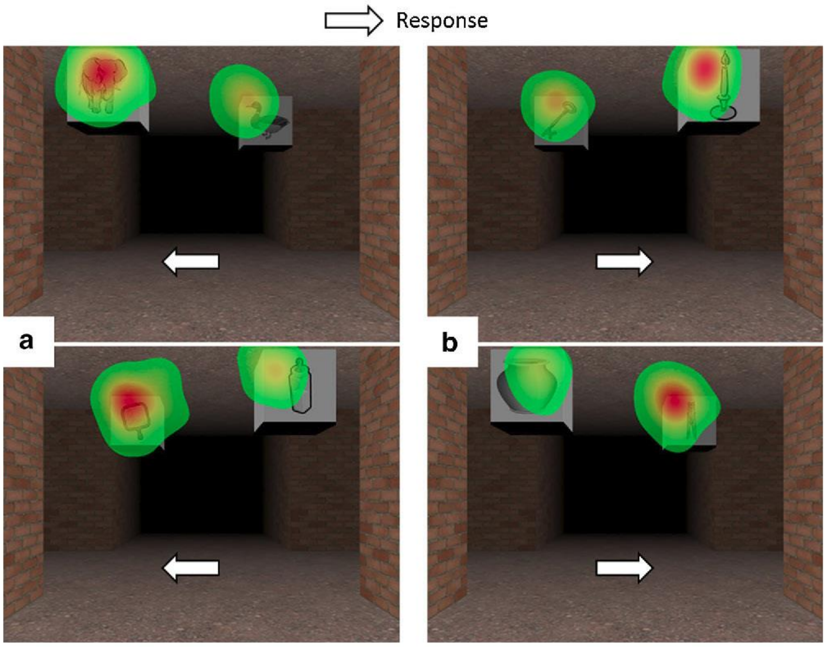
### *Same-direction trials*

An analysis of dwell times in correct same-direction trials (see Fig. 5a, b) 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 %): $t(50) = 10.32$, $p < 0.001$, $r = 0.82$). This systematic gaze bias can be explained by (1) 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, (2) anticipatory gaze behavior towards the intended movement direction, or (3) a combination of (1) and (2). 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*

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

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



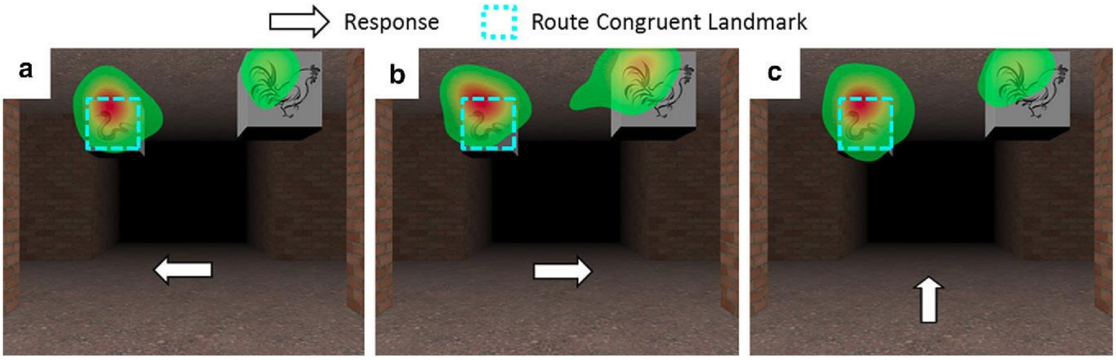


**Fig. 6** Gaze behavior at the selected different-direction trials used to identify navigation strategy. The route congruent landmark during training is located on the left of the featured intersection (the snake). **a** Beacon responses (chosen response was *left*). **b** Associative cue responses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

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

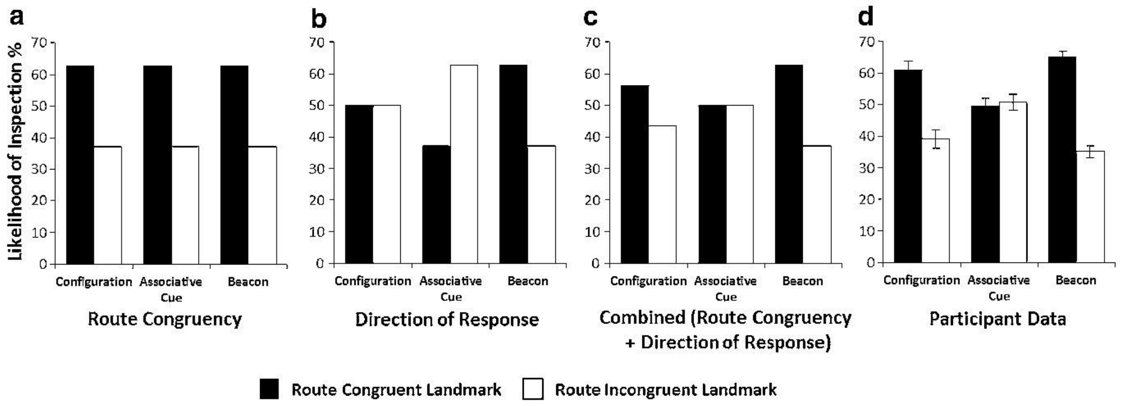


**Fig. 7** Predictive models of gaze behavior and participant data. **a** Predicted gaze behavior of different strategy users if only the location of the route congruent landmark influences visual attention. **b** Predicted gaze behavior if only the direction of the response made influences attention. **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)

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 [$\chi^2(2) = 7.72$, $p = 0.021$], 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 ($Z = -2.56$, $p = 0.01$, $r = 0.25$) ($\alpha = 0.016$) and the route congruency model ($Z = -2.34$, $p = 0.019$, $r = 0.23$) ($\alpha = 0.025$), suggesting that, irrespective of strategy, participants primarily attended to the route congruent landmark and the direction of intended movement during navigation.

## 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 (1) the landmark located in the movement direction during training and (2) 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-Torbert, 2007). Instead, our findings broadly

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[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.

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 organization 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 (1) spatial transformations to relate the viewpoints experienced during training and test or (2) 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; Matthews & 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: (1) the landmark located in the direction of movement during learning (the route congruent landmark) and (2) 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 750–500 ms 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.

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## 14.2. Appendix B

Wiener, J. M., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: effects of cognitive aging. *Frontiers in Aging Neuroscience, 4*(7).

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# Route repetition and route retracing: effects of cognitive aging

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Retracing a recently traveled route is a frequent navigation task when learning novel routes or exploring unfamiliar environments. In the present study we utilized virtual environments technology to investigate age-related differences in repeating and retracing a learned route. In the training phase of the experiment participants were guided along a route consisting of multiple intersections each featuring one unique landmark. In the subsequent test phase, they were guided along short sections of the route and asked to indicate overall travel direction (repetition or retracing), the direction required to continue along the route, and the next landmark they would encounter. Results demonstrate age-related deficits in all three tasks. More specifically, in contrast to younger participants, the older participants had greater problems during route retracing than during route repetition. While route repetition can be solved with egocentric response or route strategies, successfully retracing a route requires allocentric processing. The age-related deficits in route retracing are discussed in the context of impaired allocentric processing and shift from allocentric to egocentric navigation strategies as a consequence of age-related hippocampal degeneration.

**Keywords: route retracing, route learning, cognitive aging, spatial memory, wayfinding**

## INTRODUCTION

Age-related differences in navigation abilities are well established both in animal and human literature (Rosenzweig and Barnes, 2003; Moffat, 2009). While age-related performance declines have been reported for different navigation tasks, they seem to be particularly pronounced in unfamiliar environments (Devlin, 2001). One navigation ability crucial for navigating unfamiliar environments is retracing—navigating a recently traveled route from the end to the start—as it enables a navigator to return to a known part of the environment (Lorenz, 1952; Miller and Eilam, 2011). Specific age-related deficits in route retracing would increase the risk of getting lost when navigating novel environments and could thus explain why older adults often report avoiding unfamiliar places and routes (Burns, 1999). While route retracing is a common navigation task, especially when exploring unfamiliar environments, it has received surprisingly little attention in the literature and it is unclear how it is accomplished. In the current study we present a novel experimental paradigm to investigate the cognitive processes and strategies involved in route learning and route retracing in more detail. Moreover, by comparing route retracing performance between a younger and older age group we investigate the effects of cognitive aging on route retracing.

Route knowledge is typically conceptualized as a series of stimulus-response associations (Trullier et al., 1997). A single stimulus-response association consists of recognizing the current place (e.g., by recognizing a landmark associated with that place) and selecting the direction in which to proceed along the route (Waller and Lippa, 2007). Learning a route with multiple decision points, therefore, requires knowledge of landmarks along the routes, associations of directional information with these landmarks, and knowledge about the order of landmarks.

Note that route knowledge that takes the form of stimulus-response pairs is inherently uni-directional, allowing a route to be repeated. The stimulus-response pairs are encoded in an egocentric reference frame during learning ("Turn left at X"). During route retracing, however, the decision points are approached from a viewpoint different to that experienced before. Accordingly, the egocentric stimulus-response pairs that were encoded during route learning do not support route retracing. Route retracing requires knowledge about the spatial relationship between the direction from which a decision point is approached and the direction in which the route proceeded. Such a representation is viewpoint independent—i.e., allocentric—and would support for route retracing.

Egocentric and allocentric navigation strategies are supported by different neuronal circuits: egocentric strategies involve the parietal cortex and the caudate nucleaus, while allocentric strategies are hippocampus dependent (McDonald and White, 1994; Wolbers et al., 2004; Burgess, 2008). While cognitive aging affects egocentric strategies (Barrash, 1994; Wilkniss et al., 1997; Moffat et al., 2001; Head and Isom, 2010), allocentric strategies seem to be more severely affected (Begega et al., 2001; Moffat and Resnick, 2002). As a result, a number of studies report shifts from allocentric to egocentric strategies with increasing age (Barnes et al., 1980; Nicolle et al., 2003; Rodgers et al., 2012; Wiener et al., under review). Age-related hippocampal degeneration offers an explanation for the impaired allocentric processing and according strategy shifts (Raz et al., 2010).

In the current study we used a novel experimental paradigm to investigate the cognitive processes and strategies involved in route retracing. Specifically, we tested the hypothesis that route retracing, in contrast to route repetition, relies on allocentric processing. In the experiment, participants were navigated along a complex route with multiple decision points each featuring a unique landmark. In the subsequent test phase they were guided along sections of the route either in the direction of original travel (route repetition) or in the opposite direction (route retracing). Their tasks were, first, to indicate travel direction (route repetition or route retracing), second to indicate the direction required to continue along the route to either reach the end or the start place (depending on travel direction), and third, to identify the next landmark encountered on route if the current travel direction was maintained. Comparisons of performance in these tasks between route repetition and route retracing trials allowed for first insights into the nature of route retracing. In order to test whether route retracing in fact involves allocentric processing, we compared performance between a younger and older participant group. In line with earlier research into the effects of cognitive aging on navigation abilities (Moffat et al., 2001; Head and Isom, 2010), we expected an overall effect of age on performance in all three tasks. If route retracing—as argued above—relied on allocentric processing, we expected additional age-related performance declines for route retracing trials as compared to route repetition trials reflecting the particularly adverse effects of cognitive aging on allocentric navigation strategies (Moffat and Resnick, 2002; Iaria et al., 2009).

## MATERIALS AND METHODS

### PARTICIPANTS

Forty participants [20 younger (eight females; mean age 20.53 ± 1.84 years, range 25–30); 20 older (11 females; mean age 69.45 ± 5.48 years, range 61–85)] took part in the experiment. The montreal cognitive assessment (MoCA; Nasreddine et al., 2005) was administered to all participants to screen for mild cognitive impairment (MCI). No participant had to be excluded based on the recently recommended MoCA cut-off score for the MCI of 23 (Luis et al., 2009). The average MoCA scores for the young and old age group were 27.56 (young) and 27.65 (old).

### THE VIRTUAL ENVIRONMENT

Using Vizard 3.0 (WorldViz) we created a virtual route consisting of 11 four-way intersections (see **Figure 1**). Each intersection could be identified by a unique single landmark—an image of an object—that was mapped onto a cube suspended from the wall. During the experiment, participants were passively transported along the entire route in the training phase and along parts of the route in the test phase.

### PROCEDURE

The experiment consisted of six experimental sessions. Each experimental session was composed of a training phase and a test phase. In the training phase, participants were transported along the entire route twice. Their task was to memorize the route. The test phase consisted of 18 trials, each of which was composed of three tasks:

- **Route Direction Task.** First, participants were transported along two intersections of the original route either in the same direction as during training (route repetition, nine trials) or in the opposite direction (route retracing, nine trials). For example, in a route repetition trial they would approach the intersection with the sofa, turn left and then approach the intersection with the football where movement stopped (see **Figure 1**). Participants were asked to indicate the direction of

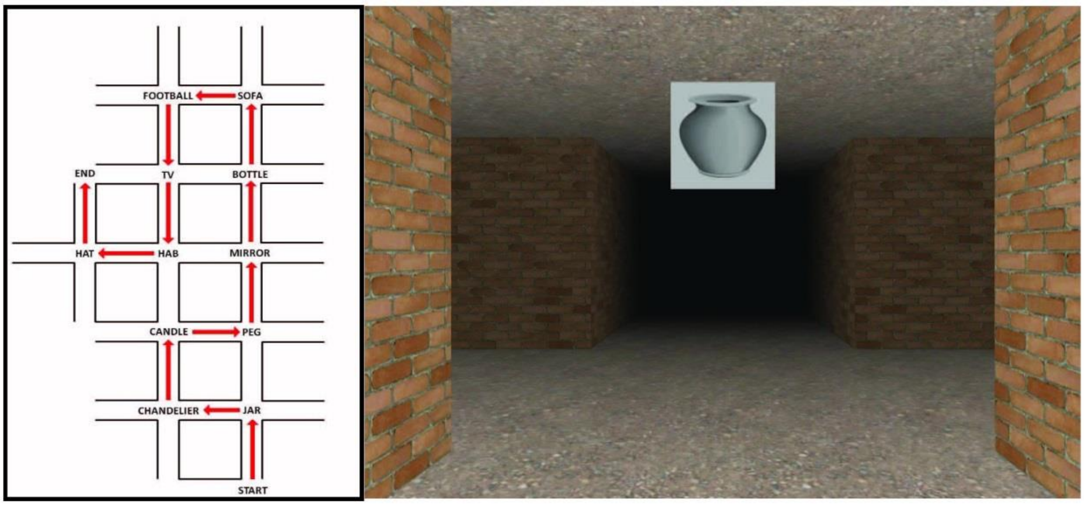

**FIGURE 1 | Left:** schematic drawing of the route consisting of 11 intersections; **right:** screen-shot of one of the intersections.

travel (repetition or retrace). Participants were instructed to respond as soon as they identified the travel direction, even if this occurred during the actual movement. Chance level for this task was 50%.

- **Intersection Direction Task.** Subsequent to the *Route Direction Task*, participants were asked to indicate the direction in which the route continued after movement stopped given the current travel direction. For route repetition trials, this involves indicating the direction required to follow the original route toward the end. In contrast, for route retracing trials this involves indicating the direction required to return to the start location while remaining on the route. With three possible movement directions and an equal amount of trials requiring a left, right, and straight responses, chance level for this task was 33.3%.
- **Landmark Sequence Task.** Finally, participants were presented with an image depicting three of the landmarks on the route. Their task was to indicate which of these landmarks would be encountered next, if the current travel direction was maintained. Chance level for this task was 33.3%.

Participants were instructed to respond as accurately and as quickly as possible by pressing the correspondingly labeled buttons on a response box (Cedrus RB-730).

The *Route Direction Task*, the *Intersection Direction Task*, and the *Landmark Sequence Task* were designed to test different aspects of route learning and route retracing. To solve the *Route Direction Task* participants needed to compare the sequence of landmarks and/or turns encountered during travel with their route memory. The *Intersection Direction Task* and the *Landmark Sequence Task* require participants to anticipate the upcoming movement direction or the next landmark, respectively. For repetition trials, these tasks are functionally equivalent to standard route learning tasks (Waller and Lippa, 2007; Head and Isom, 2010). Retracing trials, in contrast, require further processing: the *Landmark Sequence Task* requires manipulation of the temporal order of the landmarks; the *Intersection Direction Task* requires comprehending the spatial relationships between the direction from which an intersection is approached and the direction in which the route continues.

### ANALYSIS

We first analyzed performance for the *Route Direction Task*. Only trials in which participants correctly identified travel direction were included in the analyses of the *Intersection Direction* and the *Landmark Sequence Task*. As a result of removing incorrect *Travel Direction Task* trials, fewer data points were available for the remaining analyses. In order to analyze effects of learning on these two tasks we, therefore, pooled data from sessions 1–3 and 4–6.

## RESULTS

### ROUTE DIRECTION TASK

In order to enter the final data-set, participants' performance in repetition trials on the *Route Direction Task* had to exceed chance level (50%). This criterion was set to ensure that participants had acquired sufficient route knowledge during the training phases to investigate the effects of cognitive aging on route repetition. Performance for two older participants did not reach chance level. These participants were excluded from the final data-set.

To examine the impact of travel direction (route repetition and route retracing) on performance in the Route Direction Tasks between age groups, a repeated-measures ANOVA was conducted with the between-subject factors of age group (young, older) and sex and two within-subject factors of experimental session (1–6) and travel direction (repetition, retrace). We observed main effects of age [$F_{(1,\,34)} = 9.74$, $p < 0.01$, $\eta^2 = 0.22$], session [$F_{(3.2,\,111.17)} = 42.20$, $p < 0.001$, $\eta^2 = 0.55$], direction [$F_{(1,\,34)} = 26.36$, $p < 0.001$, $\eta^2 = 0.44$], but not of sex [$F_{(1,\,34)} = 0.16$, $p = 0.69$, $\eta^2 = 0.01$]. Specifically, younger participants performed better than older participants (86.19% vs. 74.97%), performance on repetition trials was better than on retracing trials (88.08% vs. 73.07%), and performance improved over experimental sessions (session 1: 60.96%, session 6: 89.94%).

The main effect of direction was primarily driven by the impaired performance of older participants on retracing trials (see **Figure 2**). This is reflected in the significant interaction of direction *x* age group [$F_{(1,\,34)} = 10.31$, $p < 0.01$, $\eta^2 = 0.23$] and by *post-hoc* tests demonstrating that younger and older participants performed comparatively during route repetition trials [*t*-test (89.31% vs. 87.25%): $t_{(35.75)} = 0.73$; $p = 0.47$], but performed differently during route retracing trials [*t*-test (84.27% vs. 63.32%): $t_{(23.50)} = 3.59$; $p < 0.01$]. Only one other interaction, direction *x* session [$F_{(2.9,\,100.7)} = 3.55$, $p = 0.02$, $\eta^2 = 0.10$] was significant.

Note that participants who entered this analysis were selected on basis of their performance on repetition trials. However, despite good performance on repetition trials, older adults showed impaired performance on retracing trials compared to young adults. In other words, the subsample of older adults that had no problems identifying travel direction during route repetition, exhibited a specific age-related impairment when traveling in the opposite direction along the route.

How did participants solve the *Route Direction Task*? In principle there are two ways: first, participants can compare the order in which the landmarks are encountered during training and test phase; second, for those test trials that feature a turn at the first intersection encountered, participants can compare the turning direction at this intersection between training and test. The analysis of response times for test trial with a turn at the first intersection allows us to distinguish between these two alternatives: Turning onset was 4.7 s after the test trial started. After 7.4 s the landmark of the second intersection was in sight. Response time for the relevant test trials was 10.25 s for young adults, 12.08 s for older adults, 11.06 s for repetition trials, and 11.26 s for retracing trials. There was a main effects of age [$F_{(1,\,36)} = 8.33$, $p < 0.01$, $\eta^2 = 0.19$] but no main effect of direction [$F_{(1,\,36)} = 1.91$, $p = 0.18$, $\eta^2 = 0.05$] and no significant interaction [$F_{(1,\,36)} = 1.52$, $p = 0.23$, $\eta^2 = 0.04$] (see **Figure 2** right). Participants made their decision 3 s (younger) to 5 s (older) after the second landmark was in sight. This strongly suggests that participants analyzed the order in which landmarks were encountered during travel to inform their decision, rather than the turning direction at the first intersection encountered.

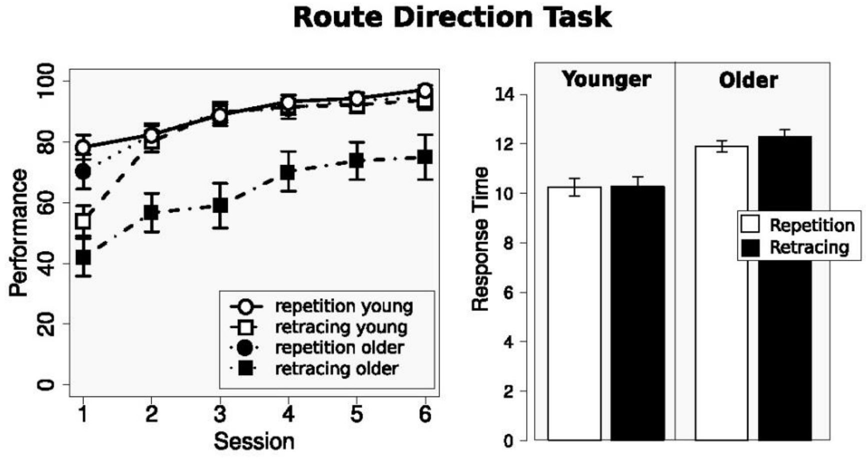

**FIGURE 2 | Left**: performance for the *Route Direction Task*; **right**: response time for test trials featuring a turn at the first intersection encountered.

## INTERSECTION DIRECTION TASK

As a result of removing two older participants from the final dataset and of excluding data from incorrect *Route Direction Task* trials from the further analysis, fewer trials from older participants (1446) than from younger participants (1720) entered the analysis of the *Intersection Direction Task* and the *Landmark Sequence Task*.

In order to examine performance differences between age groups in the *Intersection Direction Task*, a repeated-measures ANOVA was conducted with the between-subject factor of age (younger, older) and two within-subject factors of experimental session (first and second half of the experiment) and movement direction (repetition, retrace). We observed main effects of session [$F_{(1, 36)} = 29.76$, $p < 0.001$, $\eta^2 = 0.45$], direction [$F_{(1, 36)} = 29.51$, $p < 0.001$, $\eta^2 = 0.45$], and age [$F_{(1, 36)} = 17.39$, $p < 0.001$, $\eta^2 = 0.33$]. The main effect of age was driven both by repetition trials (*post-hoc*: $p < 0.001$) and by retracing trials (*post-hoc*: $p < 0.01$).

Of the interactions only direction $x$ session [$F_{(1, 36)} = 9.07$, $p < 0.01$, $\eta^2 = 0.20$] and direction $x$ session × age group [$F_{(1, 36)} = 4.12$, $p = 0.05$, $\eta^2 = 0.10$] were significant. These interactions were primarily driven by impaired learning in the older adults in the retracing trials: while young participants' performance improved over the course of the experiment for both repetition and retracing trials, the older adults' performance improved only on repetition trials, but not on retracing trials (see **Figure 3**). This is corroborated by additional separate repeated-measures ANOVAs for the young and the old age group: while main effects of direction and session were observed for both age groups (all $p < 0.05$), the interaction between direction and session was significant only in the older age group ($p = 0.02$), but not in the young age group ($p = 0.12$).

Note that performance for retracing trials in the older age group remained close to chance level performance (33%) for the entire experiment (see **Figure 3**).

## LANDMARK SEQUENCE TASK

In order to examine performance differences between age groups in the *Landmark Sequence Task*, a repeated-measures ANOVA was conducted with the between-subject factor of age (younger, older) and two within-subject factors of experimental session (first and second half of the experiment) and movement direction (repetition, retrace). We observed main effects of age [$F_{(1, 36)} = 11.54$, $p < 0.01$, $\eta^2 = 0.24$] and session [$F_{(1, 36)} = 95.07$, $p < 0.001$, $\eta^2 = 0.73$], but not of direction [$F_{(1, 36)} = 2.30$, $p = 0.14$, $\eta^2 = 0.04$]. Overall, performance was better for the young age group (young: 76.20%; old: 63.31%) and increased over the course of the experiment (first half: 62.22%; second half: 77.29%; see **Figure 3**). While none of the interactions was significant, the direction $x$ age group interaction neared significance [$F_{(1, 36)} = 4.04$, $p = 0.052$, $\eta^2 = 0.10$].

# DISCUSSION

In this study we used a novel experimental paradigm to investigate the effects of cognitive aging on the ability to retrace a route—i.e., to navigate from the end of a route back to the start location. In the experiment, participants first viewed a visual presentation of a route and were then presented with short segments of the route either in the direction experienced during training (route repetition trials) or in the opposite direction (route retracing trials). For each of these presentations, participants were given three tasks: in the *Route Direction Task* they had to indicate the overall travel direction; in the *Intersection Direction Task*, they had to indicate the direction of movement required to remain on the route given the current travel direction; in the *Landmark Sequence Task* they had to indicate which landmark they would encounter next when proceeding in the current travel direction.

Consistent with earlier findings (Barrash, 1994; Wilkniss et al., 1997; Moffat et al., 2001; Head and Isom, 2010), the older age

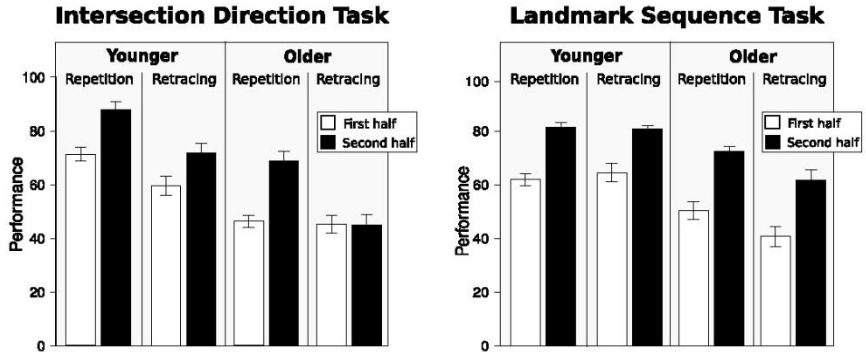

**FIGURE 3 | Left**: performance for the *Intersection Direction Task*; **right**: performancre in the *Landmark Sequence Task*.

group showed an overall performance deficit in route learning, even after removing two participants from the final data-set who did not reach chance level performance in route repetition trials in the *Route Direction Task*. In addition, older adults also showed specific deficits in retracing trials for both the *Route Direction Task* and the *Intersection Direction Task*. That is, older adults experienced difficulties when asked to identify the overall travel direction and to indicate the next movement direction when retracing the route, but not when repeating the route. Given the importance of successfully retracing a recently navigated route when exploring unfamiliar environments (Lorenz, 1952; Miller and Eilam, 2011), these effects offer an explanation for why age-related declines in navigation abilities are more striking in novel than in familiar environments (Devlin, 2001) and why older adults often report avoiding unfamiliar routes and places (Burns, 1999). In the following we consider results from the three tasks in the test phase in more detail.

### ROUTE DIRECTION TASK

The *Route Direction Task* assessed participants' ability to identify the current travel direction (route repetition or route retrace) while being passively transported along a short segment of the route. While this task can, in principle, be solved by comparing the turning direction at a single intersection during test with that experienced during training, participants of both age groups only responded after they encountered a second landmark. This suggests that they used the temporal ordering of landmarks to solve the task. Both younger and older adults performed well on route repetition trials. In contrast, for route retracing trials we found performance decrements in the older age group. In other words, while the older adults that entered the final data-set were perfectly able to recognize travel direction when it was identical to that during training, they had problems doing so when travel direction was reversed. This may be explained by the involvement of different cognitive processes during route repetition and route retracing: in the *Route Direction Task* participants are asked to identify travel direction by matching the order of landmarks experienced during the test phase to that experienced during training. Research in the area of sequence processing suggests that in repetition trials this task recruits a supervisory process that involves monitoring and selectively activating relevant items while suppressing irrelevant ones (Oberauer et al., 2000). For retracing trials, however, the sequence is reversed thus additionally requiring the coordination of the relative positions between the items. The efficiency of this coordination process has been found to be affected by cognitive aging (Bopp and Verhaeghen, 2007) which could explain the specific impairment for retracing trials in the older age group.

### LANDMARK SEQUENCE TASK

Older adults were also less accurate than young adults in the *Landmark Sequence Task* (see also Lipman and Caplan, 1992; Wilkniss et al., 1997; Head and Isom, 2010). However, the older adults reached performance levels clearly above chance level and performance increased over the course of the experiment. We did not observe a main effect of travel direction for the *Landmark Sequence Task*: both age groups performed at similar levels on repetition trials and on retrace trials. This seems surprising at first glance, but can be explained by (1) both the *Route Direction Task* and the *Landmark Sequence Task* requiring comparison between the temporal ordering of landmarks during the training phase with that experienced during the test phase; and (2) that only the data from correct *Route Direction Task* trials entered the *Landmark Sequence Task* analysis. In other words, as both tasks rely on similar processes and by pre-selecting trials on basis of performance in one task, potential effects of travel direction in the second task are reduced.

### INTERSECTION DIRECTION TASK

In line with earlier research (e.g., Head and Isom, 2010), older adults were less accurate in the *Intersection Direction Task* than young adults. This effect was observed both for route repetition trials as well as for route retracing trials. In addition, we found a specific learning deficit in retracing trials for the older age group: performance in retracing trials was close to chance level and, in contrast to repetition trials and the younger age group, did not improve over the course of the experiment. That is to say, not only did older adults perform weaker in indicating the correct direction when retracing a route, they were also unable learn the correct direction over the course of the experiment.

Egocentric route learning strategies (Trullier et al., 1997; Waller and Lippa, 2007) enable a navigator to solve the *Intersection Direction Task* in route repetition trials. Route retracing, in contrast, is not supported by egocentric strategies as intersections are approached from a different direction than during training. Route retracing, therefore, requires abstracting from the viewpoint-dependent memory encoded during the learning phase. This can be achieved by encoding the spatial relationship between the arm from which a particular intersection was approached and the arm in which the route proceeded. This form of representation is independent of the navigator's viewpoint and, therefore, allocentric. Recent research suggests that age-related deficits in allocentric processing (Moffat and Resnick, 2002; Moffat et al., 2007; Harris and Wolbers, in press) result from hippocampal degeneration during typical aging (Raz et al., 2010; Wiener et al., under review). This could also explain the age-related decline in performance on route retracing trials as these, in contrast to the route repetition trials, require allocentric processing.

In addition to the proposed deficits in allocentric processing resulting from age-related hippocampal degeneration, more general age-related declines in working memory and processing speed may contribute to the observed effects. The *Processing Speed Theory* states that declines in processing speed with increasing age can result in impairments in cognitive performance (Salthouse, 1996). This may be due to task-related time limitations or because results of earlier cognitive operations are no longer available when later operations are completed (simultaneity). While the current paradigm did not impose time limitations, allocentric processing is computationally more demanding than egocentric processes as it requires additional cognitive operations (Byrne et al., 2007). Any age-related processing speed effects are, therefore, more likely to affect retracing trials which rely on allocentric processing rather than repetition trials for which egocentric processes are sufficient.

We have argued that route retracing relies on allocentric processing. This is supported by a series of findings: route retracing provides a means to return to the start of a journey and has, therefore, been suggested to be crucial for exploring novel environments (Lorenz, 1952). Accordingly, in freely exploring rodents, route retracing is mainly observed during early stages of learning an environment (Miller and Eilam, 2011). Early stages of spatial learning primarily rely on allocentric place strategies, whereas egocentric response or route strategies only occur later (Tolman et al., 1946; Ritchie et al., 1950). Together with results from the current study this suggests that route retracing during the early stages of learning an environment relies on allocentric strategies.

Recent electrophysiological findings in rats suggest a neuronal mechanism that could support route retracing. Foster and Wilson (2006) recorded from hippocampal place cells and found that immediately after traversing a track, the hippocampal place cell activity observed during navigation was reactivated in reverse temporal order as if retracing the route. Importantly, these reverse replays were observed to a greater extent after navigating through a novel environment compared to a familiar environment, suggesting that such replays play an important role during spatial learning (see also Colgin and Moser, 2006).

To conclude, we have demonstrated age-related deficits in route retracing. Specifically, older participants showed impaired performance in both recognizing travel direction when navigating along the route in the reverse direction and in indicating the direction required to retrace the route. Given the importance of route retracing for learning novel environments these findings provide further insights into the effects of normal cognitive aging on wayfinding and orientation abilities.

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## 14.3. Appendix C

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.

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Behavioral/Cognitive

# Maladaptive Bias for Extrahippocampal Navigation Strategies in Aging Humans

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**Efficient spatial navigation requires not only accurate spatial knowledge but also the selection of appropriate strategies. Using a novel paradigm that allowed us to distinguish between beacon, associative cue, and place strategies, we investigated the effects of cognitive aging on the selection and adoption of navigation strategies in humans. Participants were required to rejoin a previously learned route encountered from an unfamiliar direction. Successful performance required the use of an allocentric place strategy, which was increasingly observed in young participants over six experimental sessions. In contrast, older participants, who were able to recall the route when approaching intersections from the same direction as during encoding, failed to use the correct place strategy when approaching intersections from novel directions. Instead, they continuously used a beacon strategy and showed no evidence of changing their behavior across the six sessions. Given that this bias was already apparent in the first experimental session, the inability to adopt the correct place strategy is not related to an inability to switch from a firmly established response strategy to an allocentric place strategy. Rather, and in line with previous research, age-related deficits in allocentric processing result in shifts in preferred navigation strategies and an overall bias for response strategies. The specific preference for a beacon strategy is discussed in the context of a possible dissociation between beacon-based and associative-cue-based response learning in the striatum, with the latter being more sensitive to age-related changes.**

## Introduction

Everyday navigation can be based on different strategies. The hippocampus plays a key role in cognitive map or place strategies that rely on allocentric processing, whereas the parietal cortex and striatal circuits are involved in route or response strategies (McDonald and White, 1994; Wolbers et al., 2004; Burgess, 2008). Aged rodents show deficits in tasks that rely on allocentric cues, whereas response strategies are less affected (Begega et al., 2001). Moreover, even when successfully trained on both place and response strategies, aged mice still show a preference for response strategies, suggesting an age-related increase in reliance on extrahippocampal systems to guide navigation (Nicolle et al., 2003).

Such age-related navigational impairments are likely to be related to the vulnerability of the hippocampus and surrounding structures to neurodegenerative processes (Lister and Barnes, 2009; Stranahan and Mattson, 2010). Given that similar physiological and morphological changes have been documented in aging humans (Raz et al., 2005, Yankner et al., 2008), it is not surprising that difficulties in using place strategies have been observed in older adults (Moffat and Resnick, 2002, Moffat et al., 2007, Iaria et al., 2009, Harris and Wolbers, 2012, Wiener et al., 2012). However, at present, the precise consequences of these changes in navigational computations are unknown.

In this study, we used a novel route-learning paradigm (1) to test whether cognitive aging does indeed lead to a shift in preferred navigation strategy and (2) to precisely identify the type of response strategy used by older adults. Response strategies are often conceptualized as a series of stimulus–response pairs in which landmarks serve as cues that become associated with motor responses defined relative to the body axis ("Turn left at the post office"; associative cue strategy). However, humans also use beacon-based strategies in which movement responses toward a landmark brings one closer to the goal but that do not require explicit encoding of directional information or motor responses ("Go toward the post office"; Waller and Lippa, 2007). Although both response strategies rely on striatal processing, some studies suggest a dissociation, with the dorsal and dorsolateral striatum implicated in associative-cue learning (Featherstone and McDonald, 2004, 2005) and the ventral and dorsomedial striatum involved in beacon-based strategies (Devan and White, 1999). Given that the dorsal striatum might be more sensitive to age-related neurodegeneration (Tupala et al., 2003), aged humans could be expected to show a preference for beacon-based over associative-cue-based strategy.

To test the hypothesis that cognitive aging not only results in a shift away from allocentric strategies but in a specific preference

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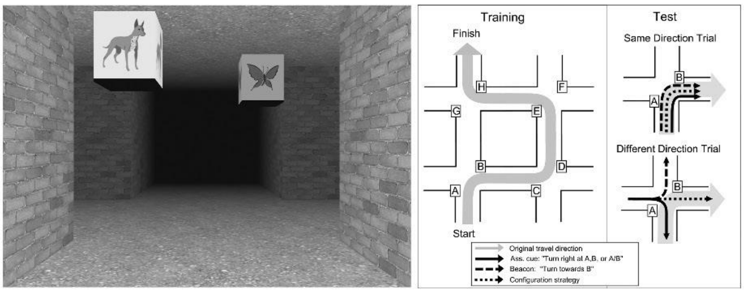

**Figure 1.** Left, Screenshot of one intersection; middle, schematic overview of the training route; right, two of the test trials. In same-direction trials, the intersections are approached from the same arm as during training: all strategies result in correct responses. In different-direction trials, the intersection is approached from an arm different from that of training. In the depicted example, the three strategies generate different responses; the associative cue strategy ["Turn right at A (or B)"] leads to a right turn, the beacon strategy ("Turn toward B") produces a left turn, whereas only the configuration strategy, relating the goal arm to the configuration of local landmarks, yields the correct response. Note that our definition of beacon strategy involves a turning response ("Turn toward"), whereas other definitions use more general responses ("Move toward"; Waller and Lippa, 2007). However, in the current paradigm, in which single landmarks are always adjacent to two arms, this would lead to ambiguity. Specifically, participants should also make "straight" responses on same-direction trials, which only happened in 3% of the same-direction trials, strongly suggesting that they adopted a "Turn toward" beacon strategy, thus eliminating any ambiguity.

for beacon-based strategies, we developed a novel experimental paradigm: participants first learned a route along a number of intersections and were then asked to rejoin the original route approaching the intersections from different directions. Trials in which participants approached the intersections from a direction different from that during training (see Fig. 1) allowed us (1) to compare the use and adoption of route-learning strategies between young and older participants and (2) to test for specific preferences for beacon-based strategies in older participants.

## Materials and Methods

Vizard 3.0 (WorldViz) was used to create the virtual environment and the route-learning task, which were presented on a 24-inch widescreen computer monitor.

*Participants.* Forty-seven participants [23 younger (12 females; mean age, 20.8 years); 24 older (12 females; mean age, 73.8 years)] took part in the experiment. The Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005) was administered to all participants to screen for mild cognitive impairment (MCI). One older participant was excluded based on the recently recommended MoCA cutoff score for MCI of 23 (Luis et al., 2009). During the analysis, one young and an additional six older participants were excluded because they did not successfully learn the route (for details, see Results). Mean age of the remaining 17 older participants (eight females) was 74.7 ± 5.03 years, and their mean MoCA score was 26.58 ± 1.94; the mean age of the remaining 22 younger participants (11 females) was 20.73 ± 1.12 years, and their mean MoCA score was 28.14 ± 1.21. Participants were paid £6/h to partake in the study, which took 60–90 min to complete.

*Procedure.* Participants learned and were tested on one route that consisted of four four-way intersections (two left turns, two right turns; Fig. 1). Each of six experimental sessions involved a training phase and a subsequent test phase. During each training phase, participants were twice passively transported along the route (speed, 5 m/s) and were instructed to memorize the route. Each intersection along the route was characterized by two unique landmarks located in diagonally opposite corners, unambiguously identifying the intersection as well as the direction from which it was approached (Fig. 1). Including black fog in the environment ensured that only one intersection was visible at any time. In the test phase, participants were guided toward the intersections within the route and were asked to indicate the direction in which the original route proceeded by pressing the left, right, or up (i.e., straight) arrow key. Both responses and response times were recorded. In the test phase, each of the four intersections was either approached from the same arm as during training (resulting in four same-direction trials) or—excluding the arm where the route proceeded during training—from the two remaining arms (resulting in eight different-direction trials), adding up to 12 trials per session. To avoid participants memorizing a series of movement directions during training (right–left–left–right), the 12 test trials were presented in randomized order. Crucially, same- and different-direction trials test different abilities: same-direction trials test participants' ability to successfully replicate the route, i.e., to replicate the direction changes experienced during the learning phase. These trials can therefore be considered a typical measure of route knowledge (Head and Isom, 2010) and can be solved using any of the three navigation strategies discussed above (beacon, associative cue, and configuration). In contrast, different-direction trials cannot be solved simply by associative cue-based or beacon-based strategies (Wiener et al., 2012). Instead, to unambiguously identify the direction in which the original route proceeded, these trials require allocentric place learning, i.e., the processing of the spatial configuration of local cues (landmarks) in relation to the goal arm. We refer to this allocentric place strategy as the configuration strategy. For two of the different-direction trials (see example depicted in Fig. 1), all three strategies produced a different response. By analyzing participants' responses for these different-direction trials for each of the six experimental blocks, we calculated the number of responses in line with each strategy, which allowed us to assess individual strategy preferences and changes thereof over the course of the experiment.

Before the experiment, participants were informed that they would approach the intersections from different directions and that they should respond as quickly and accurately as possible. To prevent learning from feedback, participants did not receive immediate feedback after making a decision in the test phase. However, repeated training sessions allowed participants to learn the spatial relationship of the local landmarks and the goal arm over the course of the experiment.

## Results

Route-learning performance—i.e., the ability to repeat the learned route—was assessed in same-direction trials in which young participants performed better than older participants (81.13 vs 64.07% correct responses; $t_{(35.64)} = 3.01, p < 0.01$). The fact that variance in the older age group was higher than in the younger age group (Levene's test, $F_{(44)} = 6.19, p = 0.02$) suggests that some of the older participants found the task hard, whereas others performed well. Using $\chi^2$ tests, we tested whether individual participants' performance for same-direction trials significantly exceeded chance-level performance (with three possible movement directions, chance level was 33% or 8 of 24 same-direction trials). In fact, performance for six older participants did not exceed chance level, whereas performance of only one younger participant did not exceed chance level. Given that the aim of this study was the investigation of aging-induced shifts in route-learning strategies and the identification of the exact type of strategy used, we excluded these participants because they did not successfully learn the routes in the first place.

Because participants were selected based on their performance on the same-direction trials, included participants in both age groups were able to learn the route (Fig. 2). However, the older participant group showed specific deficits when approaching an intersection from an arm different from that experienced during encoding (Fig. 2). A general linear model with age (young, old) and gender as between-group factors and approach direction (same, different) and session (1–6) as within-subjects factors revealed that younger participants performed better than older participants (main effect of age, $F_{(1)} = 20.601$, $p < 0.001$), that performance was better when approaching intersections from the same direction as during training than from a different direction (main effect of approach direction, $F_{(1)} = 142.49$, $p < 0.001$), and that performance increased across sessions (main effect of session, $F_{(5)} = 18.981$, $p < 0.001$). In contrast, we did not observe a significant effect of gender ($F_{(1)} = 0.012$, $p = 0.91$).

Of the two-way interactions, the session × age ($F_{(5)} = 5.682$, $p < 0.001$) and the approach × age ($F_{(1)} = 16.961$, $p < 0.001$) interactions were significant. Importantly, a significant three-way approach direction × session × age interaction ($F_{(5)} = 5.356$, $p < 0.001$) suggested that both groups differed in how performance differences between same and different-direction trials evolved across the six sessions. Planned contrasts revealed that both groups showed a linear performance increase on same-direction trials (young, $F_{(35)} = 16.56$, $p < 0.001$; old, $F_{(35)} = 7.675$, $p = 0.009$), whereas only the young group showed this effect for the different-direction trials (young, $F_{(35)} = 80.026$, $p < 0.001$; old, $F_{(35)} = 0.147$, $p = 0.70$; interaction between linear increase and age, $F_{(35)} = 31.492$, $p < 0.001$). Together, these results demonstrate that performance differences between age groups cannot be explained by a nonspecific performance decrement or inattentiveness in the older group. Rather, older adults exhibited selective problems with using the correct allocentric place strategy throughout the experiment.

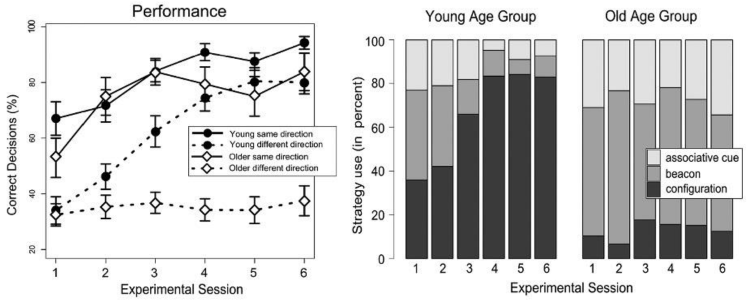

**Figure 2.** Left, Performance for same- and different-direction trials and both age groups for the six experimental sessions (mean ± SE); right, strategy use for different-direction trials for both age groups over the course of the experiment.

To assess strategy preferences, we calculated the percentage of responses in line with the three strategies (Fig. 2, right) for those different-direction trials that distinguished between all strategies (see example in Fig. 1). Because performance for different-direction trials improved over experimental sessions for young participants, so did usage of the correct allocentric navigation strategy. In contrast, the older participant group showed very little change in strategy use over the six experimental sessions. To quantify strategy preferences and changes thereof, we ran separate ANOVAs for each of the three strategies with age (young, old) as a between-group factor and session (1–6) as a within-subjects factor, and the percentage of trials the corresponding strategy was used as the dependent variable. Young participants relied more strongly on the configuration strategy than older participants ($F_{(1,37)} = 38.42$, $p < 0.001$). The main effect of session ($F_{(5,37)} = 15.32$, $p < 0.001$) was driven by the strong increase in configuration strategy use by the younger participants, which is reflected in the significant age × session interaction ($F_{(5,37)} = 8.63$, $p < 0.001$). The older participant group, compared with young participants, relied more strongly on the beacon strategy ($F_{(1,37)} = 19.59$, $p < 0.001$). Although there was a significant main effect of session for beacon strategy usage ($F_{(3.62,133.90)} = 2.99$, $p = 0.03$), the interaction did not reach statistical significance ($F_{(3.62,133.90)} = 2.37$, $p = 0.06$). The older participants also used the associative cue strategy more than the young participants ($F_{(1,37)} = 6.30$, $p = 0.02$). However, usage of the associative cue strategy did not change over experimental sessions ($F_{(3.92,145.10)} = 1.25$, $p = 0.29$), and there was no significant interaction between age group and session ($F_{(3.92,145.10)} = 0.99$, $p = 0.41$).

To investigate which of the two response strategies the older group preferred, we compared the percentage of responses in line with the beacon strategy with those in line with the associative cue strategy. This revealed that, as a group, older participants showed an overall preference for the beacon strategy ($t_{(16)} = 3.54$, $p < 0.01$). This preference already existed in the first experimental session ($t_{(16)} = 3.16$, $p < 0.01$) and did not change across the experiment (Fig. 2). Such a systematic preference for one strategy strongly suggests that the poor performance of the older group for different-direction trials was not unspecific or a result of different-direction trials being more difficult than the same-direction trials: in this case, we would have expected random behavior but no systematic bias.

Finally, the use of different navigation strategies by the two age groups should lead to a specific response time pattern: both the beacon and the associative cue strategy state that a turning response (beacon, "Turn toward …"; associative cue, "Turn left/right at …") is activated on the recognition of the corresponding place or landmark. As long as the place is identified, this process is independent of approach direction. In contrast, the configuration strategy requires the arrangement of the landmarks at the intersections to be encoded. If a place is approached from a different direction, the observer needs to use the landmark configuration to determine their facing direction. In addition, computing the correct movement direction involves a second step: either the direct computation of the correct response from an allocentric representation of the intersection or a mental transformation of the observer's current viewpoint to match the one experienced during encoding. These additional processing steps should lead to an increase in response time when approaching intersections from a novel direction, which should be greater for the young because more participants in that group used the configuration strategy. In accordance with this prediction, a repeated-measures ANOVA not only revealed significant main effects of approach direction ($F_{(1,37)} = 42.79$, $p < 0.001$) and age ($F_{(1,37)} = 26.53$, $p = 0.001$) on response time but also a significant interaction between age group and approach direction ($F_{(1,37)} = 9.80$, $p < 0.01$; Fig. 3). *Post hoc t* tests revealed shorter response times for same-direction trials than different-direction trials for the young and old participant groups (young, $p < 0.001$; old, $p = 0.02$). Although it may seem surprising that overall older participants responded more quickly than younger participants, this can be explained by the larger proportion of

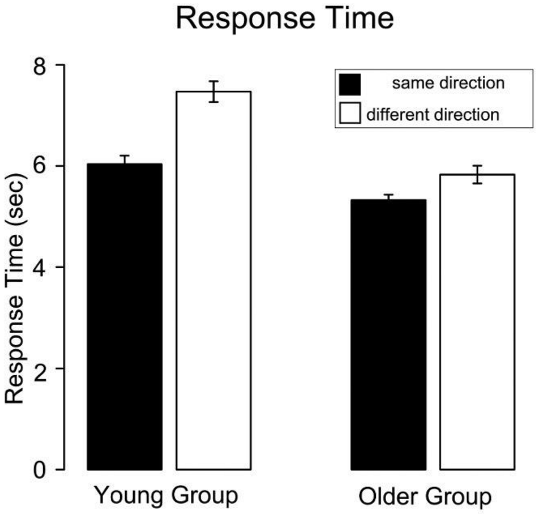

**Figure 3.** Average response times for same- and different-direction trials and both age groups. Data are collapsed across the experimental sessions (mean ± SE).

younger participants using the more time-consuming allocentric place strategy.

## Discussion

We used a novel paradigm to investigate the effects of cognitive aging on the selection and adoption of navigation strategies. Our paradigm differs from other paradigms used in aging research, such as the (human) Morris water maze and the Y-maze (Rodgers et al. 2012), in a number of important aspects. First, participants learn a route consisting of multiple intersections, which makes it a somewhat more natural task. Second, our task not only allows for the investigation of initial strategy selection biases but also of shifts in bias, which are particularly sensitive measures in detecting age-related neurodegeneration (Nicolle et al., 2003). Finally, in contrast to previous studies (Rodgers et al., 2012) addressing strategy preferences in older adults, our paradigm allows distinguishing between associative cue-based and beacon-based response strategies.

In the experiment, participants were required to follow a previously learned route encountered from an unfamiliar direction, and, to do so successfully, they needed to use an allocentric place strategy. Our younger participants showed clear evidence for adopting this superior navigation strategy. In contrast, those older participants who were able to successfully recall the route when approaching intersections from the same direction as during training showed a consistent preference for a beacon-based strategy and were unable to use the appropriate place strategy, resulting in poor performance when rejoining the learned route from a novel direction. Given that allocentric spatial processing required for place strategies is thought to critically depend on hippocampal computations, we propose that age-related hippocampal degeneration (Raz et al., 2005) induced a shift in preferred navigation strategies toward beacon-based strategy in older participants.

In contrast to the rapid learning for the same-direction trials, initial performance in young participants was poor on trials when an intersection was approached from an unfamiliar direction. However, the subsequent improvement demonstrates that this group gradually developed an understanding of the spatial configuration of each intersection and the position of the goal arm, which enabled them to use the correct configuration strategy. This strategy might have involved additional mental transformations of one's viewpoint or a direct access of the allocentric location of the goal arm, both of which have been linked to observer-independent spatial computations in the hippocampal formation (King et al., 2002; Wolbers and Büchel, 2005).

Consistent with recent findings (Head and Isom, 2010), the old age group showed an overall route-learning deficit, i.e., when repeating the route as experienced during training. A higher performance variability across participants suggested that this effect was primarily driven by a subgroup who were unable to learn the route. These underperforming older participants were removed from the final dataset, after which both age groups performed well on same-direction trials, indicating similar route-learning abilities. However, in sharp contrast, the performance of the older group on the different-direction trials remained at chance throughout the experiment, demonstrating that even the older participants who reproduced the route successfully were unable to use a place strategy. Instead, they showed a preference for a beacon-based strategy and showed no evidence of changing their behavior across the six sessions.

Rodgers et al. (2012) recently showed a similar age-related bias for response strategies in a virtual Y-maze. Critically, the probe trial was administered after subjects had shown consistent performance over five learning trials. As a consequence, the response bias could be based on the suggested inability to use place strategies. However, given that age-related deficits in strategy switching are well established in various cognitive domains (Kray and Lindenberger, 2000), it could also reflect an inability to switch from a firmly established response strategy to a place strategy in the probe trial. In our study, we observed a bias for a beacon strategy from the first session onward, with very little change occurring over the course of the experiment. These results make the strategy switching account unlikely and point instead to an age-related deficit in processing allocentric cues.

Response strategies are thought to rely on striatal circuits, whereas allocentric processing relies heavily on spatial computations in the hippocampal formation (Hartley et al., 2003; Doeller et al., 2008). Critically, the hippocampus has been shown to take over route-based navigation when the caudate is dysfunctional (Voermans et al., 2004), but the striatum is unable to take over allocentric navigation after hippocampal lesions (Goodrich-Hunsaker et al., 2010). As a consequence, because the hippocampus is particularly sensitive to the deleterious effects of aging (Yankner et al., 2008), the preferred use of response strategies might reflect an inability to successfully compensate for impaired hippocampal computations that are necessary for processing allocentric cues. Instead, our older participants relied on navigational strategies mediated by extrahippocampal structures, which we presume include the striatum.

Going beyond a general bias toward response strategies, older adults showed a consistent preference for a beacon-based strategy over an associative-cue-based strategy. This specific preference might be related to a functional dissociation between the medial/ventral and the lateral/dorsal striatum (Voorn et al., 2004). In rodents, the ventral and dorsomedial striatum receives extensive convergent input from multiple sensory and association areas of the neocortex and the limbic system, whereas the dorsal and dorsolateral striatum has a distinct topographic pattern of connections with somatosensory and motor areas (McGeorge and Faull, 1989). Similarly, in primates, the ventral striatum encompasses the medial wall of the caudate nucleus because of its inputs from regions such as the orbitofrontal cortex but not from primary or secondary motor cortices (Nakano et al., 2000; Haber, 2003). In contrast, the lateral part of the caudate receives cortical afferents from motor cortical areas as well as the somatosensory cortex. Hence, it is commonly thought of as part of the dorsal (or sensorimotor) striatum (Nakano et al., 2000). Although some functional neuroimaging studies point to a different homology (Balleine and O'Doherty, 2010), the patterns of connectivity indicate that the dorsal/dorsolateral striatum is more important for motor response learning as required for the associative cue strategy, whereas the ventral/dorsomedial striatum could be more important for beacon strategies.

Consistent with this anatomical dissociation, lesion studies in rodents implicate the dorsolateral striatum in stimulus–motor response learning (Packard and McGaugh 1996). Moreover, dorsomedial/ventral striatum lesions do not affect stimulus–motor response learning to the same extent as dorsal/dorsolateral lesions (Yin and Knowlton, 2004). Finally, dorsomedial lesions affect the learning of a beacon strategy, whereas dorsolateral lesions do not (Devan and White, 1999). However, these findings are reversed once the animal has been overtrained on the task, which suggests that the dorsomedial striatum might only be important for learning a beacon strategy, which was addressed in our experiment as well. In summary, there is ample evidence for a role of the dorsal/dorsolateral striatum in stimulus–motor response learning and somewhat weaker evidence for a role of the dorsomedial/ventral striatum in beacon-based navigation.

Given this anatomical and functional dissociation within the striatum, what could explain the bias for beacon over associative cue strategies in older adults? In humans, the caudate shows significant age-related neurodegeneration at similar rates compared with the hippocampus (Raz et al., 2005). Furthermore, dorsal striatal dopamine transporters and receptors appear to be more vulnerable to age-related decline than their ventral striatal counterparts (Tupala et al., 2003; Kim et al., 2011). Although we are not aware of any studies testing for a potential dissociation between the dorsolateral and dorsomedial striatum, we speculate that stimulus–motor response learning processes as required for the associative cue strategy might be similarly affected by aging as hippocampus-dependent place-based processes, whereas beacon-based navigation might be more resistant to age-related change.

To our knowledge, our study is the first to directly investigate the effects of cognitive aging on different response strategies. Older adults have been reported to be more likely to point out landmarks than turns as providing the most useful information for route navigation (Lipman, 1991). In addition, Alzheimer's disease patients appear to have intact representations of objects encountered during route learning, but they fail to integrate object and spatial information (Kessels et al., 2011). These findings are consistent with our findings, indicating that using landmarks as beacons—without the need to associate any directional/motor information—could be more resistant to age-related decline. This would also explain correlations between route-learning performance and changes in caudate volume during aging in route-learning paradigms that do not allow for beacon-based strategies (Head and Isom, 2010).

Together, we demonstrated an age-related deficit in allocentric processing, which may severely impair navigation when approaching a location on a known route from an unfamiliar direction. Importantly, of the egocentric response strategies that our novel task allowed us to study, older people showed a preference for the beacon strategy over the associative cue strategy. In support of animal findings, this preference points to a dissociation between beacon- and associative-cue-based learning in the striatum, with the latter being more sensitive to age-related changes. These findings not only provide additional insight into the navigational difficulties observed in normal cognitive aging, but they could also suggest directions for the development of novel navigational aids for elderly users.

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# CHAPTER 15. Glossary

## 15.1. Abbreviations

ANOVA – Analysis of variance

CSDLT – Concurrent Spatial Discrimination Learning Task

DSP – Dual Strategy Paradigm

M – Mean

MCI – Mild cognitive impairment

MoCA – Montreal Cognitive Assessment

MWMT – Morris Water Maze Task

RAM – Radial Arm Maze

RR – Rotation Reproduction

SD – Standard Deviation

TC – Triangle Completion Task