The role of attention in spatial (dis)orientation of older adults

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Abstract

Human ageing is accompanied by deficits in spatial navigation abilities. These changes are widespread and affect many components of the navigation system. Such changes have profound effects on an individual's independence as their ability to learn and find their way through novel environments diminishes. Among the widespread age-related changes are declines in landmark-based place and route learning, which are the focus of this project. The work presented in this thesis seeks to enhance our understanding of the cognitive mechanisms which contribute to declining navigation ability, with a particular emphasis on attentional processes.

Two place recognition experiments confirmed age-related deficits in overall place learning ability. These deficits were particularly pronounced when recognition depended on object-location binding mechanisms to encode the spatial arrangements of landmarks, as compared to recognition from object identity alone. Analyses of eye-tracking data revealed a specific visual encoding strategy which involved linking landmarks together through sequences of eye-movements. Importantly, the use of this strategy predicted place recognition performance. Older adults were less likely to use this encoding strategy than younger adults, reflecting a difference in the underlying visual attention mechanisms which aid place learning. These experiments also revealed that perspective taking mechanisms during place recognition were not affected by cognitive ageing.

Four route navigation experiments demonstrated a persistent deficit in route learning and recall. Specifically, during learning older adults are slower at learning landmark-direction associations and the sequence in which places and landmarks are encountered. We found that after a route was learned successfully, which took longer for older adults, landmark-direction memory was similar between age groups, but the age-related deficit in landmark sequence knowledge remained. We suggest that this pattern of results can be explained by the prioritisation of limited attentional resources by older adults to acquire specific types of route knowledge at the expense of others. Additional analyses showed that memory for sequences of landmarks exhibited similar serial memory patterns to those found for other sequences, such as word lists, in both younger and older adults.

Eye-tracking measures from one of the route navigation studies were related to navigation performance but did not differ between age groups. This finding suggests that unlike place learning, visual attention mechanisms do not contribute to age-related differences in route navigation ability. Consistent with this result, measures of attentional engagement in the

same study also revealed similar regulation of attentional resources along different portions of a route for older and younger adults.

Overall, the work presented in this thesis provides evidence of both intact and degraded mechanisms which contribute to navigation ability in older adults. Our findings show that regulation of attentional engagement, the control of overt visual attention during route learning, encoding of landmark identities, and perspective-taking mechanisms are similar between younger and older adults. In contrast, visual encoding strategies during place learning differ between age-groups, as does object-location binding mechanisms. Associating directions with landmarks during route learning does show age related slowing, which is overcome with several learning attempts. Age-related decline in landmark and place sequence learning remains impaired even after a route is learned. These results improve our understanding of the cognitive mechanisms which underlie navigation impairment in ageing humans, as well as shedding light on which cognitive mechanisms can still be relied upon for successful navigation.

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Authors declaration

I hereby declare that the work presented in this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

This thesis conforms to an ‘integrated thesis’ format in which the experimental chapters consist of articles written in a style that is appropriate for publication in peer reviewed journals. The initial and final chapters present an introduction and discussion of the field of research undertaken, respectively. The main text in each chapter is presented as exact replications of the submitted manuscript and inevitably, there is some repetition as a consequence. In addition, Chapter 2 includes a summary of a published article which the author of this thesis contributed to as a co-author but was not responsible for a majority of the work.

The articles included in this thesis are at various stages of the publication/review process, and the status of each paper is summarised below.

Journal articles

Chapter 2 is a summary of a published article, the full version of which is presented in the appendix of this thesis: Muffato, V., Hilton, C., Meneghetti, C., De Beni, R., & Wiener, J. M. (2019). Evidence for age-related deficits in object-location binding during place recognition. *Hippocampus*, *February*, 1–9. https://doi.org/10.1002/hipo.23099

Chapter 3 consists of one published article: Hilton, C., Muffato, V., Slattery, T. J., Miellet, S., & Wiener, J. (2020). Differences in Encoding Strategy as a Potential Explanation for Age-Related Decline in Place Recognition Ability. *Frontiers in Psychology*, *11*(September). https://doi.org/10.3389/fpsyg.2020.02182

Chapter 4 consists of one published article: Hilton, C., Miellet, S., Slattery, T. J., & Wiener, J. (2019). Are age-related deficits in route learning related to control of visual attention? *Psychological Research*, *0*(0), 0. https://doi.org/10.1007/s00426-019-01159-5

Chapter 5 consists of one published article: Hilton, C., Johnson, A., Slattery, T. J., Miellet, S., & Wiener, J. M. (2021). The impact of cognitive aging on route learning rate and the acquisition of landmark knowledge. *Cognition*, *207*(November 2020), 104524. https://doi.org/10.1016/j.cognition.2020.104524

Chapter 6 consists of one article currently under review: Hilton, C., Wiener, J. M., & Johnson, A. (under review). Serial memory for landmarks encountered during route navigation. *Quarterly Journal of Experimental Psychology*.

Conference meetings

Hilton, C., Miellet, S., Slattery, T. J., & Wiener, J. (2019). Serial position memory across age groups for route landmarks. *Poster presented at: 21st European Society Cognitive Psychology Conference (ESCoP)*. Tenerife, Spain.

Hilton, C., Johnson, A., Slattery, T. J., Miellet, S., & Wiener, J (2019). Route learning and ageing: Are older adults really worse navigators? *Talk presented at: Experimental Psychological Society Meeting (EPS).* Bournemouth, UK.

Hilton, C., Muffato, V., Slattery, T. J., Miellet, S., & Wiener, J. (2018). Are age-related differences in place recognition ability reflected in gaze strategy? *Poster presented at: 2nd Interdisciplinary Symposium on Spatial Cognition in Aging & Neurodegeneration (iScan).* Magdeburg, Germany.

Hilton, C., Johnson, A., Slattery, T. J., Miellet, S., & Wiener, J (2018). Aging and route learning: The impact of training and sequence knowledge. *Talk presented at: 7th International Conference Spatial Cognition (ICSC).* Rome, Italy.

Hilton, C., Johnson, A., Slattery, T. J., Miellet, S., & Wiener, J (2018). Route learning and ageing: Are older adults really worse navigators? *Poster presented at: 2nd Interdisciplinary Navigation Symposium (iNav).* Montreal, Canada.

Hilton, C., Miellet, S., Slattery, T. J., & Wiener, J. (2017). An exploration into the effects of ageing on general control of attention during route learning in a complex environment. *Poster presented at: 20thEuropean Society Cognitive Psychology Conference (ESCoP).* Potsdam, Germany.

Chapter 1

Introduction

Spatial navigation is one of the most fundamental behaviours in daily life. From small scale movement through one's home, to traversing though cities, the ability to learn and use information about space is integral to survival. As such, humans utilise a wide array of cognitive and perceptual mechanisms to achieve navigation goals. There is a vast body of evidence showing that the ability to navigate undergoes marked decline over the typical ageing trajectory. Given the importance of navigation for daily function, it is not surprising that older adults who have problems with navigation, experience a loss of independence and overall quality of life. However, what is less well understood is how age-related changes in the underlying cognitive functions which support orientation and navigation behaviour contribute to declining navigation abilities.

In this introduction I first provide a general overview of human navigation, with extra detail given to route navigation which features heavily in this thesis. I then discuss the effect of cognitive ageing on navigation ability. Finally, I will briefly discuss the underlying neural mechanisms that support navigation behaviour. The aim of the experimental work presented in this thesis is to assess the contribution of attentional and learning mechanisms to the age-related changes in spatial navigation ability. Specifically, to investigate how age-related differences in control of visual attention, visual encoding strategies, engagement of attentional resources, learning rates and strategies relate to declines in spatial abilities. More detailed discussion of the state-of-the-art that is relevant for the specific research questions addressed in this thesis will be provided in the individual experimental chapters that follow this general introduction.

1.1 An overview of human navigation

1.1.1 Spatial navigation tasks

In this section I will provide a brief overview of several purposes for which humans navigate and specify the navigation tasks covered in this thesis. On a broad level, navigation consists of locomotion and wayfinding (Montello, 2009). Locomotion refers to the guidance of movement in vista scale space (i.e. the immediate visible space surrounding the navigator) including steering, obstacle avoidance and approaching objects. Locomotion behaviour relies on current sensory-motor input to achieve safe and efficient movement, and does not involve reference to a wider representation of space in spatial memory (Mallot, 1999).

Wayfinding refers to guided movement through space which is beyond the immediate sensory input. Specifically, wayfinding can be considered as an agents' interaction with space informed by their current location, their goal location, and their spatial knowledge. According to Montello (2009), wayfinding incorporates multiple cognitive processes including memory, decision making and planning which act on perceptual information from multiple modalities (of which vision is the most prominent, Ekstrom, 2015). The work in this thesis focuses on the wayfinding aspect of navigation, specifically on self-guided wayfinding without the use of navigation aids such as maps or GPS and is not concerned with locomotion. Whilst the use of navigation aids is interesting, and important given the modern widespread availability of GPS, it taps into different mechanisms than the self-guided, unaided wayfinding under examination in the present work (Ishikawa et al., 2008; Münzer et al., 2012). Throughout this thesis, the term navigation is often used interchangeably with wayfinding.

Unaided wayfinding requires navigators to rely on their internally held representation of the environment. Wayfinding incorporates a wide array of tasks, which vary in the goal to be achieved and the mechanisms which are used. Wiener et al. (2009) proposed a taxonomy which describes different wayfinding tasks depending on the availability of spatial knowledge (see Figure 1-1). For example, if a navigator is traversing a familiar environment without a specific destination in mind, then they are pleasure walking. In this scenario, navigators are aware of their current location and the possible locations they can travel to from their position. As they move through the environment, they track their position to avoid disorientation, a process known as spatial updating (Wolbers et al., 2008). Navigation decisions for individuals on a pleasure walk are not taken with reference to a specific destination (perhaps instead taken with reference to the desired duration of walk, or the aesthetic pleasure derived from the possible to-be-visited places).

Alternatively, an individual may need to navigate from their current location to a specific goal destination. As described in the taxonomy by Wiener et al. (2009), this can take different forms depending on the representation of the environment held by the navigator. An individual on holiday in Paris may know their current location (their hotel) and have a goal location in mind (the Eiffel tower), But having never visited the city before, they may not have any knowledge about the space in between the two locations. In this case, the navigator could see the Eiffel tower in the distance and move in that direction in the process of path finding. If the holiday maker wishes to return to the Eiffel Tower on another day, they can now rely on the route they previously learned to reach their goal destination. In this case, the navigator is making decisions with reference to their goal destination. After the visit to the Eiffel Tower, the navigator must now retrace the same route (i.e. follow a route in the reverse direction) to return to their hotel.

The route-based navigation described in the scenario above is a main focus of the work presented in this thesis, specifically in Chapters 4 and 5. Humans learn and rely on specific routes through the environment for much of their daily navigation needs (e.g. commuting between home and work). Routes can be learned using different types of information from the environment, and over time the information from several routes may be integrated into a wider representation of the environment. This integrated representation may allow for yet again different navigation behaviours such as shortcutting or planning novel routes. The types and acquisition of spatial knowledge will be covered in the next section.

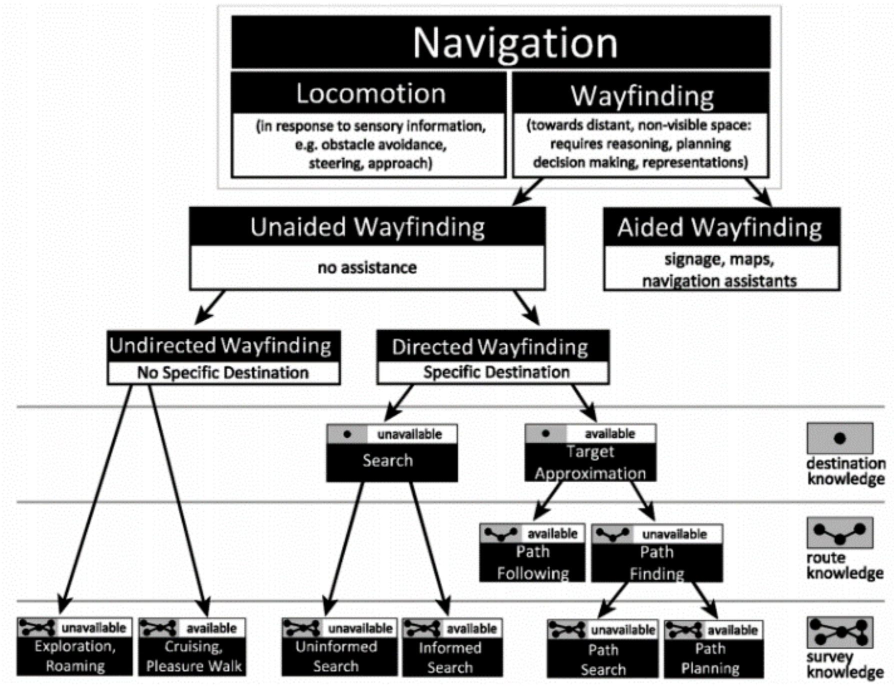

Figure 1-1 - A taxonomy of wayfinding tasks from Wiener et al. (2009), organised by the availability of different types of spatial knowledge. Figure taken from Wiener et al. (2009).

1.1.2 Spatial knowledge

Navigation behaviour is underpinned by internal spatial knowledge about the external world. The extent and type of knowledge held defines the tasks that can be completed by the navigator, as introduced in the previous section. Here I will expand on the types and nature of spatial knowledge that can be acquired and the mechanisms by which such knowledge is learned. The two fundamental navigation mechanisms are path integration and landmark navigation (Zhao & Warren, 2015).

1.1.2.1 Path integration

Path integration refers to the integration of self-motion to track the navigator's position and orientation in the environment through the estimation of distance travelled and angles of turning relative to a starting location. Self-motion information comes from the use of idiothetic information (information which is generated internally) such as vestibular feedback, proprioception, motor efference copy (McNaughton et al., 2006) and allothetic cues (external information) such as optic flow (Gramann et al., 2005; although recent evidence casts doubt on the involvement of optic flow in path integration, Chrastil & Warren, 2020). This information allows the navigator to track their movement through the environment and to acquire information about the distance between places or landmarks and the relative positioning of places to each other. However, the path integration system is not a perfect estimator of such information and accumulates error with increasing travel distance (Stangl et al., 2020). This may occur due to compounding of either path encoding errors (i.e. error when encoding the distance and angle of the current path; Klatzky et al., 1999) or homing vector errors (i.e. error when computing the return vector; Chrastil et al., 2015; Wiener et al., 2011), and recent research also implicates response execution error as a contribution to path integration errors (i.e. error in executing the planned return trajectory; Chrastil & Warren, 2020).

Path integration is sufficient for navigation in sparse environments for the purposes of returning to a start location. However, path integration alone does not allow for more advanced navigation behaviour. Moving from a start to a goal location, as in route navigation, often requires long outbound trajectories over which path integration errors accumulate (Stangl et al., 2020). In addition, complex environments often require multiple heading changes which increase the opportunity for errors. As such, landmark information is used to aid navigation. Landmarks are salient features or objects in the environment which are used as cues for navigation and serve as the foundations for spatial representations of large-scale spaces.

1.1.2.2 Landmark and place knowledge

"When I see the church, I am near the town centre"

Learning of landmarks is often considered one of the earliest stages of spatial learning. On the most basic level, landmarks allow for recognition of places in the environment which allows the navigator to know their location. Not all objects are equally suited to be a landmark. Stankiewicz and Kalia (2007) defined three important landmark properties: (1)

persistency (remain in the same location), (2) saliency (easily identifiable) and (3) informativeness (provide relevant information for the navigation task). The informativeness of a landmark depends on several dimensions. A landmark should be unique in the environment (Grzeschik et al., 2019), else confusion may arise when a similar or identical object is encountered in a different place. Additionally, for an object or feature to serve as a landmark it needs to be located at a navigationally relevant location (Chan et al., 2012).

Navigationally relevant locations can be defined as goal locations or as decision points in the environment (Allen & Kirasic, 2003; Janzen et al., 2007). Recognition memory for objects located at decision points is superior to that for objects located at non-decision points, such as simple turns with only one direction of travel (Janzen, 2006). Moreover, neuroimaging studies have demonstrated that the recognition of objects at decision points selectively recruits the parahippocampal gyrus (Janzen & van Turennout, 2004; Janzen & Weststeijn, 2007). This result suggests specific (neural) representations for objects used as landmarks during route navigation as compared to objects which are not used as landmarks. Those representations are formed rapidly and are long lasting (Janzen et al., 2007).

Using landmarks to recognise important places is often more complex than identifying one salient object. Many places in the world are made up of similar objects and features, and there is not always a unique and distinctive object to serve as a lone landmark. In these situations, navigators must integrate information about several of the objects into their representation of the place, including multiple object identities and the arrangement of those objects in space (Hartley et al., 2007). This aspect of place learning and recognition behaviour is expanded on in Chapters 2 and 3.

In summary, spatial knowledge is supported by the use of objects as landmarks. Effective landmarks fulfil several criteria including being located at navigationally relevant locations, remaining in place over time, and being visually identifiable and unique to avoid confusion. Landmarks are used to recognise places in the environment. In the next section I will discuss how landmarks are used to support route navigation.

1.1.2.3 Route knowledge

“To get from home to the town centre, I must turn left at the post office, go straight on at the school and then go past the church”

Route knowledge enables the navigation from a specific start location to a specific goal location in the environment. The simplest knowledge a navigator could acquire to learn a route between two locations is an ordered vector of directions (sometimes referred to as a simple response strategy; Iglói et al., 2009; Rondi-Reig et al., 2006). Such knowledge could allow the navigator to repeat the route by sequentially recalling the directions (e.g. turn left, then continue straight and then turn right), however this process is error prone for two reasons. First, whilst a simple response strategy is feasible for short routes where the number of turns to be encoded/recalled falls with immediate memory capacity, longer routes are likely to exceed capacity limits and result in failure to complete the route. Second, any form of error, such as taking a wrong turn, is catastrophic and cannot be corrected since the remainder of directions to be executed will no longer bring the navigator to the intended goal.

Successful learning and navigation of routes typically relies largely on the use of landmarks (Denis et al., 2014; Foo et al., 2007). Not only do landmarks allow the navigator to self-localise in the environment and identify the important decision points along routes, but they are used as cues for action (Foo et al., 2005). Waller and Lippa (2007) presented a series of experiments in which participants had to learn routes through a series of connected rooms, taking either left or right turns in each room (decision points). Rooms were either absent of landmarks such that participants had to rely on response learning (i.e. left, left, right, left), contained landmarks located above each travel direction, or contained landmarks neutrally placed equidistant between possible directions of travel. Waller and Lippa (2007) reported that participants could only rely on response learning for the intial part of the route (up to 5 intersections). Correct travel directions were learned faster at intersections where landmarks were placed in the directions of travel, as compared to when the landmarks were neutrally placed. Waller and Lippa (2007) suggested that these findings reflect two ways that a landmark can support route navigation: as beacons or as associative cues. The beacon strategy involves encoding landmarks which lie in the direction of travel such that a navigator can ‘move towards the tree’. The associative cue strategy on the other hand involves the navigator recalling a specific directional response such as ‘turn left at the tree’.

Whilst both the beacon and the associative cue strategies rely upon the encoding of landmark identities, they differ in whether the response is also encoded in memory. Associative cue knowledge relies on stimulus-response learning (SR), where the landmark and movement direction is bound together in memory. Using landmarks as beacons on the other hand requires no such SR learning, as the response is encoded in the position of the landmark in space, which the navigator simply moves towards. Here, the memory content is the identity of the correct landmarks along the route (those which indicate the necessary travel direction), and a general response rule such as “move towards the correct landmark”. As a result, the learning and memory demand for landmarks used as beacons is lower (Waller and Lippa, 2007). However, the beacon strategy relies upon specific positioning of the landmarks in space, where they are clearly indicative of a certain travel direction. In cases in which the landmark placement is not clearly indicative of a certain travel direction and thus the application of a rule ("turn towards the landmark") does not yield a clear response option, the beacon strategy is not viable whereas the associative cue strategy still allows successful navigation.

Representations of places and actions could be held in isolation, with route knowledge being formed from lists of unrelated SR associations. However, we know that navigators acquire more knowledge about routes over time (Trullier et al., 1997). Places are tied together as stimulus-response-stimulus associations (SRS; Schinazi & Epstein, 2010; Trullier et al., 1997), where a response at one location is tied to the upcoming place that will be encountered, for example: "turning left at the post office leads to the school". SRS associations provide sequence knowledge which allow navigators to generate expectations about the to-be-encountered intersection so that responses can be prepared, and the navigators' trajectory can be monitored for errors .

There are also route navigation scenarios which cannot be solved without linked SRS knowledge. Strickrodt et al. (2015) presented routes where each intersection was structurally identical, with one centrally placed landmark. Some landmarks were repeated along the route that the participants were required to learn, making these intersections visually identical. If SR knowledge was not linked to the previous or subsequent stimuli (i.e. as SRS associations), participants would not be able to disambiguate the identical intersections. In fact, the results showed that participants were able to recall directions at multiple intersections containing the same landmark, demonstrating the presence of SRS knowledge.

In order to rule out the possibility of a counting strategy (e.g. "turn left at the first church and right at the second church"), Strickrodt et al. (2015) also showed participants short segments of two intersections in a randomised order from the route, so that a counting strategy would not work. In that task, participants were passively navigated past one random intersection from the route to the next, at which they had to recall the correct direction of travel. Navigators were able to use information from the first intersection to disambiguate the second intersection when it contained a landmark which was also located elsewhere along the route. Even more impressive is that when pairs of intersections were identical along the route, the navigators could still disambiguate them based on the direction of travel that linked those places. This study not only supports the notion that route knowledge encompasses sequence information, but Strickrodt et al. (2015) argued that such sequence knowledge is integrated with directional information which can be used to resolve complex navigation problems.

1.1.2.4 Beyond route knowledge – the cognitive map

"The new shopping mall is 2km south west of the town centre"

For decades it has been accepted that spatial knowledge does not just exist in lone vectors of routes or isolated representation of places, with no knowledge of how the different places or routes relate to each other. Instead, information about several places is integrated into wider representations of the environment, known as the cognitive map (John O'Keefe & Nadel, 1978; Tolman, 1948). There is much debate as to the content of the cognitive map, its form and structure and how it is developed. Those questions are not a subject of the work presented in this thesis, and thus this section will only provide a brief introduction to cognitive maps.

So far, I have discussed spatial knowledge as associative formations between landmarks, places, and directional information. In addition to this type of information, navigators acquire more fine-grained knowledge about distances and angles between objects and places in the environment. Such knowledge is usually referred to as metric knowledge, in the sense that it represents information about space on a continuous interval or ratio scale (Ishikawa & Montello, 2006).

Traditional models of spatial learning posit stage-based development of spatial representations, where information about places and landmarks is learned first, and then information about routes is acquired (e.g. Golledge et al., 1985; Siegel & White, 1975; Thorndyke & Goldin, 1983). Only after these stages are completed, do those models suggest that navigators begin to integrate metric information into a survey knowledge representation. Montello (1998) describes such models as the dominant approach, since early navigation research relied heavily on this stage-based framework. Alternative models suggest that the different types of spatial learning happen in parallel, with the acquisition of metric information beginning immediately when exposed to a new environment (Buchner & Jansen-Osmann, 2008; Ishikawa & Montello, 2006; Montello, 1998). This has been described as the continuous model (see Figure 1-2).

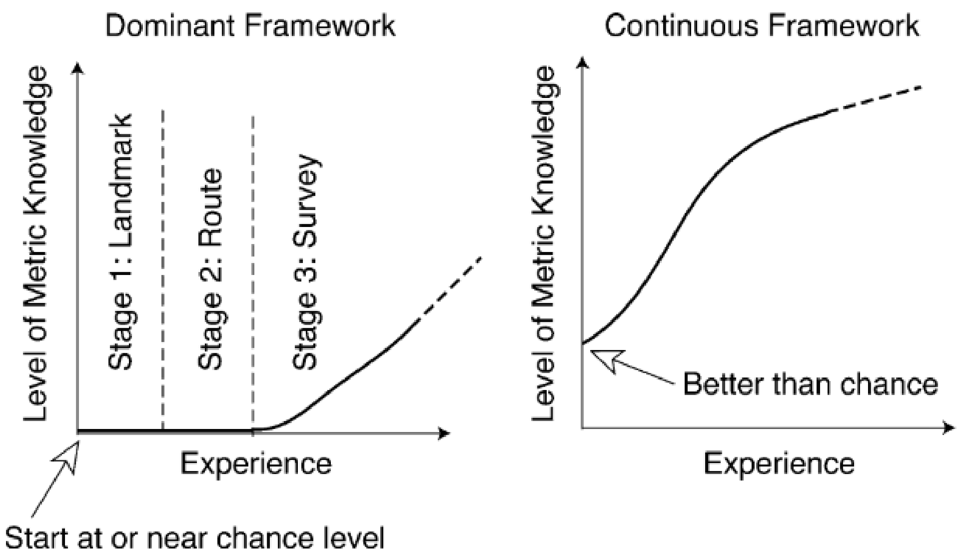

Figure 1-2 - Ishiwawa and Montello's (2006) distinction between different frameworks on the acquisition of metric knowledge. The left plot represents a stage-based approach as in Siegel and White (1975), where metric knowledge is thought to be acquired only after categorical landmark and route representations have formed. The right plot suggests that metric knowledge constantly accumulates from the very first exposure to a novel environment. Figure taken from Ishiwawa and Montello (2006).

There is now much evidence to suggest that navigators do acquire several types of spatial knowledge in parallel (Kim & Bock, 2020). However, it should be noted that there are marked individual differences in spatial learning (Hegarty & Waller, 2009; Weisberg et al., 2014). Ishikawa and Montello (2006), for example, demonstrated that some navigators develop high level metric representation of the environment astonishingly quickly, whilst other navigators take much longer, and some navigators never learn much metric information at all. On the whole, however, the prevailing current view is that as familiarity with an environment increases, navigators form more holistic representations about the environment in a continuous manner (Buchner & Jansen-Osmann, 2008; Ishikawa & Montello, 2006; Kim & Bock, 2020).

The stage model approach is still useful for understanding spatial learning, however. Although navigators acquire many types of information concurrently, not all information is of equal difficulty to encode (Poldrack et al., 2001). Many studies show that representations of landmark and place identities form quicker than accurate survey knowledge about the relationships between those places (Foo et al., 2005). Thus, although multiple types of spatial information are acquired in parallel, it is longer before metric-based survey knowledge can be relied upon for spatial decision making compared to route knowledge. Indeed, when given the opportunity to learn an environment from a map which provides accurate information about distances and configurations of places, accurate metric representations are formed quicker than when learning from unaided navigation alone (Zhang et al., 2014).

There is also a logical dependency for the development of spatial representations. For example, a navigator can hardly learn the distance between two locations, or the directions needed to travel between them, if they have not encoded the identity of the locations to begin with (discussed in Chrastil, 2013). In addition, the goal of the navigation behaviour can alter the knowledge which needs to be acquired (Hölscher et al., 2009; Meilinger et al., 2007), for example following a route typically requires S-R learning, whilst shortcutting behaviour relies on metric knowledge (Mallot & Basten, 2009). Indeed, Hartley et al. (2003) suggested that navigators predominately depend on S-R representations for route based navigation, and survey based learning (regarding the allocentric arrangement of places) for tasks that require more goal flexible behaviour such as path finding and planning. This is likely because the S-R strategy for route navigation is based on automatic, recognition triggered responses that are computationally less demanding than developing and using a survey representation (Poldrack et al., 2001).

The format of the cognitive map has often been discussed to exist as a global coordinate system (Franz et al., 2005), in which places are represented in a global, environmental reference frame (see Figure 1-3a). From this representation, navigators can plan routes between places, and even plot novel trajectories that have not been travelled before, such as shortcuts. An alternative proposal is the representation of space as a graph, which begins as a topological representation of places (nodes; see Figure 1-3b) and the categorical links between those places (edges). Over time, the edges between places become labelled with metric information (see Figure 1-3c).

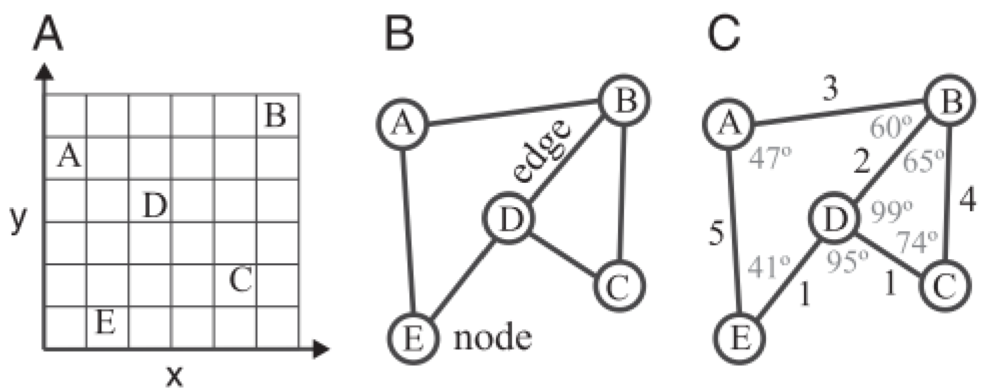

Figure 1-3 – A visualisation of a cognitive map where places are embedded in a common Euclidean coordinate system (a); or where places are represented as nodes in a linked graph in a topological format (b); or a labelled *graph where the connections between place nodes are labelled with metric distance and angle information (c). Figure taken from* Warren et al. (2017).

Chrastil (2013) proposed a framework which incorporates landmark, route, graph, and survey knowledge (see Figure 1-4). In this framework, she defines survey knowledge as the global coordinate system shown in Figure 1-3a, and graph knowledge as the topological format in Figure 1-3b. It is acknowledged that there is a parallel acquisition of multiple types of spatial knowledge, but that each category of spatial knowledge develops in a logical order. For example, navigators can, in one instance, acquire information about a landmark identity, the direction associated with it, and its preceding landmark. However, incorporation of the latter two chunks of information into a route representation depends on the first successful landmark representation being formed. The same principle is applied to survey knowledge, which is incorporated based on the skeleton of graph representations.

	Landmark	Route	Graph	Survey
1	• Place recognition *Scenes and views*	• Place recognition *Scenes and views*	• Place recognition *Scenes and views* *Place within the larger environment*	• Place recognition *Scenes and views* *Place within the larger environment*
2		• Sequence learning	• Sequence learning	
3	• Identifying decision points	• Identifying decision points	• Identifying decision points	
4		• Response learning		
5		• Forming associations	• Forming associations	
6			• Locating the goal *Relate goal and current location* *Transformation between allo- and egocentric perspectives*	• Locating the goal *Relate goal and current location* *Transformation between allo- and egocentric perspectives*
7				• Path integration

The four categories of spatial knowledge are divided into seven cognitive processes, some of which are further divided into subprocesses

Figure 1-4 - A taxonomy of spatial knowledge from Chrastil (2013) and the spatial processes which are supported by different knowledge types. Figure taken from Chrastil (2013).

In summary, navigators acquire several types of spatial knowledge which tie into specific spatial representations, such as stimulus-response associations as route knowledge, and metric distances as survey knowledge. Although these representations can develop in parallel, the task to be completed guides learning towards a dominant representation that is most appropriate given the specific task demands. While route knowledge allows navigation between two places, cognitive map like representations allow for more flexible behaviour, such as planning and navigating novel routes, and taking short cuts. There have been many other proposals about the structure and format of the cognitive map which have not been discussed here, since the work in this thesis covers predominantly landmark and route knowledge. For the purpose of this thesis, the cognitive map will be considered as any spatial knowledge that allows for goal-dependent, flexible navigation behaviour in an environment.

1.1.3 Reference frames

There are two predominant reference frames that navigators use to encode spatial information: egocentric and allocentric reference frames (Klatzky, 1998). Egocentric encoding refers to the encoding of spatial information from a person centred, viewpoint dependent frame of reference (see Figure 1-5 left). Here, the positions of objects in space are encoded relative to the observer as self-object representations. An allocentric reference frame on the other hand refers to viewpoint independent, environment centred encoding, known as object-object representations (see Figure 1-5 right).

Figure 1-5 – A visualisation of an egocentric reference frame (left) where the coordinate system axis is observer centred and objects in the environment are defined in reference to the observer; and an allocentric reference frame (right) where the object locations are defined by a coordinate system that is world centred and observer independent. Figure taken from Meilinger and Vosgerau (2010).

To illustrate the relative utility of the two reference frames, let us consider an example of place learning. The framework from Chrastil (2013) indicates that place recognition is supported by pure landmark knowledge. By identifying a unique object in the environment, the navigator can recognise that they have visited this place before. However, imagine a situation in which the navigator must recognise a place which contains objects that are found also in several other places (for example a road junction containing a stop sign, a bus stop and a tree). In this scenario, identifying the objects alone is not sufficient to distinguish this place from ones that are similar. Instead, the navigator must also use information about the way objects are positioned in space. If those object positions are encoded in an egocentric reference frame (e.g. the bus stop was to the left, the tree is directly ahead and the stop sign was to the right) then place recognition can be achieved as long as the navigator observes the place from the same viewpoint as during encoding.

However, landmark information about a place encoded in an egocentric reference frame is not sufficient for recognition if the navigator approaches the place from a different viewpoint (e.g. from a different road, the stop sign in the above example could be on the left of the navigator instead of to the right). Of course, it is possible to engage in spatial perspective taking to match other perspectives to the stored egocentric representation, however this is a computationally costly and error prone process (see Chapters 2 and 3). Additionally, the navigator must know that they have arrived at the place from a different perspective to begin with. That is, if the navigator is not aware that they arrived from a different road, then they may simply execute recognition triggered responses upon identifying the landmarks (an error which older adults are prone to making as discussed later in this chapter - Wiener et al., 2013).

Inefficiencies of an egocentric, viewpoint-dependent representation can be solved by encoding the allocentric arrangement of objects. In this case, the ability to recognise the arrangement of objects at the intersection regardless of the navigator's own position in space. This is because an allocentric representation involves the relationship between the landmarks in space, which remain the same regardless of the navigator's viewpoint. Thus, the perception of those relationships, even from a different perspective, is enough to activate that place representation for recognition.

Such methods of encoding space apply beyond the small-scale space depicted in Figure 1-5, and described in the example above. When learning a larger space, the information can be embedded in a navigator centred, egocentric reference frame such that relationships between places and the actions needed to move between them are encoded from the navigator's viewpoint. Route knowledge is largely considered to be encoded in an egocentric format. Stimulus-response information such as 'turn left at the tree' is only functional if the navigator approaches the tree from the same viewpoint each time (Wiener et al., 2013). The same is true for place sequence information, which is only accurate for a one-dimensional, unidirectional route representation (Buchner & Jansen-Osmann, 2008; Rondi-Reig et al., 2006; Trullier et al., 1997).

Survey representations of the environment on the other hand, reflect the use of an allocentric reference frame, in that the relationships between places are embedded in a reference frame that is related to the environment and is independent of the position of the navigator (Boccia et al., 2016). This involves integrating information learned from separate routes through an environment together. Such integration can be achieved via the formation of topological associations of places from different routes, particularly if the routes overlap in some way (Grzeschik et al., 2020). Additionally, metric knowledge derived from path integration mechanisms and spatial updating over time can be used to estimate the relationship between places, even if the navigator has never travelled between them.

Work from Gramann et al. (2005) demonstrates that navigators can have an inherent proclivity towards a particular reference frame (a further reflection of individual differences in navigation behaviour), or that they can even have the tendency to switch between egocentric and allocentric reference frames over time (c.f. Epstein et al., 2005; Iglói et al., 2009). Navigators do not just switch the reference frame during encoding, but also have to transform information that is already held in one reference frame into the other (Nori et al., 2018). For example, information held in an allocentric format needs to be transformed into an egocentric format so that navigational actions can be carried out (since the navigator is always experiencing the world from their egocentric viewpoint). This transformation between reference frames is considered to be a feature of graph or survey representations (see Figure 1-4, Chrastil, 2013), whilst landmark, place and route knowledge are largely confined to an egocentric format.

Given the many different types of spatial information that can be learned, and the various ways of representing that information, it is not surprising that there is not one set trajectory for learning a novel environment. In fact, different navigation tasks may be best solved using different types of knowledge, and even the same task may be solved in different ways. This variation in how a navigation task can be solved is often referred to as strategy use. The work presented in this thesis is confined to place and route learning and thus is primarily concerned with egocentric representations of space.

1.2 The effect of cognitive ageing on navigation ability

1.2.1 Typical ageing and navigation

Much research has now established the existence of a persistent decline in spatial navigation abilities along the typical ageing trajectory (for reviews see: Klencklen et al., 2012; Lester et al., 2017; Lithfous et al., 2013; Moffat, 2009; van der Ham & Claessen, 2020). Not all navigation abilities are affected equally, however. Orienting in familiar environments poses little trouble for older adults (Kirasic, 1991; Klencklen et al., 2012; Willis, 1991), but age-related deficits are apparent in the learning and navigation of novel environments.

Older adults have been shown to have difficulty with navigation tasks that require allocentric processing. They are impaired in encoding object and place positions in an allocentric reference frame (Fernandez-Baizan et al., 2019), which leads to diminished survey knowledge of the environment (Rodgers et al., 2012). This means that the survey representation that older adults possess is of lower quality than that of younger adults, and thus older adults struggle with navigation tasks such as planning novel routes between known locations. In contrast, it is generally thought that the encoding and retrieval of information in an egocentric reference frame is preserved in older adults (for a review of the effect of ageing on egocentric and allocentric reference frames see Colombo et al., 2017). However, the conversion of information between reference frames and switching between reference frames when navigating is also impaired (Harris & Wolbers, 2014).

Age-related differences between allocentric and egocentric navigation were demonstrated by Gazova et al. (2013), using a human variant of the Morris Water Maze task. In this task, participants are placed in a circular room with uniformly coloured walls and are asked to find a hidden goal location in the room. Once the participant has found the goal location, they complete a test trial which requires the participant to find the same position again. In the *egocentric only* condition, the participant starts from the same location every time, such that learning a specific set of motor movements from the start location will lead to the goal. In the *allocentric* condition, participants start at a random location in the room so that an egocentric response strategy is not viable. Instead, participants need to encode the goal location by relating it to distinctive landmarks placed on the walls. In this study, older adults performed similar to younger participants in the *egocentric only* condition but were worse at finding the goal location in the *allocentric* condition.

Despite the apparent preservation of egocentric dependent navigation in older adults, several studies showed that older adults experience difficulties with route learning, a prototypical egocentric task. Barrash (1994) found that older adults made significantly more navigation errors than younger adults when attempting to navigate a route just under 500 metres long, even after three exposures to the correct route. Indeed such route navigation deficits are acknowledged by older adults, who self-report poor spatial navigation skills (Allison et al., 2018) and that they try to avoid learning new routes though unfamiliar environments due to the increased difficulty and fear of becoming disoriented (Bryden et al., 2013; Burns, 1999; although some studies report that their older adult samples self-rated their overall sense of direction highly, e.g. De Beni et al., 2006).

Current explanations of age-related route learning deficits focus on the use of landmarks in navigation. When learning routes through a novel environment, older adults do develop at least some limited place knowledge, as evidenced by their ability to recognise and recall landmarks from a route as well as younger adults (Allison & Head, 2017; Cushman et al., 2008; Head & Isom, 2010). These findings demonstrate that older adults at least form landmark knowledge representations about the environment. Interestingly, older adults still experience decreased place recognition ability (Cushman et al., 2008; Head & Isom, 2010). This is likely because many places cannot be identified with pure landmark identity knowledge alone. Chapters 2 and 3 of this thesis focus on how place recognition which requires more than landmark identity knowledge is affected by cognitive ageing.

For route navigation, studies have shown that older adults perform worse than younger adults when recalling information associated with landmarks and places along a route. Wiener et al. (2013) conducted a route learning study in which older and younger participants first saw a video of a route and then were shown intersections from the route at which they had to indicate the correct travel direction. Each intersection contained two landmarks that were arranged such that the spatial configuration of the landmarks was visually distinctive for each possible approach direction (see Figure 1-6). In the test phase, participants were shown the intersections from a different approach direction and their response indicated their navigation strategy as a beacon, associative cue, or configuration strategy (see Figure 1-6 for a detailed method explanation). Wiener et al. (2013) showed that younger adults initially used all three strategies, but after multiple exposures to the route, overwhelmingly adopted the correct allocentric configuration strategy. This strategy involves encoding the spatial arrangement of the landmarks at the intersection which allowed the participants to identify the approach direction during test and therefore the correct direction of travel. The older adults, on the other hand, initially showed a strong preference for a beacon strategy (i.e. turn towards A) compared to either an associative cue or an allocentric configuration strategy. In contrast to the younger adults, the older participants did not shift their strategy, even after six experimental blocks.

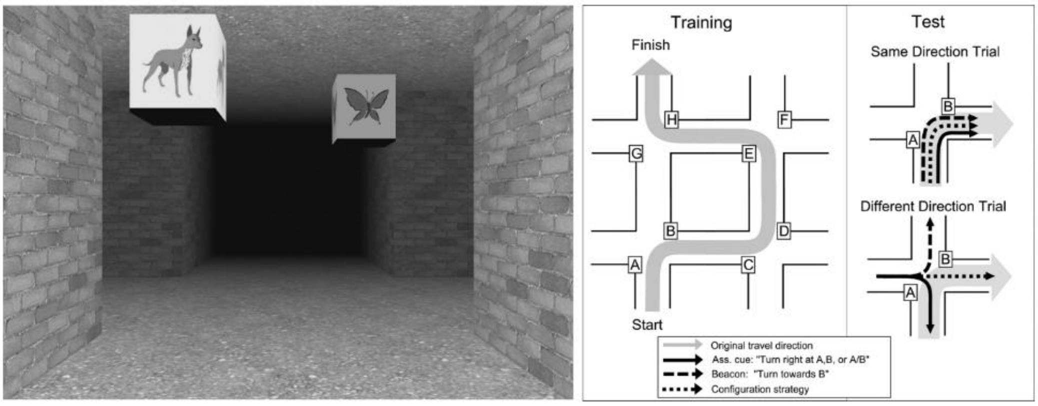

Figure 1-6 - On the left, a screenshot of an intersection used in the virtual environment from Wiener et al. (2013). On the right, a schematic of the route shown to participants during learning, and the two trial types given during the test phase. For the same direction trials, the approach to the intersection is the same as in learning, and all three strategies (beacon, associative cue and configuration) would yield a correct response. In the different direction trials the approach is from a different direction than in learning and the strategies would yield independent responses. In this example, a beacon strategy at the first intersection (turn towards B) yields a 'left response' on the different direction trial; the associative cue strategy (turn right at a/b) would yield a 'right' response; and a configuration strategy would yield a correct 'straight on' response. Figure taken from Wiener et al. (2013).

This preference for a beacon strategy could be due to the fact the movement direction is encoded in the position of the landmark itself, and therefore does not have to be explicitly encoded in memory. However, in route navigation a beacon strategy is not always possible, such as when landmarks are neutrally located (as exampled in the study by Waller & Lippa, 2007), and therefore an associative cue strategy is required. Older adults perform worse than younger adults on tests of associative cue knowledge after learning a route (Allison & Head, 2017; Head & Isom, 2010; Liu et al., 2011; Wiener et al., 2012; Zhong & Moffat, 2016). This has been interpreted as a deficit in the formation of stimulus-response associations (SR; Zhong & Moffat, 2016). In addition to a SR association deficit, older adults also show worse knowledge for the sequence in which landmarks are encountered along a route and for the locations in which landmarks are found (Allison & Head, 2017; Head & Isom, 2010; Wiener et al., 2012; Wilkniss et al., 1997).

In summary, older adults are able to learn and recall landmarks encountered in the environment but experience a range of issues when using them to support navigation. Alongside major deficits in forming allocentric representations of space, older adults display problems with associating directional information with landmarks and recalling the sequence in which landmarks are encountered. Such problems may be related to a lack of flexibility in switching strategies whilst learning a route and limit the range of navigation situations that can be solved by older adults.

1.2.2 Neuroscientific study of ageing and navigation

One major explanatory factor for the navigation deficits experienced by older adults is the atrophy of brain regions which support navigation (Ramanoël et al., 2019). Allocentric processing, and spatial learning more generally, depend on a network of structures, particularly the hippocampus and the entorhinal cortex (Herweg & Kahana, 2018; E. I. Moser et al., 2008; Spiers & Maguire, 2007). These structures contain spatially selective cells known as place cells (Ekstrom et al., 2003; O'Keefe & Dostrovsky, 1971) which are located in the hippocampus, and grid cells which are located in the entorhinal cortex (Hafting et al., 2005).

Place cells increase their firing rate when the navigator (often studied in non-human animals such as rodents in single cell recordings or, more rarely, in epilepsy patients with surgically placed depth electrodes) traverses a particular spatial location in the environment (Ekstrom et al., 2003; O'Keefe & Dostrovsky, 1971). Grid cells on the other hand, activate when the navigators position coincides with the vertices of a regularly spaced hexagonal grid (Hafting et al., 2005). Grid cells have been shown to map to the scale and boundaries of the environment (Barry et al., 2007), similar to place cells which can be tied to landmark locations (Jeffery, 1998). It is thought that these cell types are crucial for the processing and encoding of allocentric information, with place cells coding for specific locations and grid cells providing the metric for the cognitive map (Hafting et al., 2005; E. I. Moser et al., 2008; M. B. Moser et al., 2015).

The hippocampal and entorhinal brain areas which support allocentric coding are particularly prone to age-related structural and functional changes (Daugherty et al., 2015; Raz et al., 2005; Rodrigue & Raz, 2004). Indeed, when navigating, older adults have reduced activation in the hippocampus which may explain deficits in performing tasks relying on allocentric strategies (Antonova et al., 2009; Daugherty et al., 2015; Konishi et al., 2013; Meulenbroek et al., 2004; Moffat et al., 2006). Additionally, several other brain regions play a role in the navigation network, such as the translation of information between egocentric and allocentric reference frames in the retrosplenial cortex (Mitchell et al., 2018; Wolbers & Büchel, 2005). The retrosplenial cortex also shows reduced activation in older adults during navigation (Moffat et al., 2006; also in aged rodents Ash et al., 2016), possibly accounting for deficits in strategy switching for older adults (Harris & Wolbers, 2014). In contrast, brain regions which support egocentric navigation behaviour remain relatively unaffected by the ageing process.

Activation in the striatum, particularly the caudate, is associated with egocentric navigation (Bohbot et al., 2007; Burgess, 2008; Cook & Kesner, 1988; Hartley et al., 2003; Iaria et al., 2003). Older adults demonstrate sustained, and sometimes increased, activation in striatal circuits when completing a range of navigation tasks (Bohbot et al., 2012; Konishi et al., 2013; Schuck et al., 2015). Interestingly, this functional preservation occurs even though the caudate undergoes some age-related shrinkage (Raz et al., 2003), which is consistent with the lack of correlation between caudate volume and episodic memory, working memory and visuospatial abilities, which incidentally correlate with hippocampal volume (Storandt et al., 2009). This functional preservation of the caudate has been suggested as evidence for preserved egocentric coding in older adults (Wiener et al., 2013; Zhong & Moffat, 2018).

Preserved striatal activation during navigation, alongside the marked decrease in hippocampal activation (and volume) in older navigators, can account for overwhelming preference for egocentric strategies in older adults (Bohbot et al., 2012; Konishi et al., 2013; Schuck et al., 2015). Indeed, Allison et al. (2016) found that the occurrence of hippocampal atrophy in early (preclinical) Alzheimer’s Disease coincided with declines in allocentric cognitive mapping ability, whilst route learning remained relatively unaffected (compared to age matched controls) until the disease progressed to the caudate, when route navigation deficits emerge. However, despite the preservation of brain regions supporting egocentric navigation and the bias towards such strategies, older adults still experience declines in egocentric task performance, such as in route navigation.

It is possible that unlike allocentric encoding, impairments in which can be traced to the specific supporting neural coding network, difficulties in egocentric encoding cannot be fully explained by age-related decline in the specific network supporting it per se (Colombo et al., 2017). Instead, age-related difficulties in egocentric navigation may be a result of changes in other aspects of cognition which, although not navigation specific, affect the information supplied to the navigation system (Colombo et al., 2017; Zhong & Moffat, 2018). Zhong and Moffat (2018) highlighted the additional recruitment of prefrontal regions in older adults as evidence for the role of executive functions such as attention in spatial learning in older adults, as well as the role of associative learning mechanisms in route navigation deficits (also see Zhong & Moffat, 2016).

The neuroscience of cognitive ageing and spatial navigation declines is not the target of investigation for the work in this thesis, hence the omission of other neurological components of the navigation system from this discussion (e.g. head direction cells, boundary vector cells etc.). The work in this thesis is about how age-related changes in egocentric place and route learning are reflected on a cognitive level, particularly to investigate the role of attention and learning mechanisms.

1.2.3 Human ageing

Humans undergo a host of physiological and cognitive changes throughout the adult lifespan (Andrews-Hanna et al., 2007). The World Health Organisation defines the older age of life to begin between 60 and 65 years of age (WHO, 2020). Many studies of ageing and spatial navigation use such ages to define their older adult populations (as reported in a literature review by van der Ham & Claessen, 2020). In fact, there has long been the suggestion in ageing research that a fourth, older old age begins at around 70 years old (Baltes, 1998; Baltes & Smith, 2003). Some studies have also grouped their participants in such a manner, including the first study presented in this thesis (Chapter 2). In that study we found that the spatial ability of interest showed continued linear decline from our 60-70 years age group to our 70-80 years old group. This result is consistent with recent findings from large-scale studies that show a continuous decline in spatial navigation abilities beginning as early as 30 years old (Coutrot et al., 2018; van der Ham et al., 2020).

Thus, interest in age-related decline in navigation ability is not necessarily focused on a 'cliff edge' age at which navigation suddenly becomes difficult, but rather the period of the adult lifespan in which declines in spatial ability have accumulated to such an extent that they significantly impact daily life. Indeed, Barrash (1994) stated that whilst they found that navigation errors increased monotonically with age, they became particularly problematic in the 60-69 years age group and above. As a result, 'older adults' are generally represented by samples aged 60-65+. Other than the first study presented in this thesis, the remaining five experiments also used older adult groups containing participants aged 65+. Although an ideal world would see ageing studied using large and balanced participant groups for each decade of life, such an approach yields significant barriers to the research process due to the challenges of recruiting from an older adult population, and the associated research costs of substantially increased sample sizes (to cover the middle age range in addition to the younger and older adult populations). Thus, the study of older age as a singular group aged 65+ is a balanced approach between feasible research practice and results which can improve our understanding of the effect of ageing on navigation abilities.

Typically ageing humans experience physiological and cognitive changes that are a natural part of the lifespan and occur in the absence of other health conditions (Andrews-Hanna et al., 2007). However, some individuals develop a form of dementia which is associated with additional neurological atrophy that is not part of the natural ageing process. The result of such atypical ageing trajectories is a catastrophic decline in cognitive functioning that is different to that experienced by individuals ageing without dementia. Spatial navigation ability is affected in the very early stages of several forms of dementia (Cherrier et al., 2001; Cushman et al., 2008), most notably Alzheimer’s disease (Allison et al., 2016), and much research seeks to develop navigation-based screening tools to detect early signs of dementia (for a review see Coughlan et al., 2018). Although such research is valuable to improving quality of life outcomes for atypically ageing individuals, it is not a focus of the work presented in this thesis. The work in this thesis focuses on the impact of typical ageing on navigation ability and therefore atypical ageing will be sparsely mentioned.

There are several methods used to identify the presence of atypical decline including MRI scanning to detect neural atrophy, analysis of cerebral spinal fluid obtained via lumbar puncture, or blood testing. However, before such cost and time intensive techniques are employed, neuropsychological testing is often used as an initial screening tool for the presence of cognitive impairment. Tests such as the Addenbrooke's Cognitive Examination (ACE; Mathuranath et al., 2000), the Mini Mental State Examination (MMSE; Folstein et al., 1975) or the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005) have all been shown to reliably detect early signs of cognitive impairment. The research presented in this thesis uses the MoCA to screen for cognitive impairment, as is the standard in many studies of the effect of cognitive ageing on navigation (see O’Malley et al., 2018).

1.3 Summary and rationale

Overall, the literature shows that older adults experience a range of changes to their navigation systems. Whilst declines in more advanced cognitive map representations are well understood via changes in allocentric encoding mechanisms, age-related declines in landmark based place and route knowledge are not well understood. That is, older adults can learn and recall landmarks, but experience difficulty when using them to recognise places, as triggers for directional motor responses and in learning the sequences of landmarks and directions to characterise routes. The research in this thesis aims to broaden our understanding of these landmark-based place and route learning deficits by considering the influence of other cognitive domains that are relevant for navigation.

In this thesis, the first approach to understanding age-related declines in place and route learning is to investigate the contribution of changes in attention, which is characterised in multiple ways. First is via the use of eye-tracking to assess overt visual attention and encoding strategies during a place learning task (Chapter 3) and a route learning task (Chapter 4). We developed novel gaze measures that are sensitive to the spatial-temporal aspects of oculomotor behaviour. These measures are used to understand how participants encode the arrangement of objects in space, sample the environment during different parts of a route, and engage in decision making processes during navigation. The second characterisation of attention is assessing the modulation of attentional resources during route navigation. Specifically, we questioned whether older adults are engaging attention at the important decision points in the same way as younger adults, assessed in Chapter 4 via an established dual task procedure.

The second approach to understanding age-related declines in route learning is to assess the final content of landmark-based spatial representations that develop in older adults after controlling for age-related decreases in learning rates. Chapters 5 and 6 include three experiments which assess the different types of knowledge acquired by younger and older adults when they fully learn a route to completion. This study addresses a key methodological issue related to the different learning rates of older and younger adults. Specifically, we assessed fully formed route representations for a route that participants learned successfully, instead of assessing route knowledge after a fixed learning period, during which older adults may have formed only partial knowledge about the route. Using this approach allowed us to dissociate the types of knowledge that older adults eventually integrate into their representation of the environment from the types of knowledge that do not get incorporated. From this, we discuss possible strategy differences between age groups which may explain the different route representations.

Throughout this thesis we show that older adults do engage their attention at relevant decision points of the environment, and that whilst route learning they control their visual attention similarly to younger adults (Chapter 4). At navigationally relevant locations, older adults do encode and are able to recall object landmarks (Chapter 5). Landmarks can be used as cues by older adults for place recognition via landmark identity alone, but older adults struggle when the spatial arrangement of landmarks is required for recognition (Chapters 2 and 3). This deficit is related to differences in visual encoding strategy (Chapter 3). After only a few exposures to a route, older adults struggle more than younger adults to use landmarks as associative cues for navigation (Chapter 4 and 5), however when given extended learning times, landmarks are used as associative cues by older adults just as well as by younger adults (Chapter 5). In contrast, landmark sequence knowledge remains impaired compared to younger adults at both early stages of route representation formation (Chapters 4 and 5) and in final content of route knowledge (Chapter 5). This landmark sequence deficit cannot be explained by changes in serial learning mechanisms, which display similar patterns between age groups, and to other, non-navigation, sequence learning tasks (Chapter 6).

1.4 References

Allen, G. L., & Kirasic, K. C. (2003). Visual attention during route learning: A look at selection and engagement. *Lecture Notes in Computer Science (Including Subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*. https://doi.org/10.1007/978-3-540-39923-0_26

Allison, S., Babulal, G. M., Stout, S. H., Barco, P. P., Carr, D. B., Fagan, A. M., Morris, J. C., Roe, C. M., & Head, D. (2018). Alzheimer Disease Biomarkers and Driving in Clinically Normal Older Adults. *Alzheimer Disease and Associated Disorders*, *32*(2), 101–106. https://doi.org/10.1097/WAD.0000000000000257

Allison, S., Fagan, A. M., Morris, J. C., & Head, D. (2016). Spatial Navigation in Preclinical Alzheimer’s Disease. *Journal of Alzheimer’s Disease*, *52*(1), 77–90. https://doi.org/10.3233/JAD-150855

Allison, S., & Head, D. (2017). Route repetition and route reversal: Effects of age and encoding method. *Psychology and Aging*, *32*(3), 220–231. https://doi.org/10.1037/pag0000170

Andrews-Hanna, J. R., Snyder, A. Z., Vincent, J. L., Lustig, C., Head, D., Raichle, M. E. E., & Buckner, R. L. (2007). Disruption of Large-Scale Brain Systems in Advanced Aging. *Neuron*, *56*(5), 924–935. https://doi.org/10.1016/j.neuron.2007.10.038

Antonova, E., Parslow, D., Brammer, M., Dawson, G. R., Jackson, S. H. D., & Morris, R. G. (2009). Age-related neural activity during allocentric spatial memory. *Memory*, *17*(2), 125–143. https://doi.org/10.1080/09658210802077348

Ash, J. A., Lu, H., Taxier, L. R., Long, J. M., Yang, Y., Stein, E. A., & Rapp, P. R. (2016). Functional connectivity with the retrosplenial cortex predicts cognitive aging in rats. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(43), 12286–12291. https://doi.org/10.1073/pnas.1525309113

Baltes, M. M. (1998). The psychology of the oldest-old. *Current Opinion in Psychiatry*, *11*(4), 411–415. https://doi.org/10.1097/00001504-199807000-00009

Baltes, P. B., & Smith, J. (2003). New Frontiers in the Future of Aging: From Successful Aging of the Young Old to the Dilemmas of the Fourth Age. *Gerontology*, *49*(2), 123–135. https://doi.org/10.1159/000067946

Barrash, J. (1994). Age-Related Decline in Route Learning Ability. *Developmental Neuropsychology*, *10*(3), 189–201. https://doi.org/10.1080/87565649409540578

Barry, C., Hayman, R., Burgess, N., & Jeffery, K. J. (2007). Experience-dependent rescaling of entorhinal grids. *Nature Neuroscience*, *10*(6), 682–684. https://doi.org/10.1038/nn1905

Boccia, M., Guariglia, C., Sabatini, U., & Nemmi, F. (2016). Navigating toward a novel environment from a route or survey perspective: neural correlates and context-dependent connectivity. *Brain Structure and Function*, *221*(4), 2005–2021. https://doi.org/10.1007/s00429-015-1021-z

Bohbot, V. D., Lerch, J., Thorndycraft, B., Iaria, G., & Zijdenbos, A. P. (2007). Gray matter differences correlate with spontaneous strategies in a human virtual navigation task. *Journal of Neuroscience*, *27*(38), 10078–10083. https://doi.org/10.1523/JNEUROSCI.1763-07.2007

Bohbot, V. D., McKenzie, S., Konishi, K., Fouquet, C., Kurdi, V., Schachar, R., Boivin, M., & Robaey, P. (2012). Virtual navigation strategies from childhood to senescence: Evidence for changes across the life span. *Frontiers in Aging Neuroscience*, *4*(OCT), 1–10. https://doi.org/10.3389/fnagi.2012.00028

Bryden, K. J., Charlton, J. L., Oxley, J. A., & Lowndes, G. J. (2013). Self-reported wayfinding ability of older drivers. *Accident Analysis and Prevention*, *59*, 277–282. https://doi.org/10.1016/j.aap.2013.06.017

Buchner, A., & Jansen-Osmann, P. (2008). Is route learning more than serial learning? *Spatial Cognition and Computation*, *8*(4), 289–305. https://doi.org/10.1080/13875860802047201

Burgess, N. (2008). Spatial cognition and the brain. *Annals of the New York Academy of Sciences*, *1124*, 77–97. https://doi.org/10.1196/annals.1440.002

Burns, P. C. (1999). Navigation and the mobility of older drivers. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, *54*(1), 49–55. https://doi.org/10.1093/geronb/54B.1.S49

Chan, E., Baumann, O., Bellgrove, M. A., & Mattingley, J. B. (2012). From objects to landmarks: the function of visual location information in spatial navigation. *Frontiers in Psychology*, *3*(August), 1–11. https://doi.org/10.3389/fpsyg.2012.00304

Cherrier, M. M., Mendez, M., & Perryman, K. (2001). Route learning performance in Alzheimer disease patients. *Neuropsychiatry, Neuropsychology and Behavioral Neurology*.

Chrastil, E. R. (2013). Neural evidence supports a novel framework for spatial navigation. *Psychonomic Bulletin and Review*, *20*(2), 208–227. https://doi.org/10.3758/s13423-012-0351-6

Chrastil, E. R., Sherrill, K. R., Hasselmo, M. E., & Stern, C. E. (2015). There and back again: Hippocampus and retrosplenial cortex track homing distance during human path integration. *Journal of Neuroscience*, *35*(46), 15442–15452. https://doi.org/10.1523/JNEUROSCI.1209-15.2015

Chrastil, E. R., & Warren, W. H. (2020). Executing the homebound path is a major source of error in homing by path integration. *Journal of Experimental Psychology: Human Perception and Performance*. https://doi.org/10.1037/xhp0000875

Colombo, D., Serino, S., Tuena, C., Pedroli, E., Dakanalis, A., Cipresso, P., & Riva, G. (2017). Egocentric and allocentric spatial reference frames in aging: A systematic review. *Neuroscience and Biobehavioral Reviews*, *80*(February), 605–621. https://doi.org/10.1016/j.neubiorev.2017.07.012

Cook, D., & Kesner, R. P. (1988). Caudate nucleus and memory for egocentric localization.

Behavioral and Neural Biology, *49*(3), 332–343. https://doi.org/10.1016/S0163-1047(88)90338-X

Coughlan, G., Laczó, J., Hort, J., Minihane, A. M., & Hornberger, M. (2018). Spatial navigation deficits — Overlooked cognitive marker for preclinical Alzheimer disease? *Nature Reviews Neurology*, *14*(8), 496–506. https://doi.org/10.1038/s41582-018-0031-x

Coutrot, A., Silva, R., Manley, E., de Cothi, W., Sami, S., Bohbot, V. D., Wiener, J. M., Hölscher, C., Dalton, R. C., Hornberger, M., & Spiers, H. J. (2018). Global Determinants of Navigation Ability. *Current Biology*, *28*(17), 2861-2866.e4. https://doi.org/10.1016/j.cub.2018.06.009

Cushman, L. A., Duffy, C. J., Stein, K., & Duffy, C. J. (2008). Virtual reality identifies navigational defects in Alzheimer disease and cognitive aging. *Nature Clinical Practice Neurology*, *4*(12), 638–639. https://doi.org/10.1038/ncpneuro0929

Daugherty, A. M., Yuan, P., Dahle, C. L., Bender, A. R., Yang, Y., & Raz, N. (2015). Path complexity in virtual water maze navigation: Differential associations with age, sex, and regional brain volume. *Cerebral Cortex*, *25*(9), 3122–3131. https://doi.org/10.1093/cercor/bhu107

De Beni, R., Pazzaglia, F., & Gardini, S. (2006). The role of mental rotation and age in spatial perspective-taking tasks: When age does not impair perspective-taking performance. *Applied Cognitive Psychology*, *20*(6), 807–821. https://doi.org/10.1002/acp.1229

Denis, M., Mores, C., Gras, D., Gyselinck, V., & Daniel, M. P. (2014). Is Memory for Routes Enhanced by an Environment's Richness in Visual Landmarks? *Spatial Cognition and Computation*, *14*(4), 284–305. https://doi.org/10.1080/13875868.2014.945586

Ekstrom, A. D. (2015). Why vision is important to how we navigate. *Hippocampus*, *25*(6), 731–735. https://doi.org/10.1002/hipo.22449

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, *425*(6954), 184–187. https://doi.org/10.1038/nature01964

Epstein, R. A., Higgins, J. S., & Thompson-Schill, S. L. (2005). Learning places from views: Variation in scene processing as a function of experience and navigational ability. *Journal of Cognitive Neuroscience*, *17*(1), 73–83. https://doi.org/10.1162/0898929052879987

Fernandez-Baizan, C., Diaz-Caceres, E., Arias, J. L., & Mendez, M. (2019). Egocentric and allocentric spatial memory in healthy aging: Performance on real-world tasks. *Brazilian Journal of Medical and Biological Research*, *52*(4), 1–7. https://doi.org/10.1590/1414-431x20198041

Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-mental state." *Journal of Psychiatric Research*, *12*(3), 189–198. https://doi.org/10.1016/0022-3956(75)90026-6

Foo, P., Duchon, A., Warren, W. H., & Tarr, M. J. (2007). Humans do not switch between path knowledge and landmarks when learning a new environment. In *Psychological Research*. https://doi.org/10.1007/s00426-006-0080-4

Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- Versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning Memory and Cognition*.

https://doi.org/10.1037/0278-7393.31.2.195

Franz, G., Mallot, H. A., & Wiener, J. M. (2005). Graph-based models of space in architecture and cognitive science- a comparative analysis. *Proceedings of the 17th International Conference on Systems Research, Informatics and Cybernetics*, 30–38. http://eprints.bournemouth.ac.uk/13803/1/licence.txt

Gazova, I., Laczó, J., Rubinova, E., Mokrisova, I., Hyncicova, E., Andel, R., Vyhnalek, M., Sheardova, K., Coulson, E. J., & Hort, J. (2013). Spatial navigation in young versus older adults. *Frontiers in Aging Neuroscience*, *5*(DEC), 1–8. https://doi.org/10.3389/fnagi.2013.00094

Golledge, R. G., Smith, T. R., Pellegrino, J. W., Doherty, S., & Marshall, S. P. (1985). A conceptual model and empirical analysis of children's acquisition of spatial knowledge. *Journal of Environmental Psychology*, *5*(2), 125–152. https://doi.org/10.1016/S0272-4944(85)80014-1

Gramann, K., Müller, H. J., Eick, E. M., & Schönebeck, B. (2005). Evidence of separable spatial representations in a virtual navigation task. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(6), 1199–1223. https://doi.org/10.1037/0096-1523.31.6.1199

Grzeschik, R., Conroy-Dalton, R., Innes, A., Shanker, S., & Wiener, J. M. (2019). The contribution of visual attention and declining verbal memory abilities to age-related route learning deficits. *Cognition*, *187*(July 2018), 50–61. https://doi.org/10.1016/j.cognition.2019.02.012

Grzeschik, R., Hilton, C., Dalton, R. C., Konovalova, I., Cotterill, E., Innes, A., & Wiener, J. M. (2020). From repeating routes to planning novel routes : the impact of landmarks and ageing on route integration and cognitive mapping. *Psychological Research*, *0123456789*. https://doi.org/10.1007/s00426-020-01401-5

Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, *436*(7052), 801–806. https://doi.org/10.1038/nature03721

Harris, M. A., & Wolbers, T. (2014). How age-related strategy switching deficits affect wayfinding in complex environments. *Neurobiology of Aging*, *35*(5), 1095–1102. https://doi.org/10.1016/j.neurobiolaging.2013.10.086

Hartley, T., Bird, C. M., Chan, D., Cipolotti, L., Husain, M., Vargha-Khadem, F., & Burgess, N. (2007). The Hippocampus Is Required for Short-Term Topographical Memory in Humans. In *Hippocampus* (Vol. 17, Issue 1, pp. 34–48).

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, *37*(5), 877–888. https://doi.org/10.1016/S0896-6273(03)00095-3

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research*, *209*(1), 49–58. https://doi.org/10.1016/j.bbr.2010.01.012

Hegarty, M., & Waller, D. A. (2009). Individual Differences in Spatial Abilities. In *The Cambridge Handbook of Visuospatial Thinking*. https://doi.org/10.1017/cbo9780511610448.005

Herweg, N. A., & Kahana, M. J. (2018). Spatial representations in the human brain. *Frontiers in Human Neuroscience*, *12*(July), 1–16. https://doi.org/10.3389/fnhum.2018.00297

Hölscher, C., Büchner, S. J., Meilinger, T., & Strube, G. (2009). Adaptivity of wayfinding strategies in a multi-building ensemble: The effects of spatial structure, task requirements, and metric information. *Journal of Environmental Psychology*, *29*(2), 208–219. https://doi.org/10.1016/j.jenvp.2008.05.010

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *Journal of Neuroscience*, *23*(13), 5945–5952. https://doi.org/10.1523/jneurosci.23-13-05945.2003

Iglói, K., Zaoui, M., Berthoz, A., & Rondi-Reig, L. (2009). Sequential egocentric strategy is acquired as early as allocentric strategy: Parallel acquisition of these two navigation strategies. *Hippocampus*, *19*(12), 1199–1211. https://doi.org/10.1002/hipo.20595

Ishikawa, T., Fujiwara, H., Imai, O., & Okabe, A. (2008). Wayfinding with a GPS-based mobile navigation system: A comparison with maps and direct experience. *Journal of Environmental Psychology*, *28*(1), 74–82. https://doi.org/10.1016/j.jenvp.2007.09.002

Ishikawa, T., & Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive Psychology*, *52*(2), 93–129. https://doi.org/10.1016/j.cogpsych.2005.08.003

Janzen, G. (2006). Memory for object location and route direction in virtual large-scale space. *Quarterly Journal of Experimental Psychology*, *59*(3), 493–508. https://doi.org/10.1080/02724980443000746

Janzen, G., & van Turennout, M. (2004). Selective neural representation of objects relevant for navigation. *Nature Neuroscience*, *7*(6), 673–677. https://doi.org/10.1038/nn1257

Janzen, G., Wagensveld, B., & Van Turennout, M. (2007). Neural representation of navigational relevance is rapidly induced and long lasting. *Cerebral Cortex*, *17*(4), 975–981. https://doi.org/10.1093/cercor/bhl008

Janzen, G., & Weststeijn, C. G. (2007). Neural representation of object location and route direction: An event-related fMRI study. *Brain Research*, *1165*(1), 116–125. https://doi.org/10.1016/j.brainres.2007.05.074

Jeffery, K. J. (1998). Learning of landmark stability and instability by hippocampal place cells. *Neuropharmacology*, *37*(4–5), 677–687. https://doi.org/10.1016/S0028-3908(98)00053-7

Kim, K., & Bock, O. (2020). Acquisition of landmark, route, and survey knowledge in a wayfinding task: in stages or in parallel? *Psychological Research*, *0123456789*. https://doi.org/10.1007/s00426-020-01384-3

Kirasic, K. C. (1991). Spatial cognition and behavior in young and elderly adults: implications for learning new environments. *Psychology and Aging*, *6*(1), 10–18. https://doi.org/10.1037/0882-7974.6.1.10

Klatzky, R. (1998). *Allocentric and Egocentric Spatial Representations: Definitions, Distinctions, and Interconnections*. https://doi.org/10.1007/3-540-69342-4_1

Klatzky, R., Beall, A., Loomis, J., Golledge, R., & Philbeck, J. (1999). Human navigation ability: Tests of the encoding-error model of path integration. *Spatial Cognition and Computation*, *1*(1), 31–65. https://doi.org/10.1023/A:1010061313300

Klencklen, G., Després, O., & Dufour, A. (2012). What do we know about aging and spatial cognition? Reviews and perspectives. *Ageing Research Reviews*, *11*(1), 123–135. https://doi.org/10.1016/j.arr.2011.10.001

Konishi, K., Etchamendy, N., Roy, S., Marighetto, A., Rajah, N., & Bohbot, V. D. (2013). Decreased functional magnetic resonance imaging activity in the hippocampus in favor of the caudate nucleus in older adults tested in a virtual navigation task. *Hippocampus*, *23*(11), 1005–1014. https://doi.org/10.1002/hipo.22181

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers, T. (2017). The Aging Navigational System. *Neuron*, *95*(5), 1019–1035. https://doi.org/10.1016/j.neuron.2017.06.037

Lithfous, S., Dufour, A., & Després, O. (2013). Spatial navigation in normal aging and the prodromal stage of Alzheimer's disease: Insights from imaging and behavioral studies. In *Ageing Research Reviews*. https://doi.org/10.1016/j.arr.2012.04.007

Liu, I., Levy, R. M., Barton, J. J. S., & Iaria, G. (2011). Age and gender differences in various topographical orientation strategies. *Brain Research*. https://doi.org/10.1016/j.brainres.2011.07.005

Mallot, H. A. (1999). Spatial cognition: Behavioral competences, neural mechanisms, and evolutionary scaling. *Kognitionswissenschaft*, *8*(1), 40–48. https://doi.org/10.1007/s001970050074

Mallot, H. A., & Basten, K. (2009). Embodied spatial cognition: Biological and artificial systems. *Image and Vision Computing*, *27*(11), 1658–1670. https://doi.org/10.1016/j.imavis.2008.09.001

Mathuranath, P. S., Nestor, P. J., Berrios, G. E., Rakowicz, W., & Hodges, J. R. (2000). A brief cognitive test battery to differentiate Alzheimer's disease and frontotemporal dementia. *Neurology*, *55*(11), 1613–1620. https://doi.org/10.1212/01.wnl.0000434309.85312.19

McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M. B. (2006). Path integration and the neural basis of the "cognitive map." *Nature Reviews Neuroscience*, *7*(8), 663–678. https://doi.org/10.1038/nrn1932

Meilinger, T., Hölscher, C., Büchner, S. J., & Brösamle, M. (2007). How much information do you need? Schematic maps in wayfinding and self localisation. *Lecture Notes in Computer Science (Including Subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*, *4387 LNAI*, 381–400. https://doi.org/10.1007/978-3-540-75666-8_22

Meilinger, T., & Vosgerau, G. (2010). Putting egocentric and allocentric into perspective. *Lecture Notes in Computer Science (Including Subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*. https://doi.org/10.1007/978-3-642-14749-4_19

Meulenbroek, O., Petersson, K. M., Voermans, N., Weber, B., & Fernández, G. (2004). Age differences in neural correlates of route encoding and route recognition. *NeuroImage*, *22*(4), 1503–1514. https://doi.org/10.1016/j.neuroimage.2004.04.007

Mitchell, A. S., Czajkowski, R., Zhang, N., Jeffery, K., & Nelson, A. J. D. (2018). Retrosplenial cortex and its role in spatial cognition. *Brain and Neuroscience Advances*, *2*, 239821281875709. https://doi.org/10.1177/2398212818757098

Moffat, S. D. (2009). Aging and spatial navigation: What do we know and where do we go? *Neuropsychology Review*, *19*(4), 478–489. https://doi.org/10.1007/s11065-009-9120-3

Moffat, S. D., Elkins, W., & Resnick, S. M. (2006). Age differences in the neural systems supporting human allocentric spatial navigation. *Neurobiology of Aging*, *27*(7), 965–972. https://doi.org/10.1016/j.neurobiolaging.2005.05.011

Montello, D. R. (1998). A new framework for understanding the acquisition of spatial knowledge in large-scale environments. *Spatial and Temporal Reasoning in Geographic Information Systems*, 143–154. https://doi.org/10.1088/1748-6041/6/2/025001

Montello, D. R. (2009). Navigation. In *The Cambridge Handbook of Visuospatial Thinking*. https://doi.org/10.1017/cbo9780511610448.008

Moser, E. I., Kropff, E., & Moser, M. B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neuroscience*, *31*, 69–89. https://doi.org/10.1146/annurev.neuro.31.061307.090723

Moser, M. B., Rowland, D. C., & Moser, E. I. (2015). Place cells, grid cells, and memory. *Cold Spring Harbor Perspectives in Biology*, *7*(2), 1–15. https://doi.org/10.1101/cshperspect.a021808

Münzer, S., Zimmer, H. D., & Baus, J. (2012). Navigation assistance: A trade-off between wayfinding support and configural learning support. *Journal of Experimental Psychology: Applied*, *18*(1), 18–37. https://doi.org/10.1037/a0026553

Nasreddine, Z. S., Phillips, N. A., Bedirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L., & Chertkow, H. (2005). The Montreal cognitive assessment, MoCA: a brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, *53*(4), 695–699.

Nori, R., Piccardi, L., Maialetti, A., Goro, M., Rossetti, A., Argento, O., & Guariglia, C. (2018). No gender differences in egocentric and allocentric environmental transformation after compensating for male advantage by manipulating familiarity. *Frontiers in Neuroscience*, *12*(MAR), 1–9. https://doi.org/10.3389/fnins.2018.00204

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*(1), 171–175. https://doi.org/10.1016/0006-8993(71)90358-1

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

O'Malley, M., Innes, A., & Wiener, J. M. (2018). How do we get there? Effects of cognitive aging on route memory. *Memory and Cognition*, *46*(2), 274–284. https://doi.org/10.3758/s13421-017-0763-7

Poldrack, R. A., Clark, J., Paré-Blagoev, E. J., Shohamy, D., Creso Moyano, J., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature*, *414*(6863), 546–550. https://doi.org/10.1038/35107080

Ramanoël, S., York, E., Le Petit, M., Lagrené, K., Habas, C., & Arleo, A. (2019). Age-Related Differences in Functional and Structural Connectivity in the Spatial Navigation Brain Network. *Frontiers in Neural Circuits*, *13*(October), 1–13. https://doi.org/10.3389/fncir.2019.00069

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., Dahle, C., Gerstorf, D., & Acker, J. D. (2005). Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex*, *15*(11), 1676–1689. https://doi.org/10.1093/cercor/bhi044

Raz, N., Rodrigue, K. M., Kennedy, K. M., Head, D., Gunning-Dixon, F., & Acker, J. D. (2003). Differential Aging of the Human Striatum: Longitudinal Evidence. *American Journal of Neuroradiology*, *24*(9), 1849–1856.

Rodgers, M. K., Sindone, J. A., & Moffat, S. D. (2012). Effects of age on navigation strategy. *Neurobiology of Aging*, *33*(1), 202.e15-202.e22. https://doi.org/10.1016/j.neurobiolaging.2010.07.021

Rodrigue, K. M., & Raz, N. (2004). Shrinkage of the Entorhinal Cortex over Five Years Predicts Memory Performance in Healthy Adults. *Journal of Neuroscience*, *24*(4), 956–963. https://doi.org/10.1523/JNEUROSCI.4166-03.2004

Rondi-Reig, L., Petit, G. H., Tobin, C., Tonegawa, S., Mariani, J., & Berthoz, A. (2006). Impaired sequential egocentric and allocentric memories in forebrain-specific-NMDA receptor knock-out mice during a new task dissociating strategies of navigation. *Journal of Neuroscience*, *26*(15), 4071–4081. https://doi.org/10.1523/JNEUROSCI.3408-05.2006

Schinazi, V. R., & Epstein, R. A. (2010). Neural correlates of real-world route learning. *NeuroImage*, *53*(2), 725–735. https://doi.org/10.1016/j.neuroimage.2010.06.065

Schuck, N. W., Doeller, C. F., Polk, T. A., Lindenberger, U., & Li, S. C. (2015). Human aging alters the neural computation and representation of space. *NeuroImage*, *117*, 141–150. https://doi.org/10.1016/j.neuroimage.2015.05.031

Siegel, A. W., & White, S. H. (1975). The development of spatial representations of large-scale environments. *Advances in Child Development and Behavior*. https://doi.org/10.1016/S0065-2407(08)60007-5

Spiers, H. J., & Maguire, E. A. (2007). A navigational guidance system in the human brain. *Hippocampus*, *17*(8), 618–626. https://doi.org/10.1002/hipo.20298

Stangl, M., Kanitscheider, I., Riemer, M., Fiete, I., & Wolbers, T. (2020). Sources of path integration error in young and aging humans. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-15805-9

Stankiewicz, B. J., & Kalia, A. A. (2007). Acquisition of Structural Versus Object Landmark Knowledge. *Journal of Experimental Psychology: Human Perception and Performance*, *33*(2), 378–390. https://doi.org/10.1037/0096-1523.33.2.378

Storandt, M., Mintun, M. A., Head, D., & Morris, J. C. (2009). Cognitive decline and brain volume loss as signatures of cerebral amyloid-β peptide deposition identified with Pittsburgh compound B: Cognitive decline associated with Aβ deposition. *Archives of Neurology*, *66*(12), 1476–1481. https://doi.org/10.1001/archneurol.2009.272

Strickrodt, M., O'Malley, M., & Wiener, J. M. (2015). This place looks familiar-how navigators distinguish places with ambiguous landmark objects when learning novel routes. *Frontiers in Psychology*, *6*(DEC), 1–12. https://doi.org/10.3389/fpsyg.2015.01936

Thorndyke, P. W., & Goldin, S. E. (1983). Spatial Learning and Reasoning Skill. In *Spatial Orientation*. https://doi.org/10.1007/978-1-4615-9325-6_9

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*. https://doi.org/10.1037/h0061626

Trullier, O., Wiener, S. I., Berthoz, A., & Meyer, J. A. (1997). Biologically based artificial navigation systems: Review and prospects. *Progress in Neurobiology*. https://doi.org/10.1016/S0301-0082(96)00060-3

van der Ham, I. J. M., & Claessen, M. H. G. (2020). How age relates to spatial navigation performance: Functional and methodological considerations. *Ageing Research Reviews*, *58*(January), 101020. https://doi.org/10.1016/j.arr.2020.101020

van der Ham, I. J. M., Claessen, M. H. G., Evers, A. W. M., & van der Kuil, M. N. A. (2020). Large-scale assessment of human navigation ability across the lifespan. *Scientific Reports*, *10*(1), 1–12. https://doi.org/10.1038/s41598-020-60302-0

Waller, D., & Lippa, Y. (2007). Landmarks as beacons and associative cues. *Memory & Cognition*, *35*(5), 910–924. https://doi.org/10.3758/BF03193465

Warren, W. H., Rothman, D. B., Schnapp, B. H., & Ericson, J. D. (2017). Wormholes in virtual space: From cognitive maps to cognitive graphs. *Cognition*, *166*, 152–163. https://doi.org/10.1016/j.cognition.2017.05.020

Weisberg, S. M., Schinazi, V. R., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2014). Variations in cognitive maps: Understanding individual differences in navigation. *Journal of Experimental Psychology: Learning Memory and Cognition*, *40*(3), 669–682. https://doi.org/10.1037/a0035261

Wiener, J. M., Berthoz, A., & Wolbers, T. (2011). Dissociable cognitive mechanisms underlying human path integration. *Experimental Brain Research*, *208*(1), 61–71. https://doi.org/10.1007/s00221-010-2460-7

Wiener, J. M., Büchner, S. J., & Hölscher, C. (2009). Taxonomy of human wayfinding tasks: A knowledge-based approach. *Spatial Cognition and Computation*, *9*(2), 152–165. https://doi.org/10.1080/13875860902906496

Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive bias for extrahippocampal navigation strategies in aging humans. *Journal of Neuroscience*, *33*(14), 6012–6017. https://doi.org/10.1523/JNEUROSCI.0717-12.2013

Wiener, J. M., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: Effects of cognitive aging. *Frontiers in Aging Neuroscience*, *4*(MAY), 1–7. https://doi.org/10.3389/fnagi.2012.00007

Wilkniss, S. M., Korol, D. L., Gold, P. E., Jones, M. G., & Manning, C. A. (1997). Age-related differences in an ecologically based study of route learning. *Psychology and Aging*. https://doi.org/10.1037/0882-7974.12.2.372

Willis, S. . (1991). Cognition and everyday competence. In K. Schaie (Ed.), *Annual review of gerontology and geriatrics* (pp. 80–109).

Wolbers, T., & Büchel, C. (2005). Dissociable retrosplenial and hippocampal contributions to successful formation of survey representations. *Journal of Neuroscience*, *25*(13), 3333–3340. https://doi.org/10.1523/JNEUROSCI.4705-04.2005

Wolbers, T., Hegarty, M., Büchel, C., & Loomis, J. M. (2008). Spatial updating: How the brain keeps track of changing object locations during observer motion. *Nature Neuroscience*, *11*(10), 1223–1230. https://doi.org/10.1038/nn.2189

Zhang, H., Zherdeva, K., & Ekstrom, A. D. (2014). Different “routes” to a cognitive map: dissociable forms of spatial knowledge derived from route and cartographic map learning. *Memory and Cognition*, *42*(7), 1106–1117. https://doi.org/10.3758/s13421-014-0418-x

Zhao, M., & Warren, W. H. (2015). How You Get There From Here: Interaction of Visual Landmarks and Path Integration in Human Navigation. *Psychological Science*, *26*(6), 915–924. https://doi.org/10.1177/0956797615574952

Zhong, J. Y., & Moffat, S. D. (2016). Age-related differences in associative learning of landmarks and heading directions in a virtual navigation task. *Frontiers in Aging Neuroscience*, *8*(MAY), 1–11. https://doi.org/10.3389/fnagi.2016.00122

Zhong, J. Y., & Moffat, S. D. (2018). Extrahippocampal contributions to age-related changes in spatial navigation ability. *Frontiers in Human Neuroscience*, *12*(July), 1–8. https://doi.org/10.3389/fnhum.2018.00272

Chapter 2
Evidence for age-related deficits in object-location binding during place recognition

The following chapter contains a short summary of a study which I contributed to as a co-author but was not responsible for a majority of the work. The main article for this study can be found in Appendix 1, and is published as:

Muffato, V., Hilton, C., Meneghetti, C., De Beni, R., & Wiener, J. M. (2019). Evidence for age-related deficits in object-location binding during place recognition. Hippocampus, February, 1–9. https://doi.org/10.1002/hipo.23099

My main contribution to this work was the data analysis and visualisation. I was also involved in the interpretation of results, and in addressing reviewer comments in the revision of the manuscript for publication. The wider scope of this study is relevant for the following chapter of this thesis, in which we repeat the experiment as an eye-tracking study to investigate the contribution of control of visual attention to the age-related differences observed in the place recognition task introduced in the present chapter.

2.1 Introduction

In this experiment we investigated age-related differences in the mechanisms involved in place recognition. Some places can be recognised by identifying individual landmarks that distinguish them from other places. Such recognition depends on memory for object identity (Postma et al., 2008). However, many places share similar objects that are not distinctive enough for reliable recognition at a later time. In these cases, the arrangement of objects in space must also be encoded to allow for accurate recognition. This is known as object-location binding, as it involves the pairing of object identity and location in memory (Pertzov et al., 2012). Additionally, place recognition must often occur from a perspective that is different to the one from which the place was first encoded. In these cases, spatial perspective taking must be performed to reconcile the difference between the currently perceived place and those stored in memory.

Existing research is inconclusive on how the mechanisms of place recognition are affected by cognitive ageing. Object identity memory alone has been shown to be preserved (Mitchell et al., 2000) and degraded (Dai et al., 2018; Pertzov et al., 2012) in older adults, as has object-location binding mechanisms (Dai et al., 2018; Ellis et al., 1987; Mitchell et al., 2000).

However, much of the object identity, and object-location binding research prior to the current study utilised stimuli depicting 2D space, and not of a 3D space representative of real-world places (e.g. Dai et al., 2018). As a result, to our knowledge, no study prior to this one investigated object-location binding mechanisms in ageing in the presence of perspective shifts. Studies investigating perspective taking and ageing in isolation often report declines in spatial perspective taking mechanisms (Inagaki et al., 2002; Montefinese et al., 2015; Watanabe, 2011). This is mainly attributed to age-related atrophy of the hippocampus (Klencklen et al., 2012), which supports memory for the spatial arrangement of objects that allows for viewpoint independent recognition of a place (Hartley et al., 2007; King et al., 2002).

The present study involved encoding and recognition of stimuli depicting 3D places with manipulations to investigate object memory, object-location binding and spatial perspective taking mechanisms in ageing. We expected that the requirement of object-location binding would decrease recognition performance, as would increasing perspective shifts. Additionally, we expected interactions between age-group and manipulation, and age group and perspective if cognitive ageing impacts object-location binding and perspective taking mechanisms, respectively.

2.2 Method

116 participants in three age groups (20-29, 60-69, 70-79 years old) completed a place recognition task. Each trial of the task featured an encoding phase and a recognition phase. In the encoding phase, participants are shown an image of a place for 8 seconds. In the subsequent recognition phase, participants were shown a second image which was either of the same or a different place. Participants had to indicate whether the image depicted the same or different place as in the encoding phase.

Places were defined by four objects placed on an otherwise empty plain. In the recognition phase, places could be different to the place shown in the encoding phase by substituting an object for a novel object, a condition which can be solved by object memory alone via identification of the object not previously present. Alternatively, places were different because two objects had swapped locations. In this condition, all the objects were still the same as during encoding, rendering pure object identity memory insufficient to recognise that the places were different. Instead, recognising the change required object-location memory. Finally, places in the recognition phase could be presented from the same viewpoint as in encoding, or at a shifted perspective of 30° or 60°. Participants were explicitly informed that a change in perspective in itself did not constitute a change in the place, and that places could be the same even if they were being viewed from a different perspective. Figure 2-1 depicts examples of the different conditions and perspectives, as well as the trial sequence.

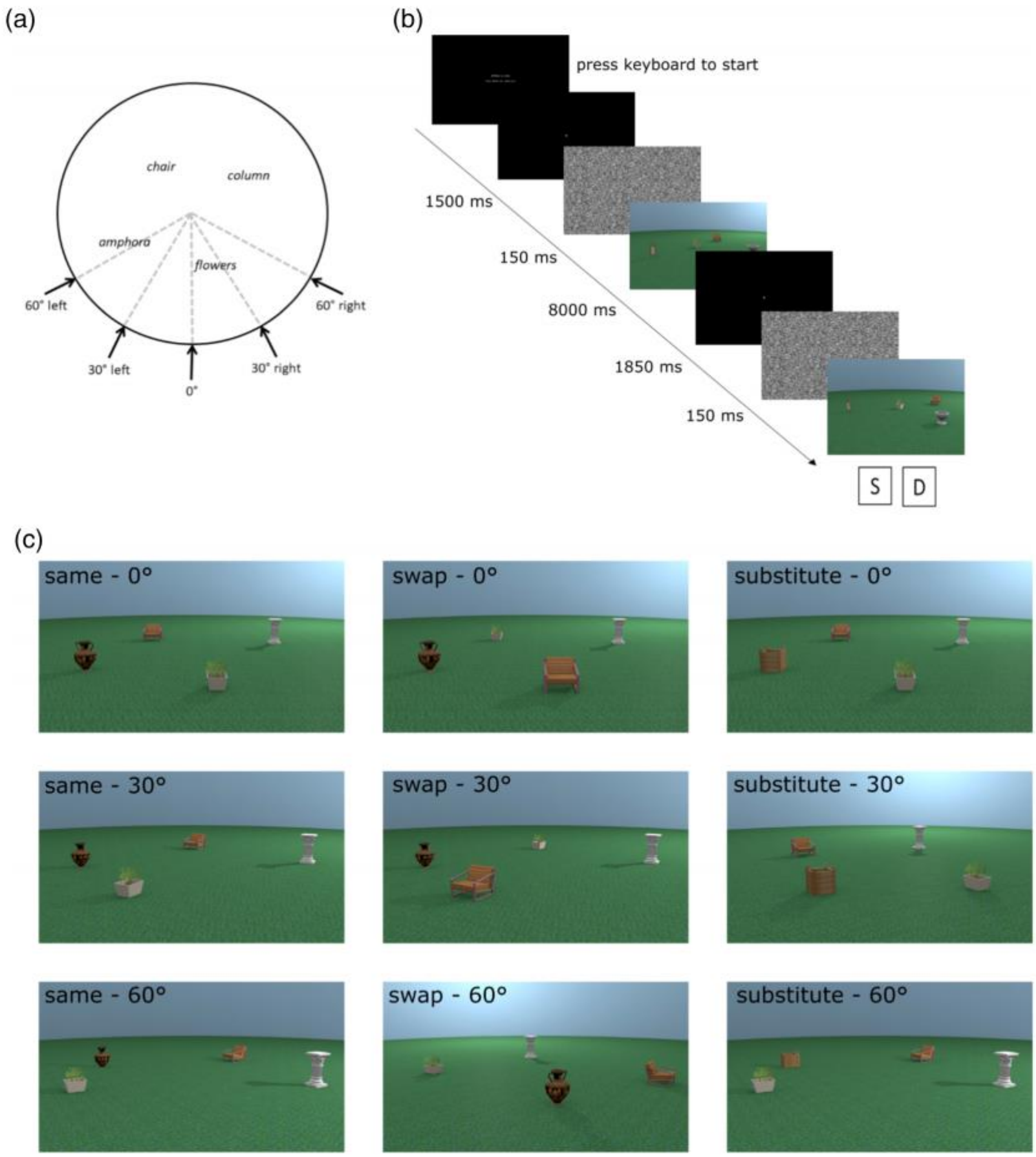

Figure 2-1 - Places and conditions in the place recognition task. Panel a: Schematic drawing of possible viewpoints from which the place was rendered (the circle represents the area in which objects could be located. The arrows indicate the direction of the cameras for the rendering); Panel b: Sequence of a trial; Panel c: Object and perspective manipulations referred to place 1.

2.3 Results

Accuracy data were converted into sensitivity scores representing ability to recognise changes in the place between encoding and recognition phases. A linear mixed effects model

(LME) was run in R (R Core Team, 2019) using the lme4 package (Bates et al., 2015). We analysed the fixed effects of age group (20-29, 60-69, 70-79; successive differences coding), sex (male, female), condition (swap, substitute) and perspective shift (0°, 30°, 60°; successive differences coding). Random by-participant slopes were included in the model for manipulation and perspective shift.

The main findings were that overall recognition ability declined from the 20-29 to the 60-69 years age group (β = -0.63, SE = 0.13, t = -4.94), and from the 60-69 to the 70-79 years age group (β = -0.47, SE = 0.14, t = -3.42). Similarly, recognition declined from the 0° to 30° perspective shift (β = -0.29, SE = 0.07, t = -4.36), and from the 30° to 60° perspective shifts (β = -0.13, SE = 0.07, t = -2.07; see Figure 2-2a). There was a main effect of condition such that recognition was poorer for the swap condition than for the substitute condition (β = -0.17, SE = 0.03, t = -5.42). Additionally, condition interacted with age-group such that recognition was even worse in the swap condition for the 60-69 compared to the 20-29 years age group (β = -0.23, SE = 0.07, t = -3.21). The interaction did not change for the 70-79 age group, showing that the additional performance deficit in the swap condition was equal for both older age groups compared to the younger group (see Figure 2-2b). There was no main effect of sex and no interactions involving sex. There were no interactions between perspective and age group, or perspective and condition, and no three-way interactions.

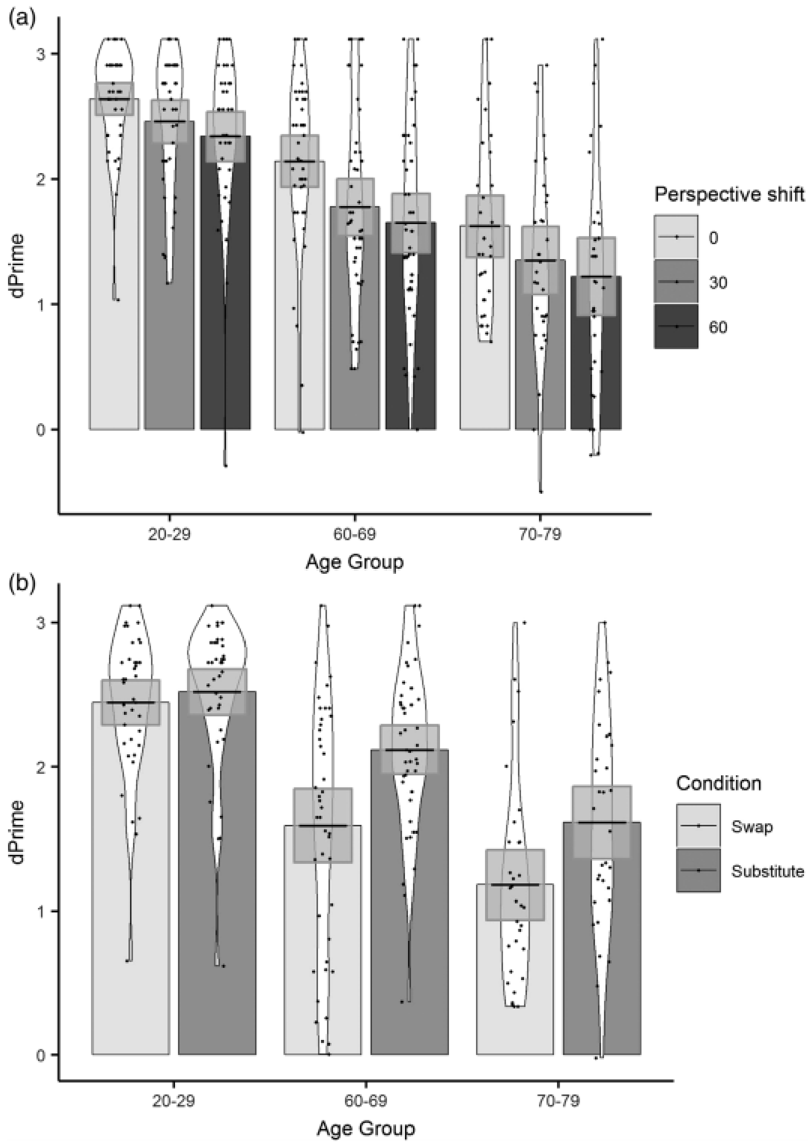

Figure 2-2 - Age group × perspective (Panel a) and age group × condition (Panel b) plots. Plots are mean averages with confidence interval error bars, individual data points and density profiles.

2.4 Discussion

In this study we investigated the involvement of object memory, object-location binding and spatial perspective taking mechanisms in place recognition and how these processes are affected by cognitive ageing. We found that older adults are worse at place recognition overall, and that this deficit is particularly pronounced when object-location binding mechanisms are involved, compared to object memory alone. Changes in spatial perspective also reduced place recognition sensitivity, but interestingly this effect was similar for younger and older age groups.

Although the effect of age on object-location binding using stimuli depicting 2D space has been mixed in previous studies, our data suggests that in a realistic place recognition task using stimuli depicting 3D space, object-location binding mechanisms are degraded in older adults. Indeed, such a result is consistent with navigation studies which demonstrate age-related impairment in the recollection of landmark locations from a previously traversed environment (Head & Isom, 2010).

Interestingly, we also found a trend suggesting a slight decline in place recognition depending on object memory alone for the older adults. This is contrary to previous studies of object memory showing preserved object or landmark memory from place, scene or route learning (Head & Isom, 2010; Mitchell et al., 2000). Considering that the places we used only differed by one object whilst the rest of the place remained identical, it is possible that our older participants demonstrated a pattern completion bias, i.e. they were more likely to accept a place as the same if it is similar (Yassa & Stark, 2011).

Consistent with previous research, we found that the introduction of a perspective shift increased place recognition errors (Hartley et al., 2007; King et al., 2002; Montefinese et al., 2015). We contrasted no shift to a small 30° shift, and 30° to a larger 60° shift. These comparisons revealed that the simple introduction of a perspective shift had an effect size nearly double that of increasing the shift from 30° to 60°. We suggest that it is the requirement to engage spatial perspective taking mechanisms, not the extent of the perspective shift per se, that contributes the largest decrement in recognition performance.

Further, we found similar declines in place recognition sensitivity in response to the perspective shifts for younger and older adults. This result was somewhat unexpected, since viewpoint independent representations are thought to rely on the hippocampus which is subject to age-related deterioration (Hartley et al., 2007; King et al., 2002), however it is consistent with some other studies (e.g. Watanabe & Takamatsu, 2014). Thus, spatial perspective taking in our study does not appear to be reliant on allocentric representations of the places. Instead, perspective shifts could have been resolved via egocentric spatial perspective taking supported by the parietal cortex (Postma & van der Ham, 2016), a brain region relatively spared from age-related atrophy (Yamamoto et al., 2019).

Overall, our study suggests that spatial perspective taking mechanisms are intact in older adults. Object memory was mostly preserved, although did show some decline with age. Much greater age-related decline was observed for object-location binding mechanisms, the requirement of which negatively impacted the ability of older adults to recognise places. Our findings could result from variations in place encoding strategies between younger and older adults. That is to say that sub-optimal encoding strategies during the limited encoding phase may result in the overall impaired place recognition ability in older adults, as well as a greater decline in their memory for the arrangement of objects in space. Conversely, those strategies may be conducive for spatial perspective taking mechanisms. This question of encoding strategies during place recognition is addressed in the following chapter of this thesis.

2.5 References

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/doi: 10.18637/jss.v067.i01

Dai, R., Thomas, A. K., & Taylor, H. A. (2018). Age-related differences in the use of spatial and categorical relationships in a visuo-spatial working memory task. *Memory and Cognition*, *46*(5), 809–825. https://doi.org/10.3758/s13421-018-0794-8

Ellis, N. R., Katz, E., & Williams, J. E. (1987). Developmental aspects of memory for spatial location. *Journal of Experimental Child Psychology*, *44*(3), 401–412. https://doi.org/10.1016/0022-0965(87)90042-7

Hartley, T., Bird, C. M., Chan, D., Cipolotti, L., Husain, M., Vargha-Khadem, F., & Burgess, N. (2007). The Hippocampus Is Required for Short-Term Topographical Memory in Humans. In *Hippocampus* (Vol. 17, Issue 1, pp. 34–48).

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research*, *209*(1), 49–58. https://doi.org/10.1016/j.bbr.2010.01.012

Inagaki, H., Meguro, K., Shimada, M., Ishizaki, J., Okuzumi, H., & Yamadori, A. (2002). Discrepancy between mental rotation and perspective-taking abilities in normal aging assessed by Piaget's Three-Mountain Task. *Journal of Clinical and Experimental Neuropsychology*, *24*(1), 18–25. https://doi.org/10.1076/jcen.24.1.18.969

King, J. A., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2002). Human hippocampus and viewpoint dependence in spatial memory. *Hippocampus*, *12*(6), 811–820. https://doi.org/10.1002/hipo.10070

Klencklen, G., Després, O., & Dufour, A. (2012). What do we know about aging and spatial cognition? Reviews and perspectives. *Ageing Research Reviews*, *11*(1), 123–135. https://doi.org/10.1016/j.arr.2011.10.001

Mitchell, K. J., Johnson, M. K., Raye, C. L., Mather, M., & D'Esposito, M. (2000). Aging and reflective processes of working memory: Binding and test load deficits. *Psychology and Aging*, *15*(3), 527–541. https://doi.org/10.1037/0882-7974.15.3.527

Montefinese, M., Sulpizio, V., Galati, G., & Committeri, G. (2015). Age-related effects on spatial memory across viewpoint changes relative to different reference frames. *Psychological Research*, *79*(4), 687–697. https://doi.org/10.1007/s00426-014-0598-9

Pertzov, Y., Dong, M. Y., Peich, M. C., & Husain, M. (2012). Forgetting What Was Where: The Fragility of Object-Location Binding. *PLoS ONE*, *7*(10). https://doi.org/10.1371/journal.pone.0048214

Postma, A., Kessels, R. P. C., & van Asselen, M. (2008). How the brain remembers and forgets where things are: The neurocognition of object-location memory. *Neuroscience and Biobehavioral Reviews*, *32*(8), 1339–1345. https://doi.org/10.1016/j.neubiorev.2008.05.001

Postma, A., & van der Ham, I. J. M. (2016). Neuropsychology of Space: Spatial Functions of the Human Brain. In *Neuropsychology of Space: Spatial Functions of the Human Brain*. https://doi.org/10.1080/23279095.2017.1326222

R Core Team. (2019). R: A language and environment for statistical computing. In *R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.*

Watanabe, M. (2011). Distinctive features of spatial perspective-taking in the elderly. *International Journal of Aging and Human Development*, *72*(3), 225–241. https://doi.org/10.2190/AG.72.3.d

Watanabe, M., & Takamatsu, M. (2014). Spatial perspective taking is robust in later life. *International Journal of Aging and Human Development*, *78*(3), 277–297. https://doi.org/10.2190/AG.78.3.d

Yamamoto, N., Fox, M. J., Boys, E., & Ord, J. (2019). Effects of orientation change during environmental learning on age-related difference in spatial memory. *Behavioural Brain Research*, *365*(February), 125–132. https://doi.org/10.1016/j.bbr.2019.03.012

Yassa, M. A., & Stark, C. E. L. (2011). Pattern separation in the hippocampus. *Trends in Neurosciences*, *34*(10), 515–525. https://doi.org/10.1016/j.tins.2011.06.006

Chapter 3

Differences in encoding strategy as a potential explanation for age-related decline in place recognition ability

The following chapter is published as: Hilton, C., Muffato, V., Slattery, T. J., Miellet, S., & Wiener, J. (2020). Differences in Encoding Strategy as a Potential Explanation for Age-Related Decline in Place Recognition Ability. *Frontiers in Psychology*, *11*(September). https://doi.org/10.3389/fpsyg.2020.02182

3.1 Abstract

Ability to recognise places is known to deteriorate with advancing age. In this study we investigated the contribution of age-related changes in spatial encoding strategies to declining place recognition ability. We recorded eye movements whilst younger and older adults completed a place recognition task first described in Muffato et al. (2019). Participants first learned places which were defined by an array of four objects, and then decided whether the next place they were shown was the same or different to the one they learned. Places could be shown from the same spatial perspective as during learning, or from a shifted perspective (30° or 60°). Places that were different to those during learning were changed either by substituting an object in the place with a novel object, or by swapping the locations of two objects. We replicated the findings of Muffato et al. (2019) showing that sensitivity to detect changes in a place declined with advancing age and declined when the spatial perspective was shifted. Additionally, older adults were particularly impaired on trials in which object locations were swapped, however they were not differentially affected by perspective changes compared to younger adults. During place encoding, older adults produced more fixations and saccades, shorter fixation durations and spent less time looking at objects compared to younger adults. Further, we present an analysis of gaze chaining, designed to capture spatio-temporal aspects of gaze behaviour. The chaining measure was a significant predictor of place recognition performance. We found significant differences between age groups on the chaining measure and argue that these differences in gaze behaviour are indicative of differences in encoding strategy between age groups. In summary, we report a direct replication of Muffato et al. (2019) and provide evidence for age-related differences in spatial encoding strategies which are related to place recognition performance.

3.2 Introduction

Knowing where you are in the world is vital to many fundamental daily tasks. Such orientation begins with recognising the place you are in. Recognising a place from a known viewpoint can be achieved by matching stored images of that place with current visual input. However, we often must recognise places from a viewpoint which is different from when we first learnt the place. In this case we must additionally engage spatial perspective taking mechanisms to resolve the difference in perspective between our representation of that place and the current viewpoint.

To successfully recognise a place, it must be distinguished from those that are similar. Humans encounter many places which share common object features, for example road signs, traffic lights or trees. Thus, there are many cases in which recognising the individual object identities alone is not sufficient for successful place recognition. To distinguish a place from those that are similar, object identity information must be supplemented with information about the arrangement of the objects in space (Pertzov et al., 2012). As such, place encoding and recognition are complex tasks requiring the binding of object identities to their spatial locations (object-location binding) integrated with the ability to retrieve these representations from a different perspective (spatial perspective taking).

Muffato et al. (2019) investigated how the mechanisms underlying place recognition are affected by ageing. In their experiment, participants first experienced an encoding phase during which they were shown an image of a place to learn. In the subsequent test phase, participants were shown a different image for which they had to decide whether the depicted place was the same or different to the place shown in the encoding phase. The places in their experiment were made up by an array of four unique objects. To test different mechanisms involved in place recognition, places in the test phase could be manipulated in several ways as follows.

Object identity memory was tested in the substitute condition, in which one object in the place was replaced with a novel object between encoding and test phase. In this condition, the recognition performance of older adults was similar to that of younger adults, suggesting that memory for the objects in a place is preserved with advancing age. This result is in line with other spatial learning experiments (Allison & Head, 2017; Cushman et al., 2008; Head & Isom, 2010) and suggests that age-related deficits in place recognition ability is not simply driven by an inability of older adults to remember object identities. Object-location binding was tested in the swap condition, during which the same objects were presented in the test place as in the encoding place, but with the spatial positions of two objects swapped. Participants would have only recognised the change in spatial arrangement if object-location binding was successful (c.f. Pertzov et al., 2012). Muffato et al. (2019) found that older adults' recognition performance was particularly affected by the swap changes. This finding suggests that object-location binding mechanisms are impaired in older adults (see Dai et al., 2018).

Muffato et al. (2019), also tested spatial perspective taking ability. In their experiment test places could be shown from either the same or from a different perspective to that during encoding. Recognition performance declined with the introduction of a perspective shift, but this decline was similar for both age groups. This finding is consistent with previous research which suggests that spatial perspective taking ability is not affected by cognitive ageing (Watanabe, 2011; Watanabe & Takamatsu, 2014). The picture is mixed however, with other studies reporting an age-related decline in spatial perspective taking ability (Inagaki et al., 2002; Montefinese et al., 2015).

Current explanations for age-related changes in place recognition ability focus on the neurodegeneration of the hippocampal circuit (see Klencklen, Després, & Dufour, 2012; Li & King, 2019). The hippocampus is involved in the development of viewpoint independent spatial representations and in spatial perspective taking (Hartley et al., 2007; Hartley & Harlow, 2012; King et al., 2002). Further, object location binding mechanisms are also thought to be hippocampus dependent (Piekema et al., 2006; Postma et al., 2008). Given the age-related neurodegeneration of the hippocampus, which underpins place recognition mechanisms, it is unsurprising that older adults are impaired in place recognition ability. What remains unclear, is the nature of the link between hippocampal decline and place recognition impairment. Older adults could simply be attempting to use the same mechanisms as younger adults, with recognition impairment resulting from sub-optimal execution due to hippocampal decline. This explanation would account for the object-location binding deficits in older adults, but conflicts with the findings of Muffato et al. (2019) showing preserved spatial perspective taking ability in older age. An alternative explanation is that ageing may be accompanied by a shift in place learning and recognition strategies in order to compensate for hippocampal decline (Gutchess et al., 2005; Zhong & Moffat, 2018). These compensatory strategies may be less effective for successful place recognition. Muffato et al. (2019) highlighted that they were unable to discriminate age-related differences in place encoding strategies as a potential explanation for decline in place recognition ability. We address this point in the current study, in which we present a replication of the task used in Muffato et al. (2019), with the addition of eye tracking to record gaze behaviour.

Eye tracking is an established method to investigate the mechanisms and strategies involved in solving cognitive tasks. Already, early eye-movement research demonstrated that gaze patterns in response to a visual stimulus changed depending on the task to be performed (Yarbus & Levy-Schoen, 1968). In fact, eye-movements can be considered as even more than just an artefact of cognitive processes, but an integral part of these processes. This view was well summarised by Neisser (1967), who argued that recall of visual information is a re-construction process involving coordination of visual memory and eye-movements rather than simple retrieval of stored pictures. More recent work supports this conception, showing that the relationship between the scan-path displayed when learning an image and later recalling an image predicts accuracy of recall (Laeng & Teodorescu, 2002). Moreover, this replay of eye-movements is accompanied by image-specific patterns of brain activity during recall (Bone et al., 2019). Indeed, eye tracking has been used to investigate strategies in many cognitive domains, such as learning (for a review see Lai et al., 2013), reading (for a review see Rayner, 1998), memory (for a review see Hannula et al., 2010), face recognition (Chaby et al., 2017), navigation (Andersen et al., 2012; Livingstone-Lee et al., 2011; Mueller et al., 2008). This link between eye-movements and cognition extends to the solving of spatial tasks (Thomas & Lleras, 2007).

Older adults display eye-movement patterns different to that of younger adults in a range of tasks. During route learning, older adults spend less time encoding landmarks, which contributes to an increased likelihood to become disoriented on subsequent attempts to traverse that route (Grzeschik et al., 2019). Age-related differences are also apparent in basic gaze parameters such as reduced saccade amplitudes and increased fixation durations (Dowiasch et al., 2015) as well as in various scan path measures, such as in reading where older adults skip more words than younger adults. This is known as the risky reader strategy (Rayner, Reichle, Stroud, Williams, & Pollatsek, 2006), which in turn leads to more regressions in text than younger adults (McGowan & Reichle, 2018). Paterson et al. (2013) demonstrated that these differences in eye-movements during reading are not a result of impaired oculomotor control which is preserved with age, but are driven by changes in reading strategy. Age-related changes in strategy use are also apparent when remembering the position of 2D objects on a screen, where older adults have been shown to rely on fixation reinstatement to a greater extent than younger adults (Wynn et al., 2018). Fixation reinstatement is the process of reapplying eye movements to the relevant screen locations which objects were shown in and has been suggested to be a strategy used to support memory (Olsen et al., 2014). Whilst there is not a universal method to characterise gaze scan paths (see Anderson et al., 2014), various implementations such as those discussed here demonstrate that spatio-temporal measures of gaze behaviour provide an insight into differences between age groups.

It is not always the case, however, that age effects are observed in eye movements. Hilton et al. (2019) had younger and older participants learn a route through a complex virtual environment whilst recording eye movements. Although they observed age-related differences in route learning ability consistent with other studies (e.g. Head & Isom, 2010; Wiener et al., 2012), they did not find differences between older and younger adults on a range of eye movement measures. This is consistent with the notion of preserved oculomotor control in ageing (Paterson et al., 2013), as well as other accounts of age-equivalence of eye-movement patterns in the absence of a task driven strategy differences (Abrams et al., 1998; Pratt et al., 1997, 2006). The existing research demonstrates that age-related differences in strategy use can be reflected in differences in gaze parameters, various scan path measures and in dwell time on relevant stimuli. Conversely, in situations where older and younger adults use the same cognitive strategies to solve a task, similar gaze behaviour across age groups can be expected.

In the present experiment we used eye tracking to study if the age-related difference in place recognition ability reported by Muffato et al. (2019) was the result of different place encoding strategies. We expected to replicate behavioural results from their study. That is, we expected (1) older adults to perform worse than younger adults overall, and (2) for age to interact with condition. Specifically, we expected a greater performance deficit for older adults in the swap condition in which object locations were swapped in the place as compared to the substitute condition in which an object was replaced with a novel object. If any observed age-related differences were to be a result of maladaptive encoding strategy use by older adults, we expected to also find differences in gaze behaviour during place encoding. Specifically, we analysed eye movement parameters (c.f. Dowiasch et al., 2015, Hilton et al., 2019) and dwell time on task-relevant regions of interest (ROI; c.f. Grzeschik et al., 2019). Finally, we introduce a novel scan-path measure which captures spatio-temporal characteristics of gaze behaviour. On all the measures listed above we report not only age group comparisons but also the extent to which gaze behaviour relates with performance to explore how they are relevant in the context of spatial learning.

3.3 Materials and Methods

3.3.1 Participants

Thirty young and 32 older participants took part in the experiment. Older participants were screened for cognitive impairment using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005) and three participants were excluded from the data using a cut off score of 23 (Luis et al., 2009; Waldron-Perrine & Axelrod, 2012). Table 3-1 summarises the demographic data of the final participant groups. Ethical approval was granted by Bournemouth University Research Ethics Panel and written informed consent was gained from all participants who participated in exchange for either course credits or monetary compensation for their time.

In the study conducted by Muffato et al. (2019), participants were split into three age groups; 20-29, 60-69, 70-79 years old. In their study the object-location binding deficit was observed between the 20-29 and 60-69 age groups, but no additional decline was observed between the 60-69 and 70-79 age groups. Since the aim of the present study was to investigate the age-related object-location binding deficit in place recognition, which did not change between the two groups of older adults in Muffato et al. (2019), we grouped all our participants over the age of 65 into one older adult participant group.

Table 3-1 – Participant demographics

	Sex		Age		MoCA	
		n	Mean	SD	Mean	SD
Younger	Female	15	21.07	3.28		
	Male	15	22.00	5.53		
Older	Female	16	71.31	5.77	27.88	1.67
	Male	13	76.54	6.51	26.85	1.86

3.3.2 Design

There were 3 independent variables in this experiment which were age group (younger, older), perspective shift (0°, 30°, 60°) and place manipulation (same, swap, substitute). The behavioural dependent variable was sensitivity (d’) to detect a place change which was calculated from the response data. There were also several eye-tracking dependent variables which are presented in the eye tracking section of the methods.

We used eight different places in the encoding phases of the experiment. For each place, test images were rendered from the same viewpoint as the encoding stimulus, and at 30° and 60° perspective shifts. The direction of the perspective shift was counterbalanced to occur equally in the left and the right directions (see Figure 3-1a). Additional images of test places were rendered from all perspectives with an object replaced for a novel object (substitute condition) or with two objects swapped in space (swap condition; see Figure 3-1c for examples of each test condition). For more detail about the creation of the stimuli see Muffato et al. (2019).

We made one change in the experiment design from the study conducted by Muffato et al. (2019). In their experiment a black and white mask was displayed before each stimulus in order to disrupt any after-images from the previous stimulus. In the present study we changed the mask to a scrambled version of one of the places in the experiment. This change was made to ensure visual consistency between the mask and the stimulus presented in the trial in terms of colour, luminosity etc. so as not to introduce artefacts into the eye-tracking data such as changes in pupil dilation at the beginning of each trial.

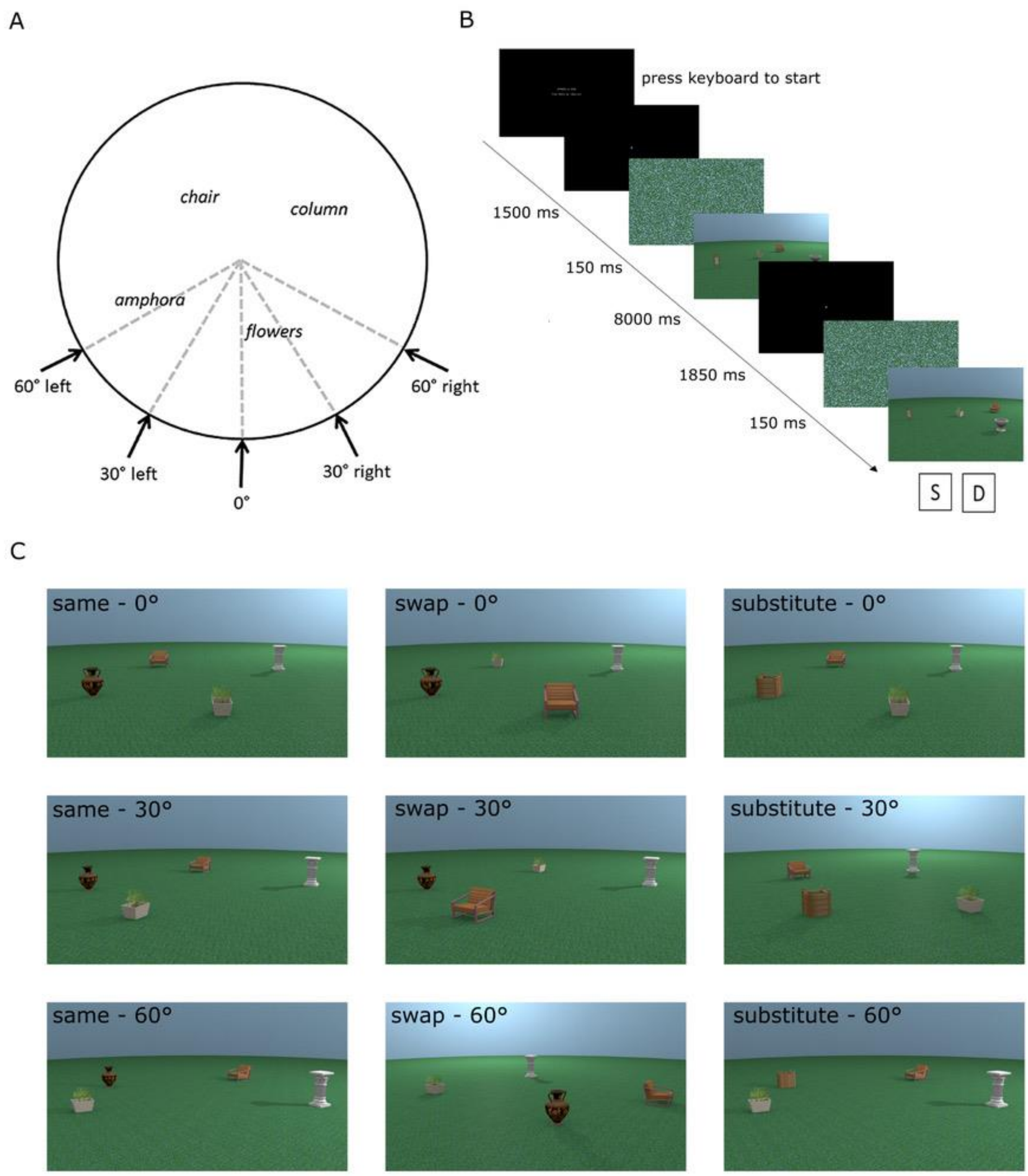

Figure 3-1 – Adapted from Muffato et al. (2019). (a) Overhead schematic of the different possible viewpoints a test place could be shown from. Encoding places were always shown from the 0° viewpoint. (b) Sequence of a trial in the experiment. (c) Examples of all possible test conditions for one encoding place incorporating manipulation (swap or substitute) and perspective shift (0°, 30° and 60°).

3.3.3 Materials

OpenSesame 3.1.4 (Mathôt et al., 2012) was used to display the stimuli and collect responses, with the PyGaze plugin for eye-tracking recording. The experiment was presented on a 102cm screen (diagonal) with an aspect ratio of 16:9 and a resolution of 1920 × 1080 pixels.

Participants sat 1m away from the screen and responded to the task using the X and M keys on the keyboard, which were labelled as S (same) and D (different) respectively. Eye movements were recorded using an Eyelink II (SR Research) head mounted eye-tracker at a rate of 500hz. Calibration used a 9-point grid, and an online drift correction was performed before every trial. Large drift errors initiated a re-calibration before continuing the experiment.

3.3.4 Procedure

Each trial comprised an encoding and test phase. During the encoding phase participants were shown an image of a place for a fixed time of 8 seconds and were instructed to learn the depicted place. In the subsequent test phase participants were shown the image of the test place. Participants had to indicate whether the test place was identical or different from the encoding place. Participants were carefully instructed that a place could be the same, even if it was presented from a different perspective in the test phase. Figure 3-1b details the exact trial procedure and timings of the different phases of the trial. There was a total of 72 trials consisting of 8 trials for each of the 9 conditions (3 place manipulation [same, swap, substitute] x 3 perspective shifts [0, 30, 60]). The trials were in three blocks which were presented in a random order, with trials from each condition evenly distributed across the three blocks.

3.3.5 Eye-tracking analysis

We restricted the analysis of the eye movement data to the encoding phase for two reasons. First, as described above, our research question focused on potential differences in visual encoding strategies. Second, response times and therefore quantity of eye-tracking data in the test phase varied widely between participants, with many participants producing a little as one or two fixations during the test phase trials. Since older adults produced longer response times than younger adults, age comparisons of eye movement data in the test phase would have been heavily confounded by differences between age groups in the amount of eye tracking data. This was not an issue in the encoding phase which had a fixed duration of 8 seconds.

Given the lack of previous work utilising eye-tracking methodology in place recognition paradigms, we performed several exploratory analyses on the gaze data in this experiment. For each analysis we first investigated if there was an age difference in the measure, and then whether that measure was predictive of place recognition performance. For analyses which focused on location of gaze, we used regions of interest (ROI). Each object had an identically sized ROI (see Figure 3-2 for example ROI placement), and the rest of the stimulus was considered as a non-object ROI for a total of 5 ROIs per stimulus. The same ROI templates were used in each analysis which required them.

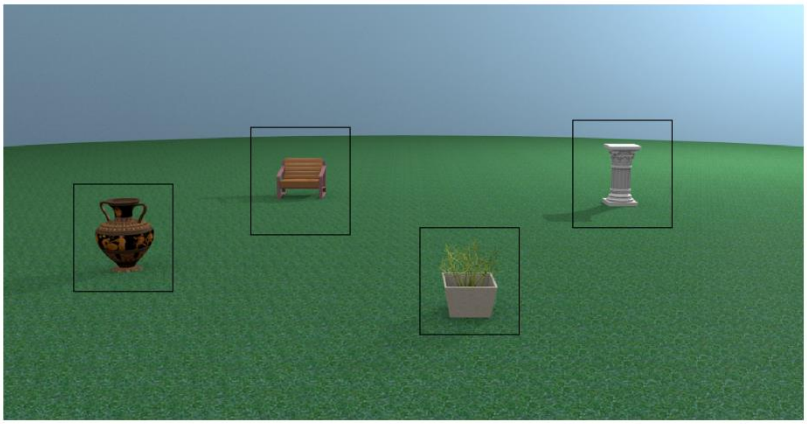

Figure 3-2 - Example ROI placement for one learning stimulus

First, we analysed dwell time on objects in the place compared to the background. On this measure, Grzeschik et al. (2019) reported that older adults spent less time than younger adults looking at objects placed at intersections during a navigation task. Therefore, we might expect that older adults would also look at objects less than younger adults in our task. On the other hand, our environment was very sparse compared to that used in Grzeschik et al. (2019), with no distinguishable features to draw attention other than the objects and thus we were unsure as to whether this finding would replicate in the present experiment. Next, we analysed fixation and saccade parameters as a descriptive insight into the oculomotor behaviour displayed in the different participant groups.

Whilst the analyses described above gives a descriptive insight into gaze behaviour, they are limited in terms of assessing encoding strategies as these measures do not capture the spatio-temporal characteristics of the gaze behaviour during encoding. As discussed earlier, eye-movements between features in the environment are an integral part of the encoding system and the order in which environmental features are looked at could provide insight into specific encoding strategies and differences in encoding strategies between age groups. To capture the order in which objects in the place were looked at during encoding, we developed a gaze measure which will be referred to as *chaining*.

Chaining: For each trial we first recorded the order in which the five interest areas (four objects + non-object background) were visited, discarding successive fixations within the same ROI. Fixations on the non-object background ROI were also removed as it did not contain any task relevant information to be processed, leaving only the sequence in which participants viewed the four object ROIs[1]. Once we obtained a vector with the order in which the four object ROIs were looked at during encoding, we used a sliding window with a size of four (reflecting the maximum possible chain of four unique objects) to calculate how many unique objects (i.e. ROIs) were looked at. This window moved through the vector and we calculated the chaining measure, i.e. the average number of ROIs participants looked at for every four ROI transitions during encoding (Figure 3-3 visualises the chaining measure in detail). The maximum value of the chaining measure is 4 and the minimum value is 2. High chaining values represent encoding strategies in which participants 'chained' all objects together in a sequence and repeatedly looked at them in the same order (see Figure 3-3a). Low chaining values, in contrast, represent trials during which gaze shifted between the same subset of available objects before moving on to newer objects, for example switching back and forth between two objects (see Figure 3-3b).

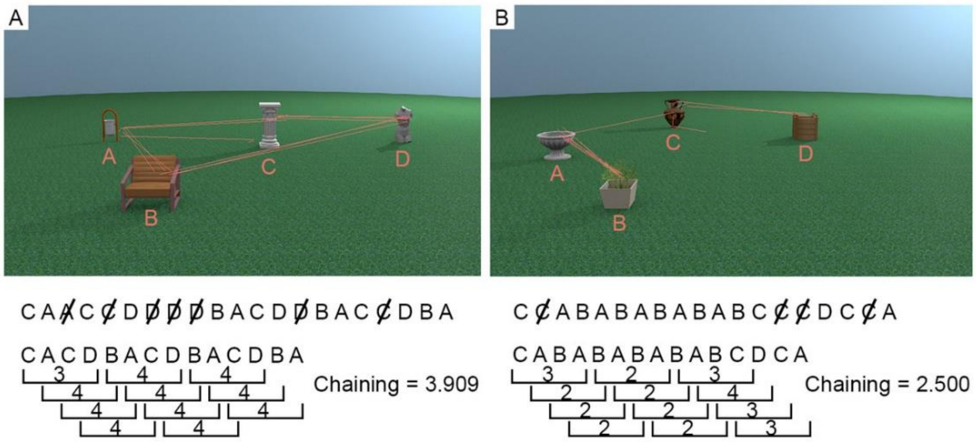

Figure 3-3 - Example chaining calculations. First, duplicates were removed from the sequence of objects gazed at, and then the number of unique objects in every window of four for the whole trial was averaged to produce the chaining measure. A: A high chaining trial in which participants' gaze was repeatedly directed towards objects which were not recently looked at. B: A low chaining trial in which participants' gaze moved back and forth between the same two objects for a large portion of the trial.

[1] In the first application of this measure, we also removed fixations which occurred in the non-object ROI since our stimuli did not feature any relevant cues in non-object ROIs that could be used to solve the task. We later also report the chaining measure without removing non-object ROIs included in a follow up analysis.

3.4 Results

We analysed the data using linear mixed effects models (LME) and generalised linear mixed effects models (GLME) in R (R Core Team, 2019) using the lme4 package (version 1.1-21; Bates et al., 2015). For each model we began with an intercept only model and iteratively added by-participant and by-item slopes. The final model was selected based on AIC comparison between models.

3.4.1 Behavioural

3.4.1.1 Sensitivity

Accuracy data was converted into d-prime scores (d' = z(false alarm rate) – z(hit rate)) for each participants' responses for every condition, which represent their ability to detect a change in the stimulus. We ran an LME on d' with fixed effects of manipulation (sum contrast coding: swap, substitute) perspective (successive differences contrasts: 0°, 30°, 60°) and age group (sum contrast coding: younger, older). We included participant as a random effect. Since d' scores are calculated across trials, item could not be included as a random effect in this model. The final model included by-participant perspective and condition slopes and was the same as in Muffato et al. (2019). Coefficients, standard errors and t-values are reported in Table 3-2.

There were effects of age group, manipulation and perspective. Specifically, younger participants had significantly higher d' than older participants, d' was significantly lower in the swap condition than the substitute condition and d' was significantly lower for a 30° perspective shift compared to a 0°perspective shift. There was no significant effect of perspective shift between 30° and 60° on d' scores.

There was a manipulation by age group interaction which showed that the decline in d' in the swap compared to the substitute condition was greater for the older adults compared to the younger adults (see Figure 3-4). There was also a three-way age group by manipulation by perspective (30° to 60°) interaction which shows that the effect of perspective shift (30° vs 60°) for older adults in the swap condition and younger adults in the substitute condition was smaller than for older adults in the substitute condition and younger adults in the swap condition. When the data was split by manipulation and models were run separately for the swap and the substitute conditions, there was no significant two way age group by perspective (30° vs 60°) interaction in either model (substitute: β = -0.10, SE = 0.10, t = 1.05; swap: β = -0.13, SE = 0.11, t = -1.19).

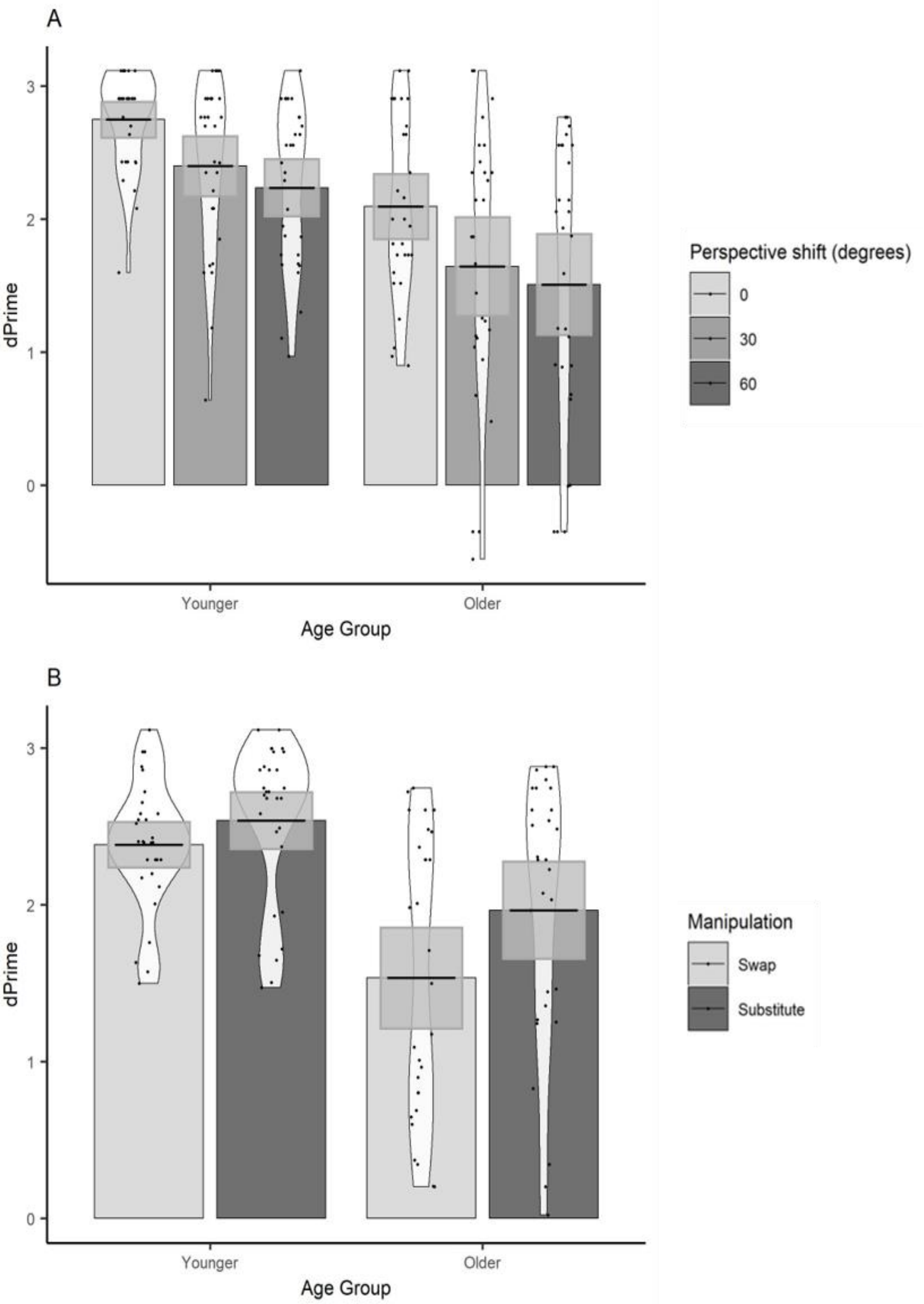

Figure 3-4 - A: d' scores for age group x perspective; B: d' scores for age group x manipulation. Plots show mean averages with confidence interval error bars, individual data points and density profiles.

Table 3-2 - LME model for d' scores

Predictors	*Estimates*	dPrime *std. Error*	*t-value*	Replication of Muffato et al. (2019)
Intercept	2.11	0.09	24.80*	-
Manipulation	-0.15	0.03	-4.84*	Yes
Age group	0.36	0.09	4.19*	Yes
Perspective 0° vs 30°	-0.40	0.09	-4.31*	Yes
Perspective 30° vs 60°	-0.15	0.08	-1.76	No
Manipulation * Age Group	0.07	0.03	2.29*	Yes
Manipulation * Perspective (0° vs 30°)	-0.06	0.05	-1.12	Yes
Manipulation * Perspective (30° vs 60°)	0.01	0.05	0.19	Yes
Age Group * Perspective (0° to 30°)	0.05	0.09	0.54	Yes
Age Group * Perspective (30° to 60°)	-0.01	0.08	-0.16	Yes
Age Group * Manipulation * Perspective (0° to 30°)	0.06	0.05	1.24	Yes
Age Group * Manipulation * Perspective (30° to 60°)	-0.11	0.05	-2.22*	No

*Significant t values (|t|>1.96)

3.4.2 Eye tracking

3.4.2.1 Pre-processing

Eye movements were parsed using SR Research algorithms. We filtered out eye movements which fell outside of the screen boundaries or contained a blink. We also removed the first fixation of every trial since this was likely an artefact of the pre-trial fixation cross in the centre of the screen. Saccades which exceeded the maximum amplitude (41.35°va) or velocity (1500°/s) that should be possible based on distance of the participant from the screen and screen size were regarded as tracker error and were removed. An LME with the fixed effect of age group (sum contrast coding; younger, older) and random factors of participant and item (intercept only) showed no significant difference in the amount of eye-tracking data removed (out of 8000ms) between older (mean = 526.72ms) and younger (mean = 576.76ms) age groups ($\beta = 25.02$, $SE = 28.91$, $t = 0.87$).

3.4.2.2 Time spent looking at objects

An LME with the fixed effect of age group (sum contrast coding: younger, older) and random factors of participant and item (intercept only) revealed that fixations on the objects represented a greater proportion of the encoding phase for younger adults compared to older adults (mean = 0.76; $\beta = 0.03$, $SE = 0.01$, $t = 2.61$)[2].

To investigate whether differences in time spent looking at objects during encoding contributed to the difference in place recognition performance, we conducted a GLME on trial performance (binomial; correct or incorrect). Fixed effects were proportion of time spent looking at objects (continuous, centred), age group (sum contrast coding: younger, older) and manipulation (sum contrast coding: same, swap or substitute), and random factors of participant and item (intercept only). Time spent looking at objects did not predict trial performance ($\beta = -0.02$, $SE = 0.07$, $z = -0.25$, $p = .799$) and did not interact with condition (swap: $\beta = 0.07$, $SE = 0.08$, $z = 0.90$, $p = .369$, substitute: $\beta = -0.07$, $SE = 0.09$, $z = -0.79$, $p = .433$) or with age group ($\beta = -0.03$, $SE = 0.07$, $z = -0.49$, $p = .624$).

3.4.2.3 Parameters

We conducted an LME model for each gaze parameter with age group as a fixed effect (sum contrast coding: younger, older) and random factors of participant and item (intercept only).

[2] Due to limitations of using LME analysis with proportion data we checked this analysis using an LME on log transformed fixation duration on objects with the same fixed and random effects structure. The result was the same as the presented model on proportion of fixation time.

Coefficients, standard errors and t-values are reported in Table 3-3. In summary, older adults produced more fixations, with shorter durations. This was accompanied by more saccades executed by older adults, which did not differ from younger adults in terms of amplitude and velocity.

Table 3-3 – Means for each age group and separate LME model results for each gaze parameter.

Parameter	Younger group mean	Older group mean	*Estimates*	*std. Error*	*t-value*
Saccade Amplitude (°va)	7.72	7.60	0.06	0.14	0.41
Saccade Peak velocity (°/s)	265.07	266.81	-0.87	5.51	-0.16
Saccade Avg. velocity (°/s)	150.20	146.32	1.94	2.44	0.80
Saccade Frequency (/s)	2.83	3.03	-0.10	0.05	-1.97*
Saccade Duration (ms)	42.36	42.96	-0.30	0.64	-0.47
Saccade Sum duration (ms)	894.35	979.96	-42.80	21.72	-1.97*
Saccade Quantity	21.18	22.76	-0.79	0.40	-1.97*
Fixation Duration (ms)	303.14	274.19	14.48	5.52	2.62*
Fixation Frequency (/s)	2.89	3.12	-0.12	0.04	-2.65*
Fixation Quantity	22.73	24.36	-0.81	0.35	-2.30*
Fixation Sum duration (ms)	6528.89	6493.32	17.79	30.16	0.59

*Significant t values ($|t|>1.96$)

To investigate whether gaze parameter profiles predicted performance, we conducted a GLME[3] on trial accuracy (binomial; correct or incorrect) with a selection of gaze parameters as fixed effects. Where multiple parameters can be considered as highly related measures, only one was selected (for example number of fixations and fixation frequency are high correlated when trial length is fixed, r = .99). Number of fixations, average fixation duration, saccade amplitude and saccade average velocity were included as fixed effects (all centred). Participant and item were included in the model as random effects (intercept only).

[3] Age group was omitted from the model due to issues with convergence.

Coefficients, standard errors and z-values are reported in Table 3-4 and show that patterns of fixation and saccade parameters did not predict trial accuracy.

Table 3-4 - GLME model for gaze parameters and trial accuracy

	Accuracy			
Predictors	*Estimates*	*std. Error*	*z-value*	*P*
(Intercept)	1.90	0.13	14.67	<0.001*
Number of fixations	-0.03	0.10	-0.32	.748
Average fixation duration	-0.02	0.10	-0.20	.840
Average saccade amplitude	0.01	0.13	0.05	.963
Average saccade velocity	-0.03	0.13	-0.25	.805

*Significant z values (|z|>1.96)

3.4.2.4 Chaining

In order to demonstrate that the chaining measure captures the extent to which gaze behaviour was actively controlled through the use of a cognitive strategy, we first compared our observed chaining values to those that would occur if gaze was randomly directed between objects. To calculate the chaining value for random gaze behaviour, we randomised the order of the observed ROI vectors for every trial. Here we used the actual data which preserves the number of visits to each ROI and the only change is to the order in which those ROIs were visited through the trial. We then conducted an LME on chaining values with data source (sum contrast coding: observed, random) and age group (sum contrast coding: younger, older) as fixed effects and random factors of participant and item (intercept only). The model revealed that chaining values were larger for the observed data than the random data ($\beta = 0.09$, $SE < 0.01$, $t = 30.84$) and that this interacted with age ($\beta = 0.02$, $SE < 0.01$, $t = 6.35$). To follow up the interaction we conduced separate models for younger and older groups which showed that observed chaining values were larger than random values for both the younger ($\beta = 0.11$, $SE < 0.01$, $t = 25.97$) and the older ($\beta = 0.07$, $SE < 0.01$, $t = 17.62$) age group (see Figure 3-5), however the effect was larger for the younger adults which explains the interaction.

Next, we used an LME model to investigate age differences in chaining behaviour. Age group was included as a fixed effect (sum contrast coding: younger, older) and participant and item were included as random factors (intercept only). The model revealed that younger adults had higher chaining values than older adults (β = 0.06, SE = 0.02, t = 2.64).

To assess whether chaining behaviour was related to task performance we conducted a GLME on trial accuracy (binomial; correct or incorrect) with chaining value (continuous, centred), age group (sum contrast coding: younger, older) and condition (sum contrast coding: same, swap, substitute) as fixed effects, and participant and item as random factors (intercept only). The model revealed that higher chaining behaviour in the encoding phase predicted better recognition performance in the test phase (β = 0.15, SE = 0.06, z = 2.71, p = .007). This effect did not interact with age group (β = 0.04, SE = 0.05, z = 0.73, p = .464) or condition (swap: β = 0.02, SE = 0.07, z = 0.36, p = .718; substitute: β = 0.07, SE = 0.08, z = 1.00, p = .319).

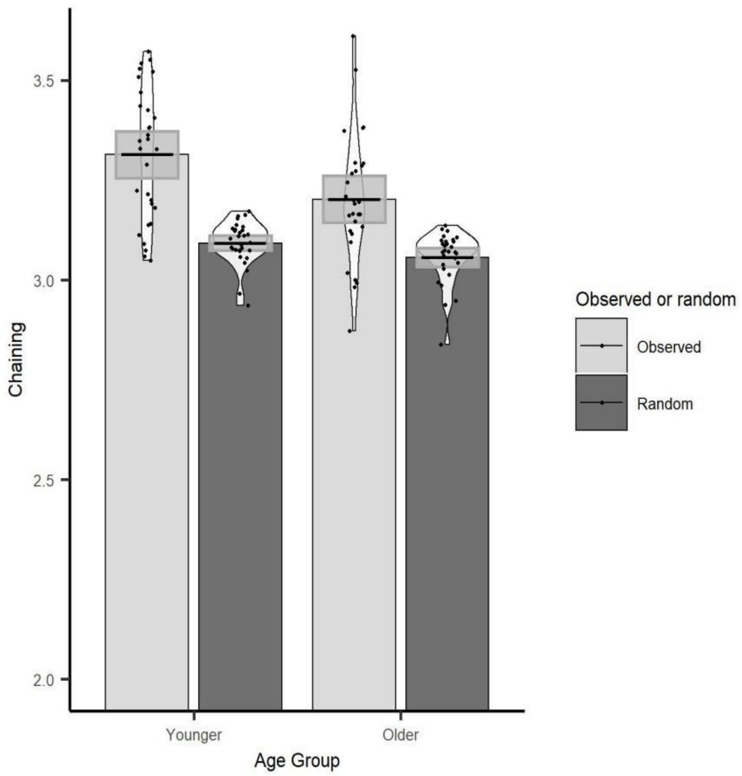

Figure 3-5 - Observed and randomised chaining across age groups with fixations on non-object ROIs removed. Plot shows mean averages with confidence interval error bars, individual data points and density profiles.

For the above analysis of chaining, non-object ROI visits were removed (see Methods section ‘Eye-tracking analysis’). Since we report above that older adults spent a larger proportion of the encoding phase looking at non-object ROIs, we re-calculated the chaining measure including non-object ROIs. Non-object ROIs were not counted as unique interest areas but as disruptions. For example, if there were 3 unique objects visited and one visit to the non-object ROI within a window of four ROI visits, the chaining measure would be 3. This decision was consistent with our original point that non-object ROIs offered no information which would aid place learning and thus may be considered as a disruption to efficient encoding strategies.

We conducted the same set of analyses as for the original chaining measure implementation. As before, the observed chaining values differed from random chaining values ($\beta = 0.06$, $SE < 0.01$, $t = 15.34$) which was the case for both older ($\beta = 0.04$, $SE = 0.01$, $t = 6.99$) and younger participants ($\beta = 0.08$, $SE = 0.01$, $t = 14.87$). Observed chaining values were still higher for younger participants than for older participants ($\beta = 0.10$, $SE = 0.03$, $t = 3.15$; see Figure 3-6). However, this version of the chaining measure did not predict trial accuracy ($\beta = 0.01$, $SE = 0.06$, $z = 0.24$, $p = .809$).

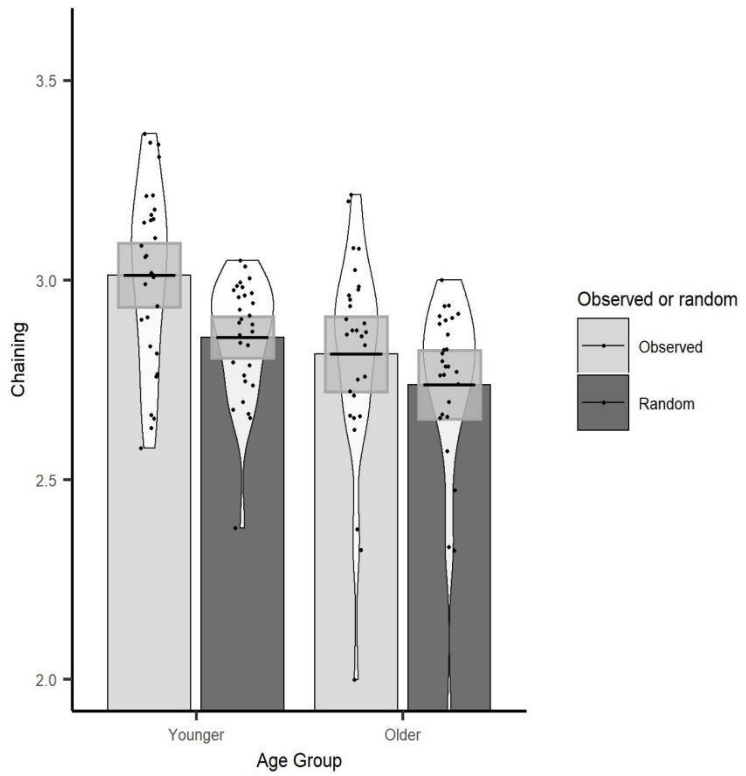

Figure 3-6 - Observed and randomised chaining across age groups with fixations on non-object ROIs included. Plot shows mean averages with confidence interval error bars, individual data points and density profiles.

3.5 Discussion

In this experiment we used eye-tracking and a place recognition task to investigate age-related changes in place encoding strategies. Participants were shown a place during the encoding phase and then had to decide whether the place was identical or had changed in a subsequent test phase. We replicated behavioural findings reported by Muffato et al. (2019). Older adults performed worse than younger adults, particularly when object positions were swapped, a manipulation that required object-location binding to solve. Recognition ability was worse when a spatial perspective shift was introduced, but older adults were not differentially affected by perspective shifts compared to younger adults. We found small age-effects in several gaze parameters and in the time spent looking at objects, however these gaze measures did not correlate with place recognition performance. We also developed a new gaze measure, chaining, which captures spatio-temporal aspects of gaze behaviour. The chaining measure was different between age groups and one variant of this new measure was related to recognition performance.

As we expected, overall sensitivity to detect changes in the places was lower for older adults than for younger adults. This result is consistent with many other accounts of age related decline in spatial learning abilities (for reviews see: Klencklen et al., 2012; Lester et al., 2017; Moffat, 2009). We also found that sensitivity to detect changes in the place was lower overall for the swap condition in which two of the four objects were exchanged between encoding and test, than for the substitute condition in which one object was replaced with a new object. The increased difficulty of the swap condition can be explained by the requirement to engage object location binding mechanisms to successfully recognise the place (Pertzov et al., 2012; Postma et al., 2008), whereas the substitute condition can be solved with object identity knowledge alone. Importantly, an interaction between age group and manipulation revealed that the drop in sensitivity between substitute and swap conditions was greater for older adults than for younger adults. Given that older adults perform better in the substitute condition than the swap condition, this deficit cannot be explained by a lack of object identity knowledge which appears to remain relatively intact in our adults (c.f. Cushman et al., 2008; Head & Isom, 2010). Instead, they can be explained by a specific age-related decline in object-location binding. These findings are consistent with other accounts of age-related decline in object location binding ability (e.g. Dai et al., 2018).

In our study we found that the initiation of a perspective shift was associated with a drop in recognition sensitivity, which did not interact with age, as reported by Muffato et al. (2019).

This can be explained by the initiation of additional spatial perspective taking mechanisms which are not active in the 0° condition, therefore incurring additional cognitive load (Holmes et al., 2018). In contrast to Muffato et al. (2019) we did not find that sensitivity continued to drop with increasing degrees of perspective change (30° vs 60°). This could be a reflection of additional perspective shifts being less costly, due to the fact that spatial perspective taking mechanisms are already engaged in the 30° condition and thus no new mechanisms need to be engaged to solve the 60° condition. Indeed the 0°-30° shift effect in Muffato et al. (2019) was more than double the size of the 30°-60° shift. In our study the 30°-60° perspective shift effect did not reach significance, although our t-value was close ($t = 1.76$). Given that our study had fewer participants than Muffato et al. (2019), and the relatively small size of their 30°-60° perspective shift effect, we may have lacked power to detect this effect. An alternative explanation is that increases in perspective change may not increase the difficulty of place recognition, however this interpretation seems unlikely since it conflicts with other evidence showing that increasing perspective changes are associated with reduced recognition performance (Diwadkar & McNamara, 1997; Montefinese et al., 2015).

The behavioural results of this study are a direct replication of those found by Muffato et al. (2019). As such, the main results are that older adults are impaired in object-location binding dependent place recognition but have preserved perspective taking ability. The novel contribution of the present study was to investigate the contribution of place encoding strategies to the age-related impairment observed in place recognition ability.

We recorded gaze behaviour to assess differences in place encoding strategies between younger and older adults. We found differences between age groups in several gaze parameters. Specifically, older adults produced more fixations in the 8 second encoding phase than younger adults, with shorter average fixation duration. Accordingly, they performed more saccades than younger adults, but saccade amplitudes and velocity was comparable between age groups. These findings conflict with those of Dowiasch et al. (2015) who reported that older adults made fewer saccades which had lower amplitudes than those performed by younger adults whilst locomoting through a real-world environment. Açik et al. (2010) also reported lower saccade amplitudes in older adults whilst viewing a complex visual image, although their results show higher saccade frequency and reduced fixation durations which is consistent with our results. Açik and colleagues suggested that because their task did not contain a recall memory element, older adults were able to employ an efficient image exploration strategy which involved performing a series of short saccades and fixations throughout the image. The same argument is true for the study conducted by

Dowiasch et al. (2015) although their study contains a locomotion element which could be responsible for the increased fixation time, since older adults are known to alter their gaze behaviour in an attempt to avoid falling (for a review see Uiga et al., 2015) .

Indeed, in paradigms which do contain a memory element, such as visual search tasks where items in the stimulus must be compared to a target object in memory, the reverse pattern of gaze behaviour is observed. Older adults fixate more often and for longer durations (Williams et al., 2009) likely due to older adults being more cautious about accepting or rejecting items as targets (Porter et al., 2010). In our task, the encoding phase did not require participants to compare the stimulus to visual memory traces which could explain why we observed reduced fixation durations and increased saccade frequency as found by Açik et al. (2010). Equivalence of saccade amplitudes and velocities between our age groups may be a result of the simple stimuli used, which is in contrast to the visually dense stimuli used in the study by Açik et al. (2010). With only four objects presented against a visually simple background, there are limited choices as to where gaze should be directed, and since older and younger adults viewed the same stimuli, eye movements between these objects would produce saccades of similar amplitudes. Following this, increased frequency of saccades between objects, with shorter fixation times on those objects, could be a result of differences in encoding strategy between age groups.

In our study, gaze parameters were not predictive of place recognition performance. The coefficients we report from our models of gaze parameters reveal that the age differences are very small (for example on the scale of less than one saccade and fixation per trial). In addition, gaze parameters are not independent of each other, and visual encoding strategies are likely reflected in a combination of these parameters as scan-paths performed throughout the trial which form part of the memory trace for that place (Bone et al., 2019). In this case we would expect that breaking those scan-paths into their component parts (gaze parameters), which also removes any temporal element in the data, would also reduce the predictive power of eye movements for recognition performance. Combined with the small effect sizes we observe between age groups, it is not surprising that individual parameters of oculomotor behaviour did not correlate with performance. To address this point and to gain a deeper understanding of visual encoding strategies, we developed the chaining measure.

The chaining measure was designed to quantify the extent to which participants are using an encoding strategy which involves chaining multiple unique objects together during encoding. High chaining values represent an encoding strategy in which participants were likely to direct their gaze to an object which had not recently been inspected, creating a sequence of eye-movements which bind (or chain) several different objects together. The chaining value is lowered when an object which has recently been attended to is revisited as opposed to gaze being directed towards a novel object.

We found that observed chaining was significantly higher than what would be expected if participants' gaze transitioned randomly between objects. The difference between observed and random chaining suggests that the measure captured strategy directed gaze behaviour. The older adults in our study chained significantly less than younger adults during encoding. This finding is consistent with accounts of age-related changes in strategy in other cognitive tasks, such as during reading, where older adults are more likely to make regressions to previously read text than younger adults, likely as a result of skipping words (Rayner et al., 2006). The tendency to under-process important task relevant information is also present during route navigation, in which older adults spend less time looking at landmarks (Grzeschik et al., 2019). In our study, we also found that older adults spent significantly less time looking at landmarks overall, alongside a reduction in individual fixation durations. In this scenario, regressions to recently attended objects to correct incidences of under-processing would have resulted in the lower chaining values. Such regressive saccades would be of similar amplitude and velocity as saccades to other objects in the place, which is consistent with our findings regarding these parameters.

One explanation for the reduced chaining patterns in our older adults could be age-related changes in working memory. It is well established that several aspects of working memory change with advancing age (D'Antuono et al., 2020; Klencklen et al., 2017). Poorer visual working memory skills for older adults result in worse retention of visual features (Brockmole & Logie, 2013) and could be why the older adults in our study were more likely to re-fixate recently viewed objects, in order to refresh their representation. The decline in working memory span has been shown to extend beyond the visual domain, with general span deficits occurring in older age (Bopp & Verhaeghen, 2005). Bopp & Verhaeghen (2005) note in their meta-analysis that age differences in working memory span become apparent around list sizes of 4, which was the maximum possible chain size in our study. Bopp & Verhaeghen (2005) further report that age-differences in span increase proportionally with increasing set sizes. If working memory span is an influencing factor in the chaining behaviour observed in our study, then more complex places with a larger quantity of objects (>4), as is common in the real world, may be even more difficult for older adults to encode.

We found that the initial implementation of the chaining measure (excluding fixations on the non-object background ROI) did predict recognition performance, which suggests that differences in visual encoding strategies contributed to the age-related place recognition deficit. There was no interaction between chaining value and condition when predicting performance, indicating that high chaining is an encoding strategy that is suited for both the substitute and the swap condition. This is not surprising, considering that the substitute condition can be solved with landmark identity information alone (as soon as an object is identified as novel the place can be accepted as different). Thus, any visual encoding strategy that is efficient to solve the swap condition would also be suited for the substitute condition. This is because the object-location binding which is required when solving swap trials, also requires object identity knowledge (Pertzov et al., 2012). Given that older adults' performance was less impaired in the substitute condition than the swap condition, their visual encoding strategy is likely to be somewhat efficient for the encoding of object identity. However, higher chaining behaviour as seen in our younger participants is better still for object identity encoding, since they outperform our older participants in the substitute condition. The reduced likelihood for older adults to sequence multiple objects together through their eye movements (lower chaining) may contribute to weaker spatial integration of the object arrangement, resulting in the additional difficulty that older adults experienced detecting the change in the swap condition.

Optimal chaining behaviour would result in a stereotyped fixation sequence with gaze being directed to the four objects repeatedly in the same order. Specifically, at the end of the object chain gaze should return to the object in which the chain began to create a circular sequence (e.g. as shown in the example scan path in Figure 3-3a). When the place does not change, the order of objects is the same, even if the viewpoint has changed provided the optimal chain is initiated from the same object. If two object positions were swapped however, the order would be disrupted, and the place can be identified as different. In this way, a temporal structure of the place is created through eye-movements (Heuer & Rolfs, 2019; Rucci et al., 2018), where a swap of object locations results in a swap along the temporal dimension. Usually such temporal encoding of space is evident when stimuli dynamically appear and disappear, or are highlighted, in a sequence (De Lillo et al., 2016) and has its own independent contribution to memory from concurrently formed spatial representations (Heuer & Rolfs, 2019).

If such viewpoint independent temporal structures were derived during place learning through gaze chaining, the need for perspective taking mechanisms would be circumvented and thus could account for the lack of interaction between age and perspective shift in recognition performance in the present study as well as in Muffato et al. (2019). It is possible that in the current and earlier studies (e.g. Muffato et al., 2019; Watanabe, 2011; Watanabe & Takamatsu, 2014), participants were able to extract temporal information as an alternative to perspective taking. This may not be the case for studies which found that spatial perspective shifts do differentially affect performance for different age groups (e.g. Montefinese et al., 2015). If such an explanation is accurate, it is unlikely that participants are relying solely on any temporal representation of the place since we did find an overall main effect of perspective shift, and thus are more likely to be used in combination with spatial information (Heuer & Rolfs, 2019). Further research would be required to reconcile the role of temporal and spatial reference frames when solving spatial perspective changes and how this is affected by age.

We also reported a subsequent calculation of the chaining measure in which we included fixations to non-objects (background). Fixations on the non-object ROI were counted as disruptions and thus the presence of non-object fixations in the scan-path reduced the chaining measure. In this implementation of the measure the age effect increased in size, reflecting the increased likelihood of older adults to disrupt their chains with fixations away from the relevant objects. However, chaining did not correlate with recognition performance anymore. This is contrary to what one might expect given that there is no information in the non-object interest areas which could aid the resolution of the task. Thus, eye-movements to these non-object regions or background should have disrupted spatial encoding (Thomas & Lleras, 2007). If this was the case, we expected the chaining measure that included non-object fixations to have a larger correlation with recognition performance, however we actually found the opposite. One explanation for the lack of association between chaining and performance using this version of the chaining measure is that whilst non-object fixations have not aided in solving the task, they were also not costly. Given that there is no complex visual information to be processed in the non-object regions, fixations in these areas may not have negatively affected the spatial representations of the place. This argument is supported by the finding that the time spent fixating at non-object regions also did not predict performance. Indeed Shih, Meadmore and Liversedge (2012) reported differences between age groups on time spent looking at objects in a spatial encoding task and they also conclude that such object-oriented viewing does not promote memory about the general layout of the objects in space. Given this explanation, the inclusion of non-object fixations in the chaining measure served only to add noise to the data and thus impacted on its predictive power.

If non-object fixations in our task were neutral with regards to place encoding, then why did older adults fixate non-object regions significantly more often than younger adults? This could be a result of reduced oculomotor accuracy in saccade landing sites for older adults (Sharpe & Zackon, 1987). If this were true however, we would also have expected lower average saccade amplitudes in older adults resulting from corrective saccades, which we did not find. Alternatively, visits to non-object regions may be an artefact of older adults attempting to rely on cues external to the object array. Indeed, older adults have been shown to rely more on geometric cues in the environment as opposed to objects or landmarks, when orienting in space (Bécu et al., 2019). Further, current work from Segen et al. (2020 preprint) found that eye movements during place encoding were more exploratory in older adults than in younger adults. Segen and colleagues suggest that older adults rely on distal environmental cues to aid spatial encoding, more so than younger adults. In our task, there were no external environmental cues such as distal objects (Segen et al., 2020 preprint) or geometric features (Bécu et al., 2019) and so attempts from older adults to fixate on extra-object cues would have been futile.

In summary, we provide further evidence for age-related impairments in place recognition ability, particularly when recognition requires the use of object-location binding mechanisms. We show differences between age groups on several measures of eye movements, including chaining of objects through gaze. We explore how these differences could be indicative of differences in place encoding strategy and provide some first insights into the nature of these strategies.

3.6 References

Abrams, R. A., Chasteen, A. L., & Pratt, J. (1998). Aging and movement: Variability of force pulses for saccadic eye movements. *Psychology and Aging*, *13*(3), 387–395. https://doi.org/10.1037/0882-7974.13.3.387

Açik, A., Sarwary, A., Schultze-Kraft, R., Onat, S., & König, P. (2010). Developmental changes in natural viewing behavior: Bottom up and top-down differences between children, young adults and older adults. *Frontiers in Psychology*, *1*(NOV), 1–14. https://doi.org/10.3389/fpsyg.2010.00207

Allison, S., & Head, D. (2017). Route repetition and route reversal: Effects of age and encoding method. *Psychology and Aging*, *32*(3), 220–231. https://doi.org/10.1037/pag0000170

Andersen, N. E., Dahmani, L., Konishi, K., & Bohbot, V. D. (2012). Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory*, *97*(1), 81–89. https://doi.org/10.1016/j.nlm.2011.09.007

Anderson, N. C., Anderson, F., Kingstone, A., & Bischof, W. F. (2014). A comparison of scanpath comparison methods. *Behavior Research Methods*, *47*(4), 1377–1392.

https://doi.org/10.3758/s13428-014-0550-3

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/doi: 10.18637/jss.v067.i01

Bécu, M., Sheynikhovich, D., Tatur, G., Agathos, C. P., Bologna, L. L., Sahel, J. A., & Arleo, A. (2019). Age-related preference for geometric spatial cues during real-world navigation. *Nature Human Behaviour*. https://doi.org/10.1038/s41562-019-0718-z

Bone, M. B., St-Laurent, M., Dang, C., McQuiggan, D. A., Ryan, J. D., & Buchsbaum, B. R. (2019). Eye movement reinstatement and neural reactivation during mental imagery. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhy014

Bopp, K. L., & Verhaeghen, P. (2005). Aging and verbal memory span: A meta-analysis. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, *60*(5), 223–233. https://doi.org/10.1093/geronb/60.5.P223

Brockmole, J. R., & Logie, R. H. (2013). Age-related change in visual working memory: A study of 55,753 participants aged 8-75. *Frontiers in Psychology*, *4*(JAN), 1–5. https://doi.org/10.3389/fpsyg.2013.00012

Chaby, L., Hupont, I., Avril, M., Luherne-du Boullay, V., & Chetouani, M. (2017). Gaze behavior consistency among older and younger adults when looking at emotional faces. *Frontiers in Psychology*, *8*(APR), 1–14. https://doi.org/10.3389/fpsyg.2017.00548

Cushman, L. A., Duffy, C. J., Stein, K., & Duffy, C. J. (2008). Virtual reality identifies navigational defects in Alzheimer disease and cognitive aging. *Nature Clinical Practice Neurology*, *4*(12), 638–639. https://doi.org/10.1038/ncpneuro0929

D'Antuono, G., Maini, M., Marin, D., Boccia, M., & Piccardi, L. (2020). Effect of ageing on verbal and visuo-spatial working memory: Evidence from 880 individuals. *Applied Neuropsychology:Adult*, *0*(0), 1–10. https://doi.org/10.1080/23279095.2020.1732979

Dai, R., Thomas, A. K., & Taylor, H. A. (2018). Age-related differences in the use of spatial and categorical relationships in a visuo-spatial working memory task. *Memory and Cognition*, *46*(5), 809–825. https://doi.org/10.3758/s13421-018-0794-8

De Lillo, C., Kirby, M., & Poole, D. (2016). Spatio-temporal structure, path characteristics, and perceptual grouping in immediate serial spatial recall. *Frontiers in Psychology*, *7*(NOV), 1–18. https://doi.org/10.3389/fpsyg.2016.01686

Diwadkar, V. A., & McNamara, T. P. (1997). Viewpoint dependence in scene recognition. *Psychological Science*, *8*(4), 302–307. https://doi.org/10.1111/j.1467-9280.1997.tb00442.x

Dowiasch, S., Marx, S., Einhäuser, W., & Bremmer, F. (2015). Effects of aging on eye movements in the real world. *Frontiers in Human Neuroscience*, *9*(FEB), 1–12. https://doi.org/10.3389/fnhum.2015.00046

Grzeschik, R., Conroy-Dalton, R., Innes, A., Shanker, S., & Wiener, J. M. (2019). The contribution of visual attention and declining verbal memory abilities to age-related route learning deficits. *Cognition*, *187*(July 2018), 50–61. https://doi.org/10.1016/j.cognition.2019.02.012

Gutchess, A. H., Welsh, R. C., Hedden, T., & Minear, M. (2005). Aging and the Neural

Correlates of Successful Picture Encoding: Frontal Activations Compensate for Decreased Medial-Temporal Activity Cognition & Aging View project Mindfulness and Self-Compassion for Trauma and PTSD View project. *Article in Journal of Cognitive Neuroscience*, 84–96. https://doi.org/10.1162/0898929052880048

Hannula, D. E., Althoff, R. R., Warren, D. E., Riggs, L., Cohen, N. J., & Ryan, J. D. (2010). Worth a glance: Using eye movements to investigate the cognitive neuroscience of memory. *Frontiers in Human Neuroscience*, *4*(October), 1–16. https://doi.org/10.3389/fnhum.2010.00166

Hartley, T., Bird, C. M., Chan, D., Cipolotti, L., Husain, M., Vargha-Khadem, F., & Burgess, N. (2007). The Hippocampus Is Required for Short-Term Topographical Memory in Humans. In *Hippocampus* (Vol. 17, Issue 1, pp. 34–48).

Hartley, T., & Harlow, R. (2012). An association between human hippocampal volume and topographical memory in healthy young adults. *Frontiers in Human Neuroscience*, *6*(DEC), 1–11. https://doi.org/10.3389/fnhum.2012.00338

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research*, *209*(1), 49–58. https://doi.org/10.1016/j.bbr.2010.01.012

Heuer, A., & Rolfs, M. (2019). Representing the spatiotemporal structure of visual events: Spatial and temporal frames of reference in working memory. *Journal of Vision*. https://doi.org/10.1167/19.10.76

Hilton, C., Miellet, S., Slattery, T. J., & Wiener, J. (2019). Are age-related deficits in route learning related to control of visual attention? *Psychological Research*, *0*(0), 0. https://doi.org/10.1007/s00426-019-01159-5

Holmes, C. A., Newcombe, N. S., & Shipley, T. F. (2018). Move to learn: Integrating spatial information from multiple viewpoints. *Cognition*, *178*(April), 7–25. https://doi.org/10.1016/j.cognition.2018.05.003

Inagaki, H., Meguro, K., Shimada, M., Ishizaki, J., Okuzumi, H., & Yamadori, A. (2002). Discrepancy between mental rotation and perspective-taking abilities in normal aging assessed by Piaget's Three-Mountain Task. *Journal of Clinical and Experimental Neuropsychology*, *24*(1), 18–25. https://doi.org/10.1076/jcen.24.1.18.969

King, J. A., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2002). Human hippocampus and viewpoint dependence in spatial memory. *Hippocampus*, *12*(6), 811–820. https://doi.org/10.1002/hipo.10070

Klencklen, G., Banta Lavenex, P., Brandner, C., & Lavenex, P. (2017). Working memory decline in normal aging: Is it really worse in space than in color? *Learning and Motivation*, *57*, 48–60. https://doi.org/10.1016/j.lmot.2017.01.007

Klencklen, G., Després, O., & Dufour, A. (2012). What do we know about aging and spatial cognition? Reviews and perspectives. *Ageing Research Reviews*, *11*(1), 123–135. https://doi.org/10.1016/j.arr.2011.10.001

Laeng, B., & Teodorescu, D. S. (2002). Eye scanpaths during visual imagery reenact those of perception of the same visual scene. *Cognitive Science*, *26*(2), 207–231. https://doi.org/10.1016/S0364-0213(01)00065-9

Lai, M. L., Tsai, M. J., Yang, F. Y., Hsu, C. Y., Liu, T. C., Lee, S. W. Y., Lee, M. H., Chiou, G. L., Liang, J. C., & Tsai, C. C. (2013). A review of using eye-tracking technology in exploring learning from 2000 to 2012. *Educational Research Review*, *10*(88), 90–115.

https://doi.org/10.1016/j.edurev.2013.10.001

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers, T. (2017). The Aging Navigational System. *Neuron*, *95*(5), 1019–1035. https://doi.org/10.1016/j.neuron.2017.06.037

Li, A. W. Y., & King, J. (2019). Spatial memory and navigation in ageing: A systematic review of MRI and fMRI studies in healthy participants. *Neuroscience and Biobehavioral Reviews*, *103*(August 2018), 33–49. https://doi.org/10.1016/j.neubiorev.2019.05.005

Livingstone-Lee, S. A., Murchison, S., Zeman, P. M., Gandhi, M., van Gerven, D., Stewart, L., Livingston, N. J., & Skelton, R. W. (2011). Simple gaze analysis and special design of a virtual Morris water maze provides a new method for differentiating egocentric and allocentric navigational strategy choice. *Behavioural Brain Research*, *225*(1), 117–125. https://doi.org/10.1016/j.bbr.2011.07.005

Luis, C., Keegan, A., & Mullan, M. (2009). Cross validation of the Montreal Cognitive Assessment in community dwelling older adults residing in the Southeastern US. *International Journal of Geriatric Psychiatry*, *24*(2), 197–201.

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, *44*(2), 314–324. https://doi.org/10.3758/s13428-011-0168-7

McGowan, V. A., & Reichle, E. D. (2018). The “risky” reading strategy revisited: New simulations using E-Z reader. *Quarterly Journal of Experimental Psychology*, *71*(1 Special Issue), 179–189. https://doi.org/10.1080/17470218.2017.1307424

Moffat, S. D. (2009). Aging and spatial navigation: What do we know and where do we go? *Neuropsychology Review*, *19*(4), 478–489. https://doi.org/10.1007/s11065-009-9120-3

Montefinese, M., Sulpizio, V., Galati, G., & Committeri, G. (2015). Age-related effects on spatial memory across viewpoint changes relative to different reference frames. *Psychological Research*, *79*(4), 687–697. https://doi.org/10.1007/s00426-014-0598-9

Mueller, S. C., Jackson, C. P. T., & Skelton, R. W. (2008). Sex differences in a virtual water maze: An eye tracking and pupillometry study. *Behavioural Brain Research*, *193*(2), 209–215. https://doi.org/10.1016/j.bbr.2008.05.017

Muffato, V., Hilton, C., Meneghetti, C., De Beni, R., & Wiener, J. M. (2019). Evidence for age-related deficits in object-location binding during place recognition. *Hippocampus*, *February*, 1–9. https://doi.org/10.1002/hipo.23099

Nasreddine, Z. S., Phillips, N. A., Bedirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L., & Chertkow, H. (2005). The Montreal cognitive assessment, MoCA: a brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, *53*(4), 695–699.

Neisser, U. (1967). Cognitive Psychology. In *Cognitive Psychology*. Meredith Publishing Company. https://doi.org/10.4324/9781315736174

Olsen, R. K., Chiew, M., Buchsbaum, B. R., & Ryan, J. D. (2014). The relationship between delay period eye movements and visuospatial memory. *Journal of Vision*, *14*(1), 1–11. https://doi.org/10.1167/14.1.8

Paterson, K. B., McGowan, V. A., & Jordan, T. R. (2013). Aging and the control of binocular fixations during reading. *Psychology and Aging*, *28*(3), 789–795. https://doi.org/10.1037/a0033328

Pertzov, Y., Dong, M. Y., Peich, M. C., & Husain, M. (2012). Forgetting What Was Where: The Fragility of Object-Location Binding. *PLoS ONE*, *7*(10). https://doi.org/10.1371/journal.pone.0048214

Piekema, C., Kessels, R. P. C., Mars, R. B., Petersson, K. M., & Fernández, G. (2006). The right hippocampus participates in short-term memory maintenance of object-location associations. *NeuroImage*, *33*(1), 374–382. https://doi.org/10.1016/j.neuroimage.2006.06.035

Porter, G., Tales, A., Troscianko, T., Wilcock, G., Haworth, J., & Leonards, U. (2010). New insights into feature and conjunction search: I. Evidence from pupil size, eye movements and ageing. *Cortex*, *46*(5), 621–636. https://doi.org/10.1016/j.cortex.2009.04.013

Postma, A., Kessels, R. P. C., & van Asselen, M. (2008). How the brain remembers and forgets where things are: The neurocognition of object-location memory. *Neuroscience and Biobehavioral Reviews*, *32*(8), 1339–1345. https://doi.org/10.1016/j.neubiorev.2008.05.001

Pratt, J., Abrams, R. A., & Chasteen, A. L. (1997). Initiation and inhibition of saccadic eye movements in younger and older adults: An analysis of the gap effect. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, *52*(2). https://doi.org/10.1093/geronb/52B.2.P103

Pratt, J., Dodd, M., & Welsh, T. (2006). Growing older does not always mean moving slower: Examining aging and the saccadic motor system. *Journal of Motor Behavior*, *38*(5), 373–382. https://doi.org/10.3200/JMBR.38.5.373-382

R Core Team. (2019). R: A language and environment for statistical computing. In *R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.*

Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, *124*(3), 372–422.

Rayner, Keith, Reichle, E. D., Stroud, M. J., Williams, C. C., & Pollatsek, A. (2006). The effect of word frequency, word predictability, and font difficulty on the eye movements of young and older readers. *Psychology and Aging*, *21*(3), 448–465. https://doi.org/10.1037/0882-7974.21.3.448

Rucci, M., Ahissar, E., & Burr, D. (2018). Temporal Coding of Visual Space. *Trends in Cognitive Sciences*, *22*(10), 883–895. https://doi.org/10.1016/j.tics.2018.07.009

Segen, V., Avraamides, M. N., Slattery, T. J., & Wiener, J. (2020, April 23). Age-related differences in visual encoding and response strategies contribute to spatial memory deficits. *PsyArXiv* https://doi.org/10.31234/osf.io/4qdey

Sharpe, J. A., & Zackon, D. H. (1987). Senescent saccades: Effects of aging on their accuracy, latency and velocity. *Acta Oto-Laryngologica*. https://doi.org/10.3109/00016488709128270

Shih, S. I., Meadmore, K. L., & Liversedge, S. P. (2012). Aging, Eye movements, and object-location memory. *PLoS ONE*, *7*(3). https://doi.org/10.1371/journal.pone.0033485

Thomas, L. E., & Lleras, A. (2007). Moving eyes and moving thought: On the spatial compatibility between eye movements and cognition. *Psychonomic Bulletin & Review*, *14*(4), 663–668.

Uiga, L., Cheng, K. C., Wilson, M. R., Masters, R. S. W., & Capio, C. M. (2015). Acquiring visual information for locomotion by older adults: A systematic review. *Ageing Research Reviews*, *20*, 24–34. https://doi.org/10.1016/j.arr.2014.12.005

Waldron-Perrine, B., & Axelrod, B. N. (2012). Determining an appropriate cutting score for indication of impairment on the Montreal Cognitive Assessment. *International Journal of Geriatric Psychiatry*, *27*(11), 1189–1194. https://doi.org/10.1002/gps.3768

Williams, C. C., Zacks, R. T., & Henderson, J. M. (2009). Age differences in what is viewed and remembered in complex conjunction search. *Quarterly Journal of Experimental Psychology*, *62*(5), 946–966. https://doi.org/10.1080/17470210802321976

Wynn, J. S., Olsen, R. K., Binns, M. A., Buchsbaum, B. R., & Ryan, J. D. (2018). Fixation reinstatement supports visuospatial memory in older adults. *Journal of Experimental Psychology: Human Perception and Performance*, *44*(7), 1119–1127. https://doi.org/10.1037/xhp0000522

Yarbus, A. L., & Levy-Schoen, A. (1968). Eye movements and vision. *Neuropsychologia*, *6*(4), 389–390. https://doi.org/10.1016/0028-3932(68)90012-2

Zhong, J. Y., & Moffat, S. D. (2018). Extrahippocampal contributions to age-related changes in spatial navigation ability. *Frontiers in Human Neuroscience*, *12*(July), 1–8. https://doi.org/10.3389/fnhum.2018.00272

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Chapter 4

Are age-related deficits in route learning related to control of visual attention?

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4.1 Abstract

Typically aged adults show reduced ability to learn a route compared to younger adults. In this experiment we investigate the role of visual attention through eye-tracking and engagement of attentional resources in age-related route learning deficits. Participants were shown a route through a realistic virtual environment before being tested on their route knowledge. Younger and older adults were compared on their gaze behaviour during route learning and on their reaction time to a secondary probe task as a measure of attentional engagement. Behavioural results show a performance deficit in route knowledge for older adults compared to younger adults, which is consistent with previous research. We replicated previous findings showing that reaction times to the secondary probe task were longer at decision points than non-decision points, indicating stronger attentional engagement at navigationally relevant locations. However, we found no differences in attentional engagement and no differences for a range of gaze measures between age groups. We conclude that age-related changes in route learning ability are not reflected in changes in control of visual attention or regulation of attentional engagement.

4.2 Introduction

Learning and recalling routes through complex environments is a common task which is essential in maintaining independence in everyday life. Typically aged adults often report difficulty with general navigation (Burns, 1999) and show a reduced ability to learn and recall routes (Head & Isom, 2010; Moffat, Zonderman & Resnick, 2001), to retrace a route backwards (Wiener, Kmecova & de Condappa, 2012), to understand the layout of a known intersection when approaching it from a novel direction (Wiener, de Condappa, Harris & Wolbers, 2013), to bind landmarks to specific locations (Newman & Kazniak, 2000; Head & Isom, 2010) and to learn the sequence of turns along a route (O'Malley, Innes & Wiener, 2017). Older adults also shift preference away from allocentric navigation strategies and use egocentric strategies more than younger adults (Rodgers, Sindone & Moffat, 2010). Age-related navigation deficits are more pronounced in unfamiliar than in familiar environments (Devlin, 2001) and typically become apparent in adults aged between 60-69 years old (Barrash, 1994). Current explanations of age-related decline in route learning ability focus on neurodegeneration of structures related to stimulus-response-based, egocentric navigation, such as the caudate (see Lester, Moffat, Wiener, Barnes & Wolbers, 2017). In contrast, the roles of other cognitive domains to age-related route learning declines have received little attention (for a review see Klencklen, Després & Dufour, 2011). In this study we investigated whether control of visual attention and attentional engagement also contribute to age-related declines in route learning.

Visual information is a vital input for successful navigation (see Ekstom, 2015), particularly in route navigation, where strategies rely heavily on visual cues (Waller & Lippa, 2007). At decision points, for example, gaze is directed towards the eventually chosen path and to specific geometric features such as long lines of sight or changes in geometry (Wiener, Hölscher, Büchner & Konieczny, 2012). In environments with landmarks that are easily identified, the selection and encoding of relevant landmarks is reflected in gaze behaviour (Hamid, Stankiewicz & Hayhoe, 2010; Wenczel, Hepperle & von Stülpnagel, 2017; de Condappa & Wiener, 2014). While these studies demonstrate that gaze behaviour is a measure which is sensitive to behaviour during route learning, so far no study has addressed the question of whether age-related differences in route learning abilities are reflected in differences in gaze behaviour.

Systematic differences in gaze behaviour between younger and older adults have been reported in non-route learning tasks. Dowiasch, Marx, Einhäuser and Bremmer (2015) measured several gaze parameters whilst older and younger participants walked through an environment. While participants did not solve a specific navigation task, older adults showed reduced saccade frequency, amplitude, peak and average velocity. This is in line with a driving study (Maltz & Shinar, 1999) in which older adults have been reported to make shorter saccades and more fixations, although fixation durations remained the same as in younger adults. This work also reports that when assessing a spatial scene, older adults focus on smaller sub-regions of the stimuli and are less exploratory than younger adults. Similarly, during locomotion older adults focused on lower portions of the visual scene and to areas closer to themselves in an effort to reduce task error (see Uiga, Cheng, Wilson, Masters & Capio, 2014). These studies include tasks which are not the focus of this experiment, such as locomotion, but they provide some insight into how cognitive ageing affects gaze behaviour.

Control of visual attention is part of the executive function network (Diamond, 2014), which is known to undergo age-related decline, often characterised by working memory deficits (Klencklen, Lavenex, Brandner & Lavenex, 2017). The ageing brain however, shows increased activation of the prefrontal cortex across both hemispheres (Cabeza, 2002) as a compensatory mechanism to complete executive functioning tasks (Kirova, Bays & Lagalwar, 2015). Dorsal frontal regions have also been implicated in the top down control of visual attention (Kastner, 2004) and show similar patterns of increased activation in older adults when completing tasks such as visual search (Madden, 2007). The extent to which both declining executive function and neural compensation in ageing contribute to differences in control of visual attention remains unclear. Given that this is not the focus of the current study, we used age as the indicator for potential decline rather than characterising it through other measures such as working memory performance. Control of visual attention measured by gaze behaviour (see Kristjánsson, 2011 for discussion of the relationship between eye movements and visual attention) may, at least partially, explain age-related route learning differences.

Not all locations in an environment are equally important for route navigation. The parts of a route where a decision about the direction of travel has to be made are known as decision points (e.g. intersections), while other parts which only allow for one possible direction of travel are referred to as non-decision points. Route navigation can be conceptualised as a series of paths between decision points (Schinazi & Epstein, 2010). Objects at such decision points, i.e. landmarks, not only yield better recognition memory and recall of associated direction than objects located at non-decision points (Janzen, 2006; von Stülpnagel & Steffens, 2012), they also selectively recruit the parahippocampal gyrus (Janzen & van Turennout, 2004; Janzen & Weststeijn, 2007). Good navigators demonstrate better memory consolidation of decision point information than poor navigators (Janzen, Jansen & van Turennout, 2008).

Given the importance of decision points for successful route learning, it is not surprising that navigators pay particular attention to these locations. Using a secondary auditory probe task, Allen and Kirasic (2003) demonstrated stronger attentional engagement at areas of high navigational relevance, such as decision points. In their task, participants learned a route from a series of photographs, whilst responding to an auditory probe (a beep). Time to disengage from the primary route learning task and respond to the probe reflects the level of attentional engagement and increased at navigationally relevant locations. Hartmeyer, Grzeschik, Wolbers and Wiener (2017) replicated these findings in an ageing study using videos instead of photographs. Interestingly, the effect was similar in the younger and older age group, even though the latter group showed marked route learning performance deficits. However, the environment used in this experiment was very simplistic, featuring empty corridors and single landmarks at decision points and turns. In view of research demonstrating that older adults have difficulty ignoring task-irrelevant stimuli (e.g. Tusch, Alperin, Holcomb & Daffner, 2016; West, 1999), it is conceivable that attentional control will be more strongly affected by age in environments which are visually more complex. If older adults directed attentional resources towards task irrelevant stimuli, fewer resources would remain available for the primary route learning task. The disadvantage of poor resource allocation may be particularly costly for older adults considering the suggestion that their overall pool of cognitive resources may already be diminished compared to younger adults (Meulenbroek et al., 2010). Assigning already diminished attentional resources to non-task relevant information in a complex environment would likely impact route learning performance.

In the present study we used a paradigm similar to that of Hartmeyer et al. (2017), but we used a more visually complex environment and we tracked participants' gaze behaviour. Our main research questions were: (1) Will previous attentional engagement findings from an auditory probe task be replicated in a complex environment? (2) Can age-related differences in route learning ability be related to differences in gaze behaviour?

The behavioural part of this study was confirmatory. We expected impaired route learning performance in our older as compared to our younger participants (c.f. Wiener et al., 2012). Moreover, we expected longer response times to the auditory probe at decision points vs. non-decision points in the younger participant group (c.f. Hartmeyer et al., 2017). If older adults were impaired in their ability to modulate engagement of attention during route learning in an information rich environment, we expected a reduced difference in response times to the auditory probe at decision points vs. non-decision points as compared to the response time difference in younger adults.

The lack of previous research investigating how cognitive ageing affects gaze behaviour during route learning warrants an exploratory approach to the eye-tracking part of this study. If control of visual attention contributes to age-related differences in route learning, we expected systematic differences in gaze behaviour between age groups.

4.3 Materials and Methods

4.3.1 Participants

Fifty-nine participants took part in the experiment. Of these, data from 13 participants had to be discarded due to technical issues with the video presentation during the experiment. Two participants also withdrew before completion of the experiment due to experiencing motion sickness and 4 more were discarded because they did not engage with the experiment and failed to follow instructions. Participants were screened for mild cognitive impairment using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005). One participant was excluded from analysis based on a cut off score of 23 (Luis, Keegan & Mullan, 2009; Waldron-Perrine & Axelrod, 2012). Twenty younger participants (10 females; mean age 24 years; mean MoCA 28.15) and 19 older participants (10 females; mean age 73.36 years; mean MoCA 27.68) were included in the final analysis. Ethical approval was granted by Bournemouth University Research Ethics Panel and written informed consent was gained from all participants who either participated in exchange for course credits or a monetary compensation for their time.

4.3.2 Design

4.3.2.1 Learning phase

Participants were passively navigated along a route through “Virtual Tübingen”, a photorealistic virtual model of Tübingen, Germany (see Figure 4-1a; van Veen, Distler, Braun & Bültoff, 1998). The route, presented as a video, consisted of 18 decision points (balanced for turning directions) and was 6 minutes and 13 seconds long (see Figure 4-1b). The video is available as supplementary material.

Participants were instructed to learn the route so that they would be able to reproduce it on their own. At the same time, we administered an auditory probe task as used in Allen and Kirasic (2003) and Hartmeyer et al. (2017): whilst the participants were watching the video of the route, auditory stimuli (a beep: 100 ms, square wave 1000 Hz) were presented, to which participants had to respond via key press as fast as possible. Twenty four auditory probes were presented along the route, with their locations balanced evenly across decision points and non-decision points. The auditory probes were presented at different locations along the route in each experimental block to avoid participants predicting their onset.

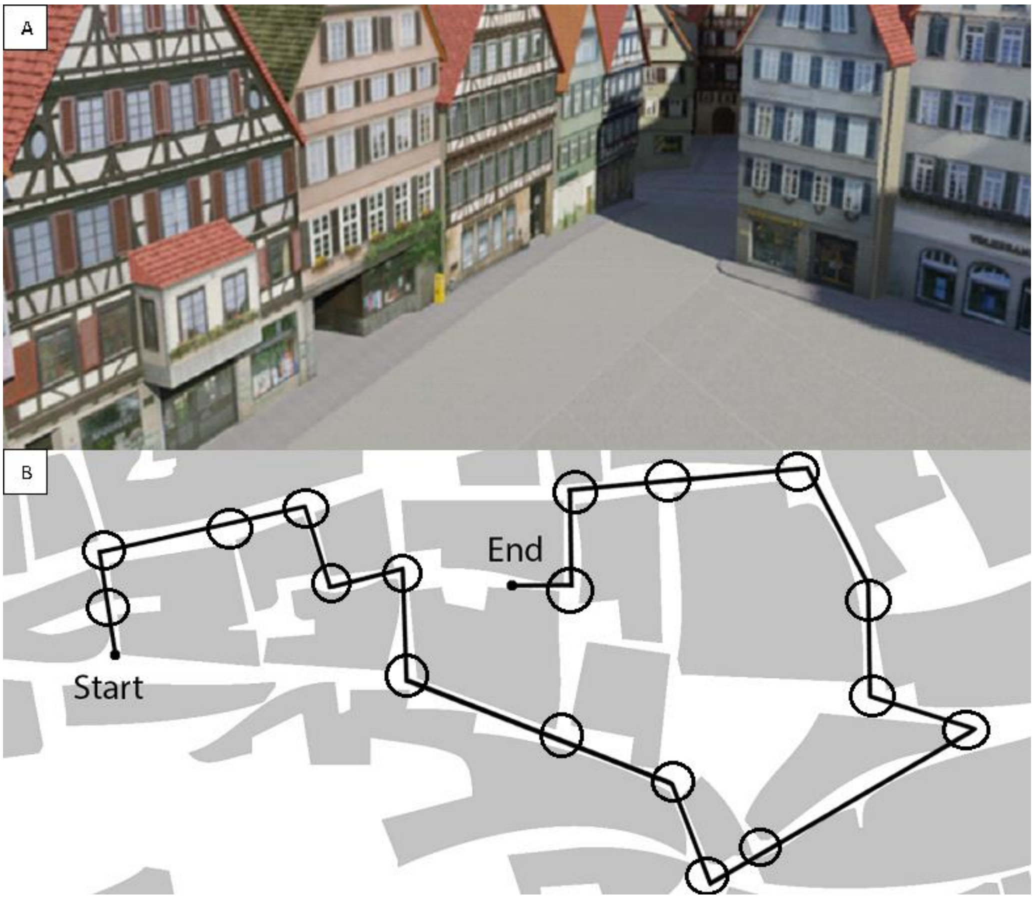

Figure 4-1 - A: a screenshot from Virtual Tübingen; B: an overhead schematic of the route with decision points circled.

4.3.2.2 Direction test

Participants were shown screenshots of all 18 decision points (intersections) along the route in a randomized order. Their task was to indicate the direction in which the route continued. Fifteen intersections had two possible turn directions and the rest had three. The Direction Test was the primary measure of route learning and was completed after each Learning Phase.

4.3.2.3 Order test

The Order Test examined participants' knowledge of the sequence in which locations along the route were encountered. Participants were presented with two screenshots from the route next to each other and asked to indicate which location they encountered first along the route during the Learning Phase. Altogether there were 54 trials split over three image pair types. The image pair types were both decision points (18 trials), both non-decision points (18 trials) or one of each (18 trials). This task was presented at the end of the experiment and participants were not informed about the order test before it was presented, to avoid intentional changes in learning strategy to acquire sequence knowledge.

4.3.3 Materials

The experiment was presented on a 102cm screen (diagonal) with an aspect ratio of 16:9 and a resolution of 1920x1080 pixels. Participants were sat 1 meter away from the screen. Responses were recorded using a Cedrus response box (RB-740, Cedrus, San Pedro, USA). Auditory stimuli were presented via speakers using an external sound card (ASIO M-Track Plus, M-Audio, Cumberland, USA). Eye movements were recorded using an Eyelink II (SR Research) head mounted eye-tracker at a rate of 500hz. Calibration used a 9 point grid and a drift correction was performed before every phase of the experiment.

4.3.4 Procedure

The experiment took approximately one hour and was divided into several phases. Before the experiment began, participants completed a short practice session to familiarise themselves with the tasks and to check their understanding of the instructions. This session used a short two-intersection route through a different part of Virtual Tübingen and included response to auditory stimuli. There was also a short Direction Test with two trials. There was no Order Test in the practice session to ensure that participants remained unaware of this task. The main experiment was comprised of two experimental blocks, each containing a Learning Phase followed by the Direction Test. Each block used the same route. The Order Test was administered once at the end of the experiment.

4.3.5 Eye-tracking measures

Given the lack of previous research linking gaze behaviour, ageing and route learning, we took an exploratory approach to analysing eye-tracking measures during route learning. As in Dowiasch et al. (2015) we compared saccade amplitude, peak velocity, average velocity and frequency (number of saccades per second) between age groups for eye-tracking data from the Learning Phase using Analysis of Variance (ANOVA). We did the same for the Direction Test with the addition of average fixation duration. We decided not to analyse gaze behaviour for the Order Test as the angular size of the stimuli was relatively small (in order to present two scenes at once).

Due to the dynamic nature of the video stimuli used in the Learning Phase and the complex spatial scenery, it was difficult to relate gaze behaviour to specific environmental features. Regions of interest analysis as described in Allen & Kirasic (2003) are not applicable to video stimuli (see also Caldara & Miellet, 2011 for a discussion on the limitations of regions of interest analyses). An alternative option would be a frame-by-frame analysis of gaze behaviour during the Learning Phase. This, however, would have been very labour intensive, for example Anderson et al. (2012) report approximately 31 hours of hand coding per hour of video data. Consequently, such methods are typically applied only to samples much smaller than in the current study (e.g. Hollands, Patla, & Vickers, 2002; Imai, Moore, Raphan, & Cohen, 2001). We opted for two other analyses for the Learning Phase.

First, we developed a new measure: gaze dispersion. Gaze dispersion is calculated as the average distance of all gaze points, within a specified time window of the video, from the centre of gravity of those points. High gaze dispersion values mean that participants' gaze is widely distributed across the stimulus and can therefore be described as more exploratory, while smaller dispersion values indicate more spatially focused and less exploratory gaze behaviour. We calculated gaze dispersion in a 1000ms moving time window, with a 500ms overlap between each successive window, and analysed how gaze dispersion changed during the last 5 seconds of approaching a decision point. We used a linear mixed effect model (LME) analysis to investigate whether time until reaching a decision point could predict gaze dispersion in younger and older participants.

Second, we analysed the effect of route learning between blocks 1 and 2 on gaze bias at decision points. Specifically, we were interested whether the likelihood of gaze being directed towards the correct direction of travel changed between the first and the second viewing of the route. Any increase in the likelihood that the correct path option was attended to would reflect learning of the route. The gaze bias analysis is spatially sensitive to where gaze is directed in the environment, while the gaze dispersion measure is temporally informative.

The Direction Test was comprised of static stimuli (screenshots) which allowed us to use iMap4 (Lao, Miellet, Pernet, Sokhn & Caldara, 2016) to analyse gaze behaviour. Specifically, we analysed whether age systematically affected what parts of the stimuli participants looked at when recalling route directions at decision points. iMap4 is a MATLAB open source toolbox implementing a pixel-wise linear mixed model approach for statistical fixation mapping of eye movement data and nonparametric tests based on resampling to assess statistical significance.

4.4 Results

4.4.1 Behavioural

4.4.1.1 Auditory probe task

Responses from one participant were not collected due to user error so they were excluded from the analysis. A repeated measures ANOVA on response times with a between groups factor of age group (young, old) and within groups factors of block number (1, 2) and section type (DP or NDP) revealed main effects of age group [$F(1, 36) = 11.02$, $p = .002$, $\eta p^2 = .234$] and section type [$F(1,36) = 52.49$, $p < .001$, $\eta p^2 = .593$], but no main effect of block [$F(1,36) = 0.87$, $p = .358$, $\eta p^2 = .024$]. Younger adults (403.52ms) responded faster to the auditory probes than older adults (487.51ms). Probes at non-decision points (425.44ms) were responded to faster than at decision points (465.29ms). Only the age group x section type interaction was significant [$F(1,36) = 8.06$, $p = .007$, $\eta p^2 = .183$].

To investigate this interaction, which indicates that the size of the section type effect is larger for the older participant group compared to the younger group, the data was split by age group and paired t-tests were performed for section type. Both younger adults [$t(18) = 5.57$, $p < .001$, $d = .22$] and older adults [$t(18) = 5.44$, $p < .001$, $d = .43$] were significantly faster at responding to the auditory probe at non-decision points (younger = 391.02ms, older = 461.03ms) than at decision points (younger = 415.71ms, older = 517.11ms; see Figure 4-2a).

4.4.1.2 Direction test

A repeated measures ANOVA on performance with a between groups factor of age group (young, old) and a within groups factor of block number (1, 2) revealed main effects of age group [$F(1,37) = 6.12$, $p < .001$, $\eta p^2 = .142$] and block number [$F(1, 37) = 39.54$, $p < .001$, $\eta p^2 = .517$]. Younger participants (75.28%) performed better than older participants (65.64%) and performance on block 2 (76.35%) was better than on block 1 (64.81%; see Figure 4-2b). There was no significant interaction.

4.4.1.3 Order test

A repeated measures ANOVA on performance with a between groups factor of age group (young, old) and a within groups factor of pair type (decision points, non-decision points, mixed) revealed a main effect of age group [$F(1,37 = 15.30)$, $p < .001$, $\eta p^2 = .293$] but no main effect of pair type [$F(1,37) = 2.07$, $p = .159$, $\eta p^2 = .053$]. Younger adults (76.57%) performed better than older adults (61.99%; see Figure 4-2c). There was no significant interaction.

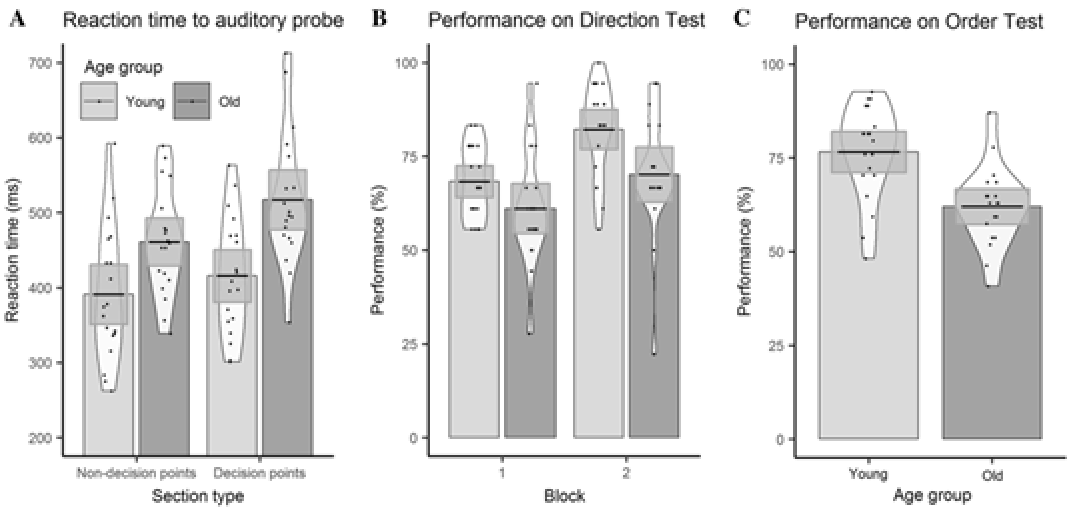

Figure 4-2 - Graphs include means, 95% confidence intervals and density profiles. A: reaction times of younger and older participants to the auditory probe at decision and non-decision points; B: performance of younger and older participants on the Direction Test over blocks 1 and 2; C: performance of younger and older participants on the Order Test

4.4.2 Eye-tracking

One older participant had a visual disorder that prevented eye-tracking. There were also calibration errors for two older participants during the Learning Phase; these participants were not included in the analysis of gaze behaviour during the Learning Phase.

4.4.2.1 Learning Phase

4.4.2.1.1 Saccade parameters

Separate repeated measures ANOVAs were conducted for saccade amplitude, frequency, peak velocity and average velocity with a between groups factor of age group and a within groups factor of block. There were no significant effects of age group or block on any of the saccade parameters (see Table 4-1 for the age differences') and no significant interactions.

Table 4-1 - Means and ANOVA results for saccade parameters between younger and older adults from the Learning Phase.

Saccade parameter	Mean(sd) young	Mean(sd) old	f-value	p-value	ηp^2
Saccade amplitude (°va)	6.58(1.30)	6.24(1.16)	0.65	.425	.012
Saccade peak velocity (°/s)	251.71(49.99)	249.10(37.72)	0.03	.871	<.001
Saccade average velocity (°/s)	139.82(17.75)	130.66(15.78)	2.57	.118	.070
Saccade frequency (/s)	2.48(0.45)	2.71(0.43)	2.44	.128	.067

Given the exploratory nature of this study, the lack of theoretically motivated prior expectations, and the sensitivity of Bayes factors to these prior expectations (Liu & Aitkin, 2008; Morey, Romejin & Rouder, 2016), we decided against using Bayes factors to support the null hypothesis of no differences between age groups. Instead, we used bootstrapped t-tests (5000 resamplings) in order to take into account the real distribution of our data. First, data were centred to the mean to ensure H0. Then a bootstrapped t-value was computed after random sampling of 20 centred data points with replacement. This procedure was repeated 5000 times. The 5000 bootstrapped t-values were then ordered, and .025 and .975 bounds determined. Finally, the observed t-value was compared to the bootstrapped bounds to assess significance. Here, there was no significant effect of age on amplitude (t-obs=0.83; 95% CI=[0.03, 2.37]; p=.404), peak velocity (t-obs=0.19; 95% CI=[0.03, 2.30], p=.847, average velocity (t-obs=1.64; 95% CI=[0.03, 2.32], p=.164) or frequency (t-obs=1.57; 95% CI=[0.04, 2.43], p=.123).

4.4.2.1.2 Gaze dispersion

Using the raw data samples, gaze dispersion for every 1000ms of the Learning Phase was calculated with a 500ms overlap for each time subsequent time window. We analysed gaze dispersion for the last 5000ms during the approach of decision points during learning, with 0ms being the arrival at the intersection, but before a turn would be initiated.

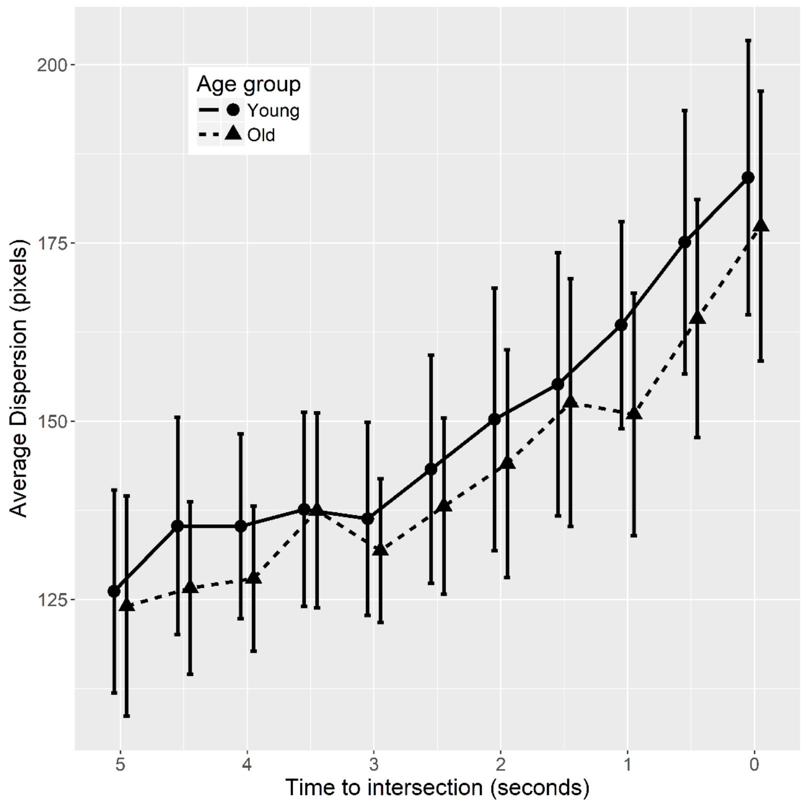

Figure 4-3 - Dispersion of gaze on the five second approach to an intersection for younger and older participants

We ran a linear mixed effects model (LME) analysis for dispersion of gaze using the lme4 package (version 1.1-14; Bates, Machler, Bolker & Walker, 2015) in R (R Development Core Team, 2013). Fixed effects were approach time to intersection (continuous, 5000ms – 0ms, centred around 0), block number (factor, 1 or 2, centred using sum contrast coding) and age group (factor, young or old, centred using sum contrast coding). Random effects were subject and intersection. We started with an intercept only model and added random by-subject and by-intersection slopes for fixed effects one by one (starting with those that accounted for the most variance) and then added interactions between random slopes. Each random slope or interaction was included only if it significantly improved the model.

Estimates, standard errors and t-values for the final model are reported in Table 4-2 and show that approach time to an intersection is a significant predictor of gaze dispersion (see Figure 4-3) whilst age group and block do not have a significant effect. There were no significant interactions.

Table 4-2 Coefficients from LME analysis

Fixed effect on dispersion of gaze (number of pixels)	Estimate	Std. error	t-value
Intercept	146.24	7.77	18.82*
Approach time	10.10	2.18	4.63*
Age group	3.05	4.84	0.63
Block	2.42	1.72	1.41

*Significant t values ($|t|\geq1.96$)

4.4.2.1.3 Gaze bias

We used the raw data samples to calculate gaze bias during the last 5000ms before entering a decision point. To do this, the screen was split into three equal regions to represent left, straight and right turns. Gaze bias is defined as the percentage of samples which were located in the region that corresponded with the correct direction of travel.

A repeated measures ANOVA on gaze bias with a between groups factor of age group (young, old) and a within groups factor of block number (1, 2) revealed a main effect of block [$F(1, 34) = 11.31$, $p = .002$, $\eta p^2 = .250$] and no main effect of age group [$F(1, 34) = 1.39$, $p = .247$, $\eta p^2 = .039$]. Gaze bias was higher during block 2 (35.79%) than during block 1 (33.15%; see Figure 4-4). There was no significant interaction.

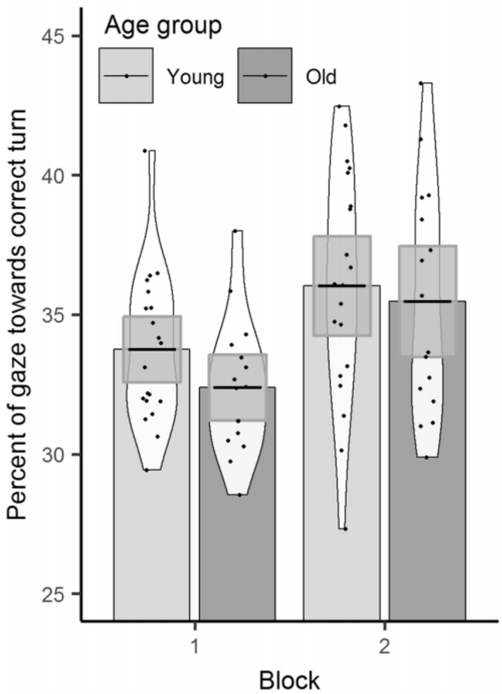

Figure 4-4 - Gaze bias towards correct direction in the learning phase across blocks for younger and older participants

4.4.2.1.4 Gaze behaviour and route learning performance

To investigate whether the gaze dispersion and gaze bias measures were in fact predictive of route learning performance we ran a multiple regression analysis with gaze bias and gaze dispersion as predictor variables and performance in the behavioural direction test as the outcome variable. We included block as an interaction term for gaze bias. This was motivated by gaze bias being a measure of learning and thus is at chance level for block 1 since this was the first time participants had seen the route. A significant regression equation was found [F(3, 68) = 5.25, p = .003] with an R^2 of .15. Gaze dispersion was a significant predictor of test phase performance [b = .04, t(68) = 2.36, p = .02)]. Gaze bias was also a significant predictor of direction test performance, but only in block 2 [block 1: b = .02, t(68) = 0.89, p = .38; block 2: b = .07, t(68) = 3.067, p = .003].

4.4.2.2 Direction Test

4.4.2.2.1 Saccade and fixation parameters

Separate repeated measures ANOVAs were conducted for saccade amplitude, frequency, peak velocity, average velocity and for average fixation duration with a between groups factor of age group and a within groups factor of block. Block only rendered a significant effect on saccade frequency [$F(1,37) = 17.58$, $p < .001$, $\eta p^2 = .322$] and the main effect of age group was only significant for saccade average velocity [F(1,37) = 6.68, p = .014, ηp^2 = .153] (see Table 4-3 for the age differences'). There were no significant interactions.

Table 4-3 Means and ANOVA results for saccade and fixation parameters between younger and older adults for the test phase.

Gaze parameter	Mean(sd) younger	Mean(sd) old	f-value	p-value	ηp^2
Saccade amplitude (°va)	8.65(1.17)	8.11(1.30)	1.44	.237	.038
Saccade peak velocity (°/s)	292.44(41.01)	285.65(42.83)	0.17	.69	.005
Saccade average velocity (°/s)	166.48(16.28)	151.31(17.86)	6.68	.014	.153
Saccade frequency (/s)	3.61(0.31)	3.44(0.50)	1.46	.235	.038
Average fixation duration (ms)	258.05(25.61)	259.40(31.34)	0.01	.923	>.001

Bootstrapped t-tests showed a significant effect of age on average velocity (t-obs=2.77; 95% CI=[0.03, 2.34], p=.008) and no significant effects of age on amplitude (t-obs=1.38; 95% CI=[0.03, 2.31]; p=.168), peak velocity (t-obs=0.51; 95% CI=[0.04, 2.34], p=.617, frequency (t-obs=1.24; 95% CI=[0.03, 2.59], p=.238) or fixation duration (t-obs=0.15; 95% CI=[0.03, 2.36], p=.888).

4.4.2.2.2 iMap

iMap 4 (Lao et al., 2016) was used to examine the regions in each test stimulus to which participants directed their gaze. Participant and test stimulus were included as random effects and fixed effects were age group and block. The model showed no significant effect of age group or block on location of gaze during the test phase.

4.5 Discussion

The overall aim of this study was to investigate the potential contribution of control of visual attention and attentional engagement to age-related changes in route learning ability. We compared an older and younger participant group using a standard route learning paradigm with eye-tracking and an auditory probe task. We found an age-related performance deficit in tests of route knowledge. Both younger and older participants were slower to respond to the auditory probe at decision points as compared to non-decision points and this slowing was statistically larger for the older participant group. We report a significant increase in gaze dispersion on the approach to an intersection and an effect of learning on gaze bias towards the correct path option. Finally, there were no age differences in both the learning phase and the direction test phase on several gaze measures, including general saccade parameters (other than average velocity in the test phase), gaze dispersion, gaze bias and iMap analysis.

4.5.1 Route learning performance and attentional engagement

Older adults performed worse than younger adults on both the Direction Test and the Order Test, which is consistent with earlier navigation studies (Hartmeyer et al., 2017; Head & Isom, 2010; Wiener et al., 2012). Difficulty in recalling directions at intersections for older adults suggest age-related deficits in place-response associations (see Strickrodt, O'Malley & Wiener, 2015). Zhong and Moffat (2016) suggest this place-response deficit is due to older adults expending more cognitive resources on the encoding of landmark/place information than on the binding of this information to a direction. In relation to the results in the Order Test, a lack of knowledge about the relative locations of intersections along the route in older adults indicates impairment in place-place associations (see Strickrodt et al., 2015). Place-place associations are important, as navigation of an environmental scale space may not be encoded in a single reference frame, but in several smaller scale reference frames which are linked by proximity and are switched between as the environment is traversed (Meilinger, 2008; Schinazi & Epstein, 2010; Wolbers & Wiener, 2014). This allows navigators to form expectations of next encounters and plan responses accordingly (Schölkopf & Mallot, 1995), a task in which older adults are impaired (Salthouse & Siedlecki, 2007).

Task focused engagement of attentional resources is reflected in the time taken to disengage and respond to a secondary auditory probe task (Posner & Boies, 1971). We show slower response times to probes presented at decision points as compared to non-decision points, suggesting engagement of more attentional resources to the navigation task at locations important for route learning (Allen & Kirasic, 2003). This effect is present for both younger and older participants. We also find an interaction between age group and probe location. However, this interaction is difficult to interpret as older adults typically show slower cognitive processing (Salthouse, 2000; Waters & Caplan, 2005), which could be amplified by the need to disengage more resources from the primary task. Our results replicate findings from Hartmeyer et al. (2017) in a complex environment, providing more evidence that route learning deficits in older adults cannot be explained by changes in the deployment of attentional resources.

4.5.2 Gaze behaviour and route learning

First, we introduced gaze dispersion as a new eye-tracking measure. We found that dispersion increased during the approach to a decision point. One possible explanation for this is that the visual features of the environment may be driving the dispersion effect. Viewers of a spatial scene will preferentially direct gaze to areas with the longest line of sight (Wiener et al., 2012). In the case of a non-decision point location this would usually be the path of travel and thus gaze would be focused here. In the case of a decision point, where multiple paths are available, gaze may be split between path options, thus leading to an increase in gaze dispersion.

Alternatively, an increase in gaze dispersion may be task driven. Given that navigators selectively encode information at decision points (Janzen, 2006; Janzen, Jansen & van Turennout, 2008); an increase in dispersion could reflect wider exploration of the environment to obtain more information about that specific navigationally relevant location. Secondly, we analysed gaze bias at decision points during route learning. We found that when participants saw the route for the second time, they were more likely to look at the correct direction of travel during the 5 second approach of decision points. This is in line with previous accounts of gaze bias for eventually chosen path options in a spatial task (Wiener et al., 2012).

The results from these two gaze measures fit with the spatial decision making framework during navigation recently reported by Brunyé, Gardony, Holmes and Taylor (2018). They suggest that decision making occurs before a decision point is entered. In their study, participants could request additional information about route direction (in the form of a beacon) and were most likely to request information during the 5 seconds before entering a decision point. In our study, gaze dispersion begins to increase around 5 seconds before an intersection is entered. We believe this reflects the acquisition of information during the approach of a decision point through wider visual exploration to aid decision making when later recalling the route. When participants approached an intersection during the second training phase, they showed a gaze bias towards the correct direction of travel. These results nicely reflect the advanced spatial decision making described in Brunyé et al. (2018). Specifically the gaze bias suggests that our participants were able to predict the direction of travel before reaching the decision point, most likely based on information obtained through the increased visual exploration of the environment at decision points in the previous exposure.

Overall, the change in gaze dispersion and in gaze bias as a function of learning demonstrates that eye-tracking measures are sensitive to the spatial environment and the route learning task. This is further corroborated by the regression analysis showing that both of these measures predicted learning performance.

4.5.3 Gaze behaviour and ageing

We compared older and younger participants on several eye movement parameters during route learning and the recall of directions at decision points. First, we focused on general gaze patterns during the learning phase. For the vast majority of measures, there were no differences between age groups, which was surprising, given evidence from Dowiasch et al. (2015), who reported age differences in general gaze parameters. The bootstrapped t-test analysis demonstrated that our observed comparisons fall well within the distribution of t-values when comparing groups without differences, suggesting our results represent no difference between age groups as opposed to a type 2 error. Further, we found no difference between age groups in gaze dispersion whilst learning a route, gaze bias in response to learning or in the distribution of gaze locations in the Direction Test. We found a difference in average saccade velocity during the test phase, however, in view of the overwhelming similarity in the other measures of eye movements; we do not attribute too much meaning to this. Our findings suggest that age-related performance differences in route learning are not reflected in gaze behaviour.

A possible explanation for the differences in results between our study and the study by Dowiasch et al. (2015) comes from the fact that participants in their study were actively locomoting through the environment, while our participants were passively transported along the route. It is conceivable that age-related differences in postural control (Jimenez et al., 2016), control of locomotion and steering cause differences in gaze behaviour. For example, Uiga et al. (2014) suggest that older adults focus more on the lower portion of the visual field, potentially because they are more afraid of falling and therefore closely monitor the space just in front of them. Here we used Montello’s (in Shah & Miyake, 2005) definition of navigation which is comprised of two components: wayfinding and locomotion. While wayfinding refers to the memory and decision making processes involved in navigation, locomotion is about coordinating movement in the local environment. As we aimed to isolate the cognitive processes involved in the route learning and spatial decision making, we decided to use passive navigation. In other words, we eliminated age effects that related to steering and other aspects of locomotory control. However, it would be interesting if future work would investigate how age-related changes in gaze behaviour related to locomotion might interact with route navigation ability.

Given the similarity of eye movement parameters between age groups, we suggest little, if any, task-related difference in oculomotor behaviour between age groups. This is in line with Pratt, Abrams and Chasteen (1997) who report a simple saccade to target task where they conclude that older adults produce saccades in fundamentally the same way as younger adults and in follow up work (Abrams, Pratt & Chasteen, 1998; Pratt, Dodd & Welsh, 2006) demonstrates equivalence between age groups on many basic eye movement parameters. Age differences in eye movements in other work can be attributed to a cognitively driven difference such as using different strategies or cues to solve a task. Thus, results from our study showing equivalence in oculomotor behaviour between age groups in route learning indicates that both age groups use similar visual strategies during route learning. As discussed earlier, performance differences could then be explained by associative learning deficits in stimulus-response associations instead of differences in oculomotor control.

4.5.4 Conclusion

In summary, we have replicated previous findings showing that attentional resources are dedicated to decision points in route navigation and that this process is not affected by ageing. Further, the general control of visual attention does not differ between older and younger participants when learning and recalling route information. Taken together, we conclude that route learning deficits in typically aged adults are not reflected in changes in attentional engagement or by general changes in visual attention. More specific gaze measures may be more sensitive in identifying precise artefacts of visual attention which could be used to further investigate changes in ageing. Our current and future work involves further development of spatially sensitive measures appropriate for dynamic stimuli, focussing on the environmental content of gaze location. Finally, we demonstrate a change in gaze bias in response to route learning and find that gaze dispersion is sensitive to changes in the spatial stimuli, both of which predict route learning performance.

4.6 References

Abrams, R. A., Pratt, J., & Chasteen, A. L. (1998). Aging and movement: Variability of force pulses for saccadic eye movements. *Psychology and Aging, 13*(3), 387-395.

doi:10.1037/0882-7974.13.3.387

Allen, G. L., & Kirasic, K. C. (2003). Visual attention during route learning: A look at selection and engagement. *Spatial Information Theory, Proceedings: Foundations of Geographic Information Science, 2825*, 390-398.

Andersen, N. E., Dahmani, L., Konishi, K., & Bohbot, V. D. (2012). Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory, 97*(1), 81-89. doi:10.1016/j.nlm.2011.09.007

Barrash, J. (1994). Age-related decline in route learning-ability. *Developmental Neuropsychology, 10*(3), 189-201. doi:10.1080/87565649409540578

Bates, D., Machler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1-48.

Brunye, T. T., Gardony, A. L., Holmes, A., & Taylor, H. A. (2018). Spatial decision dynamics during wayfinding: intersections prompt the decision-making process. *Cognitive Research-Principles and Implications, 3*. doi:10.1186/s41235-018-0098-3

Burns, P. C. (1999). Navigation and the mobility of older drivers. *Journals of Gerontology Series B-Psychological Sciences and Social Sciences, 54*(1), S49-S55.

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging, 17*(1), 85-100. doi:10.1037//0882-7974.17.1.85

de Condappa, O., & Wiener, J. M. (2014). Human place and response learning: navigation strategy selection, pupil size and gaze behavior. *Psychological Research-Psychologische Forschung, 80*(1), 82-93. doi:10.1007/s00426-014-0642-9

Diamond, A. (2013). Executive Functions. In S. T. Fiske (Ed.), *Annual Review of Psychology, Vol 64* (Vol. 64, pp. 135-168). Palo Alto: Annual Reviews.

Dowiasch, S., Marx, S., Einhauser, W., & Bremmer, F. (2015). Effects of aging on eye movements in the real world. *Frontiers in Human Neuroscience, 9*, 12. doi:10.3389/fnhum.2015.00046

Ekstrom, A. D. (2015). Why vision is important to how we navigate. *Hippocampus, 25*(6), 731-735. doi:10.1002/hipo.22449

Hamid, S. N., Stankiewicz, B., & Hayhoe, M. (2010). Gaze patterns in navigation: Encoding information in large-scale environments. *Journal of Vision, 10*(12), 11. doi:10.1167/10.12.28

Hartmeyer, S., Grzeschik, R., Wolbers, T., & Wiener, J. M. (2017). The Effects of Attentional Engagement on Route Learning Performance in a Virtual Environment: An Aging Study. *Frontiers in Aging Neuroscience, 9*, 9. doi:10.3389/fnagi.2017.00235

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research, 209*(1), 49-58. doi:10.1016/j.bbr.2010.01.012

Hollands, M. A., Patla, A. E., & Vickers, J. N. (2002). "Look where you're going!": gaze behaviour associated with maintaining and changing the direction of locomotion. *Experimental Brain Research, 143*(2), 221-230. doi:10.1007/s00221-001-0983-7

Imai, T., Moore, S. T., Raphan, T., & Cohen, B. (2001). Interaction of the body, head, and eyes during walking and turning. *Experimental Brain Research, 136*(1), 1-18. doi:10.1007/s002210000533

Janzen, G. (2006). Memory for object location and route direction in virtual large-scale space. *Quarterly Journal of Experimental Psychology, 59*(3), 493-508. doi:10.1080/02724980443000746

Janzen, G., Jansen, C., & van Turennout, M. (2008). Memory consolidation of landmarks in good navigators. *Hippocampus, 18*(1), 40-47. doi:10.1002/hipo.20364

Janzen, G., & van Turennout, M. (2004). Selective neural representation of objects relevant for navigation. *Nature Neuroscience, 7*(6), 673-677. doi:10.1038/nn1257

Janzen, G., & Weststeijn, C. G. (2007). Neural representation of object location and route direction: An event-related fMRI study. *Brain Research, 1165*, 116-125. doi:10.1016/j.brainres.2007.05.074

Jimenez, S., Hollands, M., Palmisano, S., Kim, J., Markoulli, M., McAndrew, D., Stapley, P. J. (2016). Age-related effects of increasing postural challenge on eye movement onset latencies to visual targets. *Experimental Brain Research, 234*(6), 1599-1609. doi:10.1007/s00221-016-4564-1

Kastner, S. (2004). Attentional Response Modulation in the Human Visual System. In M. I. Posner (Ed.), *Cognitive neuroscience of attention* (pp. 144-156). New York, NY, US: Guilford Press.

Kirova, A. M., Bays, R. B., & Lagalwar, S. (2015). Working Memory and Executive Function Decline across Normal Aging, Mild Cognitive Impairment, and Alzheimer's Disease. *Biomed Research International*. doi:10.1155/2015/748212

Klencklen, G., Despres, O., & Dufour, A. (2012). What do we know about aging and spatial cognition? Reviews and perspectives. *Ageing Research Reviews, 11*(1), 123-135. doi:10.1016/j.arr.2011.10.001

Klencklen, G., Lavenex, P. B., Brandner, C., & Lavenex, P. (2017). Working memory decline in normal aging: Is it really worse in space than in color? *Learning and Motivation, 57*, 48-60. doi:10.1016/j.lmot.2017.01.007

Kristjánsson, A. (2011). The intriguing interactive relationship between visual attention and saccadic eye movements. In Liversedge, S. P., Gilchrist, I. D., & Everling, S. (Eds.). *Oxford library of psychology. The Oxford handbook of eye movements (pp.455 – 466).* New York, NY, US: Oxford University Press.

Lao, J. P., Miellet, S., Pernet, C., Sokhn, N., & Caldara, R. (2017). iMap4: An open source toolbox for the statistical fixation mapping of eye movement data with linear mixed modeling. *Behavior Research Methods, 49*(2), 559-575. doi:10.3758/s13428-016-0737-x

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers, T. (2017). The Aging Navigational System. *Neuron, 95*(5), 1019-1035. doi:10.1016/j.neuron.2017.06.037

Liu, C. C., & Aitkin, M. (2008). Bayes factors: Prior sensitivity and model generalizability. *Journal of Mathematical Psychology, 52*(6), 362-375. doi:10.1016/j.jmp.2008.03.002

Luis, C. A., Keegan, A. P., & Mullan, M. (2009). Cross validation of the Montreal Cognitive Assessment in community dwelling older adults residing in the Southeastern US. *International Journal of Geriatric Psychiatry, 24*(2), 197-201. doi:10.1002/gps.2101

Madden, D. J. (2007). Aging and visual attention. *Current Directions in Psychological*

Science, 16(2), 70-74. doi:10.1111/j.1467-8721.2007.00478.x

Maltz, M., & Shinar, D. (1999). Eye movements of younger and older drivers. *Human Factors, 41*(1), 15-25. doi:10.1518/001872099779577282

Meilinger, T. (2008). The Network of Reference Frames Theory: A Synthesis of Graphs and Cognitive Maps. *Spatial Cognition Vi: Learning, Reasoning, and Talking About Space, 5248*, 344-360.

Meulenbroek, O., Kessels, R. P. C., de Rover, M., Petersson, K. M., Rikkert, M., Rijpkema, M., & Fernandez, G. (2010). Age-effects on associative object-location memory. *Brain Research, 1315*, 100-110. doi:10.1016/j.brainres.2009.12.011

Moffat, S. D., Zonderman, A. B., & Resnick, S. M. (2001). Age differences in spatial memory in a virtual environment navigation task. *Neurobiology of Aging, 22*(5), 787-796. doi:10.1016/s0197-4580(01)00251-2

Morey, R. D., Romeijn, J. W., & Roude, J. N. (2016). The philosophy of Bayes factors and the quantification of statistical evidence. *Journal of Mathematical Psychology, 72*, 6-18. doi:10.1016/j.jmp.2015.11.001

Nasreddine, Z. S., Phillips, N. A., Bedirian, V., Charbonneau, S., Whitehead, V., Collin, I., Chertkow, H. (2005). The montreal cognitive assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society, 53*(4), 695-699. doi:10.1111/j.1532-5415.2005.53221.x

Newman, M. C., & Kaszniak, A. W. (2000). Spatial memory and aging: Performance on a human analog of the Morris water maze. *Aging Neuropsychology and Cognition, 7*(2), 86-93. doi:10.1076/1382-5585(200006)7:2;1-u;ft086

O'Malley, M., Innes, A., & Wiener, J. M. (2018). How do we get there? Effects of cognitive aging on route memory. *Memory & Cognition, 46*(2), 274-284. doi:10.3758/s13421-017-0763-7

P., S., & A, M. (2005). *The Cambridge Handbook of visuospatial thinking*. New York: Cambridge University Press.

Pazzaglia, F. (2003). Mind and maze. Spatial cognition and environmental behavior. *Applied Cognitive Psychology, 17*(5), 625-626. doi:10.1002/acp.938

Posner, M. I., & Boies, S. J. (1971). Components of attention. *Psychological Review, 78*(5), 391-&. doi:10.1037/h0031333

Pratt, J., Abrams, R. A., & Chasteen, A. L. (1997). Initiation and inhibition of saccadic eye movements in younger and older adults: An analysis of the gap effect. *Journals of Gerontology Series B-Psychological Sciences and Social Sciences, 52*(2), P103-P107. doi:10.1093/geronb/52B.2.P103

Pratt, J., Dodd, M., & Welsh, T. (2006). Growing older does not always mean moving slower: Examining aging and the saccadic motor system. *Journal of Motor Behavior, 38*(5), 373-382. doi:10.3200/jmbr.38.5.373-382

Rodgers, M. K., Sindone, J. A., & Moffat, S. D. (2012). Effects of age on navigation strategy. *Neurobiology of Aging, 33*(1). doi:10.1016/j.neurobiolaging.2010.07.021

Salthouse, T. A. (2000). Aging and measures of processing speed. *Biological Psychology, 54*(1-3), 35-54. doi:10.1016/s0301-0511(00)00052-1

Schinazi, V. R., & Epstein, R. A. (2010). Neural correlates of real-world route learning. *Neuroimage, 53*(2), 725-735. doi:10.1016/j.neuroimage.2010.06.065

Tusch, E. S., Alperin, B. R., Holcomb, P. J., & Daffner, K. R. (2016). Increased Early Processing of Task-Irrelevant Auditory Stimuli in Older Adults. *Plos One, 11*(11), 24. doi:10.1371/journal.pone.0165645

Uiga, L., Cheng, K. C., Wilson, M. R., Masters, R. S. W., & Capio, C. M. (2015). Acquiring visual information for locomotion by older adults: A systematic review. *Ageing Research Reviews, 20*, 24-34. doi:10.1016/j.arr.2014.12.005

van Veen, H., Distler, H. K., Braun, S. J., & Bulthoff, H. H. (1998). Navigating through a virtual city: Using virtual reality technology to study human action and perception. *Future Generation Computer Systems, 14*(3-4), 231-242. doi:10.1016/s0167-739x(98)00027-2

von Stulpnagel, R., & Steffens, M. C. (2013). Active route learning in virtual environments: disentangling movement control from intention, instruction specificity, and navigation control. *Psychological Research-Psychologische Forschung, 77*(5), 555-574. doi:10.1007/s00426-012-0451-y

Waldron-Perrine, B., & Axelrod, B. N. (2012). Determining an appropriate cutting score for indication of impairment on the Montreal Cognitive Assessment. *International Journal of Geriatric Psychiatry, 27*(11), 1189-1194. doi:10.1002/gps.3768

Waller, D., & Lippa, Y. (2007). Landmarks as beacons and associative cues: Their role in route learning. *Memory & Cognition, 35*(5), 910-924. doi:10.3758/bf03193465

Waters, G., & Caplan, D. (2005). The relationship between age, processing speed, working memory capacity, and language comprehension. *Memory, 13*(3-4), 403-413. doi:10.1080/09658210344000459

Wenczel, F., Hepperle, L., & von Stulpnagel, R. (2017). Gaze behavior during incidental and intentional navigation in an outdoor environment. *Spatial Cognition and Computation, 17*(1-2), 121-142. doi:10.1080/13875868.2016.1226838

West, R. (1999). Visual distraction, working memory, and aging. *Memory & Cognition, 27*(6), 1064-1072. doi:10.3758/bf03201235

Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive Bias for Extrahippocampal Navigation Strategies in Aging Humans. *Journal of Neuroscience, 33*(14), 6012-6017. doi:10.1523/jneurosci.0717-12.2013

Wiener, J. M., Holscher, C., Buchner, S., & Konieczny, L. (2012). Gaze behaviour during space perception and spatial decision making. *Psychological Research-Psychologische Forschung, 76*(6), 713-729. doi:10.1007/s00426-011-0397-5

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

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Chapter 5

The impact of cognitive aging on route learning rate and the acquisition of landmark knowledge

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5.1 Abstract

Aging is accompanied by changes in general cognitive functioning which may impact the learning rate of older adults; however, this is often not controlled for in cognitive aging studies. We investigated the contribution of differences in learning rates to age-related differences in landmark knowledge acquired from route learning. In Experiment 1 we used a standard learning procedure in which participants received a fixed amount of exposure to a route. Consistent with previous research, we found age-related deficits in associative cue and landmark sequence knowledge. Experiment 2 controlled for differences in learning rates by using a flexible exposure learning procedure. Specifically, participants were trained to a performance criterion during route learning before being tested on the content of their route knowledge. While older adults took longer to learn the route than younger adults, the age-related differences in associative cue knowledge were abolished. The deficit in landmark sequence knowledge, however, remained. Experiment 3 replicated these results and introduced a test situation in which a deficit in landmark sequence knowledge yielded an increased likelihood of disorientation in older adults. The findings of this study suggest that age-related deficits in landmark associative cue knowledge are attenuated by controlling for learning rates. In contrast, landmark sequence knowledge deficits persist and are best explained by changes in the learning strategy of older adults to acquire task essential associative cue knowledge at the expense of supplementary sequence knowledge.

5.2 General Introduction

Route navigation is the most frequent daily navigation task. While many studies have shown that route learning abilities decline with the typical aging trajectory (for reviews see Lester et al., 2017; Lithfous et al., 2013), age-related changes in learning rate are often not accounted for. The result is that whilst we have a good understanding of age-related differences in the learning of a novel environment, our understanding of the final content of route knowledge possessed by older adults after a route has been successfully learned is limited. In this study we first compared route knowledge between young and older adults after limited exposure to a route. In the second experiment, we compare route knowledge between young and older adults after participants had successfully learned a route. In the last experiment, we investigated the impact of age-related differences in the final content of route knowledge on the wider navigation ability of older adults.

Frameworks of spatial knowledge acquisition suggest that early stages of learning involve the encoding of distinctive visual environmental features as landmarks (Chrastil, 2013; Foo et al., 2007; Siegel & White, 1975). In route learning, these landmarks are used as cues to execute the required motor response for successful navigation (Foo et al., 2005), which is known as the associative cue strategy (Waller & Lippa, 2007). This associative cue knowledge requires stimulus-response learning (S-R; Trullier et al., 1997) in order to bind directional information to landmarks (e.g. turn left at the church). Importantly, S-R information is not always held in isolation but can be linked to the up-coming landmark which will be encountered at the next intersection as stimulus-response-stimulus associations (S-R-S; Strickrodt et al., 2015; Trullier et al., 1997), for example "turning left at the church brings you to the post office". These S-R-S associations are thought to form the basis of route sequence knowledge which allow the navigator to generate expectations about the next location to be encountered and prepare responses (Schinazi & Epstein, 2010; Trullier et al., 1997).

Older adults have been shown to perform worse than younger adults in tests of associative cue knowledge (Head & Isom, 2010; Hilton et al., 2019; Liu et al., 2011; Wiener et al., 2012; Zhong & Moffat, 2016) and landmark sequence knowledge (Head & Isom, 2010; Hilton et al., 2019; Wiener et al., 2012; Wilkniss et al., 1997) after a period of route learning. This cannot be attributed to a failure to learn landmarks, since older adults are able to engage attention at relevant locations (i.e. intersections; Hartmeyer et al., 2017; Hilton et al., 2019), select relevant environmental features as landmarks (Grzeschik et al., 2019), and recall them from memory at similar rates to younger adults (Cushman et al., 2008; Head & Isom, 2010). Instead, it has been suggested that older adults are impaired in the actual association of spatial information and landmarks (Zhong & Moffat, 2016), which is in line with a more general age-related decline in associative learning ability in older age (Associative Deficit Hypothesis; Naveh-Benjamin, 2000). Indeed, when learning routes, older adults tend to avoid the associative cue strategy where possible, in favour of encoding landmarks which are located in the direction of travel, so that the direction of movement is coded in the visual position of the landmark and does not need to be explicitly represented in memory (Wiener et al., 2013).

Whilst current research provides substantial insight into age-related differences in acquisition of route knowledge when learning novel routes, our understanding of the final content of route knowledge is limited. One contributing factor to this contrast is the nature of the methods used to assess route learning and knowledge. Typical route learning tasks first involve a learning phase, in which participants navigate or are passively transported along a route which they are instructed to learn. This learning phase is followed by a test phase in which participants are probed on their ability to repeat the route, and on the content of their route knowledge via tests of landmark memory, associative cue, and landmark sequence knowledge. In all the route navigation studies discussed so far, the learning phase involved a set number of times participants viewed or navigated the route, or a set time limit to explore the environment. This approach will henceforth be referred to as *fixed exposure learning*.

Fixed exposure learning yields two concerns centred around the fact that the content of participants' route knowledge is being compared whilst their actual ability to successfully navigate through the environment varies. It is important to highlight at this point that the ability to navigate a route does not indicate that a participant possesses an exact, known structure of knowledge for that route. For example, on the simplest level a navigator could solely encode a vector of turns to complete a route (e.g., left-right-left-straight-right). The content of that navigator's route knowledge would be more limited than an individual who acquired associative cue and/or sequence information about the places and landmarks they encountered. Considering the vast range of individual differences apparent in navigation ability (Hegarty & Waller, 2009; Weisberg et al., 2014), setting an arbitrary cut off for exposure during learning provides only limited insights into the final content of route knowledge once successful navigation would be achieved.

The first concern with fixed exposure learning can be summarised as the *under-training* of older adults. In most route navigation studies, it is the older participant group who are less able to successfully navigate the route at the end of the fixed exposure learning protocol. This demonstrates that they have not fully developed their route knowledge by that point. Indeed, many studies using a fixed exposure approach would not be able to determine if the older participants would eventually be able to successfully complete the navigation task, and whether the means by which they would do so were comparable to the younger participants.

The second concern with the fixed exposure learning procedure is that younger participants may be *over-trained*. That is to say that participants who perform very well early on, but are required to continue the learning phase, may receive more exposure than is required to acquire only the knowledge they need to complete the route navigation task without errors. In subsequent exposures those participants may engage in supplementary learning of additional information about the route. This supplementary knowledge may then give the impression that younger adults acquired particular information that is required for successful navigation that older adults could not learn.

The concerns of under-training older adults and over-training younger adults arise from the differences in learning rates between the two age groups. Studies focusing on cognitive domains other than navigation find reduced learning rates for older adults, for example in sequence learning of visuospatial information (Turcotte et al., 2005). Older adults also acquire information slower on procedural memory tasks, notably when associative learning is involved (Vakil & Agmon-Ashkenazi, 1997), which is in line with the Associative Deficit Hypothesis (Naveh-Benjamin, 2000). Vakil and Agmon-Ashkenazi (1997) noted that age-related differences in learning rate must be considered alongside differences in baseline performance when characterizing the specific memory deficits associated with normal aging. Our study applies this notion in a navigation context, for the learning of landmark and route information.

There are several hypotheses as to why older adults acquire less information than younger adults in the same fixed time period. The Speed of Processing theory of aging (Salthouse, 1996) posits that the speed at which cognitive functions are performed decreases in older age. That is, the time available for later operations is reduced when the prerequisite functions occupy larger proportions of the available time window. The products of earlier cognitive functions may degrade during the extended time taken for subsequent processes to take place and as a result the final output may be incomplete. Park (2000) emphasises that "the effects of the slowed processing speed are hypothesized to be global and to have an impact on all aspects of cognition" (p.10). More recent evidence supports this assertion; Ebaid et al. (2017) used measurements from assessments of motor dexterity to statistically control for motor speed differences between older and younger adults when comparing response times on traditional measures of cognitive processing (subsets of the WAIS-IV, Wechsler, 2008). They reported that older adults still exhibited processing speed deficits when motor speed was controlled for, which is discussed as affecting a variety of domains including short-term visual memory, visual-motor coordination, visual discrimination, attention, and concentration.

Additionally, the Resource Deficit Hypothesis (Craik & Byrd, 1982) suggests that the pool of cognitive resources available to process information and to perform cognitive functions declines in older age. This pool is referred to as being attentional in nature but is also characterised more generally as "mental energy". As a result of declining resources, cognitive operations carried out by older adults are limited in quantity (as evidenced by reduced span, Brown, 2016). The resource deficit has been suggested as a possible mechanism underlying associative learning deficits (Craik, 2012; Craik et al., 2010; Naveh-Benjamin et al., 2005; Naveh-Benjamin & Kilb, 2014). Such a relationship between resource deficits and associative learning has also been suggested in route navigation. Zhong and Moffat (2016) argued that older adults may allocate a greater proportion of their cognitive resources to landmark encoding but do so at the expense of forming S-R associations between landmarks and required movement directions, thus leading to poorer route navigation performance. This explanation was supported by the unintuitive finding that memory for landmarks correlated positively with navigation errors in older adults. Older adults focusing more resources on the earlier stages of spatial learning, specifically landmark encoding (Siegel & White, 1975), may explain why their performance on landmark memory tasks is often similar to younger adults (Cushman et al., 2008; Head & Isom, 2010).

Age-related differences in learning rates means that differences in route knowledge that are present during fixed exposure learning may not reflect the final content of route knowledge. There are a few studies which employed an alternative approach to the fixed exposure learning procedure. Those studies instead used a performance threshold for ability to navigate through the environment as the indicator of when to terminate the learning phase. In this case, the amount of exposure to the route may vary between participants, but at the end of learning all of the participants are matched on ability to successfully navigate through the environment. We will refer to this approach as *flexible exposure learning*.

Of the studies which employed a flexible exposure learning approach one unsurprising, but reassuring, consensus is that most older participants were able to pass the learning phase by meeting a performance criterion for successful navigation (Allison & Head, 2017; Craig et al., 2016; Grzeschik et al., 2019; O'Malley et al., 2018). However, these studies report differing patterns of results: two studies reported that older adults took a greater number of trials to initially learn routes and follow up tests of route knowledge did not uncover age-related differences in associative cue (Grzeschik et al., 2019; O'Malley et al., 2018) or landmark sequence knowledge (O'Malley et al., 2018). Conversely, two other studies reported no difference between age groups in the time taken to learn a route (Allison & Head, 2017; Craig et al., 2016). However, one of the studies found that older adults performed worse on both tests of associative cue and sequence knowledge (Allison & Head, 2017), whilst the other did not conduct such tests (Craig et al., 2016).

Grzeschik et al. (2019) did not directly test the ability to navigate the route, but rather used the associative cue test as the indicator for successful navigation, by repeating interleaved videos of the route and tests of associative cue knowledge. Thus, in their study, more learning trials to reach criterion only revealed that older adults were able to successfully learn associative cue knowledge, but it took them longer to do so. This result is in line with results from O'Malley et al. (2018) who also did not report age-related differences in associative cue knowledge once a route was learned. However, O'Malley et al. (2018) assessed route knowledge with ability to provide directions at intersections during learning. Their post learning test of associative cue knowledge showed only ~60% performance, indicating that this was not the sole type of information participants used to navigate the route. This result reinforces the notion that learning a route does not necessarily result in an exact structure of route knowledge and highlights that associative cue knowledge should not serve as the sole indicator of the ability to successfully navigate a route.

O'Malley et al. (2018) also reported age equivalence on the landmark sequence task. The studies by both Grzeschik et al. (2019) and O'Malley et al. (2018) suggest that older adults have reduced route learning rate, but that their final content of route knowledge is comparable to that of younger adults. Note however, that participants in both studies were aware of the nature of the follow up tests and could have altered their learning strategy accordingly, away from what they may have learned naturally during navigation, in order to solve the up-coming tasks (Naveh-Benjamin et al., 2007). Indeed, this may have been trivial also for the older participants as both studies used short routes with only four intersections. Such a strategy could explain why, despite equal route lengths, older participants took more trials to complete learning in the study by O'Malley et al. (2018), where there were more follow up tests, than in the study by Grzeschik et al. (2019).

In contrast, Allison and Head (2017) and Craig et al. (2016) used longer routes, and somewhat paradoxically reported no differences in the number of sessions taken to reach criterion for successful navigation. Such a finding could be due to the lack of precision in assessing ability to navigate during learning. Each learning session contained either two (Allison & Head, 2017) or three (Craig et al., 2016) exposures to the route before knowledge was assessed. It is possible that testing participants' ability to navigate the route only after learning sessions which containing several exposures is not sensitive enough to reveal any age-related differences in route learning rate, which is supported by the differences reported in studies using 'per exposure' testing (Grzeschik et al., 2019; O'Malley et al., 2018).

In addition to several exposures per learning session, Allison and Head (2017) and Craig et al. (2016) also had a minimum of two learning sessions (i.e. a minimum of 4-6 total route exposures). Therefore, whilst they addressed the concern of under-training by requiring all participants to reach the same performance criterion during learning, their procedure could result in over-training. That is, participants who learned the route on the very first exposure would have had 3+ additional exposures in which to engage in supplementary learning. Indeed, Craig et al. (2016) explicitly reported that more younger than older adults could navigate the route after the first learning session (3 exposures), but required them to complete the second learning session nonetheless. This over-training of younger adults could be responsible for the age-related deficits in associative cue and landmark sequence knowledge reported by Allison and Head (2017), which conflicts with O'Malley et al. (2018).

The present study investigated the content of route knowledge in older and younger adults following route learning via a fixed exposure learning procedure (Experiment 1) and a flexible exposure learning procedure (Experiment 2). The ability to navigate the route during learning was tested during each exposure (Grzeschik et al., 2019; O'Malley et al., 2018) and we used a moderately long route length (Allison & Head, 2017; Craig et al., 2016). We conducted follow up tests of landmark memory, associative cue knowledge, and sequence knowledge (Allison & Head, 2017; O'Malley et al., 2018) which participants did not know about during learning. We provide the first direct comparison of the fixed and flexible exposure learning procedures and thus of route knowledge acquired by younger and older adults during route learning and after route learning is completed. Our approach addresses both the concerns of under-training older adults and over-training younger adults.

Finally, we aimed to assess the impact of age-related differences in specific features of route knowledge when navigators are faced with a different task along the same route. Specifically, based on the findings of Experiment 2, we introduce a novel, realistic navigation task in Experiment 3 which requires a rich representation of the environment to be solved via a combination of landmark sequence and associative cue knowledge. Other than the addition of this task, Experiment 3 is a direct replication of Experiment 2 and the flexible exposure learning procedure, assessing the reliability of our findings in view of the variations in findings from previous studies using this approach (Allison & Head, 2017; Craig et al., 2016; Grzeschik et al., 2019; O'Malley et al., 2018).

5.3 Experiment 1

5.3.1 Introduction

The aim of Experiment 1 was to test whether we could replicate previous findings with our route learning protocol and our stimuli using a fixed exposure learning procedure. Such a conceptual replication is important to reinforce our arguments that (1) older adults will be less able to navigate the route by the end of the learning phase than younger adults and (2) that older adults will perform worse in tests of landmark associative cue and sequence knowledge. Additionally, the data from this experiment provides a route and procedure matched comparison to the flexible exposure learning approach used in Experiment 2.

In this experiment participants were required to give directional responses at decision points during the learning phase. The subsequent test phase comprised tests of landmark memory, associative cue knowledge, and landmark sequence knowledge. Based on previous research we expected: (i) Older adults to make more route navigation errors than younger adults (c.f. Head & Isom, 2010; Wiener et al., 2012). (ii) No significant performance difference between older and younger adults on the test of landmark memory (c.f. Allison & Head, 2017; Cushman et al., 2008). (iii) Younger adults to perform significantly better than older adults on the test of associative cue knowledge (c.f. Hilton et al., 2019; Zhong & Moffat, 2016). (iv) Younger adults to perform significantly better than older adults on the test of landmark sequence knowledge (c.f. Head & Isom, 2010; Wiener et al., 2012).

5.3.2 Method

5.3.2.1 Participants

Twenty-nine younger participants and 27 older participants took part in this experiment. Older participants were screened for mild cognitive impairment using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005). All older participants scored above the MoCA cut off score of 23 (Luis et al., 2009; Waldron-Perrine & Axelrod, 2012). Table 5-1 summarises the demographic data of the final participant groups. Ethical approval was granted by the Bournemouth University Research Ethics Panel and written informed consent was gained from all participants who either received course credits or a monetary compensation for their time.

Table 5-1 - Participant demographics.

	Sex		Age		MoCA	
		n	Mean	SD	Mean	SD
Younger	Female	16	22.38	4.84		
	Male	13	19.69	1.11		
Older	Female	14	71.14	5.87	26.36	2.06
	Male	13	70.77	3.40	26.08	2.22

5.3.2.2 Design

The independent variables were age group (2 levels: younger and older) and for the learning phase, learning trial (1-3). The younger age group was 18-35 years old and the older age group was 65+ years old. There were a series of dependent variables: learning phase performance, landmark recall memory, associative cue knowledge, and landmark sequence knowledge.

5.3.2.2.1 Virtual Environment

We used a modified version of the environment described by Grzeschik et al. (2019), which was created using 3D Studio Max (Autodesk Inc., San Rafael, USA). The only change we made to the environment was to the landmarks at the intersections. We used two identical landmarks at each intersection, which were the only way to distinguish between different intersections (see Figure 5-1). The paths between intersections were all visually identical and of equal length.

We recorded videos of passive transportation for left, straight and right turns at each intersection. To generate routes for participants, we stitched a series of videos together in OpenSesame, an open source experiment presentation software (Mathôt et al., 2012). The routes consisted of 12 intersections (4 left turns, 4 right turns, 4 straight ahead). Every participant saw the same landmarks and could only ever see one pair of identical landmarks at a time. The order of landmarks and route directions were randomized for every participant. Routes were presented on a BenQ XL 2411-8 24-inch monitor at a resolution of 1920x1080p.

5.3.2.2.2 Learning Phase

Participants were passively transported along the route, which they were instructed to learn. During this passive transportation, the video was paused at each intersection so that movement along the route halted, and participants were required to indicate the direction of travel they thought would continue along the route using the directional keys on the keyboard. As soon as a response was given, transportation continued along the route regardless of the movement direction provided by the participant, thus providing participants with immediate feedback. Participants were informed that the route transportation always continued in the correct direction, even if their response was incorrect, and thus they could learn from the feedback. All participants navigated the route using this procedure three times sequentially during the learning phase. During the first of the three route exposures participants were required to guess their responses, since they had not seen the route before.

Figure 5-1 - A screenshot of an intersection in the environment.

5.3.2.2.3 Test Phase

Test phase tasks were not conducted using a computer. Participant responses were given verbally and recorded by the experimenter. The test phase comprised of three tasks:

5.3.2.2.3.1 Free Landmark Recall Task

This task was designed to assess memory for the landmarks along the route. Participants were asked to verbally recall as many of the landmarks as they could remember in any order (i.e. immediate free recall). Any ambiguous responses were clarified with the participant by asking for alternative names and visual descriptions of the object. Participants scored 1 for every landmark they recalled and 0 for every landmark they omitted.

5.3.2.2.3.2 Associative Cue Task

This task was designed to assess whether or not participants had associated a directional response to the landmarks along the route. Images of all the landmarks were printed out and shown to the participants individually and in a random order. Participants had to indicate the direction taken when this landmark was encountered along the route (the response was 3-alternative forced choice: left, right, and straight). Participants scored 1 for every correct response and 0 for an incorrect response.

5.3.2.2.3.3 Landmark Sequence Task

This task was designed to assess participants' knowledge of the sequence in which landmarks were encountered along the route. Participants were given all printed images of the landmarks and were required to arrange them in the order in which they were encountered along the route. This was a free reconstruction of order (ROO-free) task as described in Ward et al. (2010), in which participants are free to place landmarks into their positions in any temporal order. They were also free to change their decisions before finalising the sequence. The sequence was recorded once participants indicated they were finished.

We analysed the Sequence Task data in two ways. In the primary analysis we used absolute scoring. Each landmark placed in the correct position was scored 1 and each incorrectly placed landmark was scored 0 (c.f. Ward et al., 2010). Whilst this scoring method does indicate sequence knowledge in terms of absolute position, it is not sensitive to relative ordering of landmarks. For example, a participant could place N-1 items correctly, and then place the last landmark in position one, therefore shifting all items one place forward. This situation would result in a total score of 0, despite having the relative sequence of 11/12 landmarks in the correct order. To account for relative positioning, we calculated the Levenshtein Distance between the given sequence and the correct sequence (Levenshtein, 1966). The Levenshtein Distance is the number of moves required to transform the given sequence into the correct sequence. Moves consist of deletions, insertions and substitutions. Sequences with good relative ordering of landmarks will have lower Levenshtein Distances than those which have poor relative ordering.

5.3.2.3 Procedure

Participants first completed the Learning Phase. They were not informed about the nature of the tasks in the Test Phase to avoid any intentional changes in learning strategy. Once participants completed the Learning Phase, they immediately performed the Free Landmark

Recall Task. The Free Landmark Recall Task was always performed before the other tasks because the other tasks involve showing the landmarks to participants which would confound landmark memory. The order of the Associative Cue Task and the Landmark Sequence Task was counterbalanced between participants and age groups to control for potential interference on memory.

5.3.3 Results

We analysed the data using logistic generalized linear mixed effects models (GLME) in R (R Core Team, 2019) using the lme4 package (version 1.1-14; Bates et al., 2015). We fitted our models using the procedure described in Bates et al. (2018). We began with the maximal models which reached convergence. We then iteratively reduced model complexity using principle component analysis (PCA; R-package: RePsychLing) to remove random effects components which accounted for the least variance until we reached the least components needed to still capture 100% of the variance explained. The resulting model was compared to a model with an intercept only random effect structure from which we selected the final model based on the Akaike Information Criterion.

5.3.3.1 Learning Phase

Figure 5-2 shows the percentage of correct directions given in each trial of the learning phase. In the first learning trial, older adults (mean: 35.49%, 95% CI: 40.95%, 30.04%) and younger adults (mean: 37.36%, 95% CI: 43.50%, 31.21%) performed close to the chance level of 33% (given the three possible movement directions at each intersection) since this was their first exposure to the route.

We used a GLME model with age group (factor, younger or older, centred using sum contrast coding) and trial (factor, 1 or 2 or 3, coded using successive differences contrasts) as fixed effects, and participant and stimulus as random effects. The outcome variable was performance, which is whether the response given at each intersection was correct (1) or incorrect (0). Estimates, standard errors, z-values, and p-values for the Learning Phase model[4] are reported in Table 5-2. The model shows that younger adults performed better than older adults, and that performance improved from trial 1 to 2, and trial 2 to 3 (see Figure

[4] Learning Phase GLME model as expressed using the lme4 package:
glmer(performance ~ age_group * trial + (1|participant) + (1|stimulus), data = data, family = binomial)

5-2). The only significant interaction was age group (younger vs older) x trial (1 vs 2) which shows that the size of the age group effect increased from trial 1 to 2.

Table 5-2 - Coefficients from the Learning Phase GLME analysis.

Fixed effect on Learning Phase performance	Estimate	Std. error	z-value	p-value
Intercept	0.43	0.11	3.82	<.001*
Age group (older vs younger)	0.29	0.09	3.10	.002*
Trial (1 vs 2)	1.33	0.12	10.97	<.001*
Trial (2 vs 3)	0.45	0.12	3.55	<.001*
Age group (younger vs older) * trial (1 vs 2)	0.28	0.12	2.29	.022*
Age group (younger vs older) * trial (2 vs 3)	0.20	0.13	1.58	.113

*Significant p values (|p|<0.05)

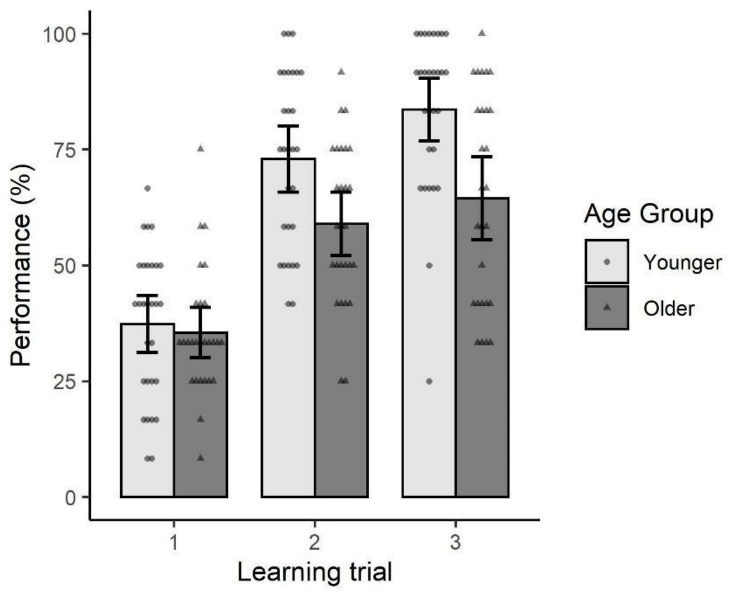

Figure 5-2 - Average performance in each learning trial for the younger and older participant groups. Bars are group means, points are individual participants and error bars are 95% confidence intervals.

5.3.3.2 Test Phase

Each model[5] included age group (factor: younger or older; centred using sum contrast coding) as a fixed effect and participant and stimulus (landmark) as random effects. The outcome variable for all models was performance which is whether each response given was correct (1) or incorrect (0).

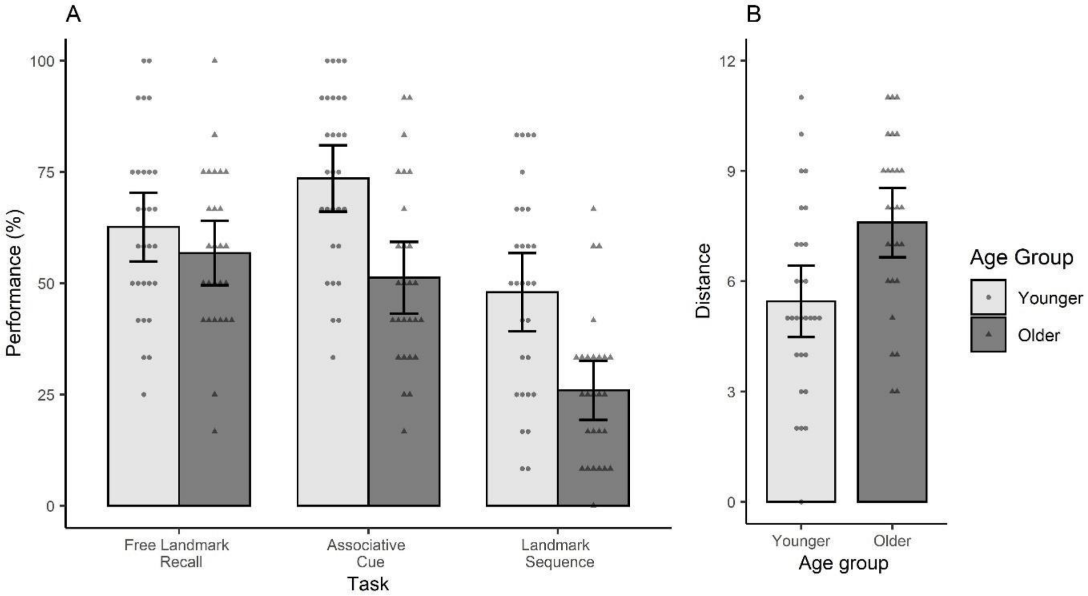

Figure 5-3 - (A) Average performance in each test task and (B) Levenshtein distances for the Landmark Sequence Task for the younger and older participant groups. Bars are group means, points are individual participants and error bars are 95% confidence intervals.

5.3.3.2.1 Free Landmark Recall Task

Estimates, standard errors, z-values, and p-values for the Free Landmark Recall Task model are reported in Table 5-3 and show that age group was not a significant predictor of performance (see Figure 5-3a).

[5] GLME model as expressed using the lme4 package:
glmer(performance ~ age_group + (1|participant) + (1|stimulus), data = data, family = binomial)

Table 5-3 - Coefficients from the Free Landmark Recall Task GLME analysis.

Fixed effect on Free Landmark Recall Task performance	Estimate	Std. error	z-value	p-value
Intercept	0.46	0.19	2.42	.016*
Age group (older vs younger)	0.14	0.12	1.18	.240

*Significant p values (|p|<0.05)

5.3.3.2.2 Associative Cue Task

Estimates, standard errors, z-values, and p-values for the Associative Cue Task model are reported in Table 5-4. Age group was a significant predictor of performance, with younger participants performing better than older participants (see Figure 5-3a).

Table 5-4 - Coefficients from the Associative Cue Task GLME analysis.

Fixed effect on Associative Cue Task performance	Estimate	Std. error	z-value	p-value
Intercept	0.64	0.20	3.26	.001*
Age group (older vs younger)	0.58	0.14	4.01	<.001*

*Significant p values (|p|<0.05)

5.3.3.2.3 Landmark Sequence Task

5.3.3.2.3.1 Absolute Scoring

Estimates, standard errors, z-values, and p-values for the Landmark Sequence Task model are reported in Table 5-5. Age group was a significant predictor of performance, with younger participants performing better than older participants (see Figure 5-3a).

Table 5-5 - Coefficients from the Landmark Sequence Task GLME analysis.

Fixed effect on Landmark Sequence Task performance	Estimate	Std. error	z-value	p-value
Intercept	-0.63	0.14	-4.41	<.001*
Age group (older vs younger)	0.54	0.13	4.08	<.001*

*Significant p values (|p|<0.05)

5.3.3.2.3.2 Levenshtein Distance

We calculated Levenshtein Distances using the stringdist package (van der Loo, 2014) version 0.9.5.2 (2019) in R (R Core Team, 2019). A Welch's two sample t-test revealed that Levenshtein Distance was significantly higher for older adults (mean = 7.59, SD = 2.37) compared to that for younger adults (mean = 5.45, SD = 2.56), $t(54) = 3.25$, $p = .002$, Cohen's $d = 0.87$ (95% CI for Cohen's d: 1.43, 0.31). Specifically, there was a difference of 2.14 (95% CI: 3.47, 0.82; see Figure 5-3b).

5.3.4 Discussion

In Experiment 1 we compared landmark memory, associative cue knowledge, and landmark sequence knowledge after a fixed exposure learning phase (three exposures to the route) between younger and older adults. As predicted, (i) younger participants correctly recalled direction changes at more intersections of the route during the learning phase than older participants. Further, the age group x learning trial interaction shows that younger participants' performance increased more than that of older adults between the first and second training trial. This result supports the notion that the learning rate of older adults is reduced compared to that in younger adults. Interestingly, some of the younger participant group reached 100% performance already in the second learning trial (see Figure 5-2), whilst none of the older adults did.

Under the fixed exposure learning procedure used in this experiment, those (young) participants who learned the route quickly were still required to continue the learning phase. This continued exposure to the route may have led to over-training. That is, since participants had already learned the route before the third learning trial, they may begin acquiring additional information about the route which was not part of their original learning strategy. Since younger adults learned the route quicker in this experiment, they may be particularly prone to over-training which may contribute to inflated age group differences.

Consistent with previous research, there was (ii) no difference between younger and older adults on the Free Landmark Recall Task whereas older adults performed worse than younger adults on tests of both (iii) associative cue knowledge and (iv) landmark sequence knowledge. The Landmark Sequence Task analyses using absolute scoring and Levenshtein Distances both showed an age-related deficit, which suggests that absolute and relative sequence knowledge is impaired in older adults when compared to young adults. This experiment provides a conceptual replication of earlier studies and demonstrates that our environment, learning procedure and tasks used to assess landmark knowledge yielded results which were similar to those reported in earlier studies addressing the effects of cognitive aging on route learning (e.g. Head & Isom, 2010; Wiener et al., 2012).

5.4 Experiment 2

5.4.1 Introduction

The aim of Experiment 2 was to investigate age-related differences of landmark knowledge after participants had successfully learned a route. We implemented a flexible exposure learning procedure which allowed participants to learn a route to a performance criterion, before moving on to the test phase. This approach controls for individual differences in learning rate, which the fixed exposure learning procedure used in Experiment 1 did not. Further to this, by ending the learning phase as soon as participants have learned the route, we avoid potentially over-training younger participants, as well as under-training older participants. We were then able to investigate specific age-related differences in the content of route knowledge irrespective of learning rate. In addition, we directly compared the content of route knowledge in this experiment as developed through flexible exposure learning to route knowledge developed through fixed exposure learning by the participants in Experiment 1.

Considering the results of Experiment 1 and previous studies showing impaired route learning ability in aging (Grzeschik et al., 2019; O'Malley et al., 2018), we expected (i) older adults to take significantly more learning trials than younger participants to reach the performance criterion. Since the older adults were not able to navigate the route to a high level by the end of learning in Experiment 1, we expected (ii) older adults to take significantly more than 3 trials to pass the learning phase in this experiment, representing the concern of under-training. Accordingly, if our younger participants were over-trained in Experiment 1, we expected them to take (iii) significantly fewer than 3 trials to pass the learning phase.

Based on the results of the test phase in Experiment 1, we predicted: (iv) no significant difference between older and younger participants in performance on the Free Landmark Recall Task. For the associative cue and landmark sequence tasks, there were several possible permutations of results. Between experiment comparisons may reveal (v) an increase in performance for older adults due to controlling for learning rates (i.e. under-training) and/or a decrease in performance for younger adults due to lack of over-training. Such changes would then result in (vi) reduced or abolished age-effects in one or both of these tasks

(O'Malley et al., 2018). Oppositely, it is possible that (vii) age-related differences in the final content of route knowledge persist independently of learning rate, therefore age-related differences on the associative cue and/or landmark sequence task would remain (Allison & Head, 2017).

5.4.2 Method

5.4.2.1 Participants

Twenty-nine younger participants and 27 older participants were included in the final analysis. An additional six older participants took part in the Experiment but did not reach the performance criteria (90% accuracy) in the learning phase and were excluded from the final analysis. All older participants scored above the MoCA cut off score of 23 (Luis et al., 2009; Waldron-Perrine & Axelrod, 2012). Table 5-6 summarises the demographic data of the final participant groups.

Table 5-6 - Participant demographics.

	Sex		Age		MoCA	
		n	Mean	SD	Mean	SD
Younger	Female	15	21.13	4.12		
	Male	14	21.79	4.44		
Older	Female	13	72.08	6.17	26.77	2.20
	Male	14	73.00	6.40	26.43	2.10

5.4.2.2 Design

The design was as described for Experiment 1 except for a change to the Learning Phase.

5.4.2.2.1 Learning Phase

Instead of repeating the route three times during the learning phase, participants navigated the route repeatedly until they recalled at least 90% of the directions correctly (i.e. at least 11 out of the 12 decisions along the route), or until 9 attempts had been made. 9 attempts was chosen as the maximum to ensure that the complete experimental session did not exceed 1.5 hours. Participants moved on to the test phase after they reached the criterion (>90% performance) or after 9 attempts (in which case the test data was excluded from the final analysis).

5.4.2.3 Procedure

The procedure was the same as described for Experiment 1.

5.4.3 Results

5.4.3.1 Learning Phase

We analysed the number of learning trials taken to reach the performance criterion which will henceforth be referred to as learning trials. A Welch's two sample t-test revealed that older adults required significantly more learning trials to reach criterion (mean = 5.82, SD = 2.29) compared to younger adults (mean = 4.07, SD = 1.49; see Figure 5-4), $t(44.13) = 3.36$, $p = .002$, Cohen's *d* = 0.91 (95% CI for Cohen's *d*: 1.48, 0.35). Specifically, there was a difference of 1.75 (95% CI: 2.79, 0.70).

In addition, to examine whether age groups were over-trained in Experiment 1, we analysed whether the mean number of trials taken to pass the learning phase was significantly different to 3. A one sample t-test revealed significantly more than 3 trials taken to pass the learning phase for both older adults (mean: 5.82, $t(26) = 6.39$, $p < .001$, Cohen's *d* = 1.23, 95% CI for Cohen's *d*: 2.09, 0.37) and younger adults (mean: 4.07, $t(28) = 3.87$, $p < .001$, Cohen's *d* = 0.72, 95% CI for Cohen's *d*: 1.50, -0.07).

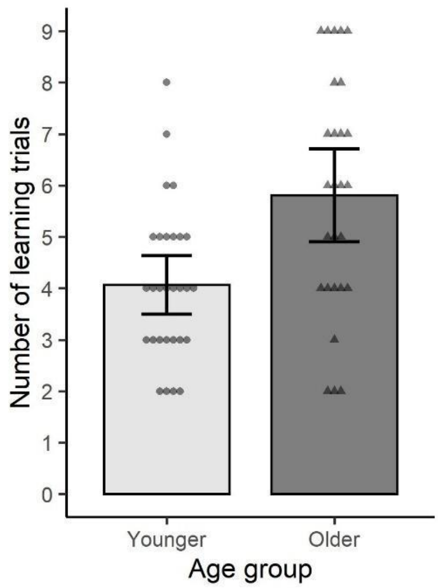

Figure 5-4 - Number of learning trials taken to reach criterion in the Learning Phase for the younger and older participant groups. Bars are group means, points are individual participants and error bars are 95% confidence intervals.

5.4.3.2 Test Phase

We conducted three GLMEs[6]; one for each test task. Each model included age group (factor: younger or older; centred using sum contrast coding) as a fixed effect. Since there was variability in the number of learning trials taken for participants to learn the route, we also included learning trials as a fixed effect (centred around 0). This was to account for the influence of varied amounts of route exposure between participants on test phase performance, similar to Allison and Head (2017) who also took into account performance at learning as a predictor of test performance. The outcome variable for all models was performance which is whether each response given was correct (1) or incorrect (0). Participant and stimulus (landmark) were included as random effects.

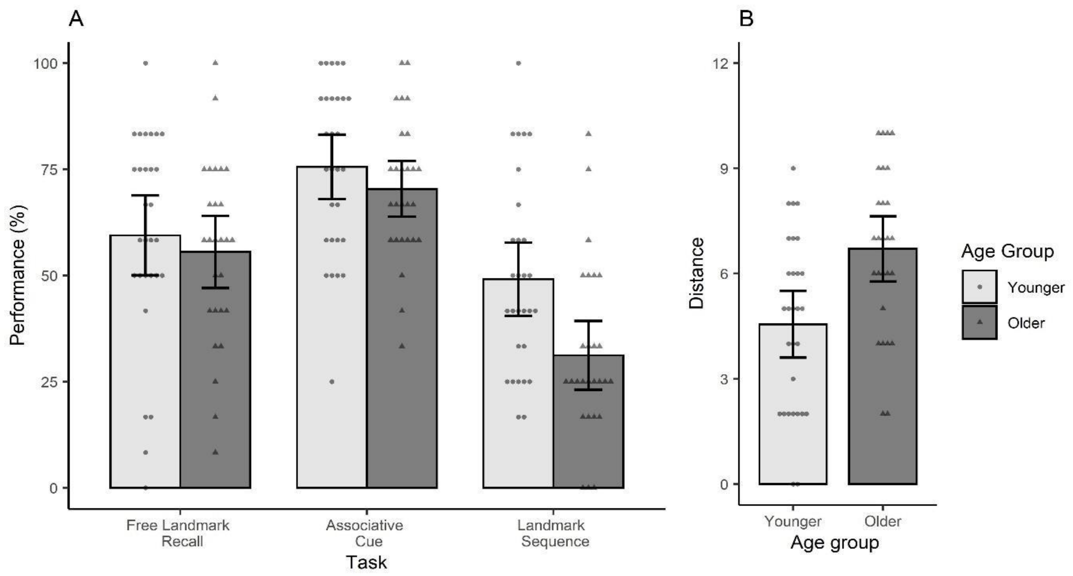

Figure 5-5 - (A) Average performance in each test task and (B) Levenshtein distances for the Landmark Sequence Task for the younger and older participant groups. Bars are group means, points are individual participants and error bars are 95% confidence intervals.

5.4.3.2.1 Free Landmark Recall Task

Estimates, standard errors, z-values, and p-values for the Free Landmark Recall model are reported in Table 5-7 and show that neither age group nor learning trials were predictors of performance (see Figure 5-5a). There was no significant interaction.

[6] GLME model as expressed using the lme4 package:
glmer(performance ~ age_group * learning_trials + (1|participant) + (1|stimulus), data = data, family = binomial)

Table 5-7 - Coefficients from the Free Landmark Recall Task GLME analysis.

Fixed effect on Free Landmark Recall Task performance	Estimate	Std. error	z-value	p-value
Intercept	0.23	0.20	1.15	.250
Age group (older vs younger)	0.04	0.16	0.22	.826
Learning trials	-0.16	0.17	-0.91	.366
Age group (younger vs older) * learning trials	-0.31	0.17	-1.77	.076

*Significant p values (|p|<0.05)

5.4.3.2.2 Associative Cue Task

Estimates, standard errors, z-values, and p-values for the Associative Cue Task model are reported in Table 5-8 and show that neither age group nor learning trials predicted performance (see Figure 5-5a). There was no significant interaction.

Table 5-8 - Coefficients from the Associative Cue Task GLME analysis.

Fixed effect on Associative Cue Task performance	Estimate	Std. error	z-value	p-value
Intercept	1.14	0.21	5.36	<.001*
Age group (older vs younger)	0.22	0.16	1.39	.164
Learning trials	.12	0.17	0.72	.469
Age group (younger vs older) * learning trials	-0.09	0.17	-0.51	.608

*Significant p values (|p|<0.05)

5.4.3.2.3 Landmark Sequence Task

5.4.3.2.3.1 Absolute Scoring

Estimates, standard errors, z-values, and p-values for the Landmark Sequence Task model are reported in Table 5-9 and show that age group was a significant predictor of performance in the Landmark Sequence Task (see Figure 5-5a). Specifically, younger participants performed better than older participants. Learning trials were not a significant predictor of performance and there was no significant interaction.

Table 5-9 - Coefficients from the Landmark Sequence Task GLME analysis.

Fixed effect on Landmark Sequence Task performance	Estimate	Std. error	z-value	p-value
Intercept	-0.40	0.15	-2.68	.007*
Age group (older vs younger)	0.44	0.15	2.93	.003*
Learning trials	0.02	0.16	0.13	.900
Age group (younger vs older) * learning trials	0.15	0.16	0.94	.346

*Significant p values (|p|<0.05)

5.4.3.2.3.2 Levenshtein Distance

A Welch's two sample t-test revealed that Levenshtein Distance was significantly higher for older adults (mean = 6.70, SD = 2.35) compared to that for younger adults (mean = 4.55, SD = 2.49), t(53.99) = 3.33, p = <.001, Cohen's *d* = 0.89 (95% CI for Cohen's *d*: 1.45, 0.33). Specifically, there was a difference of 2.15 (95% CI: 3.45, 0.86; see Figure 5-5b).

5.4.3.3 Between Experiment Comparison

We also compared performance in the test phase between Experiments 1 and 2. Since participants in Experiment 1 did not learn the route to a performance criterion but instead always completed three learning trials, we could not include number learning trials taken to reach criterion as a fixed effect in this analysis. Each model[7] included age group (factor: younger or older; centred using sum contrast coding) and Experiment (factor: 1 or 2; centred using sum contrast coding) as fixed effects. The outcome variable for all models was performance which is whether each response given was correct (1) or incorrect (0). Participant and stimulus (landmark) were included as random effects.

[7] GLME model as expressed using the lme4 package:
glmer(performance ~ age_group * experiment + (1|participant) + (1|stimulus) , data = data, family = binomial)

5.4.3.3.1 Free Landmark Recall Task

Estimates, standard errors, z-values, and p-values for the Landmark Recall model are reported in Table 5-10 and show that there was no difference between Experiment 1 and 2, and there was no significant interaction.

Table 5-10 - Coefficients from the Free Landmark Recall Task GLME analysis.

Fixed effect on Free Landmark Recall Task performance	Estimate	Std. error	z-value	p-value
Intercept	0.41	0.16	2.51	.012*
Age group (older vs younger)	0.12	0.10	1.25	.211
Experiment (1 vs 2)	-0.06	0.10	-0.58	.562
Age group (younger vs older) * experiment (1 vs 2)	-0.03	0.10	-0.29	.776

*Significant p values (|p|<0.05)

5.4.3.3.2 Associative Cue Task

Estimates, standard errors, z-values, and p-values for the Associative Cue Task model are reported in Table 5-11 and show that both age group and experiment predicted performance. These effects were qualified by the significant age group x experiment interaction. Specifically, the interaction shows that the age effect was reduced between Experiment 1 and 2. This is reflected in the individual experiment analyses in which there was a significant difference between age groups on the Associative Cue task in Experiment 1 and no significant difference in Experiment 2.

Table 5-11 - Coefficients from the Associative Cue Task GLME analysis.

Fixed effect on Associative Cue Task performance	Estimate	Std. error	z-value	p-value
Intercept	0.92	0.18	5.17	<.001*
Age group (older vs younger)	0.38	0.10	3.72	<.001*
Experiment (1 vs 2)	0.27	0.10	2.68	<.001*
Age group (younger vs older) * experiment (1 vs 2)	-0.20	0.10	-2.03	.042*

*Significant p values (|p|<0.05)

5.4.3.3.3 Landmark Sequence Task

5.4.3.3.3.1 Absolute Scoring

Estimates, standard errors, z-values, and p-values for the Landmark Sequence Task model are reported in Table 5-12 and show that age group is a significant predictor of performance on the Landmark Sequence Task. There was no difference between Experiment 1 and 2 and no significant interaction.

Table 5-12 - Coefficients from the Landmark Sequence Task GLME analysis.

Fixed effect on Landmark Sequence Task performance	Estimate	Std. error	z-value	p-value
Intercept	-0.55	0.10	-5.77	<.001*
Age group (older vs younger)	0.48	0.09	5.11	<.001*
Experiment (1 vs 2)	0.08	0.09	0.90	.371
Age group (younger vs older) * experiment (1 vs 2)	-0.05	0.09	-0.56	.575

*Significant p values (|p|<0.05)

5.4.4 Discussion

In Experiment 2 we compared younger and older adults on landmark memory, associative cue knowledge, and landmark sequence knowledge after learning a route to a performance criterion. As expected, we found that (i) older participants took significantly more trials to learn the route than younger participants, demonstrating a reduced route learning rate. The problem of under-training in Experiment 1 was highlighted by older participants in this experiment (ii) taking more than 3 attempts to learn the route. However, we did not find evidence of over-training for the younger participants since they also took more than 3 attempts on average to learn the route.

As in Experiment 1, there was (iv) no difference between younger and older adults on the Free Landmark Recall Task. In contrast to Experiment 1, there was (vi) no difference between age groups on the Associative Cue Task. This change was due to (v) higher performance for the older adults in this experiment compared to Experiment 1 which is in line with our findings of under-training for the learning phase. In contrast, the younger adults in Experiment 1 and 2 showed similar performance on the associative cue task. A different pattern of results was observed for the landmark sequence task, for which older adults in this experiment did not display greater knowledge as compared to those in Experiment 1. Consequently, the age difference remained, indicating that (vii) age-related differences in route knowledge cannot be entirely explained by differences in route learning rate, and that the route knowledge of older adults for a known route lacks sequence information compared to younger adults.

As highlighted in the General Introduction, being able to navigate a route does not mean that the navigator possesses a default route representation, and that is evident in this experiment with the reduced sequence knowledge for older adults compared to younger adults. Given that both groups of participants were able to navigate the route, it is important to consider the consequence of this limitation in the spatial knowledge of older adults. Indeed, whilst our Landmark Sequence Task and the scoring methods we used have been commonly used in previous sequence memory research (Ward et al., 2010), it remains a somewhat abstract measure. That is, it is not clear how well they capture the importance of landmark sequence knowledge for actual navigation and it is therefore not clear what impact age-related declines in landmark sequence knowledge could have for actual navigation. The following experiment will investigate the effect of an age-related landmark sequence knowledge deficit in a navigational context.

5.5 Experiment 3

5.5.1 Introduction

We have previously identified an age-related deficit in the acquisition of landmark sequence knowledge for a learned route. The older participants in Experiment 2 were still able to navigate the route successfully, despite having diminished landmark sequence knowledge, and thus the consequence of how an age-related deficit in this type of route knowledge affects navigation behaviour is not clear. The purpose of spatial representations is to allow navigators to resolve a variety of tasks to achieve goal directed wayfinding and avoid disorientation (Wiener et al., 2009). As such, whilst a deficit in sequence knowledge is not particularly harmful to the ability to repeat a route, there are a variety of other situations that sequence knowledge contributes to solving. Intersections and landmarks are tied together during learning (Schinazi & Epstein, 2010) in order to solve such situations should they arise in the future. For example, if landmarks are repeated in the environment, navigators can rely on S-R-S associations to distinguish one landmark from the other (e.g. this post box was preceded by the school whereas the other post box is located after the supermarket) and retrieve the correct motor response (Strickrodt et al., 2015).

Additionally, as familiarity with an environment increases, several known routes may intersect at certain locations. If the navigator has knowledge about the sequence of landmarks along those routes and S-R-S associations, they can integrate those routes into a larger topological representation (Grzeschik et al., 2020). Such representations can then be used to plan routes through the environment to reach different goals, by anticipating the various places that can be travelled to via different movement choices at the present location (Trullier et al., 1997).

Due to the lack of a navigation task which requires the recruitment of sequence knowledge in Experiment 2, it is not entirely clear how the use of the aforementioned processes is affected by aging in a realistic navigation situation. Indeed, although the absolute placement of items was very poor for the older participants (mean: 31.17%), the average Levenshtein Distance for the older adults was 6.7, which is almost half the maximum distance from the correct sequence (maximum = 12). Thus, the older participants clearly maintained some concept of landmark sequence, albeit of lower quality than that of the younger participants. The aim of Experiment 3 was to investigate how this observed deficit in sequence knowledge could affect the ability of older adults to solve navigation tasks with different requirements to those of simple route repetition.

To do this, we developed the Missing Landmark Task in which some landmarks were removed from the route after participants had learnt it to criterion. Participants were required to give route directions at the intersections where landmarks were missing. This task can be solved using landmark sequence knowledge, as participants can use the landmarks which they encountered at the preceding intersection to retrieve what the next landmark in the sequence should be (thus identifying the missing landmark) and recalling the associated direction. This situation presented in the Missing Landmark Task represents the dynamic nature of the real world, in which environmental cues or landmarks used when learning environments may suddenly become unavailable. For example, in residential developments or care environments it is likely that objects such as specific pieces of furniture or paintings that are used by residents as landmarks (O'Malley et al., 2018) will be moved or replaced at some point.

Other than the addition of the Missing Landmark Task, the rest of the experiment was identical to that of Experiment 2. As such, the second aim of Experiment 3 was to test the replicability of the results from Experiment 2. This replication is important, given that the results in Experiment 2 were different from those found in other studies (Allison & Head, 2017; O'Malley et al., 2018), which also vary from each other.

If knowledge about the sequence in which landmarks were encountered is weaker in older adults and this represents impaired use of S-R-S associations, they should become disoriented and unable to complete the Missing Landmark Task. Based on the results of Experiment 2, we predict: (i) Older adults to take significantly more trials to reach the performance criterion during the learning phase than younger participants. (ii) No significant difference between older and younger participants in performance on the Free Landmark Recall Task or the Associative Cue Task. (iii) Older adults to perform significantly worse on the Landmark Sequence Task and the Missing Landmark Task.

5.5.2 Method

5.5.2.1 Participants

Thirty younger participants and 23 older participants were included in the final analysis. One additional older participant did not reach the performance criterion (90% accuracy) in the learning phase and was excluded from the final analysis. All older participants scored above the MoCA cut off score of 23 (Luis et al., 2009; Waldron-Perrine & Axelrod, 2012). Table 5-13 summarises the demographic data of the final participant groups.

Table 5-13 - Participant demographics.

	Sex		Age		MoCA	
		n	Mean	SD	Mean	SD
Younger	Female	15	22.87	3.11		
	Male	15	24.07	4.33		
Older	Female	14	70.07	2.95	27.21	2.08
	Male	9	70.00	5.39	27.22	1.99

5.5.2.2 Design

The design was identical to the one described in Experiment 2, with the addition of the Missing Landmark Task to the test phase.

5.5.2.2.1 The Missing Landmark Task

In the Missing Landmark Task, participants were placed in a corridor along the route and were passively navigated past the next intersection with landmarks present. At the following intersection the landmarks were removed (see Figure 5-6) and the video was paused. The participants were required to indicate the direction of travel to continue along the route. As soon as participants responded they began the next trial, thus they did not receive feedback. There were 11 trials in total – one less than the number of intersections in the route since the last intersection has no following intersection. The trials were presented in a randomized order.

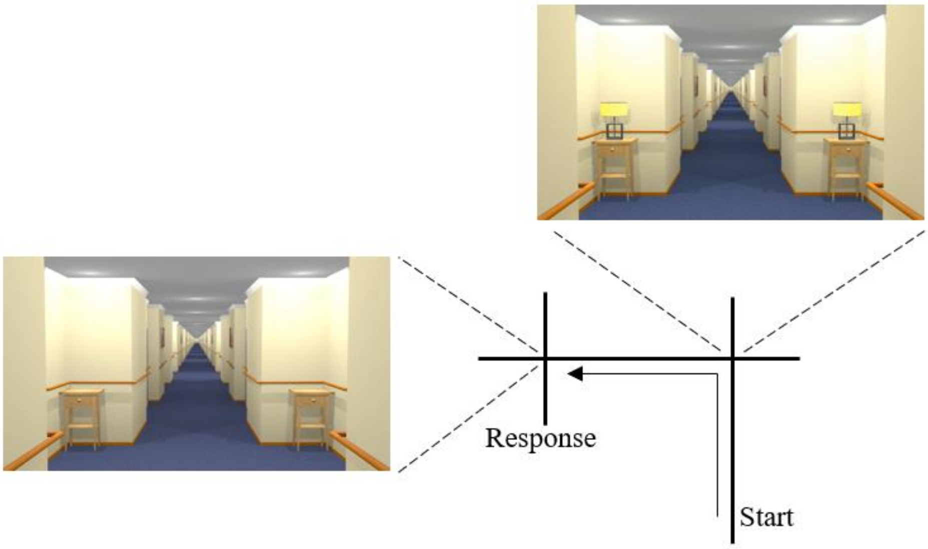

Figure 5-6 - Example Missing Landmark Task trial. Participants were passively navigated from a random start location along the route past an intersection with the landmark in place, to the following intersection where the landmark is missing. Here the video pauses and participants are required to indicate which direction continues along the route.

5.5.2.3 Procedure

The procedure was as described in Experiments 1 and 2 with the addition of the Missing Landmark Task. The Missing Landmark task was always conducted before the Landmark Sequence Task. This was done to avoid the sequence of landmarks participants created in the Landmark Sequence Task interfering with the Missing Landmark Task.

5.5.3 Results

5.5.3.1 Learning Phase

We analysed the number of learning trials taken to reach the performance criterion. As in Experiment 2, a Welch's two sample t-test revealed that the number of learning trials was significantly higher for older adults (mean = 4.61, SD = 2.50) than for than younger adults (mean = 3.37, SD = 1.54; see Figure 5-7), $t(34.48) = 2.10$, $p = .04$, Cohen's $d = 0.62$ (95% CI for Cohen's d: 1.19, 0.05). Specifically, there was a difference of 1.25 (95% CI: 2.44, 0.04).

To examine whether young participants were over-trained in Experiment 1, we analysed whether the mean number of trials taken to pass the learning phase was significantly different to 3 (the number of learning trials in Experiment 1). A one sample t-test revealed significantly more than 3 trials taken to pass the learning phase for older adults (mean: 4.61, $t(22) = 3.09$, $p = .005$, Cohen's $d = 0.64$, 95% CI for Cohen's d: 1.53, -0.24). There was no significant deviation from 3 trials for younger adults (mean: 3.37, $t(29) = 1.30$, $p < .203$, Cohen's $d = 0.24$, 95% CI for Cohen's d: 0.99, -0.51).

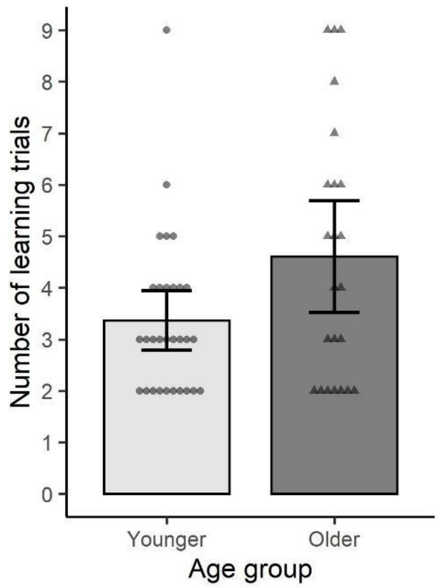

Figure 5-7 - Number of learning trials taken to reach criterion in the Learning Phase for the younger and older participant groups. Bars are group means, points are individual participants and error bars are 95% confidence intervals.

5.5.3.2 Test Phase

We conducted four GLMEs[8]; one for each test phase. Each model included age group (factor: younger or older; centred using sum contrast coding) and number of learning trials (centred around 0) as fixed effects. The outcome variable for all models was performance which is whether each response given was correct (1) or incorrect (0). Participant and stimulus (landmark) were included as random effects.

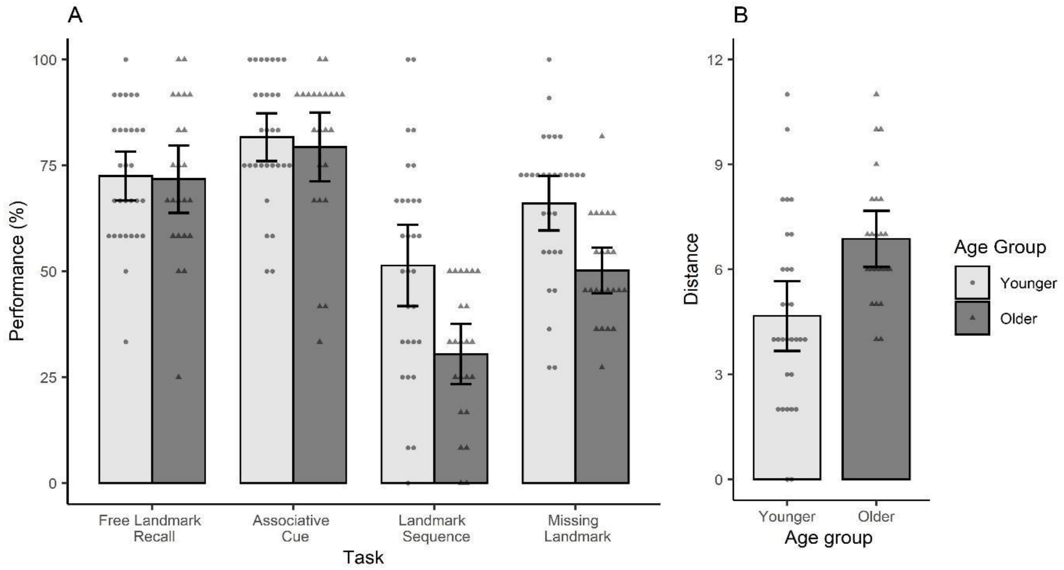

Figure 5-8 - (A) Average performance in each test task and (B) Levenshtein distances for the Landmark Sequence Task for the younger and older participant groups. Bars are group means, points are individual participants and error bars are 95% confidence intervals.

5.5.3.2.1 Free Landmark Recall Task

Estimates, standard errors, z-values, and p-values for the Free Landmark Recall model are reported in Table 5-14. As in Experiment 2, neither age group nor learning trials predicted performance (see Figure 5-8a) and there was no significant interaction.

[8] GLME model as expressed using the lme4 package:
glmer(performance ~ age_group * learning_trials + (1|participant) + (1|stimulus), data = data, family = binomial)

Table 5-14 - Coefficients from the Free Landmark Recall Task GLME analysis.

Fixed effect on Free Landmark Recall Task performance	Estimate	Std. error	z-value	p-value
Intercept	1.05	0.17	6.21	<.001*
Age group (older vs younger)	-0.01	0.13	-0.08	.936
Learning trials	-0.09	0.14	-0.64	.525
Age group (younger vs older) * learning trials	0.01	0.14	0.04	.967
*Significant p values (|p|<0.05)				

5.5.3.2.2 Associative Cue Task

Estimates, standard errors, z-values, and p-values for the Associative Cue Task model[9] are reported in Table 5-15. As in Experiment 2, neither age group nor learning trials predicted performance (see Figure 5-8a) and there was no significant interaction.

Table 5-15 - Coefficients from the Associative Cue Task GLME analysis.

Fixed effect on Associative Cue Task performance	Estimate	Std. error	z-value	p-value
Intercept	1.61	0.17	9.72	<.001
Age group (older vs younger)	0.08	0.16	0.46	.649
Learning trials	<0.01	0.16	0.03	.980
*Significant p values (|p|<0.05)				

[9] This model's fixed effects structure deviates from that of the other models in that the intercept only model would not converge with the fixed effect interaction of age group and learning trials. The model with the interaction would converge with the addition of a random by stimuli slope for learning trials. This model was not selected using our stated GLME procedure, but the fixed effects did not differ from the reported model and the interaction was non-significant.

5.5.3.2.3 Landmark Sequence Task

5.5.3.2.3.1 Absolute Scoring

Estimates, standard errors, z-values, and p-values for the Landmark Sequence Task model are reported in Table 5-16. As in Experiment 2, age group was a significant predictor of performance in the Landmark Sequence Task (see Figure 5-8a). Specifically, younger participants performed better than older participants. There was no main effect of learning trials. There was a significant age group (younger vs older) x learning trials interaction which shows that the size of the age group effect decreases as number of learning trials increases.

Table 5-16 - Coefficients from the Landmark Sequence Task GLME analysis.

Fixed effect on Landmark Sequence Task performance	Estimate	Std. error	z-value	p-value
Intercept	-0.54	0.16	-3.37	<.001*
Age group (older vs younger)	0.46	0.15	3.01	.003*
Learning trials	-0.16	0.16	-1.00	.316
Age group (younger vs older) * learning trials	-0.34	0.16	-2.10	.036*

*Significant p values (|p|<0.05)

5.5.3.2.3.2 Levenshtein Distance

A Welch's two sample t-test revealed that Levenshtein Distance was significantly higher for older adults (mean = 6.87, SD = 1.87) compared to that for younger adults (mean = 4.67, SD = 2.67), $t(50.63) = 3.53$, $p < .001$, Cohen's *d* = 0.94 (95% CI for Cohen's *d*: 1.52, 0.35). Specifically, there was a difference in Levenshtein Distance of 2.20 (95% CI: 3.46, 0.95; Figure 5-8b).

5.5.3.2.4 Missing Landmark Task

Estimates, standard errors, z-values, and p-values for the Missing Landmark Task are reported in Table 5-17 and show that age group was a significant predictor of performance on the Missing Landmark Task (see Figure 5-8). Specifically, younger participants performed better than older participants. There was no effect of learning trials and no significant interaction.

Table 5-17 - Coefficients from the Missing Landmark Task GLME analysis.

Fixed effect on Landmark Sequence Task performance	Estimate	Std. error	z-value	p-value
Intercept	0.33	0.10	3.47	<.001*
Age group (older vs younger)	0.31	0.09	3.35	<.001*
Learning trials	-0.08	0.10	-0.79	.430
Age group (younger vs older) * learning trials	-0.03	0.10	-0.32	.748

*Significant p values (|p|<0.05)

Since both the Landmark Sequence Task and the Missing Landmark Task are intended to measure the extent to which people know the sequence in which landmarks were encountered, we also analysed their relationship. There was a significant correlation between performance on the Landmark Sequence Task and the Missing Landmark Task (see Figure 5-9), *r* = 0.59, t(51) = 5.21, p < .001.

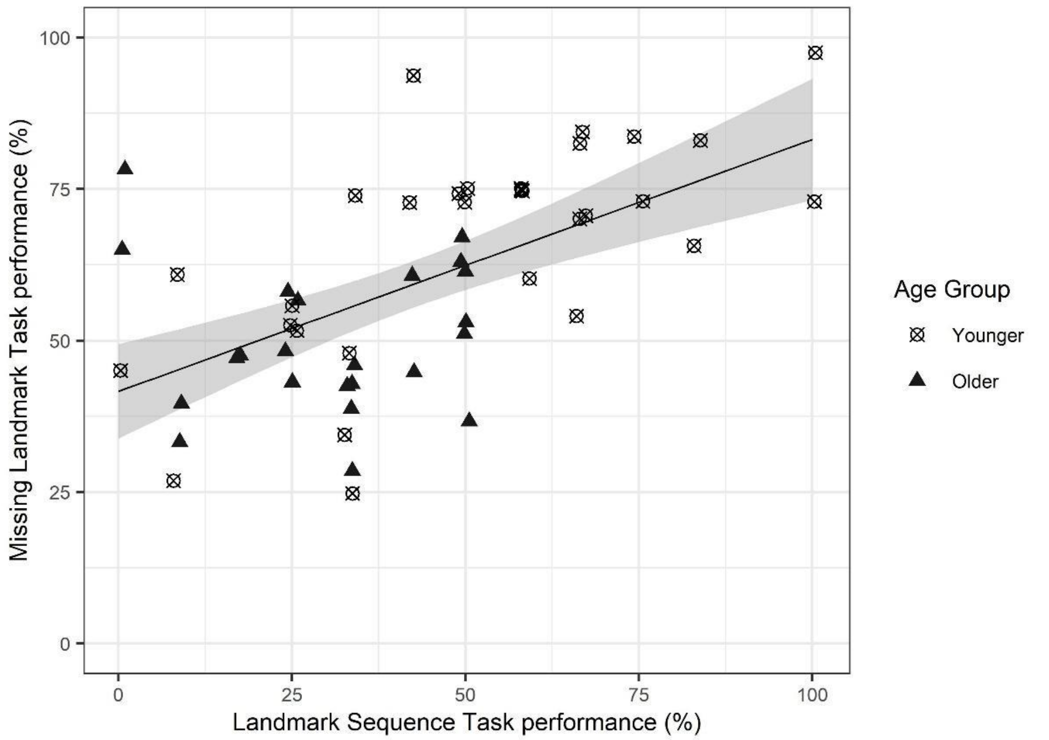

Figure 5-9 - Performance on the Landmark Sequence Task and the Missing Landmark Task for the older and younger participant groups. Data points are jittered for visibility and regression slope shows 95% confidence interval.

5.5.4 Discussion

Experiment 3 was a replication of Experiment 2 with the addition of the newly developed Missing Landmark Task. We replicated the results of Experiment 2, showing (i) that older adults took longer to learn the route, (ii) that they performed worse on the Landmark Sequence Task, and (iii) that performance in the Free Landmark Recall Task and the Associative Cue Task was similar between age groups. Finally, in the new Missing Landmark Task our older participants performed worse than our younger participants.

We developed the Missing Landmark task as a navigational test for landmark sequence knowledge. Impaired performance on the Missing Landmark Task demonstrates that older adults are more likely to become disoriented when landmark information is disrupted (in this case removed). We believe that this is a result of older adults forming weaker S-R-S associations during route learning. The correlation between the Missing Landmark Task and the Landmark Sequence Task provides evidence for the validity of the Landmark Sequence Task in assessing landmark sequence knowledge that is relevant for navigation.

Additionally, in this study the number of learning trials was not a predictor for any of the test tasks, as in Experiment 2. However, we found a sole interaction between the number of learning trials taken to reach criterion and age group on Landmark Sequence Task performance in this experiment. This interaction was not present in Experiment 2 and not found in the analysis for any of the other tasks across all experiments. Given that the age group x learning trials interaction appears unreliable and was only found in one model, we are cautious that it may be a false positive and therefore do not attribute much meaning to this finding.

5.6 General discussion

We conducted three experiments to investigate age related differences in the acquisition of route landmark knowledge after learning a route through either a fixed exposure or a flexible exposure learning procedure. Experiment 1 used a fixed exposure learning procedure in which participants navigated a route three times before being tested on their landmark knowledge. In Experiment 1 we replicated previous findings showing age-related differences in associative cue and landmark sequence knowledge (c.f. Head & Isom, 2010) but no difference between age groups on the ability to freely recall landmarks (c.f. Cushman et al., 2008). Experiment 2 used a flexible exposure learning procedure in which participants repeatedly navigated the route until they reached a 90% performance criterion. The results showed that older adults took more attempts to reach criterion than younger adults (c.f. Grzeschik et al., 2019; O'Malley et al., 2018). In contrast to Experiment 1, however, there was no difference between older and younger participants on the Associative Cue Task (c.f. O'Malley et al., 2018) while the age group difference on the Landmark Sequence Task remained (c.f. Allison & Head, 2017). Experiment 3 again used the flexible exposure learning procedure and replicated the findings from Experiment 2. In addition, participants performed the Missing Landmark Task which was designed to investigate the use of landmark sequence knowledge in a navigation context, in which older participants performed worse than younger participants.

As expected, older adults showed route learning deficits in all experiments. Specifically, in Experiment 1, older participants made more errors when navigating the route during learning (c.f. Barrash, 1994; Hartmeyer et al., 2017), showing that younger participants had learnt more about the route at the point they entered the test phase. In Experiments 2 and 3, older participants took more learning trials to reach the performance criterion (c.f. Grzeschik et al., 2019; O'Malley et al., 2018). Essentially, when given a limited amount of time to learn a route, older adults were less able to repeat the route than younger adults. However, when given the extra time/exposure that older adults required, they could learn and navigate a route to the same level as younger adults. We included number of learning trials as a predictor in our models for test phase performance. Number of exposures taken to pass learning had no predictive value on test phase performance across the experiments. This is important, since it indicates that participants who took longer to learn the route were not at an advantage in the test phase despite having had more exposure to the route than participants who completed the learning phase in fewer trials.

Greater time to learn the route in our study indicates that older adults take more time to acquire the knowledge required to repeat the route. Improved associative cue knowledge for the older adults in Experiment 2 compared to Experiment 1 suggests that they are relying on S-R learning, at least in part, to navigate successfully (Trullier et al., 1997; Waller & Lippa, 2007). This result is in line with the suggestion that reduced ability to navigate the route by the end of the learning phase under fixed exposure conditions are a result of age-related impairments in associative learning (Naveh-Benjamin, 2000; Zhong & Moffat, 2016). Indeed, our older participants showed the associative cue deficit with only three exposures to the route, and in the flexible exposure conditions they, on average, took more than three exposures to complete learning. Taken together, these findings demonstrate that under the fixed exposure learning conditions, older adults are under-trained when compared to the younger participants on the content of their route knowledge.

Under the flexible exposure learning condition, the associative cue knowledge of the older adults in our study improved to the same levels as that of the younger adults, which is consistent with Grzeschik et al. (2019) and O'Malley et al. (2018), but conflicts with results by Allison and Head (2017). Whilst the studies by Grzeschik et al. (2019) and O'Malley et al. (2018) used very short routes with four intersections, our study demonstrates that older adults are able to learn and use S-R associations to navigate longer routes (at least up to 12 intersections). In the study by Allison and Head (2017) the older adults performed at ~71% in the associative cue test, which is not dissimilar to our older adults in Experiment 2 (70.37%). The younger adults in their study, however, performed significantly higher (at ~86%) and numerically higher than our younger adults in Experiment 2 (75.57%). Since the learning procedure used by Allison and Head (2017) required participants to complete a minimum number of learning sessions even if they already could navigate the route, it is possible that their younger adults were over-trained, resulting in inflated associative cue performance. Our younger adults in Experiment 2, in contrast, were not over-trained as the learning phase was terminated as soon as they reached the performance criterion, similar to the procedures by Grzeschik et al. (2019) and O'Malley et al. (2018). This explanation could account for the conflict between our study and Allison and Head (2017) regarding the presence of age-related differences on the associative cue task.

Our findings suggest that older adults were able to overcome the deficit in associating landmarks and directions if they are given enough time in the learning phase. It is possible that cognitive resource limitations experienced by older adults (Craik & Byrd, 1982; Park & Festini, 2017) contributes to the associative learning deficit usually observed under fixed learning conditions (Craik, 2012; Naveh-Benjamin & Kilb, 2014). With our flexible learning procedure, the older navigators were able to compensate for declining resources through longer learning times to acquire the S-R associations. This explanation is further supported by the between experiment interaction showing that the older adult age group particularly benefited from the change in learning procedure with regards to associative cue performance. Indeed, the Associative Cue Task performance of younger adults was nearly identical in Experiments 1 and 2 despite the differences in learning procedure. Overcoming the associative learning deficit through additional exposure could be due to attentional depletion or attentional prioritisation (Naveh-Benjamin & Kilb, 2014).

Attentional depletion refers to the notion that cognitive resources are divided between multiple, concurrent learning streams such as the encoding of items and the binding of information to those items. For older adults, the to-be-divided resources are more limited compared to younger adults and thus the quantity and quality of encoding is reduced (Craik, 2012; Craik et al., 2010). Overcoming attentional depletion with additional learning time would involve a gradual increase in all the different types of knowledge being acquired (Naveh-Benjamin et al., 2004). Such concurrent and integrated acquisition of spatial knowledge has been demonstrated for younger adults (Ishikawa & Montello, 2006; Montello, 1998; Schinazi & Epstein, 2010). However, this was not the case for our older adults, for whom we observed a large increase in associative cue knowledge between Experiments 1 and 2, with no changes in landmark memory or sequence knowledge. Therefore, attentional depletion does not account for the pattern of results observed in this study.

Instead, our findings are more in line with attentional prioritisation, which suggests that cognitive resources are directed towards the different components of the task one after the other, in order of priority. For route learning, Zhong and Moffat (2016) suggested that older adults first prioritise the learning of landmark identities, whilst neglecting to bind directional information to those landmarks. This pattern is also evident in our study where older adults showed good knowledge for landmark identities which was already formed during the three learning trials provided in Experiment 1, but they showed relatively poor associative cue knowledge. During the additional learning trials in Experiments 2 and 3, older participants have then been able to direct their resources towards the learning of S-R associations to overcome this deficit. We believe this explanation is plausible given that dual task paradigms have shown that modulation of attentional engagement during route learning is not only preserved for older adults, but they show engagement of a greater proportion of their attention at intersections where they had to associate landmarks with directional information compared to younger adults (Hartmeyer et al., 2017; Hilton et al., 2019). Learning landmark identities before learning associative information is also in line with frameworks of spatial knowledge acquisition which state that landmarks are learned first and before associative cue or sequence knowledge is acquired (Chrastil, 2013; Foo et al., 2007; Siegel & White, 1975). Indeed, parahippocampal representations of landmarks have been shown to form after only a single exposure in younger adults (Janzen et al., 2007).

Not all aspects of route knowledge were equated across age groups in our study, however. Under the flexible learning procedures used in Experiments 2 and 3, we still observed age-related deficits in landmark sequence knowledge. This is in contrast to findings of O'Malley et al. (2018), who did not report differences between age groups. Their participants, however, were aware of the up-coming tests and therefore could amend their learning strategy to acquire such knowledge (Naveh-Benjamin et al., 2007), which is plausible considering they used only 4 landmarks. Indeed, the younger participants in their study also performed (82.81%) much better than our younger participants (47.99% - 51.39%).

Following the attentional prioritisation explanation, the results of the landmark sequence task indicate that older adults prioritised the learning of associative cue knowledge over sequence learning, once the initial encoding of landmark identities was completed. This order is intuitive, since recalling cued directions alone would be enough to repeat the route in our environment (as long as landmarks are unique and not repeated along the route, see Strickrodt et al., 2015). Importantly, this finding demonstrates that even when older navigators have learned a route successfully, the overall content of their route knowledge is impoverished compared to the richer representation held by younger navigators. Attentional prioritisation seems to allow older navigators to acquire the essential knowledge to successfully complete the basic task in the learning session, which is repeating the exact same route (Wiener et al., 2012). However, the cost of such a strategy is reduced learning of wider information about the environment.

Although sequence knowledge was not required to repeat the route during the learning phase, we still expected navigators to acquire some knowledge about the order of landmarks. This is in line with more general sequence learning studies, which show that even in the absence of explicit instruction or requirement to learn a sequence, repeated exposures are still associated with sequence learning (Oberauer & Meyer, 2009). The incidental acquisition of sequence information has also been shown to be impaired in older adults which, in line with our interpretation, is suggested to be due to differences in cognitive capacity between age groups (Vandenbossche et al., 2014). For route navigation the learning of landmark sequence knowledge may not be vital for the repeating of a route, but it would enable behaviours such as response priming (Schinazi & Epstein, 2010; Schweizer et al., 1998) and error monitoring. We did not analyse such measures in our study so although we find that older adults can repeat a route without well-formed sequence knowledge, it is possible that younger adults would have these other advantages over older adults at the point of successful navigation.

Note that environments in the real world are dynamic and ever changing, and that beside route repetition, there are several other navigation tasks that humans solve in daily life

(Wiener et al., 2009). Rich representations of environments support flexibility in navigation behaviour by affording the use of different navigation strategies and the solution of different tasks and therefore also help to deal with environmental changes. We introduced the missing landmark task in Experiment 3, which involved navigating past an intersection to the following intersection, at which point the participants were required to decide which direction the route continued in. The latter intersection had the landmark removed, requiring participants to use information about the preceding intersection to solve the task. We found that older adults performed worse on this task than younger adults. This deficit cannot be explained by either lack of familiarity with the route, since all participants underwent flexible exposure learning, or by poor landmark memory or by poor associative cue knowledge since age groups performed similarly in those tests. Instead, the impaired performance of older adults can be explained by the lack of sequence knowledge, as supported by the significant correlation between sequence task and missing landmark task performance.

The missing landmark task results highlight that even when older adults are able to navigate a familiar route, the flexibility in their navigation behaviour is reduced by their limited route knowledge. For locations frequented by an older population, such as hospitals, shopping centres or care facilities, it is important to understand that altering features may significantly affect the navigability for older adults, even if they seem familiar with the environment. A question for future research is whether older adults would be able to overcome the sequence knowledge deficit in the same way as they overcame the associative cue deficit in our study. Our explanation of attentional prioritisation would suggest that this might be achieved through changing the relevance of sequence knowledge during learning (as in O'Malley et al., 2018), or possibly via extra learning trials after successful navigation is achieved. Alternatively, it is possible that older adults would continue to struggle to intentionally acquire landmark sequence knowledge, as shown by more general sequence learning paradigms (Golomb et al., 2008; Kahana et al., 2002).

The findings of this study support Vakil and Agmon-Ashkenazi (1997) suggestion that age-related differences in learning rate of information should be considered alongside differences in baseline performance. In our study, performance after the fixed learning procedure can be considered the baseline, where immediate age-related deficits emerge in the learning of specific information. We then demonstrate that accounting for learning rate reveals dissociated development of these baseline differences. Specifically, our older adults eventually learned the associative cue information to the same performance levels as younger adults, whilst their landmark sequence knowledge still showed age-related deficits.

The flexible exposure learning procedure examined in this study may be a means by which learning research in other domains can account for age-related differences in learning-rates.

In summary, this study has replicated existing findings that under fixed exposure route learning conditions, older adults have preserved memory for landmarks but worse associative cue and sequence knowledge compared to younger adults. We then demonstrate that under a flexible exposure learning procedure, the associative cue deficit is attenuated, whilst the sequence knowledge deficit remains. We suggest that such a pattern of findings is a result of older adults prioritising their limited cognitive resources to learn in a piecemeal manner, compared to the quicker and more simultaneous learning conducted by younger participants. Attentional prioritisation leads older adults to first encode landmark identities without the association of directional information, and then to later acquire directional information that is not linked to the adjacent locations. Importantly, the cost of such a strategy is reduced flexibility in the final route representation, namely a lack of sequence knowledge even after successful navigation is achieved, which results in increased likelihood of disorientation when faced with other navigation tasks along the same route.

5.7 References

Allison, S., & Head, D. (2017). Route repetition and route reversal: Effects of age and encoding method. *Psychology and Aging*, *32*(3), 220–231. https://doi.org/10.1037/pag0000170

Barrash, J. (1994). Age-Related Decline in Route Learning Ability. *Developmental Neuropsychology*, *10*(3), 189–201. https://doi.org/10.1080/87565649409540578

Bates, D. M., Kliegl, R., Vasishth, S., & Baayen, H. (2018). Parsimonious mixed models. *ArXiv E-Print*.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/doi: 10.18637/jss.v067.i01

Brown, L. A. (2016). Spatial-sequential working memory in younger and older adults: Age predicts backward recall performance within both age groups. *Frontiers in Psychology*. https://doi.org/10.3389/fpsyg.2016.01514

Chrastil, E. R. (2013). Neural evidence supports a novel framework for spatial navigation. *Psychonomic Bulletin and Review*, *20*(2), 208–227. https://doi.org/10.3758/s13423-012-0351-6

Craig, M., Wolbers, T., Harris, M. A., Hauff, P., Della Sala, S., & Dewar, M. (2016). Comparable rest-related promotion of spatial memory consolidation in younger and older adults. *Neurobiology of Aging*. https://doi.org/10.1016/j.neurobiolaging.2016.08.007

Craik, F. I. M. (2012). Remembering items and their contexts: Effects of ageing and divided attention. In *Handbook of Binding and Memory: Perspectives from Cognitive*

Neuroscience. https://doi.org/10.1093/acprof:oso/9780198529675.003.0023

Craik, F. I. M., & Byrd, M. (1982). Aging and Cognitive Deficits. In *Aging and Cognitive Processes*. https://doi.org/10.1007/978-1-4684-4178-9_11

Craik, F. I. M., Luo, L., & Sakuta, Y. (2010). Effects of Aging and Divided Attention on Memory for Items and Their Contexts. *Psychology and Aging*, *25*(4), 968–979. https://doi.org/10.1037/a0020276

Cushman, L. A., Duffy, C. J., Stein, K., & Duffy, C. J. (2008). Virtual reality identifies navigational defects in Alzheimer disease and cognitive aging. *Nature Clinical Practice Neurology*, *4*(12), 638–639. https://doi.org/10.1038/ncpneuro0929

Ebaid, D., Crewther, S. G., MacCalman, K., Brown, A., & Crewther, D. P. (2017). Cognitive processing speed across the lifespan: Beyond the influence of motor speed. *Frontiers in Aging Neuroscience*. https://doi.org/10.3389/fnagi.2017.00062

Foo, P., Duchon, A., Warren, W. H., & Tarr, M. J. (2007). Humans do not switch between path knowledge and landmarks when learning a new environment. In *Psychological Research*. https://doi.org/10.1007/s00426-006-0080-4

Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- Versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning Memory and Cognition*. https://doi.org/10.1037/0278-7393.31.2.195

Golomb, J. D., Peelle, J. E., Addis, K. M., Kahana, M. J., & Wingfield, A. (2008). Effects of adult aging on utilization of temporal and semantic associations during free and serial recall. *Memory and Cognition*, *36*(5), 947–956. https://doi.org/10.3758/MC.36.5.947

Grzeschik, R., Conroy-Dalton, R., Innes, A., Shanker, S., & Wiener, J. M. (2019). The contribution of visual attention and declining verbal memory abilities to age-related route learning deficits. *Cognition*, *187*(July 2018), 50–61. https://doi.org/10.1016/j.cognition.2019.02.012

Grzeschik, R., Hilton, C., Dalton, R. C., Konovalova, I., Cotterill, E., Innes, A., & Wiener, J. M. (2020). From repeating routes to planning novel routes : the impact of landmarks and ageing on route integration and cognitive mapping. *Psychological Research*, *0123456789*. https://doi.org/10.1007/s00426-020-01401-5

Hartmeyer, S., Grzeschik, R., Wolbers, T., & Wiener, J. M. (2017). The effects of attentional engagement on route learning performance in a virtual environment: An aging study. *Frontiers in Aging Neuroscience*, *9*(JUL). https://doi.org/10.3389/fnagi.2017.00235

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research*, *209*(1), 49–58. https://doi.org/10.1016/j.bbr.2010.01.012

Hegarty, M., & Waller, D. A. (2009). Individual Differences in Spatial Abilities. In *The Cambridge Handbook of Visuospatial Thinking*. https://doi.org/10.1017/cbo9780511610448.005

Hilton, C., Miellet, S., Slattery, T. J., & Wiener, J. (2019). Are age-related deficits in route learning related to control of visual attention? *Psychological Research*, *0*(0), 0. https://doi.org/10.1007/s00426-019-01159-5

Ishikawa, T., & Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive Psychology*. https://doi.org/10.1016/j.cogpsych.2005.08.003

Janzen, G., Wagensveld, B., & Van Turennout, M. (2007). Neural representation of navigational relevance is rapidly induced and long lasting. *Cerebral Cortex*, *17*(4), 975–981. https://doi.org/10.1093/cercor/bhl008

Kahana, M. J., Howard, M. W., Zaromb, F., & Wingfield, A. (2002). Age Dissociates Recency and Lag Recency Effects in Free Recall. *Journal of Experimental Psychology: Learning Memory and Cognition*, *28*(3), 530–540. https://doi.org/10.1037/0278-7393.28.3.530

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers, T. (2017). The Aging Navigational System. *Neuron*, *95*(5), 1019–1035. https://doi.org/10.1016/j.neuron.2017.06.037

Levenshtein, V. (1966). Binary codes capable of correcting deletions, insertions, and reversals. *Soviet Physics Doklady*.

Lithfous, S., Dufour, A., & Després, O. (2013). Spatial navigation in normal aging and the prodromal stage of Alzheimer's disease: Insights from imaging and behavioral studies. In *Ageing Research Reviews*. https://doi.org/10.1016/j.arr.2012.04.007

Liu, I., Levy, R. M., Barton, J. J. S., & Iaria, G. (2011). Age and gender differences in various topographical orientation strategies. *Brain Research*. https://doi.org/10.1016/j.brainres.2011.07.005

Luis, C., Keegan, A., & Mullan, M. (2009). Cross validation of the Montreal Cognitive Assessment in community dwelling older adults residing in the Southeastern US. *International Journal of Geriatric Psychiatry*, *24*(2), 197–201.

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, *44*(2), 314–324. https://doi.org/10.3758/s13428-011-0168-7

Montello, D. R. (1998). A new framework for understanding thr acquisition of spatial knowledge in large-scale environments. *Spatial and Temporal Reasoning in Geographic Information Systems*. https://doi.org/10.1088/1748-6041/6/2/025001

Nasreddine, Z. S., Phillips, N. A., Bedirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L., & Chertkow, H. (2005). The Montreal cognitive assessment, MoCA: a brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, *53*(4), 695–699.

Naveh-Benjamin, M. (2000). Adult Age Differences in Memory Performance: Tests of an Associative Deficit Hypothesis. *Journal of Experimental Psychology: Learning Memory and Cognition*, *26*(5), 1170–1187. https://doi.org/10.1037/0278-7393.26.5.1170

Naveh-Benjamin, M., Brav, T. K., & Levy, O. (2007). The associative memory deficit of older adults: The role of strategy utilization. *Psychology and Aging*. https://doi.org/10.1037/0882-7974.22.1.202

Naveh-Benjamin, M., Guez, J., Craik, F. I. M., & Kreuger, S. (2005). Divided attention in younger and older adults: Effects of strategy and relatedness on memory performance and secondary task costs. *Journal of Experimental Psychology: Learning Memory and Cognition*. https://doi.org/10.1037/0278-7393.31.3.520

Naveh-Benjamin, M., Guez, J., & Shulman, S. (2004). Older adults' associative deficit in episodic memory: Assessing the role of decline in attentional resources. *Psychonomic Bulletin and Review*, *11*(6), 1067–1073. https://doi.org/10.3758/BF03196738

Naveh-Benjamin, M., & Kilb, A. (2014). Age-related differences in associative memory: The role of sensory decline. *Psychology and Aging*. https://doi.org/10.1037/a0037138

O'Malley, M., Innes, A., Muir, S., & Wiener, J. M. (2018). "All the corridors are the same": A qualitative study of the orientation experiences and design preferences of UK older adults living in a communal retirement development. *Ageing and Society*, *38*(9), 1791–1816. https://doi.org/10.1017/S0144686X17000277

O'Malley, M., Innes, A., & Wiener, J. M. (2018). How do we get there? Effects of cognitive aging on route memory. *Memory and Cognition*, *46*(2), 274–284. https://doi.org/10.3758/s13421-017-0763-7

Oberauer, K., & Meyer, N. (2009). The contributions of encoding, retention, and recall to the Hebb effect. *Memory*, *17*(7), 774–781. https://doi.org/10.1080/09658210903107861

Park, D. C. (2000). The basic mechanism, accounting for age-related decline in cognitive function. *Cognitive Aging: A Primer*.

Park, D. C., & Festini, S. B. (2017). Theories of memory and aging: A look at the past and a glimpse of the future. In *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*. https://doi.org/10.1093/geronb/gbw066

R Core Team. (2019). R: A language and environment for statistical computing. In *R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.*

Salthouse, T. A. (1996). The Processing-Speed Theory of Adult Age Differences in Cognition. *Psychological Review*. https://doi.org/10.1037/0033-295X.103.3.403

Schinazi, V. R., & Epstein, R. A. (2010). Neural correlates of real-world route learning. *NeuroImage*, *53*(2), 725–735. https://doi.org/10.1016/j.neuroimage.2010.06.065

Schweizer, K., Herrmann, T., Janzen, G., & Katz, S. (1998). *The Route Direction Effect and its Constraints*. https://doi.org/10.1007/3-540-69342-4_2

Siegel, A. W., & White, S. H. (1975). The development of spatial representations of large-scale environments. *Advances in Child Development and Behavior*. https://doi.org/10.1016/S0065-2407(08)60007-5

Strickrodt, M., O'Malley, M., & Wiener, J. M. (2015). This place looks familiar-how navigators distinguish places with ambiguous landmark objects when learning novel routes. *Frontiers in Psychology*, *6*(DEC), 1–12. https://doi.org/10.3389/fpsyg.2015.01936

Trullier, O., Wiener, S. I., Berthoz, A., & Meyer, J. A. (1997). Biologically based artificial navigation systems: Review and prospects. *Progress in Neurobiology*. https://doi.org/10.1016/S0301-0082(96)00060-3

Turcotte, J., Gagnon, S., & Poirier, M. (2005). The effect of old age on the learning of supraspan sequences. *Psychology and Aging*, *20*(2), 251–260. https://doi.org/10.1037/0882-7974.20.2.251

Vakil, E., & Agmon-Ashkenazi, D. (1997). Baseline performance and learning rate of procedural and declarative memory tasks: Younger versus older adults. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, *52*(5), 229–234.

https://doi.org/10.1093/geronb/52B.5.P229

van der Loo, M. P. J. (2014). The stringdist package for approximate string matching. *R Journal*. https://doi.org/10.32614/rj-2014-011

Vandenbossche, J., Coomans, D., Homblé, K., & Deroost, N. (2014). The effect of cognitive aging on implicit sequence learning and dual tasking. *Frontiers in Psychology*, *5*(FEB), 1–8. https://doi.org/10.3389/fpsyg.2014.00154

Waldron-Perrine, B., & Axelrod, B. N. (2012). Determining an appropriate cutting score for indication of impairment on the Montreal Cognitive Assessment. *International Journal of Geriatric Psychiatry*, *27*(11), 1189–1194. https://doi.org/10.1002/gps.3768

Waller, D., & Lippa, Y. (2007). Landmarks as beacons and associative cues. *Memory & Cognition*, *35*(5), 910–924. https://doi.org/10.3758/BF03193465

Ward, G., Tan, L., & Grenfell-Essam, R. (2010). Examining the relationship between free recall and immediate serial recall: The effects of list length and output order. *Journal of Experimental Psychology: Learning Memory and Cognition*, *36*(5), 1207–1241. https://doi.org/10.1037/a0020122

Wechsler, D. (2008). Wechsler Adult Intelligence Scale - Fourth Edition: Administration and Scoring Manual. In *Psychological Corporation*.

Weisberg, S. M., Schinazi, V. R., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2014). Variations in cognitive maps: Understanding individual differences in navigation. *Journal of Experimental Psychology: Learning Memory and Cognition*. https://doi.org/10.1037/a0035261

Wiener, J. M., Büchner, S. J., & Hölscher, C. (2009). Taxonomy of human wayfinding tasks: A knowledge-based approach. *Spatial Cognition and Computation*, *9*(2), 152–165. https://doi.org/10.1080/13875860902906496

Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive bias for extrahippocampal navigation strategies in aging humans. *Journal of Neuroscience*, *33*(14), 6012–6017. https://doi.org/10.1523/JNEUROSCI.0717-12.2013

Wiener, J. M., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: Effects of cognitive aging. *Frontiers in Aging Neuroscience*, *4*(MAY), 1–7. https://doi.org/10.3389/fnagi.2012.00007

Wilkniss, S. M., Korol, D. L., Gold, P. E., Jones, M. G., & Manning, C. A. (1997). Age-related differences in an ecologically based study of route learning. *Psychology and Aging*. https://doi.org/10.1037/0882-7974.12.2.372

Zhong, J. Y., & Moffat, S. D. (2016). Age-related differences in associative learning of landmarks and heading directions in a virtual navigation task. *Frontiers in Aging Neuroscience*, *8*(MAY), 1–11. https://doi.org/10.3389/fnagi.2016.00122

Chapter 6

Serial memory for landmarks encountered during route navigation

6.1 Abstract

The present study is the first to show similarities between route learning and classical tests of serial order memory. Here, we investigated serial memory for landmarks in a route learning task, in younger and older adults. We re-analysed data from a route learning task with 12 landmarks, reported by Hilton et al. (under review). Participants (88 younger and 77 older) learned a route using either a Fixed Learning (3 exposures to the route) or Flexible Learning (repeated exposures until successful navigation was achieved) procedure. Following route learning, participants completed Immediate Free Recall (IFR) and Free Reconstruction of Order (Free RoO) of the landmarks. We show clear acquisition of sequence memory for landmarks for both age groups, with Free RoO producing a bowed serial position curve. IFR produced recency effects but no primacy effects in fixed learning, with recency reduced following flexible learning for both age groups. Younger adults displayed a primacy bias for the first item recalled in both learning conditions, as did the older adults in the flexible learning condition. In contrast, older adults displayed a recency bias in the fixed learning condition. Findings are broadly consistent with results from typical short-term list learning procedures and support the universality of sequence learning effects, which we demonstrate are generalisable to a navigation context.

6.2 Introduction

Recall of a sequence is typically characterised by a bowed serial position function in which a memory advantage is observed for the first (primacy) and last (recency) item in the sequence. The ubiquity of this serial position function has been hypothesised to represent a general underlying feature of memory (e.g. Surprenant & Neath, 2006). The present study examines sequence knowledge during a route learning paradigm. Specifically, whether the canonical patterns of performance found with conventional sequence memory tasks can be generalised to learning of landmarks during navigation, despite the different characteristics of the two tasks.

Earlier research on serial position functions suggested that the shape of the function differs depending on the modality of stimuli being recalled (e.g. Phillips & Christie, 1977). These differences have subsequently been shown to be artefacts of methodological differences between tasks (e.g. Guérard & Tremblay, 2008; Ward et al., 2005). Specifically, when the same task demands were applied to different stimulus types, the serial position functions were qualitatively equivalent. This observation led Ward et al. (2005) to argue that the serial position function is task rather than modality dependent.

Bowed functions are not confined to episodic memory and are generalisable to the recall of semantic information. For example, when participants are instructed to order a list of category members on a given dimension, such as US presidents (Roediger & DeSoto, 2014), hymn verses (Maylor, 2002), age of actors (Kelley, Neath, & Surprenant, 2015) and books in a series (Kelley, Neath, & Surprenant, 2013), primacy and recency effects are evident. Moreover, Neath et al. (2016) instructed participants to order US States upon a range of dimensions (i.e. area in km^2, year of statehood, and population) and found that order reconstruction accuracy was determined not by the States per se but rather by where these States were positioned on the different dimensions. That is, greater accuracy was observed for the boundary items of that specific category list, regardless of the performance for those items in other lists. These results are consistent with the proposal that primacy and recency are general features of lists due to the first and last (i.e. boundary) items being more distinctive by virtue of having positional competitors on only one side (Kelley et al., 2015).

These canonical serial position functions are also found across age groups. Whilst age can produce overall differences in serial recall accuracy, bowed functions have been demonstrated in both younger (Koppenol-Gonzalez, Bouwmeester, & Vermunt, 2014) and older adults (Elliott et al., 2011; Maylor et al., 1999; Surprenant, 2007). These findings indicate that the qualitative effects of boundary items remain, even though recall accuracy can be quantitatively affected by ageing.

Serial position functions are commonly observed across a range of stimulus types using Immediate Free Recall (IFR; e.g. Cortis et al., 2015; Spurgeon et al., 2014) and Reconstruction of Order (RoO; e.g. Avons, 1998; Guérard & Tremblay, 2008; Johnson et al., 2016; Parmentier & Jones, 2000; Ward et al., 2005) tasks. IFR, particularly with longer lists (>10), typically produces a serial position function with strong recency and some primacy (e.g. Grenfell-Essam et al., 2013; Grenfell-Essam & Ward, 2012; Murdock, 1962; Ward et al., 2010). Similarly, for RoO, where output order is unconstrained (i.e. Free RoO), the serial position function exhibits primacy and recency (e.g. Lewandowsky et al., 2008, 2009; Neath, 1997; although recency was stronger for longer lists, see Ward et al., 2010). For IFR, the order in which items are outputted is contingent on list length, with latter list items outputted first for longer lists (e.g. Cortis et al., 2015; Grenfell-Essam & Ward, 2012; Grenfell-Essam et al., 2013; Spurgeon et al., 2014; Ward et al., 2010).

Recalled sequences can also be assessed using conditionalised response probabilities (CRP; see Kahana et al., 2007; Ward et al., 2010). CRPs assess response transitions for each successive pair of items (i.e. the lag in transition from the position of the first and second item in the recalled pair, where a lag of +1 indicates recall of successive items in the original sequence). The resultant CRP-lag function typically exhibits a peak at +1 lag, with an asymmetric lag recency effect illustrating more transitions for adjacent positions (i.e. transpositions close to the correct position are more frequent indicating some vague yet inexact positional knowledge) and a greater tendency to transition forward. One benefit of examining sequence CRPs is that they provide a measure of relative order memory, as opposed to serial position functions which examine absolute order knowledge (see Schoo et al., 2014 on the importance of distinguishing relative and absolute measures of order memory).

In this study, we examined the extent to which route learning produces the characteristic bowed function observed in serial memory and whether this function is affected by age. When traversing routes, navigators encounter landmarks in a sequence and need to perform actions at these landmarks (such as turning right at gas station and turning left at red house). Whilst it is possible that such landmark triggered responses (or associative cues; Waller & Lippa, 2007) could be used in isolation (i.e. independent of other landmark cues), there is a benefit to learning the sequence in which landmarks are encountered. For example, forthcoming navigational decisions are primed thus improving the efficiency of navigation (Schinazi & Epstein, 2010). Moreover, without any sequence knowledge, it would be difficult, if not impossible, to distinguish situations that feature similar or identical landmarks (Strickrodt, O'Malley, & Wiener, 2015).

The present study is a re-analysis of data presented in Hilton, Johnson, Slattery, Miellet, and Wiener (under review). In that study, younger and older participants were presented with a to-be-remembered route comprising of 12 decision-points, each containing a unique landmark. In Experiment 1, participants received three exposures to the route and in Experiments 2 and 3, they were exposed to the route repeatedly until they achieved at least 90% accuracy in repeating the movement decisions along the route. At test, participants performed (1) IFR of all the landmarks from the route, (2) an Associative Cue Task in which they were shown the 12 landmark in a randomised order and were required to indicate the direction of travel (right, left, and straight), and (3) Free RoO wherein participants were given the landmarks and required to position them in the order they were encountered along the routes. Performance of younger and older participants did not differ in their free recall of landmarks. Older adults were poorer at the Associative Cue Task (Experiment 1); however age differences were removed when participants were trained to criterion in Experiments 2 and 3. This finding highlights the differences in rate of route knowledge acquisition between age groups. Older participants also performed worse on the Free RoO task, consistent with the proposition that older adults generally learn less about the order in which landmarks are encountered (Allison & Head, 2017; Head & Isom, 2010).

The aim of this study was to investigate the extent to which serial memory effects commonly seen in list learning paradigms also featured in our route navigation experiment, despite the following clear methodological differences between the paradigms. First, list learning tasks include the explicit instruction for participants to learn the items in the list, whereas there was no explicit instruction to learn the landmarks or their sequence in our route learning task. Second, in a list learning procedure, participants will typically receive a single exposure to the to-be-remembered sequence (although not always, see Hebb, 1961) whereas in our route learning task participants received multiple (2-9) exposures. Third, the list learning procedure requires short-term retention (with trials typically lasting < 30s). In contrast, the route learning trials took several minutes per presentation. Therefore, the retention interval between presentation and test of the route was considerably longer. Notwithstanding these differences, we here examine whether sequence memory for landmarks encountered along a route exhibits some of the proposed canonical features of list memory (Kelley et al., 2015). Specifically, we assess serial position effects for IFR and Free RoO, output order effects for IFR, and conditionalised response probabilities for Free RoO.

6.3 Method

In this study we performed additional analyses on the data collected by Hilton et al. (under review). That study comprised of three experiments each containing a learning phase, followed by a series of tasks. For the present re-analysis, we focused on data from the Immediate Free Recall (IFR) and Free Reconstruction of Order (Free RoO) tasks. There were two separate learning protocols in the study which are explained in the Learning Phase section of the Methods in this paper. Experiment 1 involved a ‘Fixed Learning’ protocol (3 exposures of the route) whereas Experiments 2 and 3 employed a ‘Flexible Learning’ protocol wherein participants were trained to criterion (90%). In Flexible Learning, participants were exposed repeatedly to the route until they gave 90% of the directions correctly, at which point the participants received no more exposures to the route and moved onto the test phase. Due to their procedural similarities, and to increase statistical power, data from

Experiments 2 and 3 were combined for this study into one Flexible Learning condition and were compared against the Fixed Learning condition as a between groups design.

6.3.1 Participants

In the Fixed Learning condition there were 29 younger participants and 27 older participants. In the Flexible Learning condition there were 59 young and 50 old participants. Older participants were screened for mild cognitive impairment using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005). All older participants scored above the MoCA cut-off score of 23 (Luis, Keegan, & Mullan, 2009; Waldron-Perrine & Axelrod, 2012). See Table 6-1 for participant demographic information. Ethical approval was granted by the Bournemouth University Research Ethics Panel and written informed consent was gained from all participants who either received course credits or an honorarium.

Table 6-1 - Participant demographics

	Sex		Age		MoCA	
		n	Mean	SD	Mean	SD
Fixed Learning Condition						
Younger	Female	16	22.38	4.84		
	Male	13	19.69	1.11		
Older	Female	14	71.14	5.76	26.35	2.06
	Male	13	70.77	3.39	26.08	2.22
Flexible Learning Condition						
Younger	Female	30	22.00	3.70		
	Male	29	22.97	4.46		
Older	Female	27	71.04	4.79	27.00	2.11
	Male	23	71.83	6.08	26.74	2.05

6.3.2 Design

A 3-factor (2x2x12) mixed multifactorial design was employed. The between groups independent variables were age group (2 levels: younger and older) and learning condition (2 levels: Fixed Learning and Flexible Learning), and the within groups variable was serial position (1 – 12). The two dependent measures were serial recall accuracy for IFR and Free RoO.

6.3.3 Learning Phase

Participants were instructed to learn a route though a virtual environment. The route consisted of 12 intersections (4 left turns, 4 right turns, and 4 straight ahead). Each intersection had a pair of identical landmarks. The landmarks at each intersection were unique from all other intersections and only one pair of landmarks could be seen at a time (see Figure 6-1). The order of landmarks and route directions were randomised for every participant. They were shown videos of passive transportation along the route. At each intersection, the footage was paused and participants were required to indicate the direction of travel (right, left, straight) required to continue along the route. Transportation resumed once a response was given thus providing immediate feedback.

Figure 6-1 - A screenshot of an intersection in the environment

In the Fixed Learning condition participants navigated the route three times during the Learning Phase. Participants in the Flexible Learning condition navigated the route repeatedly until they reached a 90% performance criterion (i.e. they responded correctly at 11 out of the 12 intersections). Once participants navigated the route with at least 90% correct responses, the Learning Phase was terminated.

6.3.4 Immediate Free Recall (IFR)

At test, participants were asked to verbally free recall as many of the landmarks from the route as they could remember (i.e. recall the list in any order). Any ambiguous responses were clarified with the participant by asking for alternative names and visual descriptions of the object. Responses were recorded by the experimenter in the order they were output by the participant.

6.3.5 Free Reconstruction of Order (Free RoO)

Following IFR, participants were presented with printed images of all the landmarks from the route and were required to arrange them into the order in which they occurred along the route. Participants were able to place landmarks into their positions in any temporal order (i.e. output order was unconstrained) and were free to change their decisions before finalising the order. The sequence was recorded once participants indicated reconstruction was complete.

6.3.6 Procedure

Participants completed the Learning Phase and were not informed about the requirements of the forthcoming tasks to avoid participants intentionally adapting their learning strategy. Thus, participants did not know that the identity or sequence of landmarks would be tested. After the Learning Phase, participants completed the IFR task and then the Free RoO task. Additional tasks were included at test (see Hilton et al., under review, for full details) but are not discussed in this study. The order of the tasks in the test phase of these was counterbalanced, with the proviso that the first test was always free recall.

6.3.7 Data analysis

We analysed the data using generalised linear mixed effect models (GLME) in R (R Core Team, 2019) using the lme4 package (version 1.1-21; Bates et al., 2015). Due to the low number of observations per participant, we used intercept only random effects structures to preserve statistical power. For all models, we included participant and landmark as random factors. Due to issues with model convergence, data from flexible learning and the fixed learning groups were analysed separately, unless otherwise stated.

6.4 Results

6.4.1 Immediate Free Recall Task

6.4.1.1 Serial position memory

Responses from the IFR task were scored as described in Ward et al. (2010), with items being assigned a 1 if they were recalled and a 0 if they were not recalled.

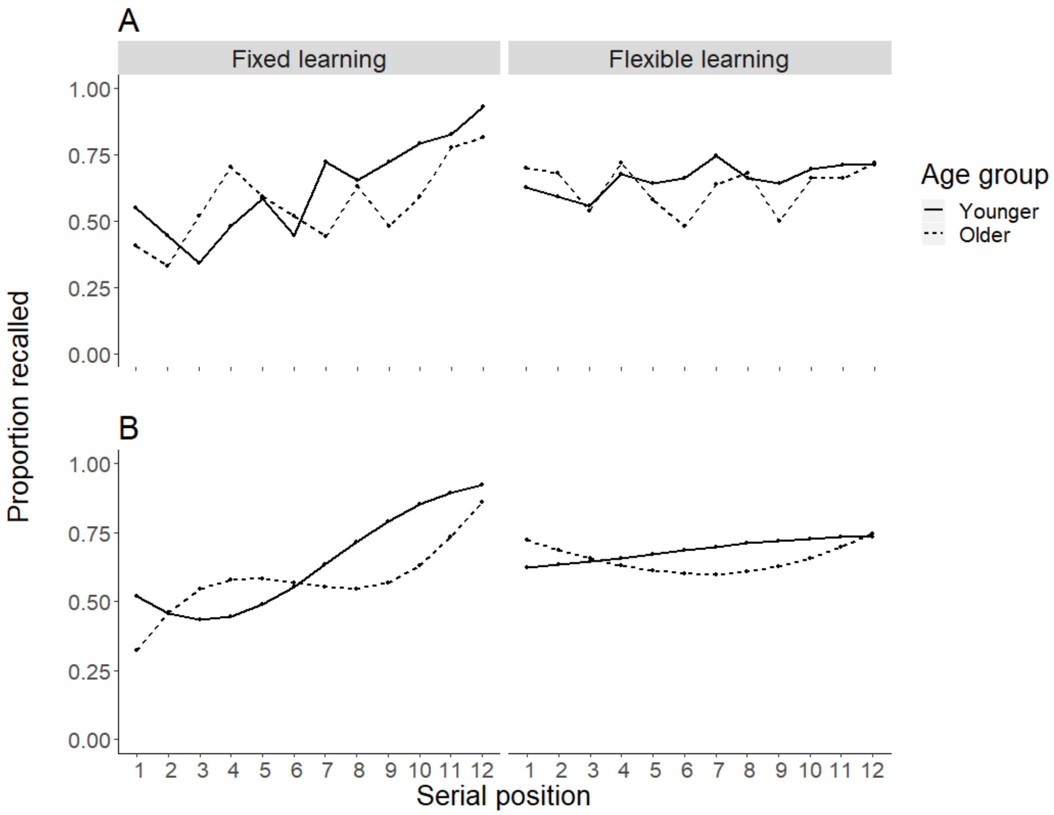

Figure 6-2 – A: Mean proportion of words recalled in the IFR task as a function of serial position. B: Trend effects from GLME models.

We ran a GLME model separately for the fixed learning and flexible learning conditions with the outcome variable as recall probability (0 or 1). Landmark position was included as an ordered factor with polynomial contrast coding to identify trends within the data, and age group was included as a fixed effect (younger or older). Estimates, standard errors, z-values, and p-values are reported in

Table 6-2. There was no significant effect of age group on recall proportions in either condition.

For the fixed learning condition, recall of landmarks as a function of serial position was best described by a linear trend and this did not interact with age. There was an age group by cubic fit interaction which suggests that recall proportions of older adults could be described by a cubic fit better than that of the younger adults. However, this interaction with a cubic fit (β = -0.74) was weaker than the overall linear fit (β = 2.35). Overall, there was a linear effect of serial position on landmark recall probability for both older and younger age groups (see Figure 6-2), for which an accuracy benefit was observed for latter route landmarks. For the flexible learning condition, there was no significant fit of any trend to the recall proportions as a function of serial position and no interactions with age. This suggests that there was no effect of serial position on recall probability in the flexible learning condition (see Figure 6-2).

This analysis indicates that in the fixed learning condition there was a recency effect on recall such that landmarks at the end of the route were more likely to be recalled than items in earlier positions along the route. In contrast, no trend was observed on recall in the flexible learning condition which suggests that serial position of landmarks along the route did not affect likelihood of that landmark being recalled.

Table 6-2 - Coefficients from the Fixed learning and Flexible learning IFR GLME analysis

	Fixed learning model				Flexible learning model			
Fixed effect on recall probability	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
Intercept	0.54	0.21	2.59	.009*	0.71	0.16	4.49	<.001*
Age group	0.19	0.14	1.34	.179	0.08	0.11	0.72	.472
Linear fit – serial position	2.35	0.35	6.72	<.001*	0.34	0.22	1.52	.129
Quadratic fit – serial position	0.72	0.33	2.17	.030*	0.34	0.22	1.55	.122
Cubic fit – serial position	0.34	0.33	1.03	.302	<0.01	0.22	0.01	.992
Age group * Linear fit	0.66	0.34	1.93	.054	0.27	0.22	1.23	.221
Age group * Quadratic fit	0.37	0.33	1.12	.263	-0.40	0.22	-1.82	.069
Age group * Cubic fit	-0.74	0.33	-2.27	.023*	-0.06	0.22	-0.28	.781

*Significant p values ($|p|<0.05$)

6.4.1.2 Order of output

In order to examine potential primacy or recency effects in recall strategy, Figure 6-3 displays the probability of first recall (PFR) for each landmark position. PFR refers to probability that the initial item recalled was located in each of the serial positions during learning. For the fixed learning condition, younger adults showed a clear primacy effect which was not present for the older adults. In contrast, the older participants showed evidence of a recency recall strategy. There was some evidence of a recency effect in the younger participants in the fixed learning condition also, with the final 2 items having higher PFR than items 2-10, however this recency peak was not as large as that of the older participants. For the flexible learning condition, the older participants showed a marked shift from recency towards primacy, compared with the older participant sample in the fixed learning condition. This tendency towards primacy in first recall was also present for the younger participants in the flexible learning condition. In fact, the reduction in recency effect was sharp for both age groups, with the final items in the flexible learning condition having equal PFR to all other items excluding the first.

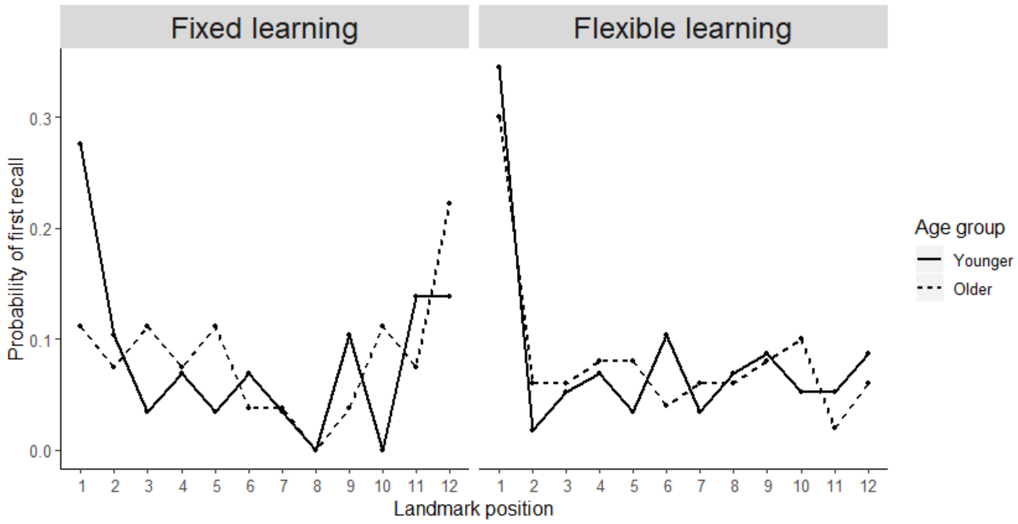

Figure 6-3- Probability of first recall for landmarks in each serial position

6.4.2 Free Reconstruction of Order Task

6.4.2.1 Serial position memory

Responses from the Free RoO task were scored as described in Ward et al. (2010), with items being assigned a 1 if they were placed in the correct position in the sequence and a 0 if they were transpositions.

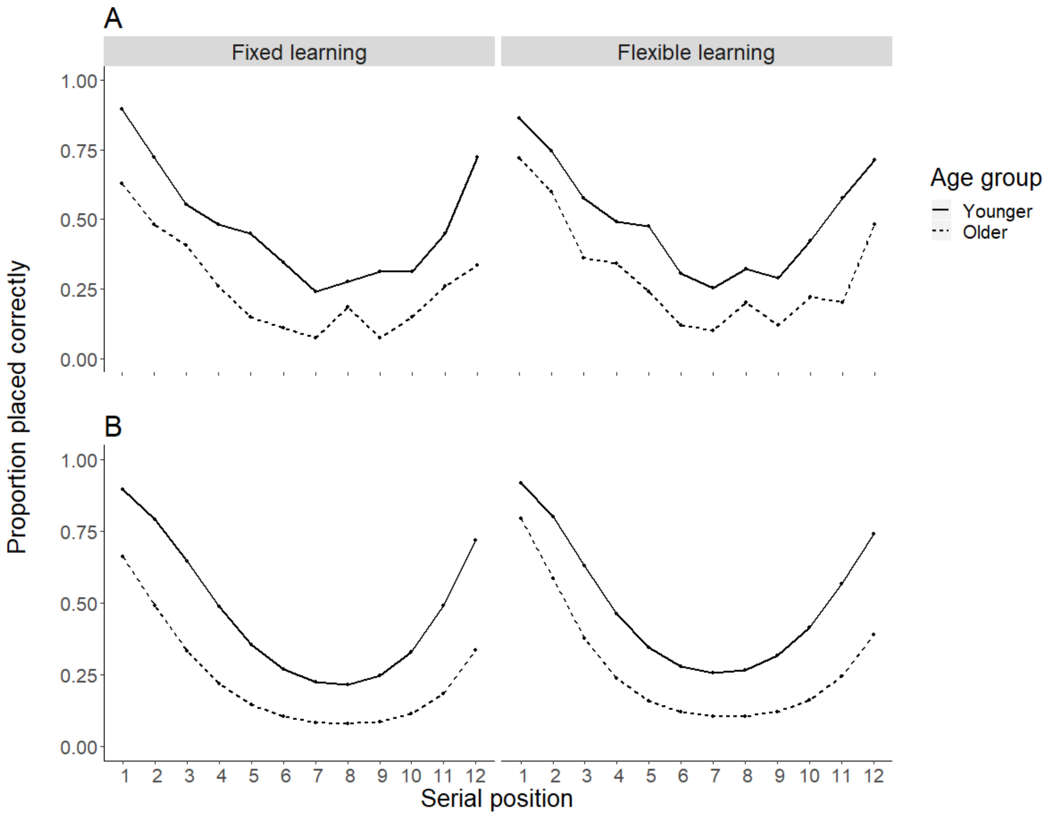

Figure 6-4 - A: Mean proportion of landmarks placed correctly in the Free RoO task as a function of serial position. B: Trend effects from GLME models.

We ran a GLME model separately for the fixed learning and flexible learning conditions with the outcome variable as performance (0 or 1). Landmark position was included as an ordered factor with polynomial contrast coding to identify trends within the data, and age group was included as a fixed effect (younger or older). Estimates, standard errors, z-values, and p-values are reported in Table 6-3.

For both conditions, there was a significant effect of age such that younger participants performed better than older participants. Both linear and quadratic trends provided a significant fit to the data. The fit of a quadratic trend was stronger than a linear trend in both fixed learning and flexible learning conditions. There were no interactions between trend fits and age group. Overall, there was a quadratic effect of serial position on probability of correct landmark placement (see Figure 6-4). This trend demonstrates primacy and recency benefit in serial order memory for both age groups and across fixed and flexible learning protocols.

Table 6-3 - Coefficients from the Fixed learning and Flexible learning Free RoO GLME analysis

	Fixed learning model				Flexible learning model[10]			
Fixed effect on recall probability	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
Intercept	-0.74	0.18	-4.11	<.001*	-0.52	0.13	-4.01	<.001*
Age group	0.65	0.16	3.96	<.001*	0.58	0.13	4.55	<.001*
Linear fit – serial position	-1.83	0.34	-5.43	<.001*	-1.71	0.24	-7.09	<.001*
Quadratic fit – serial position	2.99	0.36	8.27	<.001*	3.21	0.26	10.21	<.001*
Cubic fit – serial position	0.44	0.34	1.30	.194	-	-	-	-
Age group * Linear fit	0.05	0.33	0.16	.870	0.23	0.24	0.97	.330
Age group * Quadratic fit	0.23	0.25	0.67	.503	0.13	0.25	0.51	.610
Age group * Cubic fit	0.03	0.34	0.08	.936	-	-	-	-

*Significant p values (|p|<0.05)

6.4.2.2 Conditionalised response probabilities (CRPs)

The scoring method for the Free RoO task assesses absolute positional knowledge but is insensitive to relative order. That is, a participant may place items in the incorrect absolute position during reconstruction, but still place items in the correct order relative to last retrieved item. To analyse relative ordering of items in the Free RoO task, we computed conditionalised response probabilities (CRPs) at different lags (e.g. Kahana et al., 2007; Ward et al., 2010). Lag refers the distance between each successive item in the given sequence in terms of their serial position during learning (e.g. placing items 3 and 7 next to each other would produce a lag of 4). A lag may be negative if an item is placed before an item with a lower serial position (e.g. placing item 7, then 3 would result in a lag of -4). The CRP refers to the probability that each lag is made within a sequence, after controlling for the number of opportunities available for each lag distance (for example a lag of 11 can only occur once in a sequence of 12 items, whereas there are 10 opportunities to make a lag transition of 2). Lag-CRP curves are plotted for each condition in Figure 6-5a.

[10] To achieve model convergence, polynomial contrasts were run to identify linear and quadratic trends only.

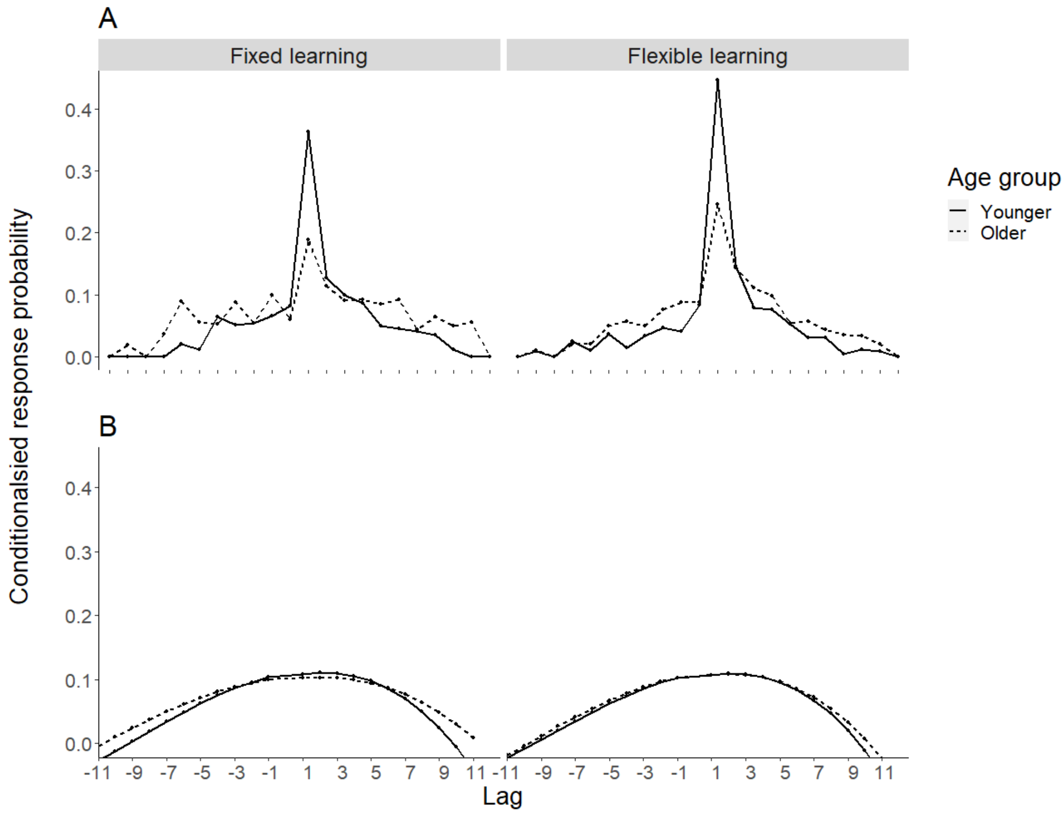

Figure 6-5 - A: Lag-CRP curves for each condition for the Free RoO task. B: Trend effects from LME model.

We ran an LME model on CRP. Lag was included as a factor with polynomial contrast coding to identify trends within the data. Age group (younger or older) and condition (fixed or flexible) were included as fixed effects using sum contrast coding. Estimates, standard errors, z-values, and p-values are reported in Table 6-4. There were significant fits of lag to linear, quadratic, and cubic trends. The fit of a quadratic trend was stronger than the fit of linear and cubic trends in both fixed learning and flexible learning conditions (see Figure 6-5b). The fit of the quadratic trend interacted with age group such that the fit was slightly weaker for the older participants, although this was still the best trend to describe their data overall. There were no other significant interactions. This inverted U shaped trend demonstrates a bias towards lags of smaller values, which shows that participants had good knowledge of the relative ordering of landmark sequence.

Table 6-4 - Coefficients from the Free RoO CRP lag LME analysis.

Fixed effect on CRP	Estimate	Std. error	t-value
Intercept	0.05	<0.01	30.61*
Age group	<-0.01	<0.01	-2.01*
Condition	<0.01	<0.01	0.92
Linear fit – lag	0.04	0.01	3.94*
Quadratic fit – lag	-0.19	0.01	-21.53*
Cubic fit – serial lag	-0.04	0.01	-4.28*
Age group * Linear fit	<-0.01	0.01	-0.43
Age group * Quadratic fit	0.02	0.01	-2.41*
Age group * Cubic fit	-0.01	0.01	-1.24
Condition * Linear fit	<0.01	0.01	0.42
Condition * Quadratic fit	0.01	0.01	1.18
Condition * Cubic fit	0.01	0.01	0.57
Condition * Age group	<-0.01	<0.01	-0.67
Condition * Linear fit* Age group	<0.01	0.01	0.15
Condition * Quadratic fit* Age group	-0.01	0.01	-1.21
Condition * Cubic fit* Age group	<-0.01	0.01	-0.37

*Significant t values (|t|>1.96)

From examination of Figure 6-5, the fit of the quadratic trend matched the data closely on almost all lag positions. However, there was a large departure of the data from the fitted trend for lag +1 across both conditions and age groups. This is not particularly surprising since a lag of +1 is special in that it reflects the correct relative placement of items in the sequence, whilst all other positions are lags in which participants made an error in the relative ordering. In a follow up analysis, we analysed CRP to make +1 lags only. Cutting down the data to only examine CRP for +1 lag resulted in only one observation per participant, thus we used a linear model without a random effects structure. CRP for lag +1 was the outcome variable with fixed effects of age group (younger, older) and condition (fixed or flexible) both coded using sum contrasts. Results of the model are presented in Table 6-5 and show an effect of age group such that the probability of +1 lags was greater for younger participants than older participants. There was no effect of condition and no significant interaction. The model presented in Table 6-4 and Figure 6-5 shows that both age groups had a relative knowledge of the sequence above chance level, however the model on +1 lags only (Table 6-5) suggests that this relative knowledge was better for the younger participants than the older participants.

Table 6-5 - Coefficients from the Free RoO lag +1 LM analysis.

Fixed effect CRP	Estimate	Std. error	t-value	p-value
Intercept	0.31	0.02	17.10	<.001*
Age group	0.09	0.02	5.17	<.001*
Condition	-0.04	0.02	-1.925	.056
Age group * condition	<-0.01	0.02	-0.36	.718

*Significant p values (|p|<0.05)

6.5 Discussion

The present study is the first to examine the role of classical sequence learning effects in the acquisition of route knowledge. Here we show evidence for the development of landmark sequence knowledge following route learning both in respect to the items and order of those items along the route. We tested sequence learning via Immediate Free Recall (IFR) and Free Reconstruction of Order (Free RoO), reporting established effects found in other sequence learning paradigms. Following both fixed and flexible learning, Free RoO produced the canonical bowed serial position effects found in conventional list learning tasks (e.g. Lewandowsky et al., 2008, 2009; Neath, 1997; Tan & Ward, 2008; Ward et al., 2010). Established patterns of sequence learning was seen also in the lag-CRP functions which revealed an asymmetric lag recency. IFR of landmarks produced serial position functions that were, however, less consistent with earlier findings. For fixed learning there was evidence of a recall benefit for latter list items, whereas the flexible learning condition produced much flatter functions. These functions were at odds with the order of output for the free recall of landmarks, which revealed a bias towards outputting early list items first. A main effect of age was found only with Free RoO.

The serial position function exhibited in the Free RoO task demonstrates that participants did acquire knowledge of the sequence of landmarks for both the fixed and flexible learning conditions. The pattern of this serial position function is consistent with studies that have explored Free RoO for short-term memory of verbal sequences (e.g. Lewandowsky et al., 2008, 2009; Neath, 1997; Tan & Ward, 2008; Ward et al., 2010). Specifically, a memory advantage was observed for boundary items at both ends of the sequence, revealing both primacy and recency effects. This finding supports the notion that serial position effects for sequences extends beyond the standard list learning tasks and generalises to a navigation context.

Bowed serial position curves in Free RoO were observed for both older and younger age groups, despite an overall impairment of recall order for older adults. The presence of both primacy and recency was consistent with the serial position functions shown in previous studies with both younger and older samples (Elliott et al., 2011; Maylor et al., 1999; Surprenant, 2007). Moreover, an age-related impairment in contextual information (i.e. impaired recall of temporal location) is consistent with age-related memory deficits disproportionately affecting context (e.g. Kessels et al., 2007). This is known as the 'associative deficit hypothesis' (e.g. Chalfonte & Johnson, 1996; Naveh-Benjamin, 2000) which posits that older adults are markedly impaired for bound/associative information. In the present study we employed a surprise test of context (i.e. item-order association) and found an age-related deficit, consistent with the age-related deficit shown for a surprise test of spatial context (Lugtmeijer, de Haan, & Kessels, 2019). In contrast with the age-related deficits we report in Free RoO, we found no significant effect of age for IFR (see also Golomb et al., 2008). This is consistent with the proposition that contextual memory information is disproportionately affected by ageing (e.g., Kessels et al., 2007; although item-based deficits have been reported in older adults, e.g. Kahana et al., 2002).

The IFR data was less consistent with established serial position effects than the Free RoO data, notably lacking the bowed serial position effects in recall of landmarks. For the fixed learning condition there was evidence of recency (but not of primacy), whereas the flexible learning condition produced a relatively flat function. Whilst stronger recency (compared to primacy) is consistent with free recall of longer lists (Grenfell-Essam & Ward, 2012; Grenfell-Essam, Ward & Tan, 2013; Spurgeon et al., 2014; Ward et al., 2010), this enhanced recency was accompanied by a tendency to initiate recall with latter list items. Analysis of output order in the present study revealed a bias towards outputting early list items first. Such a finding is inconsistent with the explanation that initiating recall with an item improves recall accuracy due to an absence of output interference (e.g. see Tan & Ward, 2008). That is, recall for the latter list items was superior despite recall being initiated with early list items.

The lack of typical serial position effects in the IFR task cannot be attributed to the lack of serial memory in our participants, since those canonical curves are clearly present in the Free RoO task. Yet despite participants acquiring such sequence memory, it was not evident in free recall of items in the same way as in other sequence learning paradigms (e.g. Ward et al., 2010). One might argue that it is not overly surprising that some differences exist in our study given the vastly different task characteristics in the present study compared to typical sequence learning tasks. Nevertheless, despite those task differences, the serial position functions are stark in the Free RoO task. It appears that the task differences did not affect the acquisition of serial order knowledge but did differentially affect how serial order memory was manifested in the IFR and Free RoO tasks. It is beyond the scope of the current study to provide a full framework for this phenomenon, but we discuss the possibilities here as avenues for future research.

One difference in our task compared to standard paradigms is the number of exposures to the sequence. In the present protocol, participants are presented with a single sequence to which they are exposed multiple times. This contrasts with the conventional protocols where participants respond following a single exposure to the sequence. Moreover, in the route learning task both presentation of the sequence and the retention interval is considerably longer in duration than the conventional paradigms. Our study demonstrates that the bowed Free RoO function is resistant to longer intervals and multiple exposures to the list. Whereas the sensitivity of IFR to changes in list exposure is evident in the differences between the fixed and flexible learning conditions on both recall position and output order measures. The recency component is reduced for flexible learning relative to fixed learning (see Figure 6-2). Similarly, the extent to which participants initiate recall with the last item is reduced for flexible learning. It is not clear why flexible learning should result in a shift in recall strategy but the only difference between conditions is the number of exposures to the sequence (3 for fixed learning compared to a mean of 4.42 for flexible learning).

Given this shift towards a primacy-based output order, it is surprising that primacy is absent in the present free recall functions. Tan and Ward (2000) suggested that rehearsal of early list items, specifically the recency of that rehearsal, contributed to primacy. It is possible therefore that participants stopped rehearsing early list items in our study due to the lengthy presentation procedure (or did not engage in rehearsal at all). Indeed, interrupting rehearsal during list learning has been shown to eliminate primacy, but not recency serial position effects in recall (Marshall & Werder, 1972; see also Tan & Ward, 2000), which would explain the lack of primacy in both learning conditions. The existence of recency in the fixed learning condition can be explained by the benefit of recency in output order which is not affected by the lack of rehearsal (Marshall and Verder 1972; Tan & Ward, 2008).

Another methodological difference in our task is that participants were not explicitly instructed to learn the landmarks or their order in the route learning task. Notwithstanding this lack of instruction, we observed the serial position effect in Free RoO. Indeed, the same landmarks are not repeated within a sequence, therefore, in order to learn the route participants could 'simply' associate each landmark with a directional response (Waller & Lippa, 2014). Despite the non-essential nature of sequence information for the specific route learning task, participants acquired order memory as shown by both absolute (the Free RoO function) and relative (CRP-lag functions) measures of serial memory. The acquisition of sequence knowledge despite not knowing the forthcoming test is consistent with Tan and Ward (2007) who showed that pre-cueing the forthcoming reconstruction procedure (compared to post-cueing after the sequence has been presented) does not qualitatively affect the Free RoO serial position function. It is also unlikely that naivety of the upcoming tasks was responsible for the inconsistent IFR results, since null effects of task expectancy has previously been reported with IFR tasks (Bhatarah, Ward, & Tan, 2008; Grenfell-Essam & Ward, 2012).

In summary, this study provides clear evidence of typical serial position memory effects for landmarks encountered during route navigation. The Free RoO task produced strong primacy and recency benefits for landmarks found at the beginning at the end of the route. This function existed for both age groups, despite an overall reduction in sequence knowledge for older adults. Interestingly the serial position effects were not observed in IFR of landmarks which could be due to the several differences between our task and standard sequence learning tasks, although this avenue requires further empirical research. Despite these task differences, the serial position curves in the Free RoO task supports the ubiquity of this function and the notion that primacy and recency are general properties of memory which extend to a navigation context.

6.6 References

Allison, S., & Head, D. (2017). Route repetition and route reversal: Effects of age and encoding method. *Psychology and Aging*, *32*(3), 220–231. https://doi.org/10.1037/pag0000170

Avons, S. E. (1998). Serial report and item recognition of novel visual patterns. *British Journal of Psychology*, *89*(2), 285–308. https://doi.org/10.1111/j.2044-8295.1998.tb02685.x

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/doi: 10.18637/jss.v067.i01

Bhatarah, P., Ward, G., & Tan, L. (2008). Examining the relationship between free recall and immediate serial recall: The serial nature of recall and the effect of test expectancy. *Memory and Cognition*, *36*(1), 20–34. https://doi.org/10.3758/MC.36.1.20

Chalfonte, B. L., & Johnson, M. K. (1996). Feature memory and binding in young and older adults. *Memory and Cognition*, *24*(4), 403–416. https://doi.org/10.3758/BF03200930

Cortis, C., Dent, K., Kennett, S., & Ward, G. (2015). First things first: Similar list length and output order effects for verbal and nonverbal stimuli. *Journal of Experimental Psychology: Learning Memory and Cognition*, *41*(4), 1179–1214. https://doi.org/10.1037/xlm0000086

Elliott, E. M., Cherry, K. E., Brown, J. S., Smitherman, E. A., Jazwinski, S. M., Yu, Q., & Volaufova, J. (2011). Working memory in the oldest-old: Evidence from output serial position curves. *Memory and Cognition*, *39*(8), 1423–1434. https://doi.org/10.3758/s13421-011-0119-7

Golomb, J. D., Peelle, J. E., Addis, K. M., Kahana, M. J., & Wingfield, A. (2008). Effects of adult aging on utilization of temporal and semantic associations during free and serial recall. *Memory and Cognition*, *36*(5), 947–956. https://doi.org/10.3758/MC.36.5.947

Grenfell-Essam, R., & Ward, G. (2012). Examining the relationship between free recall and immediate serial recall: The role of list length, strategy use, and test expectancy. *Journal of Memory and Language*, *67*(1), 106–148. https://doi.org/10.1016/j.jml.2012.04.004

Grenfell-Essam, R., Ward, G., & Tan, L. (2013). The role of rehearsal on the output order of immediate free recall of short and long lists. *Journal of Experimental Psychology: Learning Memory and Cognition*, *39*(2), 317–347. https://doi.org/10.1037/a0028974

Guérard, K., & Tremblay, S. (2008). Revisiting Evidence for Modularity and Functional Equivalence Across Verbal and Spatial Domains in Memory. *Journal of Experimental Psychology: Learning Memory and Cognition*, *34*(3), 556–569. https://doi.org/10.1037/0278-7393.34.3.556

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research*, *209*(1), 49–58. https://doi.org/10.1016/j.bbr.2010.01.012

Hebb, D. O. (1961). Distinctive features of learning in the higher animal. *Brain Mechanisms and Learning: A Symposium*.

Hilton, C., Johnson, A. J., Slattery, T. S., Miellet, S., & Wiener, J. M. (under review). The impact of learning rate on age-related differences in the acquisition of landmark knowledge during route navigation

Johnson, A. J., Shaw, J., & Miles, C. (2016). Tactile order memory: evidence for sequence learning phenomena found with other stimulus types. *Journal of Cognitive Psychology*, *28*(6), 718–725. https://doi.org/10.1080/20445911.2016.1186676

Kahana, M. J., Howard, M. W., & Polyn, S. M. (2007). Associative retrieval processes in episodic memory. *Learning and Memory: A Comprehensive Reference*, (January), 1–24. https://doi.org/10.1016/B978-012370509-9.00185-6

Kahana, Michael J., Howard, M. W., Zaromb, F., & Wingfield, A. (2002). Age Dissociates Recency and Lag Recency Effects in Free Recall. *Journal of Experimental Psychology: Learning Memory and Cognition*, *28*(3), 530–540. https://doi.org/10.1037/0278-7393.28.3.530

Kelley, M. R., Neath, I., & Surprenant, A. M. (2013). Three more semantic serial position functions and a SIMPLE explanation. *Memory and Cognition*, *41*(4), 600–610. https://doi.org/10.3758/s13421-012-0286-1

Kelley, M. R., Neath, I., & Surprenant, A. M. (2015). Serial position functions in general knowledge. *Journal of Experimental Psychology: Learning Memory and Cognition*, *41*(6), 1715–1726. https://doi.org/10.1037/xlm0000141

Kessels, R. P. C., Hobbel, D., & Postma, A. (2007). Aging, context memory and binding: A comparison of “what, where and when” in young and older adults. *International Journal of Neuroscience*, *117*(6), 795–810. https://doi.org/10.1080/00207450600910218

Koppenol-Gonzalez, G. V., Bouwmeester, S., & Vermunt, J. K. (2014). Short-term memory development: Differences in serial position curves between age groups and latent classes. *Journal of Experimental Child Psychology*, *126*, 138–151. https://doi.org/10.1016/j.jecp.2014.04.002

Lewandowsky, S., Brown, G. D. A., & Thomas, J. L. (2009). Traveling economically through memory space: Characterizing output order in memory for serial order. *Memory and Cognition*, *37*(2), 181–193. https://doi.org/10.3758/MC.37.2.181

Lewandowsky, S., Nimmo, L. M., & Brown, G. D. A. (2008). When temporal isolation benefits memory for serial order. *Journal of Memory and Language*, *58*(2), 415–428. https://doi.org/10.1016/j.jml.2006.11.003

Lugtmeijer, S., de Haan, E. H. F., & Kessels, R. P. C. (2019). A comparison of visual working memory and episodic memory performance in younger and older adults. *Aging, Neuropsychology, and Cognition*, *26*(3), 387–406. https://doi.org/10.1080/13825585.2018.1451480

Luis, C., Keegan, A., & Mullan, M. (2009). Cross validation of the Montreal Cognitive Assessment in community dwelling older adults residing in the Southeastern US. *International Journal of Geriatric Psychiatry*, *24*(2), 197–201.

Marshall, P. H., & Werder, P. R. (1972). The effects of the elimination of rehearsal on primacy and recency. *Journal of Verbal Learning and Verbal Behavior*, *11*(5), 649–653. https://doi.org/10.1016/S0022-5371(72)80049-5

Maylor, E. A. (2002). Serial position effects in semantic memory: Reconstructing the order of verses of hymns. *Psychonomic Bulletin and Review*, *9*(4), 816–820. https://doi.org/10.3758/BF03196340

Maylor, E. A., Vousden, J. I., & Brown, G. D. A. (1999). Adult age differences in short-term memory for serial order: Data and a model. *Psychology and Aging*, *14*(4), 572–594. https://doi.org/10.1037/0882-7974.14.4.572

Murdock, B. B. (1962). The serial position effect of free recall. *Journal of Experimental*

Psychology, *64*(5), 482–488. https://doi.org/10.1037/h0045106

Nasreddine, Z. S., Phillips, N. A., Bedirian, V., Charbonneau, S., Whitehead, V., Collin, I., … Chertkow, H. (2005). The Montreal cognitive assessment, MoCA: a brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, *53*(4), 695–699.

Naveh-Benjamin, M. (2000). Adult Age Differences in Memory Performance: Tests of an Associative Deficit Hypothesis. *Journal of Experimental Psychology: Learning Memory and Cognition*, *26*(5), 1170–1187. https://doi.org/10.1037/0278-7393.26.5.1170

Neath, I. (1997). Modality, concreteness, and set-size effects in a free reconstruction of order task. *Memory and Cognition*, *25*(2), 256–263. https://doi.org/10.3758/BF03201116

Neath, I., Kelley, M. R., & Surprenant, A. M. (2016). Three Semantic Serial Position Functions at the Same Time. *Experimental Psychology*, *63*(6), 351–360. https://doi.org/10.1027/1618-3169/a000344

Parmentier, F. B. R., & Jones, D. M. (2000). Functional Characteristics of Auditory Temporal-Spatial Short-Term Memory: Evidence from Serial Order Errors. *Journal of Experimental Psychology: Learning Memory and Cognition*, *26*(1), 222–238. https://doi.org/10.1037/0278-7393.26.1.222

Phillips, W. A., & Christie, D. F. M. (1977). Components of visual memory. *Quarterly Journal of Experimental Psychology*, *29*(29), 117–133. https://doi.org/10.1080/00335557743000080

R Core Team. (2019). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria. URL Http://Www.R-Project.Org/.*

Roediger, H. L., & DeSoto, K. A. (2014). Forgetting the presidents. *Science*, *346*(6213), 1106–1109. https://doi.org/10.1126/science.1259627

Schinazi, V. R., & Epstein, R. A. (2010). Neural correlates of real-world route learning. *NeuroImage*, *53*(2), 725–735. https://doi.org/10.1016/j.neuroimage.2010.06.065

Schoo, L. A., Van Zandvoort, M. J. E., Reijmer, Y. D., Biessels, G. J., Kappelle, L. J., & Postma, A. (2014). Absolute and relative temporal order memory for performed activities following stroke. *Journal of Clinical and Experimental Neuropsychology*, *36*(6), 648–658. https://doi.org/10.1080/13803395.2014.925093

Spurgeon, J., Ward, G., & Matthews, W. J. (2014). Why do participants initiate free recall of short lists of words with the first list item?: Toward a general episodic memory explanation. *Journal of Experimental Psychology: Learning Memory and Cognition*, *40*(6), 1551–1567. https://doi.org/10.1037/xlm0000028

Strickrodt, M., O'Malley, M., & Wiener, J. M. (2015). This place looks familiar-how navigators distinguish places with ambiguous landmark objects when learning novel routes. *Frontiers in Psychology*, *6*(DEC), 1–12. https://doi.org/10.3389/fpsyg.2015.01936

Surprenant, Aimee M. (2007). Effects of noise on identification and serial recall of nonsense syllables in older and younger adults. *Aging, Neuropsychology, and Cognition*, *14*(2), 126–143. https://doi.org/10.1080/13825580701217710

Surprenant, Aimée M, & Neath, I. A. N. (2006). The 9 Lives of Short-Term Memory. *Interactions between Short-Term and Long-Term Memory in the Verbal Domain*, 1–21. Retrieved from https://memory.psych.mun.ca/pubs/chapters/reprints/Surprenant & Neath (2009).pdf

Tan, L., & Ward, G. (2000). A recency-based account of the primacy effect in free recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*(6), 1589–1625. https://doi.org/10.1037/0278-7393.26.6.1589

Tan, L., & Ward, G. (2008). Rehearsal in immediate serial recall. *Psychonomic Bulletin and Review*, *15*(3), 535–542. https://doi.org/10.3758/PBR.15.3.535

Waldron-Perrine, B., & Axelrod, B. N. (2012). Determining an appropriate cutting score for indication of impairment on the Montreal Cognitive Assessment. *International Journal of Geriatric Psychiatry*, *27*(11), 1189–1194. https://doi.org/10.1002/gps.3768

Waller, D., & Lippa, Y. (2007). Landmarks as beacons and associative cues. *Memory & Cognition*, *35*(5), 910–924. https://doi.org/10.3758/BF03193465

Ward, G., Avons, S. E., & Melling, L. (2005). Serial position curves in short-term memory: Functional equivalence across modalities. *Memory*, *13*(3–4), 308–317. https://doi.org/10.1080/09658210344000279

Ward, G., Tan, L., & Grenfell-Essam, R. (2010). Examining the relationship between free recall and immediate serial recall: The effects of list length and output order. *Journal of Experimental Psychology: Learning Memory and Cognition*, *36*(5), 1207–1241. https://doi.org/10.1037/a0020122

Chapter 7

Discussion

The work presented in this thesis contributes to our understanding of how typical cognitive ageing affects spatial navigation ability. In this final chapter, I will first summarise the key findings and interpretations from the work presented in this thesis. Since discussion of the findings from the individual experiments have already been presented in detail in the chapters dedicated to those studies, I will avoid repeating that here. This discussion chapter will focus on common implications that the work as a whole has for our understanding of navigation behaviour and how it is affected by cognitive ageing.

7.1 Thesis summary

Place recognition processes were examined in two experiments presented in Chapters 2 and 3. The paradigm involved participants first encoding a place which was defined by four objects on an otherwise empty plain for 8 seconds. They then viewed a second image of a place for which they had to make a same or different judgement. The test place could differ from the encoded place by either substituting an object for a novel object, or by swapping the positions of two objects in the place. Additionally, test places could be presented from the same perspective as the encoded place, or from a different perspective, changed by either 30 or 60 degrees.

In the first experiment we found an overall deficit in place recognition ability for older adults in the 60-69 and 70-79 years old age groups compared to the younger participants. Swap changes were more difficult to detect than substitute changes and the introduction of a perspective shift negatively impacted recognition. Age group interacted with condition such that swap changes particularly impacted the performance of the older age groups. In contrast, there was no interaction between age group and perspective shift. We interpreted these findings as evidence of a specific object-location binding deficit that contributed to place recognition impairment in older adults, where the requirement to learn the spatial locations of objects in the place yielded particularly poor recognition performance. This pattern of results was replicated in the second experiment, for which we also recorded eye movements.

Initial analysis of the eye tracking data showed only small effects of age on saccade and fixation parameters, specifically that older adults fixated for shorter times and executed saccades more frequently during place encoding. Further, we analysed a specific visual encoding strategy: chaining. The chaining strategy involves gaze being directed sequentially between each object in the place before returning to a recently viewed object. Through this strategy, the spatial arrangement of objects in the place is represented as a temporal sequence of eye movements. Gaze chaining was a predictor of performance such that stronger chaining during place encoding was related to improved recognition performance. We found a significant effect of age group on the chaining measure, such that older adults used the chaining strategy less during place encoding, with their gaze more likely to regress to a recently viewed object rather than moving on to the next object in the place.

Overall, we suggest that the shift in encoding strategy during place learning results in poorer recognition performance for older adults. It is possible that older adults were less efficient with the chaining strategy because it requires retention of multiple objects in memory, which may have exceeded their limited capacity. Thus, the older adults were more likely to regress gaze to a recently viewed object to refresh their representation. Finally, we found that older adults spent more time fixating non-object areas of the stimuli which could reflect an attempt to employ an alternative encoding strategy which would utilize distal features of a place.

In Chapter 4 I presented a route learning and eye-tracking study in which older and younger participants were shown a video of a route through a town which they were instructed to learn. In addition to eye tracking, we also gave participants the secondary task of responding via button presses to an auditory stimulus presented intermittently throughout the route video. This auditory probe was taken as a measure of attentional engagement. The secondary task logic is that time taken to respond to the probe reflects the time taken to disengage attention from the primary route learning task and engage with the probe response. After viewing the route, participants were shown screenshots of locations from the route and asked to provide directions. There were two experimental blocks of learning and test, followed by a final test of place sequence knowledge. In the test of sequence knowledge participants had to indicate which location was encountered first along the route from two concurrently shown locations.

Consistent with the existing literature, we found that older participants performed worse than younger participants in recalling directions after learning, and in the test of route sequence knowledge. During learning, we found that participants took longer to respond to the auditory probe at decision points compared to non-decision points along the route. This effect interacted with age group such that the reaction time cost of responding to the probe at a decision point was greater for the older adults. For the gaze data we found no differences between age groups on basic fixation and saccade parameters, nor on two further measures: gaze bias and dispersion. Gaze bias reflects the direction of gaze to the correct direction of travel, which increased in the second block as a result of increased familiarity with the route. The dispersion measure captures the spread of gaze across the scene, which we analysed for the approach to decision points in the environment. We found that dispersion increased on the approach to decision points similarly for both age groups.

We interpret these results as evidence that age-related deficits in route learning ability cannot be explained by changes in attentional control. Indeed, attentional resources and control of visual attention for both age groups are modulated along a route in response the navigational relevance of the current location. Our findings suggest that more attention is engaged at decision points, and that visual attention is spread more widely across the space, possibly in search of landmarks. Despite similar patterns of these attentional measures for both age groups, the older participants still showed a performance deficit compared to young adults on the route knowledge tests: recall of directions and route sequence information.

In Chapter 5 we continued to investigate age-related differences in route knowledge, this time with a focus on learning rates and the final content of route knowledge once a route is known. This study contained three experiments. The first was a standard route learning experiment similar to the procedure of the experiment in Chapter 4. Participants navigated a route three times before being tested on their landmark memory, associative cue knowledge and landmark sequence knowledge. As in the previous chapter, we found that older adults were worse at recalling directional and sequence information. In Experiments 2 and 3 of this chapter, the learning phase was altered into flexible learning procedure, where participants navigated the route repeatedly until they provided at least 90% of the movement decisions correctly. Only once the participants could navigate the route to the 90% criterion did they complete the test tasks. This procedure controlled for age-related differences in route learning rates and allowed us to compare the final content of route knowledge between age groups.

Using the flexible learning procedure eliminated age-related differences on the associative cue task, which were present in Experiment 1 of this study and the results of Chapter 4. However, the landmark sequence knowledge deficit for older adults persisted. We interpreted this differential development of variation in types of route knowledge as evidence of attentional prioritisation during learning for older adults. That is, to compensate for reduced capacity, older adults adopted a route learning strategy which involved piecemeal learning of landmark identities in the first exposures to the route followed by association of directions to those landmarks in later exposures. We argued that this piecemeal direction of attentional resources to individual types of route knowledge comes at the cost to other, non-attended types of knowledge. In this experiment, that is evident in the persistent landmark sequence knowledge deficit for the older adults.

Landmark sequence knowledge was expendable for the older adults since it was not strictly required to solve the route repetition task at hand (for which landmark-direction associations is sufficient). However, the wider purposes of spatial representations is to allow for flexible navigation behaviour for a range of situations. For example, in Experiment 3 of this study participants were presented with parts of the learned route again but with some landmarks removed. Participants with good sequence knowledge could still recall correct directions at these locations by using preceding landmarks to retrieve the missing information from memory. Due to impoverished landmark sequence knowledge in older adults, they were more likely to become disoriented in this navigation scenario than younger adults.

In Chapter 6, we conducted further analysis of the data presented in Chapter 5. Specifically, in view of the importance of sequence knowledge, we investigated the extent to which serial memory for the landmarks learned during navigation reflected more general memory processes. We identified quadratics trends in the serial position curves of the landmark sequence task which revealed strong primacy and recency effects. These curves are similar to those found in other forms of sequence memory such as that from word list learning. Interestingly, despite the overall age-related impairment in sequence knowledge identified in Chapter 5, the serial response curves showed very similar patterns between age groups. Taken together, these findings suggest that landmark and route learning recruits similar general memory mechanisms to non-navigational learning such as for lists of words. The recruitment of these processes is similar for older adults and thus does not explain the overall deficit in landmark sequence knowledge. As discussed above, diminished landmark sequence knowledge in older adults can instead be explained by a shift in learning strategy during navigation.

Overall, the work presented in this thesis evidences an array of intact and diminished mechanisms involved in place and route learning. The following section will discuss four themes which are relevant for multiple chapters of this thesis: age-related differences in representations of space; the contribution of general learning processes to spatial navigation; the allocation of attentional resources as an underlying factor of strategy use; the use of eye-tracking to investigate spatial learning mechanisms.

7.2 General discussion

7.2.1 Age-related differences in representations of space

The work presented in this thesis has replicated, refined and added to our understanding of how cognitive ageing affects the development of spatial knowledge when learning a novel environment. Learning of landmark identities is often touted as one of the early and fundamental building blocks of spatial representations (Chrastil, 2013; Siegel & White, 1975). Our older adults showed relatively intact knowledge of landmarks encountered along routes and from place learning, which is in line with previous findings (Cushman et al., 2008; Head & Isom, 2010). One contributing factor to this is the ability of older adults to identify decision points as important locations for navigation, a known component of landmark and route knowledge (Chrastil, 2013), as shown in Chapter 3 (Hilton et al., 2019). This is consistent with other research showing that older adults memorized and recalled landmarks from decision points more than from non-decisions points along a route, at similar rates to younger adults (Hartmeyer et al., 2017; Zhong & Moffat, 2016).

Preservation of landmark memory and place knowledge (at least for non-changing places that can be identified via object identity alone; Hilton et al., 2020; Muffato et al., 2019) is somewhat surprising in view of research showing the importance of the parahippocampal gyrus for landmark and place representations (Janzen & Weststeijn, 2007). This is because the parahippocampal gyrus is involved in encoding the navigational relevance of landmarks (Janzen & Weststeijn, 2007), and for landmark recognition (Epstein & Vass, 2014), and is among the hippocampal structures that are affected by ageing (Gutchess et al., 2005).

This issue was investigated in a recent functional neuroimaging study (Ramanoël et al., 2020), where participants navigated a simple Y-maze with landmarks present at the central intersection. In this task, participants locate a target object in one of the arms of the maze in an encoding phase, and then have to relocate the objects in the navigation phase. Use of landmarks (compared to a no landmark condition) was associated with parahippocampal activation in younger adults, whilst older adults showed additional activation of the occipital place area. These findings indicate that older adults use visual encoding areas to mitigate the effects of medial temporal atrophy on landmark memory (see also Gutchess et al., 2005). Ramanoël et al. (2020) suggested that whilst this compensation allows for preserved landmark memory, older adults are impaired on the actual use of landmarks in navigation (such as remembering the locations or associated directions). Indeed, in their study the older adults made more errors and had longer trajectories when finding the goal location.

Impairments in using landmarks to support navigation are evident in the studies presented in this thesis (Hilton et al., 2019, 2021). Indeed, despite the relative preservation of brain regions which support egocentric encoding (Colombo et al., 2017), it is clear that route knowledge is affected by cognitive ageing (Allison & Head, 2017; Grzeschik et al., 2020; Head & Isom, 2010; Klencklen et al., 2012; Lithfous et al., 2013; Moffat, 2009; Rodgers et al., 2012; Wiener et al., 2013; Wiener, Kmecova, et al., 2012; Zhong & Moffat, 2016). We demonstrated that landmarks are not efficiently bound to their spatial locations in place representations in older adults (Hilton et al., 2020; Muffato et al., 2019). Of the features of route knowledge defined by Chrastil (2013), our older adults show deficits in sequence learning, forming associations and response learning.

Deficits in associations of landmarks and directions were reported in Chapter 4 of this thesis (Hilton et al., 2019) but we only used two sessions of route learning in that study. In Chapter 5 we showed that when given more trials for route learning, older adults do reach similar levels of associative cue knowledge to younger adults (Hilton et al., 2021). Even in the study of Chapter 4, as well as other studies, older adults do show trial-to-trial improvements in associative cue knowledge (Hilton et al., 2019; Wiener, Kmecova, et al., 2012; Zhong & Moffat, 2016). Thus, this is in line with the notion that route representations of older adults include associative learning of motor responses and landmarks, at least for familiar environments.

In contrast to associative cue knowledge, knowledge for the sequence in which landmarks were encountered does not seem to reach similar levels in young and older adults, even for routes that have been learned well (Hilton et al., 2021). In the study reported in Chapter 5 we demonstrated a navigation situation in which older adults become disoriented as result of incomplete landmark sequence knowledge. This highlights a wider point that even when an environment is familiar to older adults, there are still navigation situations that they cannot solve as well as younger adults.

The full extent to which the lack of sequence knowledge impacts spatial navigation ability is still unclear. The more advanced forms of spatial representation such as graph and survey knowledge, are known to be degraded in older adults (Klencklen et al., 2012). Atrophy of medial temporal lobe structures are often used to explain this deficit (Lester et al., 2017). An additional contribution could be the coarser sequence knowledge possessed by older adults.

Chrastil (2013) suggests that survey knowledge arises from the integration of metric information and topological graphs. Those topological graphs of the environment contain information about the connections between places, contributed to by route sequence learning. From the work in this thesis, we can conclude that older adults do not possess fine grained sequence knowledge, even for familiar routes/environments. Thus, an open question is how (presumably egocentric) route sequence knowledge contributes to allocentric/topological graph and survey representations. Following on from this, to what extent is the age-related deficit in route sequence knowledge preventing the advanced formation of cognitive graph or survey representations?

A possible line of research to address these research questions could utilise the flexible learning procedure introduced in Chapter 5 (Hilton et al., 2021) to encourage the acquisition of sequence knowledge. This would involve a route learning phase that not only required participants to demonstrate high level route knowledge as in the existing procedure, but also to reach a performance criterion on a test of sequence knowledge. Once participants reach criterion on the route learning phase, tests of metric knowledge could be used to compare the survey representation of the participants against a control condition in which participants did not have a sequence knowledge criterion during learning. The frequently used pointing task, which requires participants to provide dead reckoning pointing vectors from a current location to another location in the environment, would be a good candidate to test survey knowledge (e.g. Craig et al., 2016). The pointing task is a good measure of survey representations because it requires precise knowledge about the distances and angles between places to compute the correct pointing vector.

If sequence knowledge contributes to survey representations, then we would expect lower pointing errors for the condition which acquired sequence knowledge during route learning. For a group of older participants, the same would be true, however even in the sequence learning condition we would expect older adults to produce greater point errors than younger adults due to other factors impacting their survey representation (such as declines in allocentric coding mechanisms). The effect size of any reduction in pointing error between the sequence learning and control conditions could serve as a quantification of the extent to which sequence knowledge contributes to survey representations. This is a line of research that we have recently started as a follow up to the work presented in this thesis, but is beyond the scope of the current PhD project.

Overall, this thesis confirms preservation of landmark memory in older adults, and degradation of route knowledge. Specifically, reduced landmark-location memory, associative cue and landmark sequence knowledge. The findings that older adults can overcome associative cue deficits through additional learning time, but the same is not true for sequence learning, extends our understand of age-related route learning deficits. Possible consequences for diminished sequence knowledge on spatial representations have been discussed with open research questions highlighted alongside consideration of an experiment design to address them.

7.2.2 The contribution of general learning processes to spatial navigation

In Chapter 6 we argued that memory for landmark sequences is similar to other forms of serial memory (Hilton et al., under review). We found that the canonical serial position curves that are usually observed in non-spatial tasks such as recalling lists of words (Ward et al., 2010) or the order of US presidents (Roediger & DeSoto, 2014), are also present for landmark sequence memory. Thus, landmark sequence memory may not rely on distinct navigation specific processes, but instead may rely on more general memory processes.

Indeed, on a wider scale it is well known that other, non-spatially specific, cognitive processes contribute to the navigation system. Input from the visual (Ekstrom, 2015), auditory (Gröhn et al., 2005), olfactory (Wu et al., 2020) systems as well as executive functions (Taillade et al., 2013), working memory (Meilinger et al., 2008), motor planning (Chersi et al., 2013), and even emotional and personality factors (Pazzaglia et al., 2018) are among the cognitive contributions to the spatial navigation network. However, the extent to which each system contributes is not well understood.

Thus, although we know the importance of the hippocampus and its related structures for spatial processing, a full understanding of spatial navigation ability must take into account the wider network of neurocognitive contributions. After all, hippocampectamised rats can still solve an array of navigation tasks (Alyan et al., 2000; Alyan & McNaughton, 1999) including using a cognitive map like representation of space, which highlights that spatial memory is supported by more than just the hippocampal circuit. It is possible that general learning and memory functions support spatial knowledge to a greater extent than is currently thought. This notion is supported by the research showing that the hippocampus is functionally connected to many extrahippocampal brain regions during navigation (Burte et al., 2018), and that the strength of this functional network relates to navigation ability (Izen et al., 2018).

The idea that more general cognitive processes contribute to spatial navigation is not new but is still a contemporary issue in spatial navigation research as shown by a recent journal special issue on the topic titled "Spatial Navigation: Memory Mechanisms and Executive Function Interactions" (for the editorial see Brown & Chrastil, 2019). A recent review (Zhong & Moffat, 2018) highlights the need to investigate the role of executive functioning in age-related navigation decline. The work in this thesis contributed to that goal by investigating control of visual attention, attentional engagement and the discussion of resource allocation during spatial learning.

Zhong and Moffat (2018) also suggested that despite the now well-known deficit in associative learning of landmarks and directions in older adults, it remains unclear whether the binding of landmarks and directions relies on the same associative learning mechanisms that bind non-spatial information (e.g. face-name pairs). In agreement with this question, we would add the investigation of serial learning of landmarks, which we argued is similar to general serial learning mechanisms (Hilton et al., under review; see also Buchner & Jansen-Osmann, 2008).

Moving forward, the gap between spatial navigation research and more general memory research should be closed. This type of research will highlight what is special about spatial learning and navigation, if it is in fact different to general cognitive functions. It may be the case that theories of spatial learning can take advantage of the many theories and well documented effects known in the memory literature that may also apply to navigation. For landmark sequence memory we have applied traditional analysis of serial position memory in Chapter 6 and found effects similar to those reported in traditional word list learning paradigms. Further research could include the investigation of other effects, such as the Hebb repetition effect which shows a gradual improvement of sequence knowledge for items that are presented repeatedly over time but are hidden amongst non-repeated items (Hebb, 1961). This effect has been shown for many types of stimuli (see Johnson & Miles, 2019), but never for items encountered during navigation. The presence or absence of such effects would indicate the similarity or distinction of general memory processes and spatial memory.

From the work in this thesis, it is clear that general memory processes do play an important role in route navigation, such as for landmark associative or sequence learning. Further research is important to reveal the exact nature and extent of the role of general memory processes in route navigation. Then we may have a better understand of how ageing, and other neurological, cognitive, or developmental disorders may impact spatial navigation ability. Perhaps the best summation of this discussion can be paraphrased from Brown and Chrastil (2019): that we should look beyond the traditional boundaries of spatial navigation research.

7.2.3 The allocation of attentional resources as an underlying factor of strategy use

Throughout the work presented in this thesis is the notion of attentional resources as a limiting factor for spatial learning in older adults. More widely, the theory of limited resources (Craik & Byrd, 1982) is often paired with the inhibition deficit hypothesis (Hasher & Zacks, 1988) as a driving factor of age-related declines in cognition (e.g. Park & Festini, 2017). Our pattern of findings afford a slightly different account of how changes in attentional capacity and modulation may impact spatial learning.

A central pillar of the inhibition deficit hypothesis is that distraction of attention by irrelevant stimuli is result of ageing stemming from a lack of top-down control of attention (Chao & Knight, 1997; Gazzaley et al., 2005). However, our route navigation work has shown that older adults can modulate their attention along the temporal dimension. That is, the engagement and disengagement of attention over time in response to the changing relevance of the environment for the current task (Hilton et al., 2019; also see Hartmeyer et al., 2017). Indeed, even the distribution of attention in space seems preserved in older adults, who not only showed similar patterns of visual attention at decision points along a route to younger adults in our work (Hilton et al., 2019), but in other work have shown active inhibition of attention towards irrelevant landmarks (Grzeschik et al., 2019; Zhong & Moffat, 2016). Although older adults do display slightly differing gaze patterns when encoding an arrangement of objects in our place recognition work, we interpreted this not as a failure to control attention (e.g. an inhibition deficit) but as a reflection of strategy differences. Indeed, other recent work has demonstrated that the differing patterns of gaze for older adults reflects the use of different cues during spatial learning (Segen et al., 2020; also see Bécu et al., 2020).

This is not to say that older adults do not experience any attention inhibition deficit. It is important to highlight that older adults have been shown to be more prone to distraction than younger adults. For example, during road crossing situations, older adults are more likely to focus on pedestrians or cyclists when determining a safe point to cross a road (Nicholls & Miellet, 2019). Such changes in the control of visual attention are linked to unsafe road crossing behaviour. In route navigation, older adults are also distracted by crowds of people to a greater extent than younger adults, which results in even greater performance decrements for older adults on measures of route knowledge (Merriman et al., 2018). These studies include dynamic, moving stimuli that distract older adults, whereas the studies in this thesis used only static environments that were devoid of dynamic objects.

Given that dynamic objects are known to capture visual attention in general (Abrams & Christ, 2003), and that moving distractors specifically disrupt spatial memory (Postle et al., 2005), this is an important consideration for the lack of distraction shown by the older participants in this thesis. Interestingly, Merriman et al. (2018) showed that older adults were not more prone to distraction when simple moving objects were used as distractors, only when human avatars were present in the environment. Thus, it is likely that deficits in inhibition of attention in older adults emerge under specific circumstances such as with dynamic, but not with static, distractors, and with specific stimuli such as humans compared to simple objects. In contrast, they do not emerge under the experimental conditions in this thesis or other studies with static environments (Grzeschik et al., 2019) and thus cannot account for the observed age-related deficits in spatial learning.

Let us now assume that older adults maintain the ability to actively guide and modulate their attention and are not prone to involuntary distraction during spatial learning in environments without dynamic distraction. An alternative explanation for age-related changes in spatial learning ability is an active change in learning strategies. In Chapter 3 (Hilton et al., 2020) we suggested that a possible explanation for an alternative strategy was that older participants exceeded their capacity for the sequences of objects held in memory during place encoding. That is, they had to interrupt the sequence to revisit a recently attended object in order to refresh their representation, whereas younger adults linked more objects together before re-fixating a previously viewed object.

In the route navigation study of Chapter 5 (Hilton et al., 2021), we proposed a similar explanation for age-related differences in route knowledge, based around attentional resource limitation. We suggested that older participants actively directed their cognitive resources towards learning associative cue knowledge at the expense of landmark sequence knowledge. This strategy would be necessary because older adults do not have the attentional resource capacity to encode as much information as younger adults in a given time window during navigation. Of course, it is possible that the pattern of results could be explained by a more general deficit in serial learning, however the further analyses we conducted in Chapter 6 showed that older adults did display typical serial learning effects similar to the younger adults (i.e. primacy and recency). We therefore concluded that the diminished sequence knowledge did not manifest because of an interruption to sequence learning mechanisms, but as an overall decrement that can be explained by a general disengagement of serial learning during navigation.

It is a theme of this thesis that age-related decline in attentional resources is a driving factor for changes in spatial learning strategies. Changes in strategies can be explained by prioritisation of some forms of information over others, such as landmark identity and associative cue knowledge over sequence knowledge during route navigation. Additionally, limited resources may result in the sub-optimal execution of strategies, such as the reduction in landmark chaining when encoding a place compared to younger adults.

7.2.4 The use of eye-tracking to investigate spatial learning mechanisms

It is well established that the visual system plays an important role in spatial learning and navigation (see Ekstrom, 2015). It is also well evidenced that eye-tracking methods provide a window into the dynamics of visual attention and cognitive functioning during navigation (for a review see Kiefer et al., 2017). For example, eye-tracking has been used to investigate the use of landmarks (e.g. Hamid et al., 2010), spatial decision making dynamics (e.g. Wiener, Hölscher, et al., 2012) or cognitive effort whilst navigating (e.g. de Condappa & Wiener, 2016).

The eye-tracking work presented in Chapters 3 and 4 of this thesis seems to present two opposing views on the role of visual attention in age-related changes in spatial learning and navigation ability. In the place recognition study (Chapter 3) we suggested that changes in visual encoding strategies affect place learning (Hilton et al., 2020), a finding that has since been substantiated by other work in our lab (Segen et al., 2020). In the route navigation study (Chapter 4), in contrast, we did not observe difference in gaze behaviour that could explain age-related performance deficits (Hilton et al., 2019).

This juxtaposition can be explained by differences in the specific measures used in each study. For the route navigation study in Chapter 4, the measure of dispersion quantifies the spread of gaze over the visual scene within a certain time window. The spatial distribution of that gaze is not taken into account and thus the same dispersion value could be achieved through very different scanpaths. Therefore, this measure reveals that both age-groups increased their dispersion when approaching an intersection during navigation, but is not informative about the specific scanpaths that were used. Variations in scanpaths between age groups could reflect different strategies even though they show the same dispersion. Of course, this does not render the measures used in Chapter 4 uninformative. It shows that older adults change the way they sample the environment based on location in a similar way to younger adults; a finding which, alongside similarity on other gaze measures, we interpreted as a reflection that general control of visual attention during navigation is not affected by cognitive ageing.

The place recognition study of Chapter 3, on the other hand, did involve specific evaluation of gaze scanpaths during place learning. As in Chapter 4, age groups showed very small, or no differences in general saccade and fixation parameters (c.f. Hilton et al., 2019; Pratt et al., 1997; Segen et al., 2020). The scanpaths, however, showed small but systematic differences between older and younger participants which related to place recognition performance. In that study, we argued that this difference was not due to age-related changes in general control of visual attention but resulted from specific changes in encoding strategy.

The difference in analysis approaches for the two studies were driven not only by differences in the tasks (place recognition vs route navigation), but by the options afforded by the stimuli used in each experiment. That is, in-depth analysis of scanpaths was not viable for the study in Chapter 4, because the environment was visually complex enough that each participant could have relied on different features of the environment, even if they were using similar strategies (e.g. using a brightly coloured rooftop as a landmark vs using a shop sign as a landmark). In addition, the visual features of the environment varied between locations, and so a description of gaze at one location may not be applicable to another location along the route. This is a challenge with which spatial navigation and eye-tracking research is confronted with in general. Specifically, the visually complex nature of many of the environments which humans must navigate.

Other research areas utilising eye-tracking methodology do not suffer the problem described above, such as in reading tasks where text is always presented in the same place on the screen, and gaze is expected to follow a specific pattern (i.e. to go from left to right, from the end of one line to the beginning of the next etc.). Similarly, research in the field of face recognition can define features that exist in all (most) faces (i.e. the eyes, mouth, nose). In contrast, the visual characteristics of spatial environments can vary substantially, with large amounts of visual information which may or may not be relevant for a given task.

Much existing spatial navigation research utilising eye-tracking has circumvented this issue by using simple environments with few plainly definable landmarks that exist within an otherwise visually plain environment (e.g. Andersen et al., 2012; De Condappa & Wiener, 2014; Farran et al., 2016; Grzeschik et al., 2019; Hamid et al., 2010; Livingstone-Lee et al., 2011; Mueller et al., 2008). Just as in the environment we used in Chapters 5 and 6 of this thesis, intersections are usually visually identical except for one feature. Thus, it is possible to define regions of interest (ROI) for analysis of gaze behaviour. Whilst these studies are no doubt informative, they provide only a limited representation of real-world places and thus can only answer a limited pool of research questions about the dynamics of gaze during navigation. Indeed, in the earlier discussion of control of attention in simplistic environments, we highlighted that older adults are much more able to inhibit distraction in simple, static environments than when more complex situations are presented (e.g. Merriman et al., 2018). Thus, the simplistic situations used in many eye-tracking studies may be masking potential age-related differences that would be present in complex real-world environments.

In contrast to this approach, the environment in Chapter 4 of this thesis was visually complex, using Virtual Tübingen (Van Veen et al., 1998), which is a photo-realistic virtual model of a real town. As previously discussed, the measures that are available to analyse oculomotor behaviour recorded from such experiments are not currently advanced enough to tap into differences in strategy use between age-groups. The conundrum of this challenge then, is that simple environments with unrealistic features (e.g. only one object at each intersection) are conducive for in-depth analysis but are limited in ecological validity and in eliciting natural behaviour, but complex environments which are more representative of the real-world make eye-tracking data difficult to analyse and to create measures which are applicable to multiple stimuli.

An alternative approach in eye-tracking research is a data driven analysis of gaze behaviour. Such analysis options include the pixel-wise comparison of gaze heat maps as an alternative to researcher defined ROIs, as is possible with the iMap toolbox (Caldara & Miellet, 2011; Lao et al., 2017) or the statistical clustering of scanpaths (e.g. scasim; Von der Malsburg & Vasishth, 2011). Such tools are useful for understanding gaze behaviour when it is clear how the characteristics of the stimuli are related to the task at hand. For example, in road crossing scenarios, it is clear that the road, the sidewalks and the cars are all task-relevant, whilst pedestrians, a bench or a lamppost are not relevant for a road crossing task. The implementation of iMap for these scenarios is useful and informative because the implication that gaze was focussed on one region or another of the scene is relatable to whether that region is conducive for the task or not (Nicholls et al., 2019; Nicholls & Miellet, 2019).

In contrast to the above described scenario with definable task relevant and irrelevant parts of a scene, spatial navigation research has shown that many parts of a scene can be involved in spatial learning. For example eye-tracking studies have highlighted parts of stimuli such as objects (Chan et al., 2012; Hamid et al., 2010), the geometric structure (Keinath et al., 2017; Meilinger et al., 2012), the lines of sight (Wiener, Hölscher, et al., 2012), features aligned with current heading (Hollands et al., 2002) and the gist of a scene (Sampanes et al., 2008) as relevant for spatial tasks. Thus, understanding how a data driven representation of gaze in a visually complex environment relates to a navigation task is much less clear because almost all parts of the scene could represent a task relevant engagement of attention.

An additional barrier with such data driven analysis options is that they are mostly designed for use with static stimuli. Spatial navigation behaviour is fundamentally dynamic, using either pre-recorded videos such as in Chapters 4 and 5 of this thesis, or allowing individuals to generate unique self-guided trajectories (e.g. Andersen et al., 2012). One solution to this issue is conducting manual frame-by-frame analysis of gaze behaviour that was recorded in dynamic situations. However, this is a time and resource intensive endeavour, as shown by studies such as the one by Andersen et al. (2012), who reported 63 hours of frame-by-frame data processing per participant for analysis of eye-tracking data recorded from an actively controlled virtual navigation task.

Overall, it is clear from existing research that eye-tracking is a valuable source of information which can provide insights into navigation behaviour. In this thesis we related measures of gaze dispersion and gaze bias to route navigation performance, as well as gaze chaining to place recognition performance. However, differences between age groups may be subtle and highly dependent on the individual stimuli, and thus are poorly characterised and detected by general measures of gaze, as well as by the basic parameters of fixations and saccades. Instead, the next steps for eye-tracking methods in spatial research is to develop better analysis techniques that can be applied to visually complex, and importantly, to dynamic, stimuli. Such analysis techniques may be better suited to investigate the subtle differences between age groups than current, more general, measures of gaze behaviour.

7.3 Conclusion

The work in this thesis has extended our knowledge of how cognitive ageing affects the formation of spatial representations of places and routes. Whilst the chapters of this thesis have dealt with a range of topics, there are several significant implications for our understanding of cognitive ageing and navigation, and related future research on the topic.

We have considered the allocation of attentional resources in older adults as a driving factor behind strategy selection during place learning and route navigation. Thus, the cognitive demands of spatial tasks and how these might prompt a change in strategies should be considered when interpreting the effect of cognitive ageing. On the dynamics of visual attention, we have demonstrated that age-related differences in spatial learning are not reflected in general control of visual attention in older adults, but in specific visual encoding strategies. We suggest that future eye-tracking studies in this area are designed in such a way that task specific strategies can be identified, in order to tap into the subtle, but important, differences between age groups. For the formation of route knowledge, we found that age-related differences in separate knowledge types that are immediately apparent after few trials evolve distinctly when a route is learned to completion over longer learning sessions. We suggest that future studies investigating route navigation should consider at which stage of learning they wish to assess route knowledge, as differences reflected in early stages of learning may not reflect the final content of route knowledge. Finally, we also found that landmark sequence knowledge from route learning shows similar serial position effects as non-spatial sequence knowledge, which are similar across age-groups despite an overall decline in the sequence knowledge of older adults. It would be beneficial to link more general learning and memory research to our understanding of the spatial navigation system since these processes are unlikely to be fully independent.

7.4 References

Abrams, R. A., & Christ, S. E. (2003). Motion Onset Captures Attention. *Psychological Science*, *14*(5), 427–432. https://doi.org/10.1111/1467-9280.01458

Allison, S., & Head, D. (2017). Route repetition and route reversal: Effects of age and encoding method. *Psychology and Aging*, *32*(3), 220–231. https://doi.org/10.1037/pag0000170

Alyan, S., Jander, R., & Best, P. (2000). Hippocampectomized rats can use a constellation of landmarks to recognize a place. *Brain Research*, *876*(1–2), 225–237. https://doi.org/10.1016/S0006-8993(00)02585-3

Alyan, S., & McNaughton, B. L. (1999). Hippocampectomized rats are capable of homing by path integration. *Behavioral Neuroscience*, *113*(1), 19–31. https://doi.org/10.1037/0735-7044.113.1.19

Andersen, N. E., Dahmani, L., Konishi, K., & Bohbot, V. D. (2012). Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory*, *97*(1), 81–89. https://doi.org/10.1016/j.nlm.2011.09.007

Bécu, M., Sheynikhovich, D., Tatur, G., Agathos, C. P., Bologna, L. L., Sahel, J. A., & Arleo, A. (2020). Age-related preference for geometric spatial cues during real-world navigation. *Nature Human Behaviour*, *4*(1), 88–99. https://doi.org/10.1038/s41562-019-0718-z

Brown, T. I., & Chrastil, E. R. (2019). Editorial: Spatial navigation: Memory mechanisms and executive function interactions. *Frontiers in Human Neuroscience*, *13*(June), 1–3. https://doi.org/10.3389/fnhum.2019.00202

Buchner, A., & Jansen-Osmann, P. (2008). Is route learning more than serial learning? *Spatial Cognition and Computation*, *8*(4), 289–305. https://doi.org/10.1080/13875860802047201

Burte, H., Turner, B. O., Miller, M. B., & Hegarty, M. (2018). The neural basis of individual differences in directional sense. *Frontiers in Human Neuroscience*, *12*(October), 1–20. https://doi.org/10.3389/fnhum.2018.00410

Caldara, R., & Miellet, S. (2011). iMap: A novel method for statistical fixation mapping of eye movement data. *Behavior Research Methods*, *43*(3), 864–878. https://doi.org/10.3758/s13428-011-0092-x

Chan, E., Baumann, O., Bellgrove, M. A., & Mattingley, J. B. (2012). From objects to landmarks: the function of visual location information in spatial navigation. *Frontiers in Psychology*, *3*(August), 1–11. https://doi.org/10.3389/fpsyg.2012.00304

Chao, L. L., & Knight, R. T. (1997). Prefrontal deficits in attention and inhibitory control with aging. *Cerebral Cortex*, *7*(1), 63–69. https://doi.org/10.1093/cercor/7.1.63

Chersi, F., Donnarumma, F., & Pezzulo, G. (2013). Mental imagery in the navigation domain: A computational model of sensory-motor simulation mechanisms. *Adaptive Behavior*, *21*(4), 251–262. https://doi.org/10.1177/1059712313488789

Chrastil, E. R. (2013). Neural evidence supports a novel framework for spatial navigation. *Psychonomic Bulletin and Review*, *20*(2), 208–227. https://doi.org/10.3758/s13423-012-0351-6

Colombo, D., Serino, S., Tuena, C., Pedroli, E., Dakanalis, A., Cipresso, P., & Riva, G. (2017). Egocentric and allocentric spatial reference frames in aging: A systematic review. *Neuroscience and Biobehavioral Reviews*, *80*(February), 605–621. https://doi.org/10.1016/j.neubiorev.2017.07.012

Craig, M., Wolbers, T., Harris, M. A., Hauff, P., Della Sala, S., & Dewar, M. (2016). Comparable rest-related promotion of spatial memory consolidation in younger and older adults. *Neurobiology of Aging*. https://doi.org/10.1016/j.neurobiolaging.2016.08.007

Craik, F. I. M., & Byrd, M. (1982). Aging and Cognitive Deficits. In *Aging and Cognitive Processes*. https://doi.org/10.1007/978-1-4684-4178-9_11

Cushman, L. A., Duffy, C. J., Stein, K., & Duffy, C. J. (2008). Virtual reality identifies navigational defects in Alzheimer disease and cognitive aging. *Nature Clinical Practice Neurology*, *4*(12), 638–639. https://doi.org/10.1038/ncpneuro0929

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. https://doi.org/10.1007/s00426-014-0642-9

Ekstrom, A. D. (2015). Why vision is important to how we navigate. *Hippocampus*, *25*(6), 731–735. https://doi.org/10.1002/hipo.22449

Epstein, R. A., & Vass, L. K. (2014). Neural systems for landmark-based wayfinding in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1635). https://doi.org/10.1098/rstb.2012.0533

Farran, E. K., Formby, S., Daniyal, F., Holmes, T., & Van Herwegen, J. (2016). Route-learning strategies in typical and atypical development; eye tracking reveals atypical landmark selection in Williams syndrome. *Journal of Intellectual Disability Research*, *60*(10), 933–944. https://doi.org/10.1111/jir.12331

Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience*, *8*(10), 1298–1300. https://doi.org/10.1038/nn1543

Gröhn, M., Lokki, T., & Takala, T. (2005). Comparison of Auditory, Visual, and Audiovisual Navigation in a 3D Space. *ACM Transactions on Applied Perception*, *2*(4), 564–570. https://doi.org/10.1145/1101530.1101558

Grzeschik, R., Conroy-Dalton, R., Innes, A., Shanker, S., & Wiener, J. M. (2019). The contribution of visual attention and declining verbal memory abilities to age-related route learning deficits. *Cognition*, *187*(July 2018), 50–61. https://doi.org/10.1016/j.cognition.2019.02.012

Grzeschik, R., Hilton, C., Dalton, R. C., Konovalova, I., Cotterill, E., Innes, A., & Wiener, J. M. (2020). From repeating routes to planning novel routes : the impact of landmarks and ageing on route integration and cognitive mapping. *Psychological Research*, *0123456789*. https://doi.org/10.1007/s00426-020-01401-5

Gutchess, A. H., Welsh, R. C., Hedden, T., & Minear, M. (2005). Aging and the Neural Correlates of Successful Picture Encoding: Frontal Activations Compensate for Decreased Medial-Temporal Activity. *Journal of Cognitive Neuroscience*, 84–96. https://doi.org/10.1162/0898929052880048

Hamid, S. N., Stankiewicz, B., & Hayhoe, M. (2010). Gaze patterns in navigation: encoding information in large-scale environments. *Journal of Vision*, *10*, 28. https://doi.org/10.1167/10.12.28

Hartmeyer, S., Grzeschik, R., Wolbers, T., & Wiener, J. M. (2017). The effects of attentional engagement on route learning performance in a virtual environment: An aging study. *Frontiers in Aging Neuroscience*, *9*(JUL). https://doi.org/10.3389/fnagi.2017.00235

Hasher, L., & Zacks, R. T. (1988). Working Memory, Comprehension, and Aging: A Review and a New View. *Psychology of Learning and Motivation - Advances in Research and Theory*. https://doi.org/10.1016/S0079-7421(08)60041-9

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research*, *209*(1), 49–58. https://doi.org/10.1016/j.bbr.2010.01.012

Hebb, D. O. (1961). Distinctive features of learning in the higher animal. *Brain Mechanisms and Learning: A Symposium*.

Hilton, C., Johnson, A., Slattery, T. J., Miellet, S., & Wiener, J. M. (2021). The impact of cognitive aging on route learning rate and the acquisition of landmark knowledge. *Cognition*, *207*(November 2020), 104524. https://doi.org/10.1016/j.cognition.2020.104524

Hilton, C., Miellet, S., Slattery, T. J., & Wiener, J. (2019). Are age-related deficits in route learning related to control of visual attention? *Psychological Research*, *0*(0), 0. https://doi.org/10.1007/s00426-019-01159-5

Hilton, C., Muffato, V., Slattery, T. J., Miellet, S., & Wiener, J. (2020). Differences in Encoding Strategy as a Potential Explanation for Age-Related Decline in Place Recognition Ability. *Frontiers in Psychology*, *11*(September). https://doi.org/10.3389/fpsyg.2020.02182

Hilton, C., Wiener, J. M., & Johnson, A. (n.d.). Serial memory for landmarks encountered during route navigation. *Quarterly Journal of Experimental Psychology*.

Hollands, M., Patla, A., & Vickers, J. (2002). "Look where you're going!": Gaze behaviour associated with maintaining and changing the direction of locomotion. *Experimental Brain Research*, *143*(2), 221–230. https://doi.org/10.1007/s00221-001-0983-7

Izen, S. C., Chrastil, E. R., & Stern, C. E. (2018). Resting state connectivity between medial temporal lobe regions and intrinsic cortical networks predicts performance in a path integration task. *Frontiers in Human Neuroscience*, *12*(October), 1–12. https://doi.org/10.3389/fnhum.2018.00415

Janzen, G., & Weststeijn, C. G. (2007). Neural representation of object location and route direction: An event-related fMRI study. *Brain Research*, *1165*(1), 116–125. https://doi.org/10.1016/j.brainres.2007.05.074

Johnson, A. J., & Miles, C. (2019). Visual Hebb repetition effects: The role of psychological distinctiveness revisited. *Frontiers in Psychology*, *10*(JAN), 1–11. https://doi.org/10.3389/fpsyg.2019.00017

Keinath, A. T., Julian, J. B., Epstein, R. A., & Muzzio, I. A. (2017). Environmental Geometry Aligns the Hippocampal Map during Spatial Reorientation. *Current Biology*, *27*(3), 309–317. https://doi.org/10.1016/j.cub.2016.11.046

Kiefer, P., Giannopoulos, I., Raubal, M., & Duchowski, A. (2017). Eye tracking for spatial research: Cognition, computation, challenges. *Spatial Cognition and Computation*, *17*(1–2), 1–19. https://doi.org/10.1080/13875868.2016.1254634

Klencklen, G., Després, O., & Dufour, A. (2012). What do we know about aging and spatial cognition? Reviews and perspectives. *Ageing Research Reviews*, *11*(1), 123–135. https://doi.org/10.1016/j.arr.2011.10.001

Lao, J., Miellet, S., Pernet, C., Sokhn, N., & Caldara, R. (2017). iMap4: An open source toolbox for the statistical fixation mapping of eye movement data with linear mixed modeling. *Behavior Research Methods*, *49*(2), 559–575. https://doi.org/10.3758/s13428-016-0737-x

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers, T. (2017). The Aging Navigational System. *Neuron*, *95*(5), 1019–1035. https://doi.org/10.1016/j.neuron.2017.06.037

Lithfous, S., Dufour, A., & Després, O. (2013). Spatial navigation in normal aging and the prodromal stage of Alzheimer's disease: Insights from imaging and behavioral studies. In *Ageing Research Reviews*. https://doi.org/10.1016/j.arr.2012.04.007

Livingstone-Lee, S. A., Murchison, S., Zeman, P. M., Gandhi, M., van Gerven, D., Stewart, L., Livingston, N. J., & Skelton, R. W. (2011). Simple gaze analysis and special design of a virtual Morris water maze provides a new method for differentiating egocentric and allocentric navigational strategy choice. *Behavioural Brain Research*, *225*(1), 117–125. https://doi.org/10.1016/j.bbr.2011.07.005

Meilinger, T., Franz, G., & Bülthoff, H. H. (2012). From isovists via mental representations to behaviour: First steps toward closing the causal chain. *Environment and Planning B: Planning and Design*, *39*(1), 48–62. https://doi.org/10.1068/b34048t

Meilinger, T., Knauff, M., & Bulthoff, H. H. (2008). Working memory in wayfinding - A dual task experiment in a virtual city. *Cognitive Science*, *32*(4), 755–770. https://doi.org/10.1080/03640210802067004

Merriman, N. A., Ondřej, J., Rybicki, A., Roudaia, E., O'Sullivan, C., & Newell, F. N. (2018). Crowded environments reduce spatial memory in older but not younger adults. *Psychological Research*, *82*(2), 407–428. https://doi.org/10.1007/s00426-016-0819-5

Moffat, S. D. (2009). Aging and spatial navigation: What do we know and where do we go? *Neuropsychology Review*, *19*(4), 478–489. https://doi.org/10.1007/s11065-009-9120-3

Mueller, S. C., Jackson, C. P. T., & Skelton, R. W. (2008). Sex differences in a virtual water maze: An eye tracking and pupillometry study. *Behavioural Brain Research*, *193*(2), 209–215. https://doi.org/10.1016/j.bbr.2008.05.017

Muffato, V., Hilton, C., Meneghetti, C., De Beni, R., & Wiener, J. M. (2019). Evidence for age-related deficits in object-location binding during place recognition. *Hippocampus*, *February*, 1–9. https://doi.org/10.1002/hipo.23099

Nicholls, V., Jean-Charles, G., Lao, J., de Lissa, P., Caldara, R., & Miellet, S. (2019). Developing attentional control in naturalistic dynamic road crossing situations. *Scientific Reports*, *9*(1), 1–10. https://doi.org/10.1038/s41598-019-39737-7

Nicholls, V., & Miellet, S. (2019). Ageing and Visual Attentional Control in Naturalistic, Dynamic Road Crossing Situations. *PERCEPTION*, *48*, 52.

Park, D. C., & Festini, S. B. (2017). Theories of memory and aging: A look at the past and a glimpse of the future. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, *72*(1), 82–90. https://doi.org/10.1093/geronb/gbw066

Pazzaglia, F., Meneghetti, C., & Ronconi, L. (2018). Tracing a Route and Finding a Shortcut: The Working Memory, Motivational, and Personality Factors Involved. *Frontiers in Human Neuroscience*, *12*(May), 1–11. https://doi.org/10.3389/fnhum.2018.00225

Postle, B. R., D'Esposito, M., & Corkin, S. (2005). Effects of verbal and nonverbal interference on spatial and object visual working memory. *Memory & Cognition*, *33*(2), 203–212. https://doi.org/10.3758/BF03195309

Pratt, J., Abrams, R. A., & Chasteen, A. L. (1997). Initiation and inhibition of saccadic eye movements in younger and older adults: An analysis of the gap effect. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, *52*(2). https://doi.org/10.1093/geronb/52B.2.P103

Ramanoël, S., Durteste, M., Bécu, M., Habas, C., & Arleo, A. (2020). Differential Brain Activity in Regions Linked to Visuospatial Processing During Landmark-Based Navigation in Young and Healthy Older Adults. *Frontiers in Human Neuroscience*, *14*(October), 1–16. https://doi.org/10.3389/fnhum.2020.552111

Rodgers, M. K., Sindone, J. A., & Moffat, S. D. (2012). Effects of age on navigation strategy. *Neurobiology of Aging*, *33*(1), 202.e15-202.e22. https://doi.org/10.1016/j.neurobiolaging.2010.07.021

Roediger, H. L., & DeSoto, K. A. (2014). Forgetting the presidents. *Science*, *346*(6213), 1106–

1109. https://doi.org/10.1126/science.1259627

Sampanes, A. C., Tseng, P., & Bridgeman, B. (2008). The role of gist in scene recognition. *Vision Research*, *48*(21), 2275–2283. https://doi.org/10.1016/j.visres.2008.07.011

Segen, V., Avraamides, M. N., Slattery, T. J., & Wiener, J. M. (2020). Age-related differences in visual encoding and response strategies contribute to spatial memory deficits. *Memory and Cognition*, *1*. https://doi.org/10.3758/s13421-020-01089-3

Siegel, A. W., & White, S. H. (1975). The development of spatial representations of large-scale environments. *Advances in Child Development and Behavior*. https://doi.org/10.1016/S0065-2407(08)60007-5

Taillade, M., Sauzéon, H., Dejos, M., Arvind Pala, P., Larrue, F., Wallet, G., Gross, C., & N'Kaoua, B. (2013). Executive and memory correlates of age-related differences in wayfinding performances using a virtual reality application. *Aging, Neuropsychology, and Cognition*, *20*(3), 298–319. https://doi.org/10.1080/13825585.2012.706247

Van Veen, H. A. H. C. H. C., Distler, H. K., Braun, S. J., & Bülthoff, H. H. (1998). Navigating through a virtual city: Using virtual reality technology to study human action and perception. *Future Generation Computer Systems*, *14*(3–4), 231–242. https://doi.org/10.1016/s0167-739x(98)00027-2

Von der Malsburg, T., & Vasishth, S. (2011). What is the scanpath signature of syntactic reanalysis? *Journal of Memory and Language*, *65*(2), 109–127. https://doi.org/10.1016/j.jml.2011.02.004

Ward, G., Tan, L., & Grenfell-Essam, R. (2010). Examining the relationship between free recall and immediate serial recall: The effects of list length and output order. *Journal of Experimental Psychology: Learning Memory and Cognition*, *36*(5), 1207–1241. https://doi.org/10.1037/a0020122

Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive bias for extrahippocampal navigation strategies in aging humans. *Journal of Neuroscience*, *33*(14), 6012–6017. https://doi.org/10.1523/JNEUROSCI.0717-12.2013

Wiener, J. M., Hölscher, C., Büchner, S., & Konieczny, L. (2012). Gaze behaviour during space perception and spatial decision making. *Psychological Research*, *76*(6), 713–729. https://doi.org/10.1007/s00426-011-0397-5

Wiener, J. M., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: Effects of cognitive aging. *Frontiers in Aging Neuroscience*, *4*(MAY), 1–7. https://doi.org/10.3389/fnagi.2012.00007

Wu, Y., Chen, K., Ye, Y., Zhang, T., & Zhou, W. (2020). Humans navigate with stereo olfaction. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(27), 16065–16071. https://doi.org/10.1073/pnas.2004642117

Zhong, J. Y., & Moffat, S. D. (2016). Age-related differences in associative learning of landmarks and heading directions in a virtual navigation task. *Frontiers in Aging Neuroscience*, *8*(MAY), 1–11. https://doi.org/10.3389/fnagi.2016.00122

Zhong, J. Y., & Moffat, S. D. (2018). Extrahippocampal contributions to age-related changes in spatial navigation ability. *Frontiers in Human Neuroscience*, *12*(July), 1–8. https://doi.org/10.3389/fnhum.2018.00272

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Chapter 8

Appendix

8.1 Appendix 1: published manuscript of Chapter 2: Evidence for age-related deficits in object-location binding during place recognition

The following manuscript appears as it is published as: Muffato, V., Hilton, C., Meneghetti, C., De Beni, R., & Wiener, J. M. (2019). Evidence for age-related deficits in object-location binding during place recognition. Hippocampus, February, 1–9. https://doi.org/10.1002/hipo.23099

Note that this article was published in the journal specific 'Rapid Communication' format, which differs from the format used for the other manuscripts presented in this thesis.

8.1.1 Abstract

Deciding whether a place is the same or different than places encountered previously is a common task in daily navigation which requires to develop knowledge about the locations of objects (object-location binding) and to recognize places from different perspectives. These abilities rely on hippocampal functioning which is susceptible to increasing age. Thus, the question of the present study is how they both together impact on place recognition in aging. Forty people aged 20–29, 44 aged 60–69, and 32 aged 70–79 were presented with places consisting of four different objects during the encoding phase. In the test phase, they were then presented with a second place and had to decide whether it was the same or different. Test places were presented from different perspectives (0°, 30°, 60°) and with different object conditions (same, a swap of two objects, a substitution with a novel object). The sensitivity for detecting changes (d') decreased from 20–29 to 60–69 and to 70–79 years old, and with increasing perspective shifts. Importantly, older adults were less sensitive to object swapping than to object substitution, while young participants did not show any difference. Overall, these results suggest specific age-related difficulties in object-location binding in the context of place recognition.

8.1.2 Introduction

The ability to recognize a previously visited place, even if experienced from a viewpoint different to that during initial encoding, is crucial for successful navigation (Waller & Nadel, 2013). While many places can easily be identified by single distinctive environmental features (i.e., landmarks), other places are recognized by the spatial relationships between a number of more common environmental features. In this study we examined how cognitive aging, which is known to affect navigation and orientation abilities (Lester, Moffat, Wiener, Barnes, & Wolbers, 2017), impacts on the recognition of places that are defined by a specific spatial arrangement of several objects. In particular, we were interested in how substituting or swapping object locations as well as perspective shifts affected place recognition.

Recognizing a place, defined by a number of objects, requires memory of object identity as well as of their locations (Postma, Kessels, & van Asselen, 2004). To associate these separate memory systems, the object identity must be bound to their locations (Pertzov, Dong, Peich, & Husain, 2012). Successful retrieval of object-location representations allows individuals to identify a place on basis of an arrangement of objects and to distinguish it from other, similar arrangements. However, if object-location binding fails, “swap” errors may arise, that is, errors in which objects are believed to have been in a location occupied by a different object (Pertzov et al., 2012). So far, object-location binding has been studied in small-scale two-dimensional spaces, often with abstract shapes that are presented at different screen positions (Dai, Thomas, & Taylor, 2018). Here we translated these paradigms into a context more relevant for orientation and navigation. Specifically, we used virtual environments technology to create images of three-dimensional places that were defined by the spatial arrangement of different objects and that could be presented from different viewpoints.

The evidence for how aging affects object memory, location memory and object-location binding in small scale space is currently mixed. While some studies report that memory for object identity and object locations was unaffected by aging (Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000), other studies report decreased precision in identifying both object identity (Dai et al., 2018) and location (Pertzov, Heider, Liang, & Husain, 2015). Similarly, object-location binding has been reported to be preserved in older adults (Ellis, Katz, & Williams, 1987), whereas other studies suggest that binding performance decreases in older age (Dai et al., 2018; Mitchell et al., 2000). The fact that at least some studies report age-related deficits in object and location memory and object-location binding, raises the important question of whether this process is also involved in declining recognition of three-dimensional spaces or places, therefore potentially contributing to age-related declines in navigation abilities.

Place recognition during everyday navigation is different from remembering and recognizing a layout of objects in 2D space, insofar as places are often experienced from a perspective that differs from that during initial encoding. Such perspective changes can change the visual appearance of a place markedly and typically results in declining place recognition performance (Diwadkar & McNamara, 1997; Waller, 2006). To recognize a place after a perspective changes, it is not sufficient to compare the current visual image with that during encoding (Friedman & Waller, 2008). Instead, it has been argued that hippocampal-dependent topographical memories, which represent the spatial relationship between objects locations, allow for place recognition after perspective changes (Hartley et al., 2007; King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002). As the hippocampus undergoes functional and morphological changes already in typical aging (Klencklen, Després, & Dufour, 2012), it is not surprising that a series of studies has reported age-related deficits in perspective taking abilities (e.g., Inagaki et al., 2002; Montefinese, Sulpizio, Galati, & Committeri, 2015; Watanabe, 2011).

Previous studies have investigated age-related changes in spatial perspective taking or object-location binding in isolation. The present study aimed to combine these fields of inquiry to investigate how these mechanisms interact and how aging affects object-location binding in the context of 3D place recognition. Specifically, we presented participants with a spatial scene comprised of four different objects during encoding. In the test phase, they were then presented with the same or a similar place from the same or a different perspective. Places were changed by either substituting one object with a new object (substitute condition) or by swapping the locations of two objects (swap condition). Participants' task was to indicate whether or not the place had changed.

We expected to replicate earlier findings by showing (a) declining performance with increasing perspective shifts (Diwadkar & McNamara, 1997); (b) higher performance in the substitution than the swap condition as the former can be solved solely by object memory, while the latter relies on binding objects to their locations (Pertzov et al., 2012). For the same reason we expected that (c) perspective shifts affected the swap condition more than the substitute condition, resulting in an interaction between condition and perspective. Overall, we expected (d) worse performance in the older as compared to the younger participant group (Klencklen et al., 2012). Finally, if aging affected object-location binding also in the context of place recognition, we expected (e) an age × condition interaction, with a stronger performance decrement in the older age group in the swap as compared to the substitute condition.

A total of 116 participants gave their written informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013) to take part to the study: 40 people aged 20–29 (18 males; M age = 23.35, SD = 2.41), 44 people aged 60–69 (21 males; M age =

64.55, SD = 3.50), and 32 people aged 70–79 (19 males; M age = 72.69, SD = 2.48). We have chosen these specific age groups (see Baltes, 1998) based on earlier studies demonstrating an agerelated decline in spatial learning from 60 years of age onward, which accelerates beyond the age of 70 (e.g., Barrash, 1994; Gazova et al., 2013).

Participants attended two separate sessions, lasting ~40 min each. In the first session, participants completed a socio-demographic questionnaire, the MoCA (older participants only) and the vocabulary test. In the second session, they performed the place recognition task presenting 72 trials in a randomized order (see Figure 8-1 for places and conditions in the place recognition task).

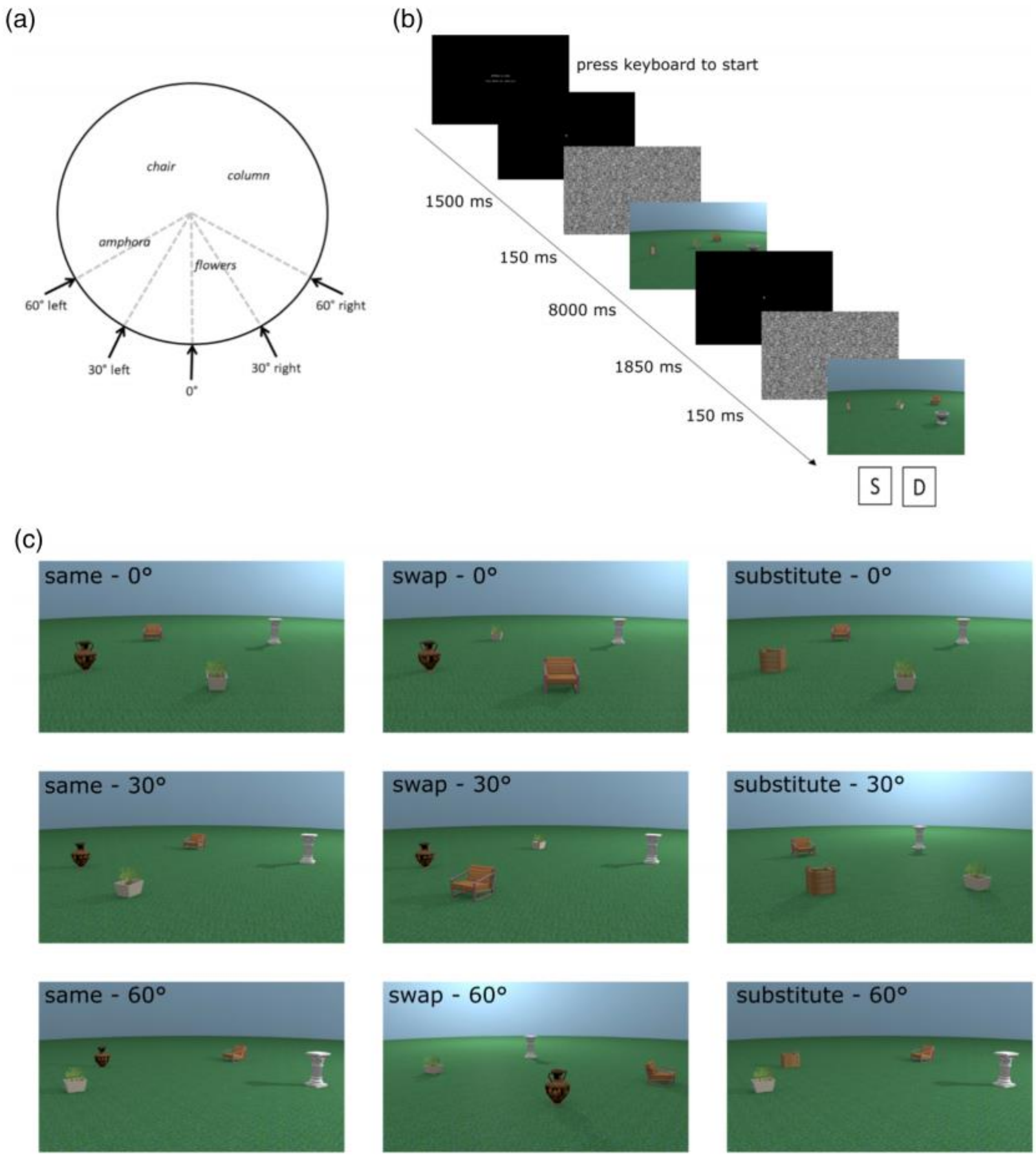

Figure 8-1 -Places and conditions in the place recognition task. Panel a: Schematic drawing of possible viewpoints from which the place was rendered (the circle represents the area in which objects could be located. The arrows indicate the direction of the cameras for the rendering); Panel b: Sequence of a trial; Panel c: Object and perspective manipulations referred to place 1. Place 1 had a chair, a column, an amphora, and flowers. The second place featured a lion statue, a vase, a table, and a basket. The third place featured a basket, the flowers, a chair, and a vase. The fourth place featured a bust, a lion statue, a box, and a table. The fifth, the flowers, a vase, an amphora, and a box. The sixth, a chair, a basket, a column, and a bust. The seventh, a column, a table, a basket, and an amphora. The eighth, a vase, a bust, a box, and a lion statue. Light and shadows changed accordingly to the perspective shift in the place

Accuracy in the place recognition task was converted into sensitivity (d') scores (we calculated also response bias, see Section 2). We ran a linear mixed effects (LMEs) model analysis for d' scores using the lme4 package (version 1.1–14; Bates, Mächler, Bolker, &

Walker, 2015) in R (R Development Core Team, 2013). Fixed effects were age group as a factor (20–29, 60–69, 70–79 years old) coded using successive differences contrast coding, gender as a factor (male, female) coded using sum contrast coding, condition as a factor (swap, substitute) coded using sum contrast coding and perspective shift as a factor (0°, 30°, 60°) coded using successive differences contrast coding. Participant was included a random factor. We started with an intercept only model and added random by-participant slopes for fixed effects one by one and then added interactions between random slopes. Each random slope or interaction was included only if the model converged and it significantly improved the model (the final model code was: model = lmer (dPrime ~ condition * ageGroup * perspective * gender + [1 + perspective + condition|participantNumber], data).

Coefficients, standard errors, and t-values for the final model are reported in Table 8-1 and shows that age group, perspective and condition are all significant predictors of d’ scores. Specifically, for age group both advances from 20–29 to 60–69 years old, and from 60–69 to 70–79 years old predicts a significant reduction in d’ scores. Perspective shift from 0° to 30°, and from 30° to 60° significantly predicts a reduction in d’ prime scores. The significant condition main effect shows that d’ scores are significantly lower in the swap condition then in the substitute condition. Importantly, the model reveals a significant age group × condition interaction. Specifically, this interaction shows that when age changes from 20–29 to 60–69, performance drops more in the swap condition than for the substitute condition (see Figure 8-2, Panel b).

Overall, the sensitivity to detect changes in the object layout decreased with increasing perspective shifts and increasing age and was lower when objects swapped locations as compared to situations in which objects were substituted. Our older adults had particular problems with the swap condition, which suggests a specific age-related object-location binding deficit. This effect was present already in our participants aged 60–69 and did not significantly worsen in our older participant group (aged 70–79). Our results demonstrate that older adults show deficits in memory for layouts of objects experienced across different perspectives (in line with Hartley et al., 2007; Montefinese et al., 2015). Age-related neurodegeneration in the hippocampal circuit is crucial for establishing topographical or allocentric spatial memories that provide the viewpoint independence required to recognize places from different perspectives (King et al., 2002).

Table 8-1 - Effect on d' scores model

Predictor	Coefficient	SE	t statistic
(Intercept)	**1.91**	**0.05**	**35.00**
Age group			
60-69 vs. 20-30	**-0.63**	**0.13**	**-4.94**
70-79 vs. 60-69	**-0.47**	**0.14**	**-3.42**
Gender			
Female vs. Male	0.04	0.05	0.73
Perspective			
30° vs. 0°	**-0.29**	**0.07**	**-4.36**
60° vs. 30°	**-0.13**	**0.07**	**-2.07**
Condition			
Substitute vs. Swap condition	**-0.17**	**0.03**	**-5.42**
Age group × perspective			
60-69 vs. 20-30 × 30° vs. 0°	-0.19	0.15	-1.24
70-79 vs. 60-69 × 30° vs. 0°	0.07	0.17	0.43
60-69 vs. 20-30 × 60° vs. 30°	-0.01	0.15	-0.08
70-79 vs. 60-69 × 60° vs. 30°	-0.05	0.16	-0.29
Age group × condition			
Substitute vs. Swap condition × 60-69 vs. 20-30	**-0.23**	**0.07**	**-3.21**
Substitute vs. Swap condition × 70-79 vs. 60-69	0.05	0.08	0.68
Perspective × condition			
Substitute vs. Swap condition × 30° vs. 0°	-0.05	0.04	-1.25
Substitute vs. Swap condition × 60° vs. 30°	-0.03	0.04	-0.87
Age group × gender			
Female vs. Male × 60-69 vs. 20-30	0.01	0.13	0.04
Female vs. Male × 70-79 vs. 60-69	-0.03	0.14	-0.20
Perspective × gender			
Female vs. Male × 30° vs. 0°	-0.01	0.07	-0.10
Female vs. Male × 60° vs. 30°	0.12	0.06	1.80
Condition × gender			

Female vs. Male × Substitute vs. Swap condition	0.01	0.03	0.24
Age group × perspective × condition			
Substitute vs. Swap × 60-69 vs. 20-30 × 30° vs. 0°	-0.16	0.09	-1.70
Substitute vs. Swap × 70-79 vs. 60-69 × 30° vs. 0°	-0.01	0.10	-0.11
Substitute vs. Swap × 60-69 vs. 20-30 × 60° vs. 30°	0.10	0.09	1.07
Substitute vs. Swap × 70-79 vs. 60-69 × 60° vs. 30°	-0.07	0.10	-0.69
Gender × perspective × condition			
Female vs. Male × Substitute vs. Swap × 30° vs. 0°	-0.00	0.04	-0.01
Female vs. Male × Substitute vs. Swap × 60° vs. 30°	0.01	0.04	0.33
Age group × gender × perspective			
60-69 vs. 20-30 × Female vs. Male × 30° vs. 0°	-0.09	0.15	-0.59
70-79 vs. 60-69 × Female vs. Male × 30° vs. 0°	0.30	0.16	1.83
60-69 vs. 20-30 × Female vs. Male × 60° vs. 30°	-0.07	0.15	-0.43
70-79 vs. 60-69 × Female vs. Male × 60° vs. 30°	0.17	0.16	1.06
Age group × gender × condition			
60-69 vs. 20-30 × Female vs. Male × Substitute vs. Swap	-0.05	0.07	-0.70
70-79 vs. 60-69 × Female vs. Male × Substitute vs. Swap	-0.04	0.08	-0.58
Age group × gender × perspective × condition			
60-69 vs. 20-30 × Female vs. Male × 30° vs. 0° × Substitute vs. Swap	-0.01	0.09	-0.07
70-79 vs. 60-69 × Female vs. Male × 30° vs. 0° × Substitute vs. Swap	0.01	0.10	0.10
60-69 vs. 20-30 × Female vs. Male × 60° vs. 30° × Substitute vs. Swap	0.04	0.09	0.42
70-79 vs. 60-69 × Female vs. Male × 60° vs. 30° × Substitute vs. Swap	-0.08	0.10	-0.78

Note. |t|>1.96 in bold.

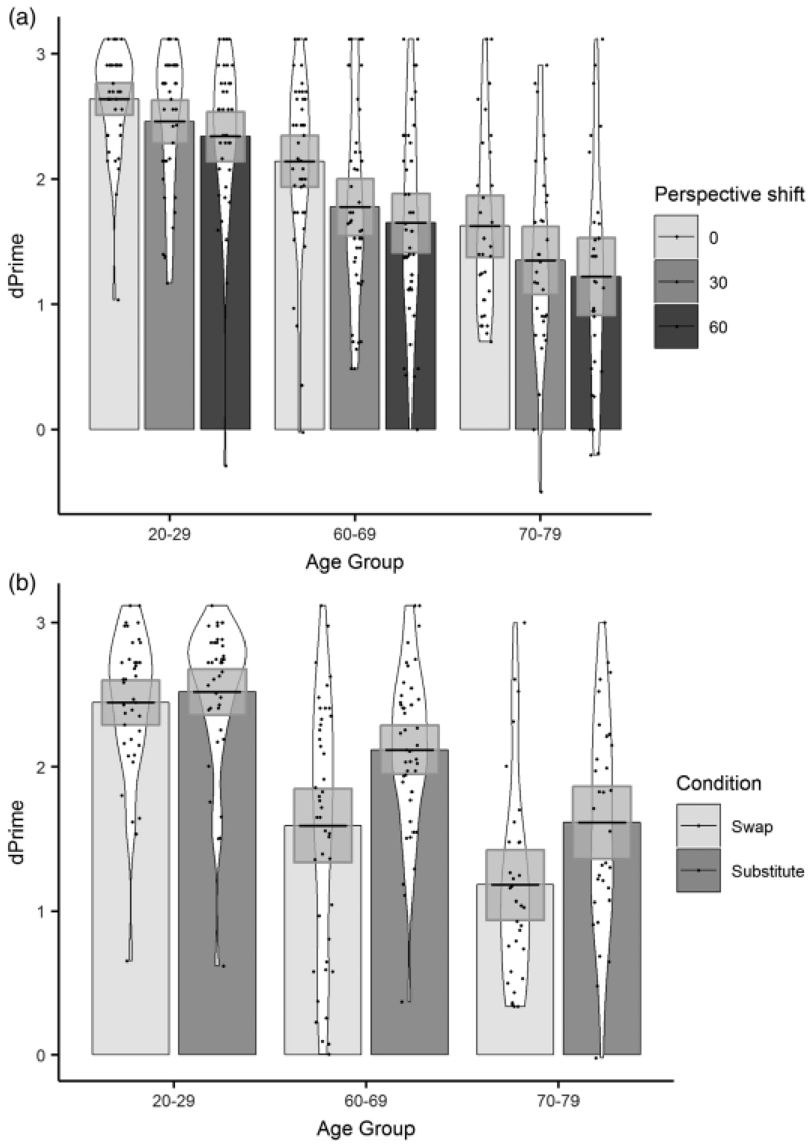

Figure 8-2 - Age group × perspective (Panel a) and age group × condition (Panel b) plots. Plots are mean averages with confidence interval error bars, individual data points and density profiles.

However, to our knowledge, no study so far has investigated whether object-location binding contributed to the age-related impairments reported in spatial memory for places. Our older age groups were less likely to detect that two objects had been swapped than that one object had been substituted. This cannot be explained by general memory deficits. Instead, it highlights a specific deficit in binding objects to their locations, which could also have contributed to age differences reported in earlier studies. Recent reviews highlight the involvement of the left hippocampus and other related brain areas (such as, bilateral medial temporal lobe, Postma & van der Ham, 2016; Zimmermann & Eschen, 2017) in object-location binding, brain areas that are susceptible to age-related functional and anatomical changes (Klencklen et al., 2012).

The performance in the substitute condition was higher than in the swap condition. This was expected as the substitute condition can be solved by object identity memory alone, while the swap condition requires object as well as location memory (Pertzov et al., 2012). It should be noted at this point that there was a trend of declining performance in the older age groups also in the substitute condition. One explanation for this decline is age-related differences in object memory (Dai et al., 2018) which would have also contributed to the overall decline in place recognition performance in older adults. However, as other studies suggested preserved memory for objects/landmarks in older age (e.g., Mitchell et al., 2000), an alternative explanation for this result relates to age-related differences in strategy use when solving the task. The current data does not allow us to distinguish between age-related differences in encoding strategies or age-related differences in object-location binding, but we are currently running a follow up eye-tracking study to address this issue.

We argue that the age x condition interaction resulted from a specific age-related deficit in object-location binding, a cognitive process, which is required to solve the swap but not the substitute condition. However, one might argue that our older participants were simply more affected than our young participants by the increased task difficulty in the swap condition, resulting from the additional information processing required, but independent of the specific nature of the addition cognitive processes involved. This explanation, however, seems unlikely, given that the additional difficulty resulting from engaging perspective taking mechanisms is handled equally well by all age groups, that is, it did not result in an age × perspective interaction. Another important point to briefly address here is the role of the hippocampus in pattern completion and pattern separation (Yassa & Stark, 2011), which is required to discriminate whether a place was identical or different from a place encoded before. Aging is typically associated with a pattern completion bias (Vieweg, Stangl, Howard, & Wolbers, 2015), which would suggest that older adults produce more miss errors, rather than false positives. In fact response bias analyses (see Section 2) show that our older participants were more conservative (more likely to accept a different place as identical) than our young participants in the swap condition. This result is in line with the idea of an age-related pattern completion bias and our results suggest that declining object-location binding may contribute this bias.

While object-location binding is typically studied with small-scale two-dimensional stimuli (e.g., Dai et al., 2018), we here used virtual environments technology to design three-dimensional places. In other words, we have translated the standard paradigm into a slightly more realistic context that also allowed us to present the places from different viewpoints

(Friedman & Waller, 2008). Recognizing places from viewpoints different to those during encoding is an important ability when navigating. For example, recognizing an intersection from a different perspective when navigating routes that are crossing is crucial for integrating route knowledge into cognitive maps. However, our study did not directly assess participants' ability to navigate, which is a limitation that should be addressed in future studies.

In line with earlier research (Montefinese et al., 2015) we found that performance declined with increasing perspective shifts. Note, however, that the size of the effect was more than twice as large between 0° and 30° than between 30° and 60°. These findings are consistent with either the idea of an allocentric representation that provides preferential access from the perspective aligned with the learning viewpoint (Diwadkar & McNamara, 1997) or with a two abilities account, in which the 0 condition is solved by a "simple" image comparison (i.e., the place is stored as a visual scene, Milner & Goodale, 2008), while perspective taking is only being applied if the perspective actually changed. Our current study was not designed to distinguish between these different possible explanations.

Interestingly, we did not find an interaction between age and perspective shifts: while both older age groups performed worse than our younger age group, this difference did not compound with increasing perspective shifts. These findings suggest that the ability to perform perspective-taking tasks is preserved in older age (e.g., Watanabe, 2011). These findings are in line with neuropsychological studies which suggest that egocentric perspective use is supported by parietal cortex activation (Postma & van der Ham, 2016), a brain area which is relatively resilient against functional changes resulting from age-related structural changes when compared to the medial temporal lobe (Yamamoto, Fox, Boys, & Ord, 2019).

Instead—and as discussed above—we argue that performance differences between age groups in our place recognition task relate to other processes involving the ability to form topographic representations, object identity memory, and object-location binding.

To conclude, the present study suggests a specific age-related object-location binding—but not a perspective shift—deficit in the context of place recognition.

8.1.3 Detailed methods

8.1.3.1 Participants

Participants met the inclusion criteria requiring them (a) living independently, (b) healthy as measured through history of diseases capable of causing cognitive, visual, auditory and/or motor impairments (Crook et al., 1986), (c) cognitively normal function as measured by a score of 26+ on the Montreal Cognitive Assessment (MoCA, Nasreddine et al., 2005) for older participants. None of the participants were excluded. Older adults aged 60–69 (M years of education = 11.18, SD = 3.35) and 70–79 (M = 12.19, SD = 3.15) had a lower education level than the young adults (M = 15.42, SD = 2.23), $F(2,115) = 23.05$, $\eta 2 = .29$, $p < .001$, consistent with the socio-demographic differences due to the cohort effect. All groups, however, showed similar performance (20–29 years old: M = 54.55, SD = 9.14; 60–69 years old: M = 52.73, SD = 9.45; 70–79 years old: M = 54.90, SD = 8.78; $F < 1$, $p = .52$) in the vocabulary test (Wechsler, 1981) which assesses crystallized abilities.

8.1.3.2 Place recognition task

We created eight places using Blender 2.66. Each place depicts the same garden (green grass, light blue sky, and the light of the sun) with four objects in different positions. For each of the places, we created two further places: one with the position of two objects swapped, one with an object substituted with a novel object. Each place was rendered from five different viewpoints, the original viewpoint and then from a viewpoint that differed by 30° and 60° to the left and to the right (see Figure 8-1, Panel a). The positions of the objects in the place were chosen to minimize occlusion, such that all objects were visible from all viewpoints. The place recognition task was prepared using OpenSesame 3.1.4 (Mathôt, Schreij, & Theeuwes, 2012). There were 72 trials (see Figure 8-1, Panel b for the time sequence of the trial) comprising of nine trials for each of the eight places including three trials presented in the same condition (from 0°, 30°, and 60°), three in the swap condition (from 0°, 30°, and 60°), and three in the substitute condition (from 0°, 30°, and 60°; see Figure 8-1, Panel c, for an example of manipulations referring to place 1).

8.1.3.3 Response bias analyses

We calculated response bias and ran a LME analysis using the same factors as in the analyses of d’ presented in the main text. Coefficients, standard errors, and t-values for the final model are reported in Table 8-2Table 8-2 - Effect on response bias model. It shows a reliable main effect of perspective and condition, while gender and age group were not significant. Specifically, perspective shift from 0° to 30° and from 30° to 60° significantly predicts a reduction bias scores. Response biases are significantly higher in the swap condition then in the substitute condition. The model also reveals a number of significant interactions. Concerning the age group × condition, older adults groups had a more positive bias than our younger group only in the swap, but not in the substitute condition; see Figure 8-3). Concerning age group × perspective, people aged 70–79 had a higher positive bias at 0° than 30°, while people aged 60–69 had not; the latter had a higher positive bias at 30° than 60°, while people aged 20–29 did not show this. An interaction age × gender was also found. Specifically, males aged 70–79 had a more positive bias than female aged 70–79, while no difference between males and females was found for people aged 60–69.

Table 8-2 - Effect on response bias model

Predictor	Coefficient	SE	t statistic
(Intercept)	**0.27**	**0.03**	**8.71**
Age group			
60-69 vs. 20-30	0.09	0.07	1.18
70-79 vs. 60-69	-0.03	0.08	-0.36
Gender			
Female vs. Male	0.01	0.03	0.40
Perspective			
30° vs. 0°	**-0.23**	**0.04**	**-5.24**
60° vs. 30°	**-0.12**	**0.03**	**-3.83**
Condition			
Substitute vs. Swap condition	**0.08**	**0.02**	**5.42**
Age group × perspective			
60-69 vs. 20-30 × 30° vs. 0°	-0.13	0.10	-1.33
70-79 vs. 60-69 × 30° vs. 0°	**-0.23**	**0.11**	**-2.12**
60-69 vs. 20-30 × 60° vs. 30°	**-0.20**	**0.07**	**-2.72**
70-79 vs. 60-69 × 60° vs. 30°	-0.03	0.08	-0.34
Age group × condition			
Substitute vs. Swap condition × 60-69 vs. 20-30	**0.12**	**0.04**	**3.20**
Substitute vs. Swap condition × 70-79 vs. 60-69	-0.03	0.04	-0.68
Perspective × condition			
Substitute vs. Swap condition × 30° vs. 0°	0.02	0.02	1.25
Substitute vs. Swap condition × 60° vs. 30°	0.02	0.02	0.87
Age group × gender			
Female vs. Male × 60-69 vs. 20-30	-0.02	0.07	-0.22
Female vs. Male × 70-79 vs. 60-69	**0.18**	**0.08**	**2.36**
Perspective × gender			

Female vs. Male × 30° vs. 0°	0.02	0.04	0.39
Female vs. Male × 60° vs. 30°	0.04	0.03	1.20
Condition × gender			
Female vs. Male × Substitute vs. Swap condition	-0.00	0.02	-0.24
Age group × perspective × condition			
Substitute vs. Swap × 60-69 vs. 20-30 × 30° vs. 0°	0.08	0.05	1.69
Substitute vs. Swap × 70-79 vs. 60-69 × 30° vs. 0°	0.01	0.05	0.11
Substitute vs. Swap × 60-69 vs. 20-30 × 60° vs. 30°	-0.05	0.05	-1.07
Substitute vs. Swap × 70-79 vs. 60-69 × 60° vs. 30°	0.03	0.05	0.69
Gender × perspective × condition			
Female vs. Male × Substitute vs. Swap × 30° vs. 0°	0.00	0.02	0.01
Female vs. Male × Substitute vs. Swap × 60° vs. 30°	-0.01	0.02	-0.33
Age group × gender × perspective			
60-69 vs. 20-30 × Female vs. Male × 30° vs. 0°	-0.04	0.10	-0.36
70-79 vs. 60-69 × Female vs. Male × 30° vs. 0°	0.09	0.11	0.83
60-69 vs. 20-30 × Female vs. Male × 60° vs. 30°	-0.05	0.07	-0.70
70-79 vs. 60-69 × Female vs. Male × 60° vs. 30°	0.09	0.08	1.17
Age group × gender × condition			
60-69 vs. 20-30 × Female vs. Male × Substitute vs. Swap	0.03	0.04	0.70
70-79 vs. 60-69 × Female vs. Male × Substitute vs. Swap	0.02	0.04	0.58
Age group × gender × perspective × condition			
60-69 vs. 20-30 × Female vs. Male × 30° vs. 0° × Substitute vs. Swap	0.00	0.05	0.07
70-79 vs. 60-69 × Female vs. Male × 30° vs. 0° × Substitute vs. Swap	-0.01	0.05	-0.10
60-69 vs. 20-30 × Female vs. Male × 60° vs. 30° × Substitute vs. Swap	-0.02	0.05	-0.42
70-79 vs. 60-69 × Female vs. Male × 60° vs. 30° × Substitute vs. Swap	0.04	0.05	0.78

Note. |t|>1.96 in bold.

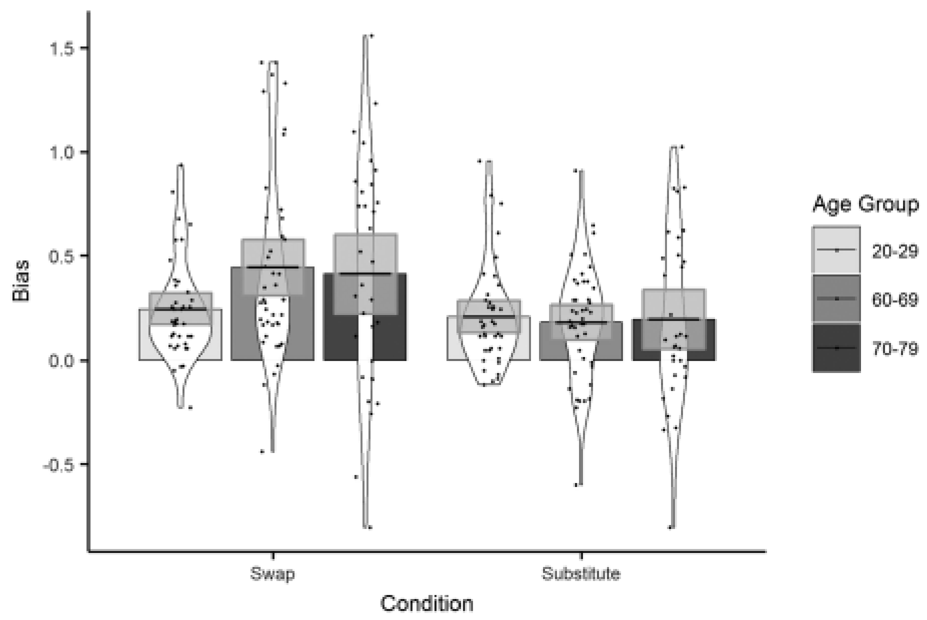

Figure 8-3 - Bias scores plot for age group x condition interaction.

8.1.4 References

Baltes, M. M. (1998). The psychology of the oldest-old: The fourth age. *Current Opinion in Psychiatry*, *11*(4), 411-415. https://doi.org/10.1097/00001504-199807000-00009

Barrash, J. (1994). Age-related decline in route learning ability. *Developmental Neuropsychology*, *10*, 189–201. https://doi.org/10.1080/87565649409540578

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Crook, T., Bartus, R. T., Ferris, S. H., Whitehouse, P., Cohen, G. D., & Gershon, S. (1986). Age-associated memory impairment: Proposed diagnostic criteria and measures of clinical change — report of a national institute of mental health work group. *Developmental Neuropsychology*, *2*, 261–276. https://doi.org/10.1080/87565648609540348

Dai, R., Thomas, A. K., & Taylor, H. A. (2018). Age-related differences in the use of spatial and categorical relationships in a visuo-spatial working memory task. *Memory & Cognition*, *46*(5), 809–825. https://doi.org/10.3758/s13421-018-0794-8

Diwadkar, V. A., & McNamara, T. P. (1997). Viewpoint Dependence in Scene Recognition. *Psychological Science*, *8*(4), 302–307. https://doi.org/10.1111/j.1467-9280.1997.tb00442.x

Dixon, R. A., Bäckman, L., & Nilsson, L. G. (2004). *New Frontiers in Cognitive Aging*. Oxford: Oxford University Press.

Ellis, N. R., Katz, E., & Williams, J. E. (1987). Developmental aspects of memory for spatial location. *Journal of Experimental Child Psychology, 44*(3), 401–412. doi.org/10.1016/0022-0965(87)90042-7

Friedman, A., & Waller, D. (2008). View combination in scene recognition. *Memory and Cognition*, *36*(3), 467–478. https://doi.org/10.3758/MC.36.3.467

Gazova, I., Laczó, J., Rubinova, E., Mokrisova, I., Hyncicova, E., Andel, R., … Hort, J. (2013). Spatial navigation in young versus older adults. *Frontiers in Aging Neuroscience*, *5*. https://doi.org/10.3389/fnagi.2013.00094

Hartley, T., Bird, C. M., Chan, D., Cipolotti, L., Husain, M., Vargha-Khadem, F., & Burgess, N. (2007). The hippocampus is required for short-term topographical memory in humans. *Hippocampus*, *17*, 34–48. https://doi.org/10.1002/hipo.20240

Inagaki, H., Meguro, K., Shimada, M., Ishizaki, J., Okuzumi, H., & Yamadori, A. (2002). Discrepancy Between Mental Rotation and Perspective-Taking Abilities in Normal Aging Assessed by Piaget's Three-Mountain Task. *Journal of Clinical and Experimental Neuropsychology (Neuropsychology, Development and Cognition: Section A)*, *24*(1), 18–25. https://doi.org/10.1076/jcen.24.1.18.969

King, J. A., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2002). Human hippocampus and viewpoint dependence in spatial memory. *Hippocampus*, *12*(6), 811–820. https://doi.org/10.1002/hipo.10070

Klencklen, G., Després, O., & Dufour, A. (2012). What do we know about aging and spatial cognition? Reviews and perspectives. *Ageing Research Reviews*, *11*, 123–135. https://doi.org/10.1016/j.arr.2011.10.001

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers, T. (2017). The aging navigational system. *Neuron, 95,* 1019-1035. https://doi.org/10.1016/j.neuron.2017.06.037

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, *44*(2), 314–324. https://doi.org/10.3758/s13428-011-0168-7

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774-785. https://doi.org/10.1016/j.neuropsychologia.2007.10.005

Mitchell, K. J., Johnson, M. K., Raye, C. L., Mather, M., & D'Esposito, M. (2000). Aging and reflective processes of working memory: Binding and test load deficits. *Psychology and Aging*, *15*(3), 527–541. https://doi.org/10.1037/0882-7974.15.3.527

Montefinese, M., Sulpizio, V., Galati, G., & Committeri, G. (2015). Age-related effects on spatial memory across viewpoint changes relative to different reference frames. *Psychological research*, *79*(4), 687-697. https://doi.org/10.1007/s00426-014-0598-9

Nasreddine, Z. S., Phillips, N. A., Bèdirian, V., Charbonneau, S., Whitehead, V., Collin, I., … Chertkow, H. (2005). The Montreal Cognitive Assessment, MoCA: A Brief Screening

Tool For Mild Cognitive Impairment. *Journal of the American Geriatrics Society*, *53*, 695–699. https://doi.org/10.1111/j.1532-5415.2005.53221.x

Pertzov, Y., Dong, M. Y., Peich, M. C., & Husain, M. (2012). Forgetting What Was Where: The Fragility of Object-Location Binding. *PLoS ONE*, *7*(10). https://doi.org/10.1371/journal.pone.0048214

Pertzov, Y., Heider, M., Liang, Y., & Husain, M. (2015). Effects of healthy ageing on precision and binding of object location in visual short term memory. *Psychology and Aging*, *30*(1), 26–35. https://doi.org/10.1037/a0038396

Postma, A., Kessels, R. P., & van Asselen, M. (2004). The neuropsychology of object-location memory. In G. Allen (Ed.), *Remembering where: Advances in understanding spatial memory* (pp. 143–160). Mahwah, NJ: Lawrence Erlbaum Associates.

Postma, A., & van der Ham, I. J. (2016). *Neuropsychology of space: spatial functions of the human brain.* Academic Press.

Vieweg, P., Stangl, M., Howard, L. R., & Wolbers, T. (2015). Changes in pattern completion– A key mechanism to explain age-related recognition memory deficits?. Cortex, 64, 343-351. https://doi.org/10.1016/j.cortex.2014.12.007

Waller, D. E., & Nadel, L. E. (2013). *Handbook of spatial cognition.* Washington, DC, US: American Psychological Association.

Waller, D. (2006). Egocentric and nonegocentric coding in memory for spatial layout: Evidence from scene recognition. *Memory & cognition*, *34*(3), 491-504. http://dx.doi.org/10.3758/BF03193573

Watanabe, M. (2011). Distinctive features of spatial perspective-taking in the elderly. *International Journal of Aging & Human Development*, *72*(3), 225–241. https://doi.org/10.2190/AG.72.3.d

Wechsler, D. (1981). *Manual for the Wechsler Adult Intelligence Scale - Revised*. San Antonio, TX: Psychological Corporation.

Yamamoto, N., Fox, M. J., Boys, E., & Ord, J. (2019). Effects of Orientation Change during Environmental Learning on Age-Related Difference in Spatial Memory. *Behavioural Brain Research, 365,* 125-132. https://doi.org/10.1016/j.bbr.2019.03.012

Yassa, M. A., & Stark, C. E. (2011). Pattern separation in the hippocampus. *Trends in neurosciences*, *34*(10), 515-525. https://doi.org/10.1016/j.tins.2011.06.006

Zimmermann & Eschen (2017). Brain regions involved in subprocesses of small-space episodic object-location memory: a systematic review of lesion and functional neuroimaging studies. *Memory, 25*, 487-519, https://doi.org/10.1080/09658211.2016.1188965