Age-related changes in memory for object locations across different perspectives

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Copyright Statement

Abstract

One important aspect of spatial cognition is the ability to recognize and remember spatial locations across different viewpoints. Previous research has suggested that those abilities decline in older adults. The aim of the current PhD project is to develop a clearer understanding of what may be contributing to age-related declines in recognising object locations from different perspectives. Specifically, focusing on how ageing effects encoding strategies that are used to memorize spatial configurations and the precision with which object/landmark locations are remembered.

In Chapter 2, gaze behaviour was recorded during a task in which young and older adults judged whether previously encoded objects have remained in the same position or were displaced following perspective shifts. Ageing was associated with declines in spatial processing abilities. Additionally, older adults displayed a more conservative decision style and relied more on encoding object positions using room-based cues compared to young adults, who focused on the spatial relations among the to-be remembered objects during encoding. In Chapter 3, age-related differences in encoding strategies were further investigated using a modified version of the task used in Chapter 2 in which the availability and utility of the room-based cues was manipulated. Performance accuracy was similar across both age groups, yet, older adults displayed a greater preference towards a more categorical encoding strategy in which they formed spatial relations between objects and room-based cues.

In the remaining chapters the focus shifted to investigating the precision with which object locations are remembered across different perspectives. In Chapter 4 participants memorized the position of an object in a virtual room and then judged from a different perspective, whether the object has moved to the left or to the right. Results revealed that participants exhibited a systematic bias in their responses that was termed the reversed congruency effect. Specifically, participants performed worse when the camera and the object

moved in the same direction than when they moved in opposite directions. In Experiment 2, it was shown that the presence of additional objects in the environment reduced the reversed congruency effect whilst in Experiment 3 the reversed congruency effect was greater in older adults, suggesting that the quality of spatial memory and perspective-taking abilities are critical in mediating the reversed congruency effect.

In Chapter 5, a novel task was used to investigate the systematic bias reported in Chapter 4. In this task participants encoded the position of an object in a virtual room and then estimated the object's position following a perspective shift. In addition, memory load was manipulated. Overall, participants systematically overestimated the position of the object in the direction of the perspective shift. This bias was present in both memory and perception conditions. In Chapter 6, these results were replicated in an online-based version of the study.

Lastly in Chapter 7, the influence of camera translations and camera rotations on the perspective shift related bias was decoupled. Additionally, the study investigated whether adding more information into the scene would reduce the bias and if there are age-related differences in the precision of object location estimates and the tendency to display the bias related to perspective shift. Overall, camera translations led to a greater systematic bias than camera rotations. Furthermore, the use of additional spatial information improved the precision with which object locations were estimated and reduced the bias associated with camera translation. Finally, although older adults were as precise as younger participants when estimating object locations, they benefited less from additional spatial information and their responses were more biased in the direction of camera translations.

Overall, by combining eye-tracking and diffusion modelling the current thesis shows that ageing is associated with changes in the type of information that is used to encode object locations across different perspectives. Additionally, ageing was found to be particularly associated with impairments in the formation of fine-grained spatial representations.

Furthermore, a novel bias in spatial memory across different perspectives has been identified. It is proposed that the perspective shift related bias is driven by uncertainty about object position following a perspective shift that leads participants to rely on an egocentric anchor when estimating the location of an object.

Thesis Structure

This thesis conforms to an `integrated thesis' format in which chapters (Chapters 2-7) 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. The articles included in this thesis are at various stages of the publication/review process, and the status of each paper is summarised below. The main text in each chapter is presented as exact replications of the submitted manuscript and inevitably, consequently there is some repetition. Additionally, since each experimental chapter is written as a standalone manuscript, reference sections for each chapter are included at the end of each chapter.

Status of articles from this Thesis

Chapter 2 has been published as:

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Segen, V., Avraamides, M. N., Slattery, T. J., & Wiener, J. M. (in prep). Biases in object location estimation: the role of camera rotations and translation

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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.

Chapter 1: Introduction and Theoretical Background

The world's population is ageing at an unprecedented rate, and a significant proportion of older adults will have to cope with normative or pathological cognitive decline. While decades of research into cognitive ageing have traditionally focused on functions such as memory and attention, more recent efforts have investigated how spatial cognition is affected by ageing and age-related pathologies such as Alzheimer's disease (AD). Spatial cognition is a fundamental cognitive function that enables us to plan routes and find our way in complex environments (Wolbers & Hegarty, 2010). It also allows attending to and manipulating objects as well as communicating information about the objects and the environment with others (Spence & Feng, 2010). As a result, declines in spatial orientation and navigation abilities can have severe consequences for everyday life and can lead to reduced mobility and isolation due to fear of getting lost (Burns, 1999).

To date, research has highlighted that ageing has deleterious effects on spatial cognition (for reviews see Lester et al., 2017; Moffat., 2009; Lithfous et al., 2013; Colombo et al., 2017). For example, ageing has been associated with difficulties in route learning (Head & Isom, 2010; Hilton, Miellet, Slattery, & Wiener, 2019; Liu, Levy, Barton, & Iaria, 2011; Wiener, Kmecova, & de Condappa, 2012; Zhong & Moffat, 2016, Hilton et al., 2021), impaired integration of self-motion information needed to infer one's position in space (Stangl, Kanitscheider, Riemer, Fiete, & Wolbers, 2020; Allen, Kirasic, Rashotte & Haun, 2004; Mahmood, Adamo, Briceno & Moffat, 2009; Harris & Wolbers, 2012; Stangl et al., 2018), as well as a decline in the ability to remember spatial locations across different perspectives (Hartley et al., 2007; Barnes et al., 1988). Those declines are often linked to age-related neurodegeneration of the medial temporal lobe (Lester et al., 2017), a key region within the brain's spatial navigation circuit (For detailed review see Hinman, Dannenberg, Alexander & Hasselmo, 2018). Specifically, several studies have shown that the hippocampus and the entorhinal cortex are particularly vulnerable to age-related alterations (Antonova et al., 2009; Lester et al, 2017; Meulenbroek, Petersson, Voermans, Weber, & Fernández, 2004; Moffat, Kennedy, Rodrigue, & Raz, 2007). They are also the first regions to show accumulation of pathological forms of proteins, such as amyloid-β plaques and tau in neurofibrillary tangles, which are closely associated with Alzheimer's disease (Braak & Del Tredici, 2015; Mufson et al., 2016; Jagust, 2018).

One important aspect of spatial cognition is the ability to recognize and remember spatial locations across different viewpoints (Epstein, Harris, Stanley, & Kanwisher, 1999; Waller & Nadel, 2013). This ability allows us to orient in situations when we encounter familiar places from a variety of perspectives, e.g., when approaching an intersection from a different direction than on our usual way or when entering our kitchen through the backdoor. Broadly, in order to recognise locations from different perspectives, we need to bind objects/landmarks that define the place to their spatial locations (Postma, Kessels & van Asselen, 2004). This is achieved by a specific type of memory known as object location memory (Postma, Kessels, & Van Asselen, 2008). In addition, memory for object locations across different viewpoints requires the ability to retrieve these object location representations from different perspectives (Epstein, Harris, Stanley, & Kanwisher, 1999; Waller & Nadel, 2013; Spatial Perspective-taking). Despite the importance of memory for object locations across different perspectives for orientation and navigation, limited research has addressed how these abilities are affected by ageing. Thus, the main aim of this thesis is to investigate age-related changes in object location memory across different perspectives. In this chapter, an overview of previous research that investigated object location memory and spatial perspective-taking independently, will be provided. This will be followed by a detailed focus on age-related changes in these abilities. The chapter will conclude by providing the rationale and the aims of this PhD project.

1.1. Object location memory

Object location memory supports spatial orientation and navigation by facilitating recognition of places defined by an arrangement of objects or landmarks (Postma et al., 2008). According to a neurocognitive model of object–location memory (Postma et al., 2004), object location memory is a subtype of spatial memory, that is supported by three separate processes: 1) object identity, (2) encoding of spatial location, and (3) binding of this information into a single representation. The existence of three separate processes is consistent with the more recent models of object location memory (Eichenbaum, Yonelinas, & Ranganath, 2007; Montaldi & Mayes, 2010). The representations of object locations can differ in their resolution (Postma et al., 2004). For example, a coarse spatial representation may only contain the categorical positions of the objects such as “the door is in the far right of the room”. Fine-grained representations, in contrast, contain precise metric information about the locations of objects (Evensmoen et al., 2013). The model’s conjecture that object location memory varies in its precision is consistent with more recent research demonstrating that successfully recollected memories of object locations often differed in their precision (Berryhill et al., 2007, Harlow & Donaldson, 2013, Harlow & Yonelinas, 2016).

Converging evidence from neuroimaging research further supports the notion that object location memory is guided by three distinct processes that are supported by different brain regions (see Zimmermann & Eschen, 2017 for a review). Specifically, memory for object identity was reported to depend on the inferior temporal-lobe structures, predominantly in the right hemisphere (Schiavetto et al., 2002; Passaro et al., 2013). Whilst memory for spatial location processing (independent of object identity) has been linked to the posterior parietal cortex, with the right hemisphere preferentially responding to more precise representations and the left hemisphere preferentially responding to more coarse representations (Baumann, Chan & Mattingley, 2012; Jager & Postma, 2003). Additionally, the prefrontal and hippocampal areas have also been linked to spatial-location processing (van Asselen et al., 2009; Baumann, Chan & Mattingley, 2012). More recently, the hippocampal areas have been reported to be critical for the binding memory of object identity and location into a single representation (Diana, Yonelinas & Ranganath; Eichenbaum et al., 2007; Montaldi & Mayes, 2010; Stepankova et al., 2004; Ekstrom & Yonelinas, 2020). Lastly, the parietal cortex has also been associated with the binding of object location information (Zimmermann & Eschen, 2017). In healthy older adults, the hippocampus is one of the regions that is particularly affected, both structurally and functionally (Antonova et al., 2009; Lester, et al, 2017; Meulenbroek, et al., 2004; Moffat et al, 2007; Feng et al., 2020), thus it is possible that older adults may have particular difficulties in binding object-location information as well as memorising the spatial locations of objects. Interestingly, the right hemisphere shows greater age-related decline than the left hemisphere (Albert & Moss, 1988; Brown & Jaffe, 1975; Dolcos, Rice, & Cabeza, 2002), suggesting that ageing may particularly affect the formation of fine-grained representations of object locations.

1.1.1. 2D object location memory and Ageing

Typically, object location binding is studied in two-dimensional spaces where objects are presented in different locations on a blank screen and participants are asked to remember their positions (Dai, Thomas, & Taylor, 2018; Mitchel et al., 2000; Pertzov, Heider, Liang, & Husain, 2015; Nilakantan, Bridge, VanHaerents, & Voss, 2018). This is then followed by a recognition phase, where participants are shown an object on the screen and are asked whether it is the correct location of this object (Dai, Thomas, & Taylor, 2018; Mitchel et al., 2000). Alternatively, participants may be asked to select the previously encoded object and position it back into its original position (Pertzov et al., 2015; Nilakantan et al., 2018).

Results from such tasks support the notion that object location binding consists of three separate processes that involve remembering of object identity and location as well as binding of this information together. For example, Pertzov, Dong, Peich & Hussain (2012) found that over time the links between object identity and location may be broken such that participants remember the identity of objects that were presented and the locations, yet they may make “swap” errors by placing a previously seen object in the position of a different object. Additionally, the ability to remember object locations declines with increasing load with participants showing a substantial reduction in performance when five compared to three items are presented (Dent & Smyth, 2005).

Results from tasks using similar paradigms to investigate age-related changes in memory for object identity, memory for location and object location-binding have been mixed. For example, Mitchel et al. (2000) investigated age-related differences in object location memory using a two-alternative forced-choice task during which participants either responded if they had seen the presented object previously (object identity memory), if an object, independent of its identity, was previously presented in this location (location memory) and, lastly, object location memory was tested by asking participants if the object occupied a correct location. Older adults performed on par with younger adults when no binding was needed, i.e. when location or identity had to be recalled separately. However, older adults were impaired when object location binding was required. This finding is consistent with age-related degeneration of the hippocampus, a region which is thought to be critical for object location binding (Postma, et al., 2008; Zimmerman & Eschen, 2017). Binding deficits were also reported in a more recent study by Dai et al., (2018) who found that when they had to remember object identity, location or both, older adults were impaired in memory for object identity and in object location binding. Age-related deficits in object-identity memory are in line with earlier studies that reported a decline in object identity memory whilst location memory remained relatively unaffected (Schiavetto et al., 2002; Ellis, Katz, & Williams, 1987; Mandler, Seegmiller & Day, 1977). However, when a slightly different experimental set up was used with participants completing each type of task in separate blocks, they reported age-related deficits for object identity and location memory separately, but no specific binding deficits were found. Overall, the results for age-related changes in object location memory are inconclusive and the discrepancy in findings as a result of different experimental procedures suggest that the findings highly depend on how object location memory is assessed.

A slightly different approach to studying object location memory was taken by Pertzov et al. (2015). In their task participants remembered the position of either 1 or 3 abstract objects on the screen. Participants were then presented with two objects, one of which was previously presented and the other was a new object. Participants' task was to recognize the previously seen object (object identity memory) and then drag it to the location it had previously occupied (location memory). Object location binding was investigated by comparing "swap" errors i.e. errors in which objects were placed at the location occupied by a different object (Pertzov et al., 2012). Results showed that older adults were impaired in their ability to remember object identity and that after controlling for memory for object identity there were no age-related deficits in object location binding. Older adults were also less precise in estimating object locations, independently of object location binding. In a later study, Petzov and colleagues, however, report pronounced object location binding deficits in older adults with AD (Liang et al., 2018). Based on these results, the authors concluded that it is possible that in typical ageing the neuropathy of the hippocampal regions is less pronounced and people can cope with object location binding when objects are viewed in 2D space and require no additional manipulations such as remembering locations from different perspectives.

Using a similar approach to that used by Pertzov et al., (2015), a more recent study investigated age-related differences in the precision of object location memory (Nilakantan et al., 2018). To do so, Nilakantan et al., (2018) examined age-related differences in the ability to position target objects in the correct quadrant on the screen (coarse representation) as well as the ability to remember the more fine-grained position of the object on the screen by focusing on the distance to the correct position of the object. Their results highlight that older adults were able to successfully place the object in the correct quadrant, thus not displaying a binding deficit, however, they were significantly less precise than younger adults in placing the object in its precise position. The findings of possible deficits in precision are in line with recent proposals that the hippocampus, which undergoes marked age-related neural degeneration (Nilakantan et al., 2018), is particularly important for binding of precise information, rather than binding per se (Yonelis & Ekstrom, 2020). The evidence for this comes from patients with hippocampal lesions (Kolarik et al., 2016; Kolarik et al., 2018), who were able to remember coarse spatial locations of target objects, although they were substantially less precise than healthy control participants.

Overall, the research on age-related change in object location binding has yielded inconsistent results, often emphasizing impairments in memory for object identity (Pertzov et al., 2012; Schiavetto et al., 2002; Ellis et al, 1987; Mandler et al., 1977; Dai et al., 2018). In addition, studies using different paradigms led to different results regarding object location memory. For example, studies that used 2AFC procedures and presented stimuli in which the target object was either placed in the correct location or a more distant location/or in a location of a different object, did not report age-related decline in memory for locations (Dai et al., 2016; Mitchel et al. ,2000; Ellis et al, 1987; Mandler et al., 1977). Conversely, studies in which participants were required to reposition the objects in their exact locations (Pertzov et al., 2015; Nilakantan et al., 2018), report age-related deficits in the precision of location memory. The differences are likely to be driven by the ability to solve the former task using coarser spatial memories whilst the latter tasks require more fine-grained memories. Additionally, the lack of age-related object location memory deficits is inconsistent with reports of older adults exhibiting difficulties in remembering object locations i.e. keys in their apartment (Mammarella & Fairfield, 2012) or difficulties in remembering landmark locations within an environment (Burns, 1999). Lastly, studies investigating route learning and route navigation, report that memory for object identity typically remains unimpaired and does not explain age-related deficits in these tasks (Allison & Head, 2017; Cushman, Stein, & Duffy, 2008; Head & Isom, 2010, Hilton et al., 2019; Hilton et al., 2021).

The key difference between the tasks assessing object location memory in 2D space and memory for object locations in everyday life is that in everyday situations we often need to remember and recognise layouts of objects from different perspectives. Specifically, tasks that assess object location memory from a single viewpoint can be solved by accessing the learning scene from memory and using image matching to detect changes (Milner & Goodale, 2008; Nardini et al., 2009). However, when the perspective changes between encoding and test, the visual appearance of the arrangement of objects can markedly change, thus preventing the use of image matching to solve the task. Instead, additional mental transformations of the stored representation of object locations are needed (Hegarty & Waller, 2004), and typically such tasks result in greater difficulty in remembering object locations (Diwadkar & McNamara, 1997; Waller, 2006). Assessing object location memory in 3D space, i.e., across different perspectives, allows us to tap into spatial memory implicated in everyday tasks such as those mentioned above (recognising object places from different perspectives or remembering the location of keys when entering the hall from a different room). To set the context for research that focused on age-related changes in object location memory across different perspectives, a brief overview on age-related changes in spatial perspective taking will be presented below (section 1.2).

1.2. Spatial perspective-taking

Recognising object locations or a place from a different perspective than during encoding is a non-trivial process that is essential for spatial orientation. In situations in which self-motion information is available i.e. people move from one place to another, they can rely on visual, vestibular and proprioceptive inputs to spatially update the representation and align it with their new perspective (Bulthoff & Christou, 2000; Waller, Montello, Richardson & Hegarty, 2002). In the absence of self-motion inputs, recognition of places or object arrays from different perspectives can be achieved either by the formation of a viewpoint independent representation (i.e. cognitive map) or by mental manipulation of the stored representation (Holmes, Newcombe & Shipley, 2018; Klencklen, Despres & Dufour, 2012; King et al., 2002; Fields & Shelton, 2006; Waller et al., 2002). Engaging in those mental transformations, in the absence of self-motion information, is cognitively demanding and typically results in increased response times and error rates compared to tasks where the learning and test viewpoints are aligned (Shelton & McNamara,1997).

There are multiple explanations of how stored representations can be mentally manipulated to allow recognition of places/object layouts from other perspectives (Holmes, Newcombe & Shipley, 2018; Klencklen et al., 2012; King et al., 2002). For example, the manipulation could include: 1) mentally rotating the spatial array in alignment with the stored representation 2) rotating the stored representation to match the array viewed from the current perspective, and 3) imagining moving around the array (King et al., 2001; Hegarty & Waller, 2004). All of these manipulations would give rise to indistinguishable outcomes, yet, mental rotations that involve rotation of the array and perspective-taking that involves imagining moving around the array have been found to be related but independent abilities (Hegarty & Waller, 2004). Nevertheless, in the majority of cases when no specific instructions are given to participants in terms of how they should perform these transformations, it is likely that there are substantial individual differences in the type of mental transformation that individuals undertake in order to align two viewpoints. As a result, in the remainder of this chapter and throughout this thesis, these mental transformations will collectively be referred to as spatial perspective-taking (Hegarty & Waller, 2004).

Typically, spatial perspective taking tasks present participants with an array of objects (drawings or real objects) or a map with a number of landmarks (house, church etc) and ask participants to imagine facing a target object or landmark. The ability to successfully engage in spatial perspective taking is then assessed by asking participants to indicate the direction of a different object i.e., imagine that you are facing the house and point to the church (i.e. object perspective taking task; Kozhevnikov & Hegarty, 2001; Hegarty & Waller, 2004). Alternatively, participants may be shown a series of images and asked to select one that corresponds to the arrangement of objects or landmarks that they would see if they were at the imagined perspective or to select the orientation of an object given the view presented on an image (i.e. the 3 Mountain Task [Piaget & Inhelder, 1956]; Spatial Orientation Test [Guilford & Zimmerman, 1948]). Such tasks typically do not require memory for object locations, as all the objects/locations are visible to the participant during the task. Instead, they tap into the cognitive processes implicated specifically in spatial perspective taking. For example, one of the best-known spatial perspective taking tasks, the object perspective taking task (Kozhevnikov & Hegarty, 2001) requires participants to indicate the direction of a target object from an imagined perspective defined by two other objects i.e. imagine facing a car and point to the watch. Common results from this task are that as the angular difference between the imagined perspective and the participant's egocentric perspective increases, such that participants need to imagine larger movements, greater pointing errors are observed (Kozhevnikov & Hegarty, 2001; Hegarty & Waller, 2004)

Neuroimaging studies suggest the involvement of parieto-occipital sulcus, supplementary motor areas and frontal areas during spatial perspective taking (Zacks, Gilliam & Ojemann, 2003; Kaiser et al, 2008). More recently, the retrosplenial cortex has also been found to be implicated in spatial perspective taking (Chrastil, 2018; Sulpizio et al., 2016). In addition, the hippocampal circuit has also been found to support the computations involved in spatial-perspective taking and the ability to develop viewpoint-independent representations of the environment (King et al., 2002; Vargha-Khadem et al., 1997; Goodrich-Hunsaker & Hopkins, 2010; Hartley, Maguire, Spiers, & Burgess, 2003; Morris, Garrud, Rawlins & O'Keefe, 1982; Wolbers & Büchel, 2005). In healthy ageing the frontal lobe areas (Cabeza, & Dennis, 2012; Nyberg et al., 2010; Raz et al., 2004), the retrosplenial cortex (Moffat et al., 2006) and the hippocampal circuit (Antonova et al., 2009; Lester et al, 2017; Meulenbroek, et al., 2004; Moffat et al, 2007; Feng et al., 2020) show pronounced and reliable functional and structural changes. Given the overlap between the areas engaged in spatial perspective taking and areas that are susceptible to age-related functional and anatomical changes suggests that older adults may have greater difficulties in spatial perspective taking.

1.2.1. Ageing and spatial perspective taking

One of the first studies to assess spatial perspective taking in older adults used a variant of the 3 Mountains task (Piaget & Inhelder, 1956) in which participants were presented with two blocks in front of them and were asked to imagine what the view would be if the blocks were rotated, or if the participant was on a different side of the array (Inagaki et al., 2002). In this study they found that older adults had deficits in both variants of the task with more pronounced deficits when older adults had to imagine moving to a different side of the array. Similar findings were reported by Herman and Coyne (1980), who showed that older adults were particularly impaired when they were asked to determine the location of target objects from imagined locations when compared to younger adults.

In a more recent study Zancada-Menendez et al. (2016), assessed age-related changes in spatial perspective taking using the Object Perspective Taking task (Kozhevnikov & Hegarty, 2001). Interestingly, they found that older participants made more errors overall compared to younger adults, yet older adults' performance did not depend on the size of the perspective changes. This was not the case in the younger group which showed a linear decline in performance with the increase in the size of the perspective shift. Similar findings were reported by Watanabe (2011), who examined age-related changes in spatial perspective using a different task in which participants were given a map of a town and asked to imagine which locations a given building would occupy on a map when it was misaligned with the orientation of the town. Overall, older adults took longer to respond and made more errors, however, both age groups were similarly affected by manipulations of the size of the perspective shifts. In a follow-up study, where the task was adapted in the form of a video game in which participants had to indicate the position of cartoon characters once a house that they occupied was rotated, Watanabe & Takamatsu (2014), reported that spatial perspective-taking remained robust in normal ageing. It is possible that the inconsistencies regarding age-related differences in spatial perspective taking across those two studies are driven by differences in task difficulty. Specifically, the task used by Watanabe & Takamatsu (2014) was specifically adapted to make it easier and to allow the assessment of spatial perspective taking in young children.

Given the mixed findings and lack of more pronounced deficits in older adults with the increase in the perspective shift it remains unclear whether the differences reported in the previous studies are driven by spatial perspective taking deficits or are a manifestation of a more general slowing down of the speed of processing in ageing (Salthouse, 2000) and cognitive decline (Harada et al., 2014; Raz, 2009; Reuter-Lorenz, et al., 2008). For example, the results by Watanabe (2011), that older adults took longer to respond may be driven by reduction in speed of processing. It is also possible that older adults have lower performance on spatial perspective tasks (Watanabe, 2011; Inagaki et al., 2002; Zancada-Menendez et al., 2016) due to speed-accuracy trade-offs, whereby older adults sacrifice accuracy in order to perform the task quicker, in such cases performance would be particularly affected since older adults are likely to require more time to solve the task due to reductions in processing speed. Additionally, lower performance in older adults may be a manifestation of general age-related deficits in attention (Ruthruff, & Lien, 2016) or other cognitive abilities that are engaged during the task i.e. visuospatial working memory (Salthouse, Miitchell, Skovronek & Babcock 1989) as well as executive functions (Buckner, 2004). This account is consistent with older adults being similarly affected by the size of the perspective shift as younger adults. Lastly, some of the studies that reported age-related deficits in spatial perspective taking (i.e. Inagaki et al. 2002; Herman & Coyne, 1980), did not manipulate the size of the perspective shift, thus making it difficult to conclude what the underlying nature behind age-related reduction in performance was. As a result, more research that attempts to disentangle spatial perspective from other cognitive abilities that are used during spatial perspective taking tasks are needed

1.3. Ageing and Memory for object locations across different perspectives

To date, only a few studies have investigated how ageing affects object location memory across different perspectives. Typically, such studies involve tasks in which an array of objects or environmental features are encoded from one perspective. During test, the array is presented from a different perspective and participants have to judge whether or not the arrangement of objects has changed (Hartley et al., 2007; Montefinese, Sulpizio, Galati, & Committeri, 2015; Muffato, Hilton, Meneghetti, De Beni & Wiener, 2019).

One such study used the Four Mountains task (Hartley et al., 2007) to investigate age-related differences in memory for the arrangement of environmental features across different perspectives. In this task, participants viewed a “target” image of a place defined by four mountains. They were then presented with four new images. One of these images depicts the same place but from a different perspective while the other images display a slightly different arrangement of the mountains. Participants were asked to select the image that corresponded to the same place they had seen during encoding. The tasks consisted of a perceptual variant where participants simultaneously view the “target” image and the four new images, and a memory version, where the four new images are presented after a short delay. Hartley and colleagues also included a “nonspatial” variant of the task, where instead of selecting the same mountain arrangement, participants' task was to select an image that matched the prevailing conditions of when the target image was taken (i.e. time of day, weather and time of the year). Older adults performed worse than younger participants but only in the spatial memory condition, highlighting that older adults are specifically impaired in memory for arrangements of objects across different perspectives rather than showing deficits in the processing of visual features of the stimuli and memory for non-spatial components of the scene.

This study also included patients with hippocampal lesions, whose deficits in the memory variant were substantially larger than in healthy older adults. Hartley et al. (2007) concluded that the hippocampus is implicated in memory for object locations across different perspectives and that the performance reduction in older adults compared to younger adults may also be related to age-related hippocampal atrophy. The task has been successfully used to differentiate between healthy older adults and those with a subtype of MCI that is considered a risk factor for AD, as well as between MCI, AD and Frontotemporal Dementia patients (Chan et al., 2016; Bird et al., 2010). The sensitivity of the task to distinguish between those groups may be driven by its dependence on the medial temporal lobe (including the hippocampus), which undergoes more pronounced degradation in MCI and AD (Berron et al., 2021) compared to normal ageing. The authors do not report the effect that different sizes of the perspective shift have on participants' performance; thus, it is not clear if younger and older adults are differentially affected by the introduction and size of the perspective shift.

Another study that investigated memory for object locations across different perspectives was carried out by Montefinese et al. (2015). Primarily the authors were interested in age-related differences in memory for object locations in relation to different types of information that is used to encode object locations. To do so, they used an environment that consisted of a room with distinguishable cues on the walls, an array of objects in the middle of the room, as well as a target object placed within close proximity to the central object arrangement. Participants' task was to encode the position of the object either in relation to the room, the central object arrangement or in relation to their own (camera) position. At test, the target object remained stationary in half of the trials and was displaced in the remaining half. Participants were asked if the object occupied the same or different position. This procedure allowed them to investigate memory for object location in relation to more distal cues, to more local cues and in relation to their own position. Additionally, the amount of the perspective shift that was introduced was also manipulated and included small (45°) and large (135°) perspective shifts.

Montefinese et al. (2015) found that both age groups took longest and showed lowest performance when object position had to be remembered in relation to the more distal room-based cues when a perspective shift was present. Also, in this condition, older adults showed lower performance than younger adults in situations when no or small perspective shifts were introduced. A slightly different performance pattern was observed in the condition where the object had to be encoded in relation to the arrangement of objects, with no overall impairments observed in older adults. They, however, performed slightly worse when a larger perspective shift was introduced compared to younger adults. In both of these conditions, older adults were more affected by the introduction of the perspective shift, as their performance was better described by a step function, whilst younger participants showed a more gradual, linear, decline in performance with the increase in the perspective shifts. This suggests that older adults may have greater difficulties in initiating the processes required to achieve spatial perspective taking and the lack of a gradual decline in performance may therefore be driven by floor level effects with older adults having difficulties in solving the trials that involve smaller perspective shifts. Alternatively, older adults may engage different strategies during spatial perspective taking compared to younger adults. For example, younger adults may engage in mental rotations of the array, a process that is typically associated with a linear decrease in performance (Lohman, 1986; Shepard & Metzler, 1971). Older adults, on the other hand may solve the task by imagining moving around the array to either match the test viewpoint with the encoded viewpoint or vice versa (King et al., 2002). These types of mental transformations do not necessarily result in increased cognitive costs with increasing angular disparity (Hegarty & Waller, 2004).

Conversely, performance was not affected by either the presence of the perspective shift or age group in situations when participants had to encode object positions in relation to their own position. This condition, across all perspective shifts, can be solved by memorising the absolute position of the object on the screen, and as a result, does not necessarily require the formation of a “spatial” representation. Thus, the lack of differences between age groups is consistent with some of the findings from 2D literature (Dai et al., 2018; Pertzov et al., 2015), showing that older adults performed similarly to younger adults when they had to memorise object positions on the screen. However, in situations when participants can no longer rely on the absolute position of the object on the screen and have to engage in mental transformations that enable spatial perspective taking, then memory for object locations, in particular in reference to more distal cues is impaired in older adults. These findings are consistent with the idea that older adults are more likely to rely on proximal than distal cues when encoding positions within virtual rooms (Moffat & Resnick, 2002).

Muffato et al. (2019) investigated age-related differences in memory for object locations across different perspectives using a slightly different task to that used by Montofinesse et al., (2015). Specifically, there were no external cues available, and participants had to remember an arrangement of four objects in an open field. To assess memory for object locations across different perspectives, Muffato et al. (2019) manipulated the position of objects within the array, by swapping two objects with each other. In addition, they also included a manipulation where one of the objects was replaced by a novel object, this allowed them to account for potential age-related differences in memory for object identity. Results revealed a specific age-related performance deficit when objects within a scene swapped positions compared to when they were substituted with a new object. These results suggest that object identity memory is relatively intact in ageing (c.f. Allison & Head, 2017; Head & Isom, 2010; Cushman et al., 2008). However, the greater difficulties in older adults when object locations were swapped suggest a specific age-related deficit in binding the remembered objects to their locations. In contrast to Montefinese et al. (2015), Muffato et al. (2019) did not find age-related differences in performance across different perspectives, with both younger and older participants showing a similar decline in performance with an increase in the perspective shifts. The results reported by Muffato et al. were more recently replicated by Hilton et al. (2020), in a study where age-related differences in encoding strategies have been examined (more information provided below).

Overall, the results from both the tasks that assess spatial perspective taking and object location memory separately using 2D stimuli as well as tasks investigating memory for object locations across different perspectives suggest that older adults have difficulties in situations when they have to engage in both spatial perspective taking and object location memory simultaneously. For example, the lack of age-related differences in performance in the spatial perception version of the 4 Mountain Task (Hartley et al., 2007) suggests that spatial perspective taking itself may not be affected by ageing, thus concurring with studies exclusively assessing spatial perspective taking (i.e the Object Perspective Taking task; Kozhevnikov & Hegarty, 2001) that do not report age-related deficits. Instead, it appears that older adults have difficulties in situations that are more akin to everyday navigation, where they need to remember locations of specific landmarks or objects across different perspectives. This conjecture also extends to age-related changes in object location memory, as robust age-related deficits are observed in situations when older participants have to remember object locations across different perspectives (Montefinese et al., 2015; Muffato et al., 2019; Hilton et al., 2020), yet, in situations when the tasks involve 2D object arrays, the results are mixed with many studies reporting intact object location memory (Dai et al., 2018; Pertzov et al., 2015).

1.3.1. Age-related differences in visual encoding strategies in tasks assessing memory for object locations across different perspectives

Together, results from the studies reviewed above suggest that older participants should have greater difficulties in establishing accurate, fine-grained representations of spatial layouts containing multiple objects or landmarks. They may also experience greater difficulties in recognizing these layouts across different perspectives. However, little is known about the effects of ageing on the encoding strategies that are used during these tasks. Recording participants' gaze behaviour can provide a window into the encoding strategies that they are using. Previously, eye-tracking has been successfully applied to study strategies that underlie the execution of spatial tasks (Schmidt et al., 2007; Livingstone-Lee et al, 2011). Livingstone-Lee et al. (2011), for example, showed that the environmental features participants gazed at in the first second of a navigation trial allowed distinguishing between navigation strategies. Similarly, Becu et al. (2020) argued that gaze dynamics are predictive of the spatial cue preferences that participants use to anchor their spatial representations.

Despite the potential utility of eye-tracking to investigate encoding strategies during spatial tasks, only a few studies have used it to study age-related differences, with the majority of studies focusing on route learning and navigation (Grzeschik et al., 2019; Hilton et al., 2019; Becu et al., 2020). To date, only one study by Hilton et al. (2020), has looked at age-related differences in gaze behaviour during a task assessing memory for object locations across different perspectives using the task described in Muffato et al. (2019). Interestingly, they did not report differences in gaze behaviour, despite age-related differences in memory for object locations. However, in that study, only the to-be-remembered objects were present and arranged in an open field. It is possible that the lack of differences in encoding strategies was driven by the limited amount of information being present in the environment that can be gazed at. This contrasts with findings by Becu et al (2020), who showed that older adults use different information when reorienting during real-world navigation. Specifically, they found that older adults were more likely to gaze at room geometry, whilst younger participants showed a preference towards landmarks. Furthermore, Grzeschik et al. (2019) found that older adults spent less time looking at navigationally relevant landmarks during route learning, compared to younger adults. It is therefore possible that when additional information is available, younger and older adults will rely on different types of information when trying to remember object locations across different perspectives.

1.5. Rationale and aims of this thesis

To date, no study has investigated age-related differences in visual encoding strategies in tasks that require memory for object locations across different perspectives in environments containing distal cues. Additionally, it remains unclear if older adults exhibit a specific deficit in spatial perspective taking. For example, Muffato et al., (2019) and Hilton et al., (2020) found that perspective shifts between encoding and test resulted in similar performance declines in young and older adults. Other studies, however, report specific age-related deficits in perspective taking abilities in spatial memory tasks (e.g., Inagaki et al., 2002; Montefinese, et al., 2015; Watanabe, 2011). Lastly, given reports of age-related decline in the precision with which object locations are remembered in tasks using 2D stimuli (Pertzov et al., 2015; Nilakantan et al., 2018), it is possible that older adults may have greater difficulties in formulating precise representation of object locations across different perspectives. However, to date, studies that have investigated memory for object location across different perspectives have either introduced coarse spatial changes and did not parametrically manipulate how object locations have been changed. For example, in the task used by Montefinese et al., (2015) the object was always displaced by 135° around an invisible circle.

Whilst in Muffato et al. (2019) and Hilton et al. (2020) two objects swapped places. Although such tasks allow investigating age-related differences in memory for object location across different perspectives, they do not allow tapping into the precision with which older adults remember the locations of objects.

Thus the overarching goals of this thesis are 1) to investigate how ageing impacts visual strategies that are used to encode object locations and retrieve them following perspective shifts; 2) to investigate age-related differences in memory for object locations across different sizes of perspective shifts and to 3) to investigate if ageing affects the resolution/precision with which object locations are remembered across different perspectives.

The first study reported in Chapter 2, set out to address all three overarching goals outlined above. To do so, a novel paradigm was designed in which participants were asked to encode locations of several objects within a room that contained additional cues such as windows, a painting, and a door. Then, following a short delay, participants were presented with the view of the same room but from a different perspective. Their task was to judge if the object locations have changed or remained the same. As participants performed the task, gaze behaviour was recorded, which enabled us to test if younger and older adults used different encoding strategies when memorising object locations. In addition, to investigate age-related changes in spatial perspective taking, there were conditions without perspective shifts, with small (45°) or large (135°) perspective shifts. Lastly, to test if ageing leads to deficits in the fine-grained encoding of object locations, two different types of object location manipulations were introduced. This included a manipulation that has been used in previous research (Muffato et al.,2019; Hilton et al., 2020) and involved swapping two objects clusters with each other, which constituted a coarse spatial change. The second object location manipulation involved a rotation of one of the object clusters, such that the categorical relationship between the object clusters was maintained. This manipulation required a more fine-grained memory of object locations. Lastly, to investigate differences in response strategies, diffusion modelling (Ratcliff, 1978) was used.

The study reported in Chapter 3 builds up on the results from Chapter 2 which suggested that older adults' gaze was more widely distributed during encoding of object positions. To investigate the potential causes of such differences, the availability and the informative value of room-based cues was manipulated. This manipulation allowed us to investigate if older adults used additional room-based cues to encode object positions, or whether they displayed more distributed gaze due to being distracted by the presence of additional information as a result of reduced attentional control (Hasher & Zacks, 1986).

From Chapter 4 onwards, the focus of the thesis shifted to exploring the precision with which object locations can be remembered across different perspectives. Although Chapter 2 investigated the resolution with which older and younger adults remembered object locations across different perspectives, there were only two types of spatial changes and therefore it was not possible to quantify the precision with which object locations are remembered across different perspectives. Thus, the main aim of Experiment 1 in Chapter 4 was to develop a task that would allow a quick and accurate assessment of the precision with which participants remember object location across perspective shifts. The task involved participants memorising a position of a single object in a virtual room. Then, a perspective shift was introduced, and the object was displaced either to the left or to the right. The participants' task was to correctly identify the displacement direction. A psychophysics approach was adopted, and the amount by which the object was displaced was systematically manipulated to quantify precision. Experiment 2 and 3 in Chapter 4 explored how the use of additional spatial information and ageing affects task performance and the type of errors that participants make. An unexpected bias in participants' responses was reported.

Chapter 5 set out to replicate the results reported in Chapter 4 using a different experimental paradigm. Specifically, instead of asking participants to judge the direction in which the object has moved, as was done in Chapter 4, participants were asked to estimate the object position following perspective shift. In addition, given previous reports of distortions introduced by spatial memory (Wang & Schwering, 2009; Uttal, Friedman, Liu & Warren, 2010; Huttenlocher et al., 1991), this study investigated if the bias in participants' responses is present in conditions with and without a memory component. In Chapter 6, the results from a lab-based and online version of the task reported in Chapter 5 (only the memory condition was tested) was compared. This study was largely motivated by the move to online data collection as a result of Covid-19 related restrictions on in-person data collection and examined if online data yields results comparable to those collected in the lab.

Finally, in Chapter 7, the perspective shift was separated into camera rotations and translations and memory for object locations were investigated across different combinations of camera rotation and translations across younger and older adults. By separating the perspective shift into camera rotations and translations, it was also possible to identify what factors drove the bias reported in Chapters 4-6 and whether older and younger were differentially affected by camera rotations and translations. Lastly, the role of additional spatial information on participants estimates of object locations was also investigated.

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Chapter 2: Age-related differences in visual encoding and response strategies contribute to spatial memory deficits

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2.1 Introduction

The ability to recognize a place from different perspectives is crucial for everyday functioning. It requires remembering the locations of objects relative to each other or relative to the environment (Epstein, Harris, Stanley & Kanwisher, 1999) and depends on the binding of the memory for object identity with the memory for its location (Postma, Kessels & van Asselen, 2004; Waller, 2006). The quality of such spatial representations depends on the resolution with which spatial information is encoded (Ekstrom & Yonelinas, 2020; Cowell, Barense & Sadil, 2019). A coarse spatial representation, for example, may only contain the categorical positions of the objects such as “the door is in the far right of the room”. Fine-grained representations, in contrast, contain precise metric information about the locations of objects (Evensmoen et al., 2013).

Once a spatial representation of a place is created, visual, vestibular and proprioceptive inputs during active movement can be used to update the representation to allow place recognition from a different perspective (Bülthoff & Christou, 2000; Waller, Montello, Richardson & Hegarty, 2002). However, if physical movement is absent, recognition across different perspectives can be achieved through the formation of a view-point independent representation or by mental manipulations of the new or stored representation (Holmes, Newcombe & Shipley, 2018; Klencklen, Despres & Dufour, 2012; King et al., 2002). Possible manipulations include: 1) mentally rotating the new representation in alignment with the stored representation 2) imagining moving around, and 3) rotating the stored representation to match the representation viewed from the current perspective (King et al., 2002; Hegarty & Waller, 2004). Hereafter, we will refer to these mental transformations collectively as spatial perspective taking (Hegarty & Waller, 2004).

Neuroimaging research suggests that the hippocampal circuit and the retrosplenial cortex support the computations involved in spatial perspective taking (King et al., 2002; Vargha-Khadem et al., 1997). The hippocampus may also allow place recognition across different perspectives by enabling the development of viewpoint-independent representations of the environment (Goodrich-Hunsaker & Hopkins, 2010; Hartley et al., 2003; Morris et al., 1982; Wolbers & Büchel, 2005). Furthermore, the hippocampus is involved in object-location binding (Zimmermann & Eschen, 2017) and the binding of high-resolution perceptual information, including spatial information (Kolarik et al., 2016; Kolarik et al., 2018), into a single representation (Erez, Lee & Barense, 2013). Together, these studies demonstrate that the hippocampus plays an important role in development of flexible fine-grained spatial representations and the processes involved in place recognition across different perspectives.

Several studies have shown that the hippocampal circuit is particularly vulnerable to age-related alterations (Antonova et al., 2009; Meulenbroek, Petersson, Voermans, Weber & Fernández, 2004; Moffat, Kennedy, Rodrigue & Raz, 2007). Thus, it is not surprising that ageing is associated with declines in spatial memory (Hartley et al., 2007; Montefinese, Sulpizio, Galati & Committeri, 2015; Muffato, Hilton, Meneghetti, De Beni & Wiener, 2019). Muffato et al., (2019) investigated the nature of spatial memory deficits in ageing by presenting participants with images of places defined by the spatial arrangement of four different objects in an open field. At test, the places were presented from different perspectives and participants decided whether the place was the same or different to that seen during encoding. Age-related performance deficits were found when objects within a scene swapped positions but not when they were substituted with new objects. This highlights a specific age-related deficit in binding the remembered objects to their locations whilst object identity memory remained relatively intact in ageing (c.f. Allison & Head, 2017; Head & Isom, 2010; Cushman, Stein & Duffy, 2008).

As Muffato et al. (2019) did not parametrically manipulate the amount of spatial change within the scene, it remains unclear if cognitive ageing also affects the resolution with which spatial representations are formed. That is, older adults may experience difficulties in forming detailed, fine-grained spatial representations, therefore, relying more on coarser representations compared to younger adults. This idea is consistent with findings from a spatial working memory study in which older participants were able to memorise the coarse position of objects on a computer screen, but were less precise than younger participants (Nilakantan, Bridge, Van Haerents & Voss, 2018). The authors proposed that age-related hippocampal neurodegeneration could explain the difficulties in forming fine-grained representations. This interpretation is in line with patient research showing that young patients with hippocampal damage can form coarse memories of environments but have problems identifying the precise locations of previously encoded objects (Kolarik et al., 2016; Kolarik et al., 2018). Given that ageing is associated with hippocampal atrophy (Moffat et al., 2007) we expect spatial memory to be less fine-grained in older individuals than in young adults. To our knowledge this has not yet been demonstrated empirically.

There is currently no consensus on how ageing affects spatial perspective taking. Some studies showed that perspective shifts resulted in similar performance declines in young and older adults (e.g., Muffato et al., 2019), while other studies have reported specific age-related deficits in perspective taking abilities (Inagaki et al., 2002; Montefinese et al., 2015; Watanabe, 2011). It thus remains unclear whether there is a specific age-related deficit in spatial perspective taking over and above general age-related slowing and cognitive decline.

Here we present an exploratory study combining eye-tracking and diffusion modelling to study age-related differences in their abilities to recognize spatial configuration across different perspectives. Similar to earlier studies (Muffato et al., 2019; Montefinese et al., 2015) participants encoded object positions from one perspective and then reported if the objects were in the same or different positions when presented with the scene from a new perspective. To investigate age-related differences in the resolution of spatial representations we manipulated the spatial arrangement of objects in two different ways: we either changed the precise position of objects within the spatial arrangement between encoding and test so that participants would need to employ fine-grained spatial knowledge to respond correctly, or we introduced a change in the whole spatial arrangement that could be detected using a coarser representation. We unpacked the processes involved in decision making using diffusion modelling which assumes that decisions are based on evidence that is accumulated over time (Ratcliff & Rouder, 1998). Diffusion modelling combines response times and accuracy to estimate a number of parameters, including response bias (tendency to classify stimuli more as "same" or "different"), response boundaries (the amount of information needed to make a decision), drift rate (the rate of information accumulation), and the time required to execute the motor response (Ratcliff, Smith, Brown & McKoon, 2016).

In ageing research, traditional response time analyses are complicated by age-related delays in non-decisional processes such as visual processing speed and response execution (Owsley, 2011; Ren, Wu, Chan & Yan, 2013). This may lead to the incorrect conclusion that ageing is associated with processing deficits and may discourage researchers from using response times in their analysis (e.g. Muffato et al., 2019; Hartley et al., 2007), despite the informative value of this measure in identifying decisional styles in particular speed-accuracy trade-offs. Diffusion modelling can overcome this by modelling separately task-specific information processing (i.e. performance), decisional styles that depend on response conservativeness, and non-decisional processes. By doing so it provides a cleaner measure of the information processing efficiency (drift rate) whilst allowing the investigation of speed-accuracy trade-offs using a single parameter, response boundaries (Ratcliff et al., 2016; Voss, Nagler & Lerche, 2013). This is particularly relevant to ageing research in which the patterns of accuracy and response times often differ across age groups (Ratcliff, Thapar & McKoon, 2006; Watanabe, 2014).

In tasks with a memory component, drift rate typically represents the quality of the match between the memory trace and the test stimuli (Ratcliff et al., 2004; Spaniol, Madden & Voss, 2006; White, Ratcliff, Vasey & McKoon, 2009). For example, in word recognition tasks, words that are more strongly encoded result in higher drift rates (Ratcliff et al., 2004), whilst deficits in episodic memory lead to reduced drift rates (Spaniol et al., 2006). In other words, drift rates depend on the ability to accurately encode information and to access the corresponding representation at test. Drift rates are independent from non-decisional processing and decision styles. In the current task, participants needed to encode the locations of objects in the environment, access and compare those representations at test following a perspective shift to determine if the objects were in the same or different positions. Thus, drift rate represents participants' ability to encode the locations of objects in the environment and to access and manipulate these representations after a perspective shift (Hegarty & Waller, 2006).

In addition to collecting accuracy and response time measures, we used eye-tracking to further investigate potential age-related changes in encoding of spatial relationships. Past research demonstrates that gaze behaviour is sensitive to the strategies adopted in solving spatial tasks (Schmidt et al., 2007). For example, Livingstone-Lee et al. (2011), showed that the environmental features participants gazed at in the first second of a navigation trial allowed distinguishing between different navigation strategies. Similarly, Becu et al., (2020) showed that gaze dynamics are predictive of the spatial cue preferences that participants use to anchor their spatial representations. Here, we rely on eye-tracking data to also delineate the automatic processes that may influence encoding strategies (Schütt et al., 2019).

Although, encoding strategies have not yet been investigated in place recognition, some navigation studies suggest that ageing is associated with changes in encoding of spatial information. For example, Grzeschik, Conroy-Dalton, Innes, Shanker & Wiener (2019) report that older adults spent less time than younger adults looking at unique, navigationally relevant landmarks during route learning. Also, Becu et al. (2020) reported that older adults engage less in explorative gaze behaviour when reorienting during real-world navigation when compared to young adults. These age-related changes in visual encoding strategies may be relevant also to our task. Specifically, participants need to “reorient” after a perspective shift in order to solve the task. This reorientation likely involves attending to the same “relevant” environmental cues during encoding and test.

Given that age-related differences during spatial encoding in tasks similar to the one presented here have not been previously investigated, we adopted an exploratory approach to the analysis of gaze behavior. If differences in encoding strategies contributed to age-related differences in spatial memory, we expect systematic differences across several gaze parameters between younger and older adults and correlations between gaze parameters and behavioral performance.

With respect to the behavioural results, we expected to replicate earlier findings showing greater difficulties with spatial memory in older adults, to observe declining performance with increasing perspective shift, and to find lower performance in trials that require fine-grained spatial knowledge than in trials that can be solved using a coarser representations. Finally, if older adults have greater difficulties than younger adults in encoding fine-grained spatial information, we expected an interaction between age group and condition with older adults showing greater performance reduction in trials that require fine-grained spatial knowledge.

For the diffusion modelling analysis, the key prediction is that drift rates would be lower in older compared to younger participants. In addition, we predicted that older adults would be more conservative in their responses, which would be reflected in wider response boundaries. This prediction is based on research from other cognitive domains showing age-related widening of response boundaries (recognition memory: Spaniol et al., 2006, perceptual learning: Ratcliff, et al., 2006 and language: Ratcliff et al., 2004). Furthermore, ageing is associated with a greater tendency to identify novel places as familiar as a result of a pattern completion bias (Vieweg, Stangl, Howard, & Wolbers, 2015). We therefore expected older adults to show a greater bias towards responding that stimuli are the same even if a change was introduced. Lastly, since ageing is associated with reductions in motor speed (Ren et al., 2013) and visual function (Owsley, 2011) we expect longer non-decision response rates in older than younger participants.

2.2. Method

2.2.1. Participants

Thirty-eight young (mean age = 21.82 years, SD = 6.92; age range = 18–31 years; 23 females and 15 males) and 38 adults aged 60 years and over (mean age=70.1, SD=4.79, age range= 60-83; 23 females and 15 males) took part in this study. Participants were recruited either through Bournemouth University's participant recruitment system or through opportunity sampling in the community. Older adults received monetary compensation for their time. Younger participants either received course credits or monetary compensation. Participants were screened for mild cognitive impairment using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005). Based on a threshold score of 23/30 (Luis, Keegan & Mullan, 2009; Waldron-Perrine & Axelrod, 2012) no participants were excluded from the final analyses. All participants gave their written informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

Given the reports of sex differences in navigation and spatial cognition (Coutrot et al., 2019; Mueller et al., 2008), we first ran an exploratory analysis focusing on sex, but did not find any performance differences between sexes (see Supplementary Materials). As the current study was not designed to investigate sex differences, we did not include sex as a factor in any further analyses.

2.2.2. Materials

2.2.2.1. Virtual environment

The virtual environment was designed using SketchUp Make 2017 (Trimble Inc., 2017) and depicted a rectangular room (13.5 m x 14.6 m) that contained visual cues on the walls including a door, windows, and a painting. The room also contained 6 identical objects, pink vases on metal stands, that were placed in the centre of the room (Figure 2.1).

The experimental stimuli were renderings of the environment from eight different viewpoints with a horizontal field of view of 50°. These viewpoints were arranged at 45° intervals on a circle with a radius of 6.5m surrounding the target objects (Figure 2.1). The objects were arranged in clusters of one, two and three objects. The cluster positions within the room were changed to provide six unique configurations that were used in the experiment. Stimuli were presented with OpenSesame 3.1.7 (Mathôt, Schreij, & Theeuwes, 2012) and a standard computer keyboard was used to record responses.

2.2.2.2. Eye-tracking recording

Eye movements were recorded using an Eyelink II (SR Research) head mounted eye-tracker at a rate of 500Hz. Calibrations were performed at least three times and drift correction was performed prior to each trial. The experiment was presented on a 102cm screen (diagonal) with an aspect ratio of 16:9 and a resolution of 1920x1080 pixels. Participants were seated at 100 cm from the monitor. The physical horizontal field of view of the screen at this distance was 47.7°.

2.2.3. Design

The experiment followed a mixed 2 (Age Group: young vs. older adults) × 3 (Condition: Rotate, Same, Swap) x 3 (Perspective Shift: 0°, 45°, 135°) design with Condition and Perspective Shift manipulated within participants.

2.2.4. Procedure

Both younger and older adults completed the MoCA (Nasreddine, et al., 2005) before taking part in the experiment. To familiarise participants with the virtual environments, we asked them to watch a 24 second video clip providing a 360° overview of the virtual room without the objects.

Each experimental trial started with a fixation cross and a scrambled stimuli mask (1500 msec). In the subsequent learning phase, participants were presented with a rendering of one of the six unique configurations of the objects from one of the eight possible viewpoints (48 different renderings) for 12 seconds. After this learning phase, participants were again presented with a fixation cross and a scrambled stimuli mask for 1500 msec. In the test phase, participants were presented with a rendering of the room either from the same viewpoint (0°) or from a different viewpoint that involved a 45° or 135° perspective shift. Each perspective level (0°, 45°, and 135°) was used in a third of all trials.

Participants' task was to decide whether or not the locations of the objects (the pink vases) in the test phase were identical to those in the learning phase. In 50% of the trials the objects remained in the same locations, whilst they moved between learning and test in the remaining 50% of the trials. Specifically, the locations of the objects were changed either by swapping the locations of two of the three clusters (Swap condition) or by rotating either the cluster consisting of two or three objects by 60° (Rotate condition, Figure 2.1B). While the Swap manipulation changed the whole spatial arrangement and could be detected using coarse spatial representation, the Rotate manipulation was more subtle. It maintained the overall configuration of objects and required a fine-grained spatial representation. It should be noted that the cluster consisting of one object was never rotated, as this would not yield a change in the position/orientation of that cluster.

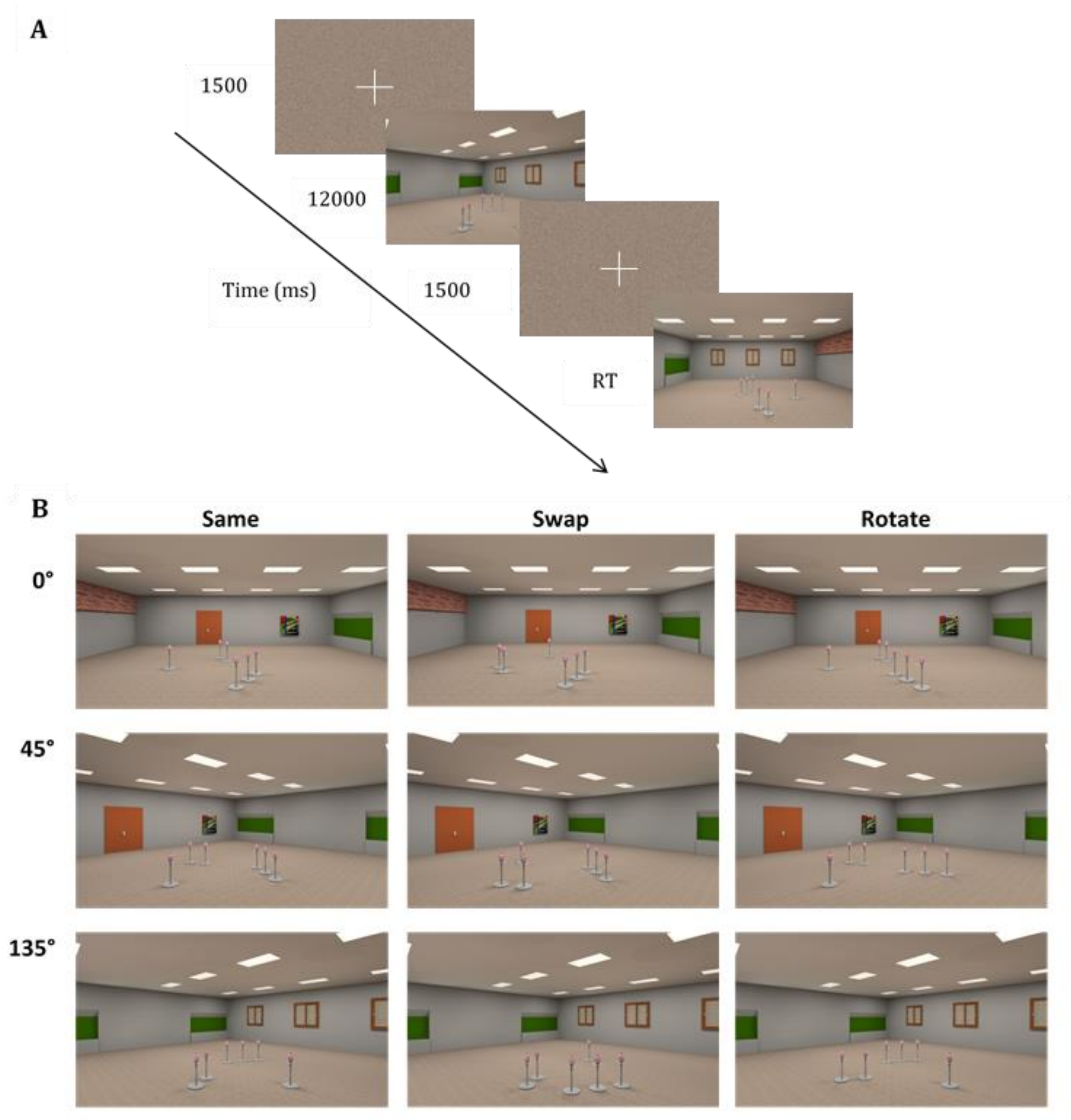

Figure 2.1 Experimental protocol; B: Examples of experimental stimuli for different conditions (Same, Swap and Rotate) and perspective shift (0°, 45°, 135°)

The experiment consisted of 192 experimental trials presented in randomised order and preceded by 10 practice trials. The entire study took around 2 hours to complete and participants were free to take breaks when they wished. Overall, 96% of our participants completed the entire study with two older adults withdrawing from the experiment after completing 144 trials and one younger adult after completing 168 trials.

2.2.3. Data analysis

Stastitical analyses were carried out using R (R Core Team, 2013) with the exception of diffusion modelling which was carried out using fastDM (Voss & Voss, 2007). The parameters that were obtained from diffusion modelling (drift rate, response conservativeness, non-decision response times) as well as behavioural data (d' and Bias, sdt.rmcs package in R; Todorova, 2017) were analysed with linear mixed effects models (LME) using LME4 (Bates et al. 2015) in R (R Core Team, 2013). For the d' and the bias LMEs we defined the contrasts as follows: Age Group and Condition (Rotate/Swap) were coded using effect coding; Perspective Shift was defined as successive difference contrasts (MASS package in R; Venables & Ripley, 2002) so that the 0° was compared to 45° and 45° was compared to 135°. For drift rate and response conservativeness analysis the same contrasts were used for Age Group and Perspective Shift whilst Condition (No Change/Rotate/Swap) was coded using treatment coding with the No Change condition as the baseline. Age group, perspective and condition were used as fixed factors across all LMEs. All models included the maximal random effects structure justified by the design: for d' a random by-subject intercept and slope for Condition and Perspective Shift (no interaction) were used. For drift rate and boundary separation analysis only a random by-subject intercept was used.

Differences between age groups in gaze parameters, non-decision response times and starting bias were examined using the Bootstrap-t method (5000 resampling) with 20% trimmed means (Wilcox & Keselman, 2003). This method provides a more robust estimation of central tendency than a standard t-test as it reduces the probability of type 1 error and bias and does not compromise power as compared to median-based methods (Wilcox & Keselman, 2003).

To estimate the parameters of the diffusion model we used the Kolmogorov–Smirnov (KS) test statistic T (Kolmogorov, 1941), as the optimization criterion in an iterative search for the best-fitting model solution (Voss, Voss & Lerche, 2015). We estimated the drift rate (v) and response conservativeness for each participant across each experimental condition (Perspective Shift [0°, 45°, 135°] and Condition [Swap, Rotate]). We also estimated the starting point bias (z) for each participant and the non-decision response time (t0). Based on the procedure suggested by Voss, Nagle, and Lerche (2013), outliers were removed from the individual response time distributions using the interquartile range method. This allowed estimating the specified parameters for 37 young adults and 36 older adults.

2.3. Results

2.3.1. Behavioural Data

Estimates of sensitivity (d') and bias (c) were obtained for each participant in the Swap and Rotate condition and across the different perspective shifts (0°, 45°, 135°). Coefficients, standard errors and t-values are reported in Table 2.1 and show that age group, perspective and condition were all reliable predictors of d' scores (Figure 2.2A). Specifically, we found a significant reduction in sensitivity in older adults when compared to younger adults. Perspective shifts from both 0° to 45° and from 45° to 135° also resulted in a significant reduction in sensitivity. Overall, sensitivity was lower in the Rotate than in the Swap condition.

We also found a significant interaction between Age Group and Perspective Shift from 45° to 135° (Figure 2.2B). There also was a trend towards significance for the interaction between Age Group x Perspective Shift at 0° to 45° degrees. Specifically, the decline in performance was lower in older adults when the perspective shift increased from 45° to 135°. Finally, there was an interaction between Condition and Perspective Shift (0° to 45°) with a larger decline in performance for the Swap condition than the Rotate condition with the introduction of the 45° perspective shift (Figure 2.2C).

Bias analysis suggested that participants were more conservative in the Rotate condition than in the Swap condition. Moreover, participants were less conservative with the introduction and increase of the perspective shift. The LME analysis of bias is reported in Supplementary Materials.

Table 2.1 Coefficients from d’ LME analysis

	dPrime		
Predictors	Estimates	std. Error	t-value
Intercept	1.604	0.085	18.887
Age Group	-0.179	0.085	-2.106
Condition (Rotate)	-0.243	0.027	-9.081
Perspective (0° to 45°)	-0.705	0.063	-11.085
Perspective (45° to 135°)	-0.450	0.062	-7.295
Age Group: Condition (Rotate)	-0.015	0.027	-0.542
Age Group: Perspective (0° to 45°)	-0.114	0.064	-1.796
Age Group: Perspective (45° to 135°)	0.144	0.062	2.341
Condition (Rotate): Perspective (0° to 45°)	0.154	0.040	3.878
Condition (Rotate): Perspective (45° to 135°)	0.145	0.040	3.642
Age Group: Condition (Rotate): Perspective (0° to 45°)	0.044	0.040	1.103
Age Group: Condition (Rotate): Perspective (45° to 135°)	-0.045	0.040	-1.119

Significant t values (|t|≥1.96) in bold type

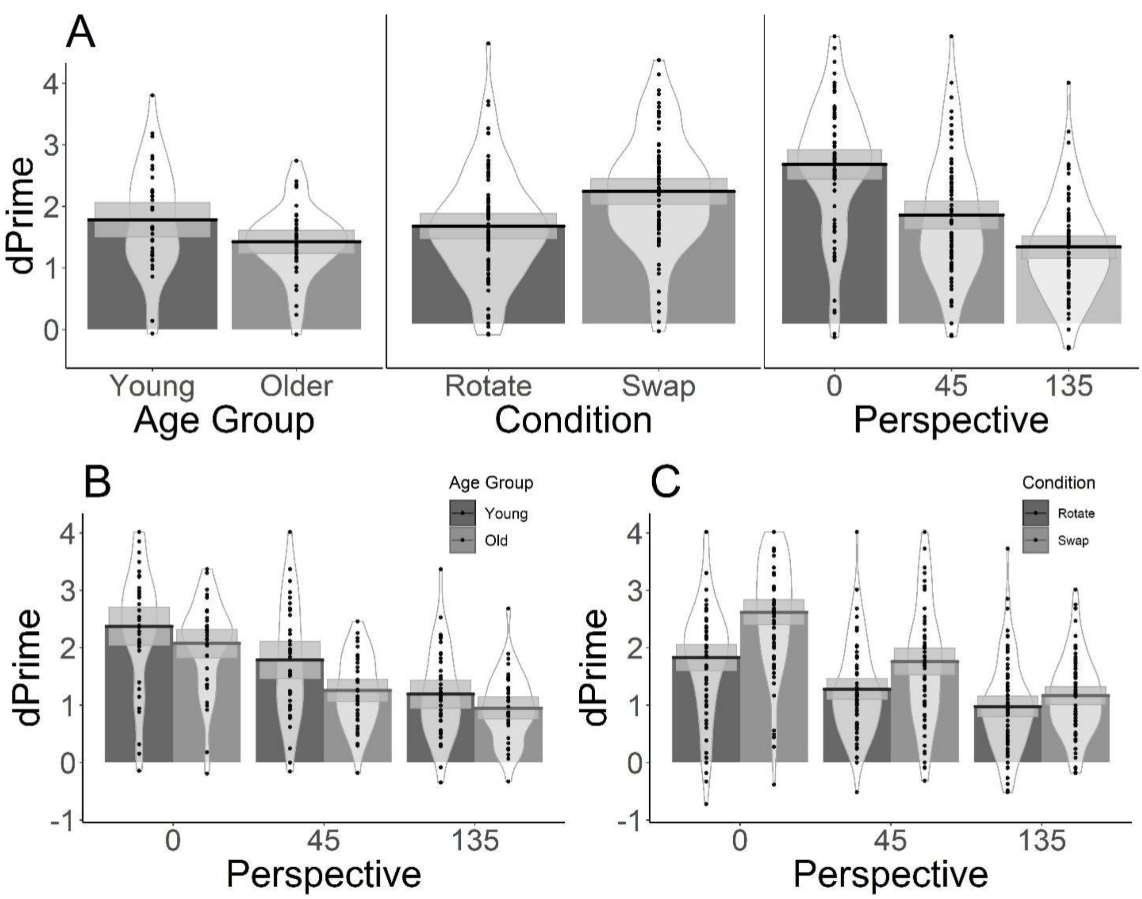

Figure 2.2 dPrime values Bar plots with mean (solid line) and 95% CIs (grey shaded area) with individual data points and violin plots A: Performance across age groups, condition and perspective; B: Younger and older participants' as a function of perspective shift; C: Performance in the Swap and Rotate conditions as a function of perspective shift

2.3.2. Diffusion Modelling

Model fit

Models that were at $p < .05$ level indicated model misfit. We removed five participants, four from the older group and one from the younger group, who had at least one significant model. For the purposes of visual representation and statistical analysis the drift rates in the no change condition were multiplied by -1, as the correct answer in the No Change condition was the opposite to that in the Swap and Rotate conditions.

Starting bias: We did not find a starting bias (z) in older adults ($M= 0.48$, $p=.165$), but there was a slight bias towards the No Change response in the younger group ($M=0.47$, $p=.026$). The differences in starting bias between age groups were not statistically significant ($p=.77$).

Non-decision response times: As expected, we did find that older adults had higher non-decision response times ($t0$) than younger adults ($M_{young}=1.00$ sec and $M_{old}=1.99$ sec, $p<.001$).

Coefficients, standard errors and t-values for the drift rate (v) and response conservativeness (a) values are reported in Table 2.2.

Drift rate: We found that Age Group, Perspective and Condition were all significant predictors for drift rate. Specifically, drift rate in our older participants was lower than in the younger participants. In addition, across both age groups there was a reduction in drift rate in the Rotate and the Swap condition compared to the No Change condition. We also found that the introduction (0° - 45°) and the increase (45°- 135°) of the perspective shift led to a reduction in drift rate, with the introduction of the perspective shift leading to a larger decline in drift rate.

The reduction in the drift rate was smaller in the Rotate and Swap condition compared to the No Change condition when the perspective shift was introduced and when it increased from 45° to 135° in the Rotate condition. This is likely to be due to relative ease of the No Change condition when no perspective shift is present (see Figure 2.3).

Given that drift rates of zero indicate that participants are not extracting useful information from the stimuli, we also compared if drift rates across each Age Group, Perspective and Condition were significantly different from zero (Figure 2.3). Overall, using the alpha level of 0.01, only the drift rates for older adults in the Rotate Condition across all levels of perspective shift have yielded results that are not significantly different from zero.

Response Boundaries: We found main effects of Age Group, Condition, and Perspective on response boundaries. Consistent with previous research using diffusion modelling in ageing (Starns & Ratcliff, 2010), older adults had wider response boundaries, indicating that they needed to accumulate more information before making a decision and, as a result, took longer to make the decision. We also found that the response boundaries were wider in the Swap condition compared to No Change condition. The introduction of perspective shift (0° vs 45°) led to a substantial widening of the response boundaries. A lesser increase was observed when perspective shift was further increased from 45° to 135°. We also found that older adults' response boundaries increased in the Swap as compared to the No change condition. There also was a trend for an interaction between Age Group and Perspective ($t= 1.92$), whereby older adults response boundaries showed a larger increase compared to younger adults when the perspective shift was introduced (0° to 45°). The increase in the response boundaries was smaller in the Swap and Rotate condition compared to No Change when the perspective shift was introduced (0° to 45°).

Table 2.2 Coefficients from Drift rate (v) and Response Boundaries (a) LME analysis

Predictors	Drift rate			Response Boundaries		
	Estimates	std. Error	t-value	Estimates	std. Error	t-value
(Intercept)	0.614	0.034	18.149	2.973	0.086	34.410
Age Group	-0.103	0.034	-3.053	0.246	0.086	2.849
Condition (Rotate)	-0.473	0.033	-14.423	0.063	0.043	1.452
Condition (Swap)	-0.215	0.033	-6.551	0.261	0.043	6.040
Perspective (0°-45°)	-0.400	0.057	-7.028	0.968	0.075	12.961
Perspective (45°-135°)	-0.118	0.057	-2.078	0.357	0.075	4.780
Age Group: Condition (Rotate)	0.000	0.033	0.013	0.055	0.043	1.265
Age Group: Condition (Swap)	-0.004	0.033	-0.117	0.129	0.043	2.994
Age Group: Perspective (0°-45°)	-0.030	0.057	-0.524	0.143	0.075	1.915
Age Group: Perspective (45°-135°)	-0.001	0.057	-0.020	0.112	0.075	1.503
Condition (Rotate): Perspective (0°-45°)	0.306	0.080	3.802	-0.428	0.106	-4.049
Condition (Swap): Perspective (0°-45°)	0.222	0.080	2.757	-0.583	0.106	-5.521
Condition (Rotate): Perspective (45°-135°)	0.166	0.080	2.067	-0.064	0.106	-0.602
Condition (Swap): Perspective (45°-135°)	0.031	0.080	0.379	-0.188	0.106	-1.779
Age Group: Condition (Rotate): Perspective (0°-45°)	0.103	0.080	1.276	-0.056	0.106	-0.529
Age Group: Condition (Swap): Perspective (0°-45°)	0.086	0.080	1.075	-0.119	0.106	-1.127
Age Group: Condition (Rotate): Perspective (45°-135°)	0.011	0.080	0.131	-0.083	0.106	-0.785
Age Group: Condition (Swap): Perspective (45°-135°)	0.066	0.080	0.822	-0.054	0.106	-0.512

Significant t values ($|t| \geq 1.96$) in bold type

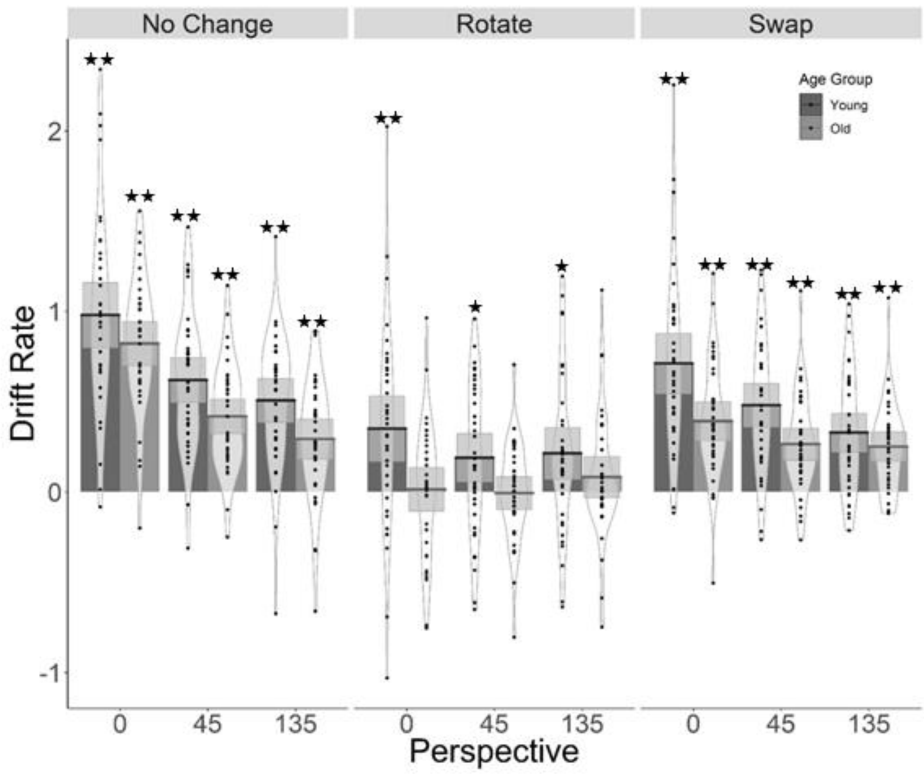

Figure 2.3 Drift Rate Bar plots for the drift rate values as a function of perspective shift, condition and age group with mean (solid line) and 95% CIs (grey shaded area) with individual data points and violin plots. Stars indicate response bias significantly different from 0 (1 star [p < 0.01] and 2 stars [p < 0.001])

2.3.3. Eye-tracking results

The aim of the eye-tracking analysis was to investigate age differences in encoding strategies and was therefore limited to the encoding phase.

2.3.3.1. General saccade and fixation parameters

Looking at general saccade and fixation parameters we found differences between young and older age groups in saccade frequency, saccade average velocity, saccade peak velocity, saccade amplitude and saccade duration as well as fixation duration and fixation frequency (Table 2.3). Specifically, older adults made more saccades and of higher in velocity and amplitude. They also made more, but shorter, fixations compared to the younger adults. Similar results were observed when trials were split into correct and incorrect trials (see Supplementary Materials). There were no differences in blink frequency between the groups. Although these results suggest that older and younger adults were using different gaze strategies when encoding the stimuli, it is rather difficult to deduce the nature of these strategies from these general eye-tracking measures.

Table 2.3 Means and inferential statistics for saccade and fixation parameters between younger and older adults from the Learning Phase

Gaze measure	Mean Young	Mean Older	Confidence Interval	t-value	p-value
Saccade Frequency	2.94	3.80	[-1.15, -0.57]	-5.52	<.001
Average velocity	100.94	110.68	[-16.74, -2.75]	-2.66	.007
Peak velocity	180.60	214.62	[-53.60, -14.46]	-3.40	.003
Amplitude	3.86	4.49	[-1.06, -0.19]	-2.76	.007
Saccade duration (ms)	32.48	34.95	[-4.87, -0.07]	-2.07	.046
Fixation Frequency	3.15	4.08	[-1.24, -0.63]	-6.08	<.001
Fixation Duration (ms)	325.33	270.15	[31.89, 78.48]	4.82	<.001
Blink Frequency	0.44	0.38	[-0.06, 0.18]	0.96	.328

Note: significant p values are in bold

Therefore, to further explore the differences in gaze characteristics between age groups and to develop a better understanding of how these relate to encoding strategies, we visually inspected the gaze paths for a random subset of the trials. This exploration suggested that our older adults tended to “look around more”, while the younger participants focused more on the target objects (see Figure 2.4 for examples of gaze paths). There was substantial overlap of objects in the stimulus set used in this study, which made the stimuli not suitable for interest area analysis. For a post-hoc analysis aiming to capture and quantify these observed differences and to compare gaze behaviour across different stimuli, we used a stimulus-independent grid cell measure.

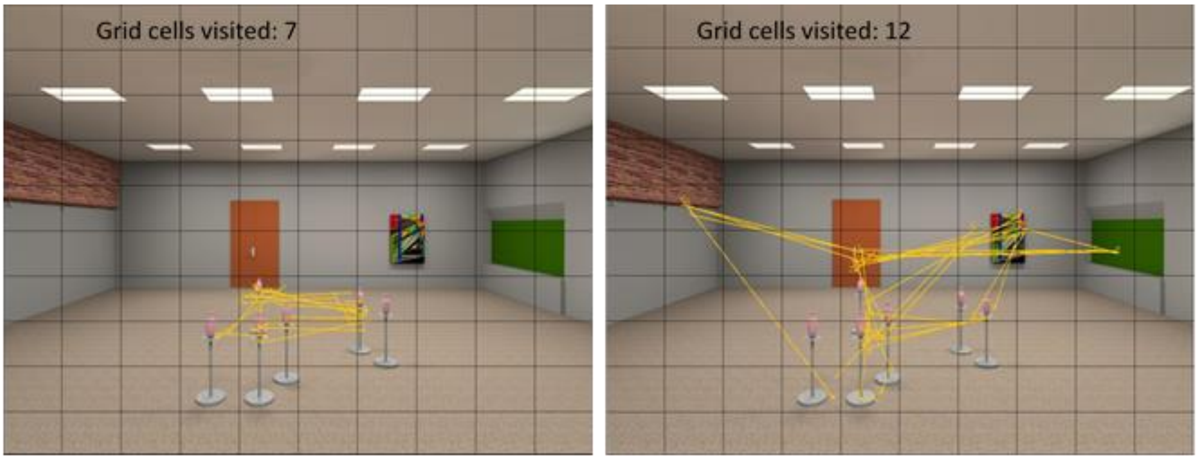

Figure 2.4 Trial examples with participant scan paths in a single trial with corresponding number of grid cells visited

2.3.3.2. Grid cell measure

To quantify the proportion of the stimulus that were examined during a trial, we superimposed a 10 x 10 grid on the stimulus display (Figure 2.4). For each trial, we then calculated the total number of grid cells that received at least one fixation similar to the method used in Livingstone-Lee et al. (2011). We found that older adults examined a larger proportion of the display (M=12.06), compared to younger adults (M=10.12); t=-5.60, p = <.001, CI= [-2.62, -1.27]. Note that both age groups fixated only on a relatively small proportion of the display (10.12% and 12.06%). The fact that younger participants can perform the memory task better than the older participants while at the same time viewing less of the overall stimulus indicates that they were better at identifying the features within the display that were important for solving the task.

2.3.3.3. Gaze behaviour across the experiment

We also investigated if gaze behaviour changed across the experiment by correlating the number of grid cells visited with trial number for younger and older participants. There was a large negative correlation in younger (r-.74, p<.001) but not in older participants (r=-.01, p=.621), suggesting that younger participants adapted their gaze strategy and explored less of the stimuli over the course of the experiment whilst older participants gaze behaviour did not change. The correlation coefficients between younger and older adults were statistically different (z=-9.13, p<.001).

2.3.3.4. Partial correlation analysis

To investigate whether differences in the number of grid cells visited during encoding were, in fact, associated with performance, we ran partial correlations between drift rates and sensitivity (d') with the number of grid cells visited, partialling out chronological age. There were no significant correlations between drift rate and the number of grid cells visited (r=-.18, p=.166) or between d' and number of grid cells visited (r=-.11, p=.383).

However, given the differences between the Rotate and Swap conditions in the behavioural findings, it is possible that the relationship between the number of grid cells visited and drift rate or d' might be different across those two conditions. We, therefore, ran partial correlations separately for the Rotate and Swap conditions and found a significant correlation between the number of grid cells visited and drift rate in the Rotate condition (r=-0.29, p .022), but not in the Swap condition (r=-0.13, p=0.339). Similarly, there was a trend for a negative correlation between number of grid cells visited and d' in the Rotate condition (r=-.22, p=.070) but not in the Swap condition (r=.02, p=.885).

2.4 Discussion

In this study we used eye-tracking and diffusion modelling to investigate age-related changes in spatial memory for object locations. To ensure that the task indeed addressed spatial memory and could not simply be solved by image comparisons, we introduced perspective shifts in two thirds of the trials (Nardini et al., 2009). To investigate potential age-related differences in the resolution of spatial representations we changed the spatial configuration between encoding and test by either swapping clusters of objects (coarse change) or by rotating a cluster within a scene (fine-grained change).

As expected, and in line with earlier research, we found that older adults had overall greater difficulties with the task than younger adults (c.f. Muffato et al., 2019; Montefinese et al., 2015; Hartley et al., 2007) which was reflected in performance and drift rate differences between age groups. We also found that older adults were generally more conservative in their decision making and needed to accumulate more information prior to deciding on a response. The introduction of perspective shifts between encoding and test negatively affected performance in both age groups. Performance and drift rates were lower in the Rotate condition which required more fine-grained spatial representations than the Swap condition. In addition, both age groups became more conservative with the introduction of a perspective shift and in the Swap condition, but this effect was more pronounced in older adults. We also found differences in gaze behaviour between younger and older adults, suggesting differences in encoding strategies.

The lower sensitivity to detect changes and the lower drift rates in older adults suggest that they had greater difficulty in detecting whether or not object positions within the room had changed. These results are in line with previous research demonstrating age-related deficits in memory for layouts of objects or environmental features experienced from different perspectives during encoding and recall (Muffato et al., 2019; Montefinese et al., 2015; Hartley et al., 2007). Given that the target objects were present in learning and test, it is likely that age-related reductions in performance were in part driven by an inability to successfully bind the objects in the array to their specific locations (Muffato et al., 2019). The current study builds on previous research and suggests that an age-related decline in object-location binding is not mediated by the presence or absence of visual and geometrical cues (Muffato et al., 2019). The decline in older adults' performance can be explained by age-related functional and morphological changes in the hippocampal circuit (Antonova et al., 2009; Meulenbroek et al., 2004; Moffat et al., 2007) which is crucial for development of spatial memories and manipulation of spatial memories to allow for perspective taking (King et al., 2002) as well as object-location binding (Postma & van der Ham, 2016; Zimmermann & Eschen, 2017).

To the best of our knowledge, the current study is the first to apply diffusion modelling to investigate age-related changes in spatial memory. Previously, diffusion modelling was mostly used to analyse data from relatively fast and simple reaction time tasks, such as lexical decision or letter discrimination tasks (Ratcliff, Gomez, & McKoon, 2004; Thapar, Ratcliff & McKoon,2003). Our findings, consistent with Lerche & Voss (2019), suggests that diffusion modelling can also be used to study decision making in more complex tasks with longer response times. The observed age-related shift towards a more conservative response strategy is consistent with research that used diffusion modelling to study cognitive ageing across a number of different domains including memory (Spaniol, Madden, & Voss, 2006; Ratcliff, Thapar, & McKoon, 2004), perceptual learning (Ratcliff, Thapar, & McKoon, 2006) and language (Ratcliff, Thapar, Gomez, & McKoon, 2004). Thus, it appears that this age-related shift towards a more conservative response strategy is not task/domain specific but extends across several cognitive domains and tasks including those related to spatial memory. This shift is likely to be driven by emphasis on different aspects of the task between younger and older adults, with older adults being less accepting of errors at the expense of time (c.f. Starns & Ratcliff, 2010).

Notably, older adults were not only more conservative in their responses, but also had longer non-decision response times. This could be due to slower visual encoding in older adults, driven by age-related declines in visual function (Owsley, 2011) and reduced motor speed (Ren, Wu, Chan & Yan, 2013). These findings highlight the importance of distinguishing information processing from decisional style and non-decisional components when analysing response time data when studying cognitive ageing as age-related changes were evident in all these components. Together these components may explain the overall increase in response times in older adults during spatial perspective taking reported in previous research (Watanabe,2011; Watanabe & Takamatsu 2014). In addition, we did not find starting bias in older adults suggesting that older participants did not exhibit pattern completion bias in the current task (Vieweg et al., 2015).

Unlike previous research in other cognitive domains that used diffusion modelling to study cognitive ageing (Ratcliff, Thapar, & McKoon, 2004; Ratcliff, Thapar, & McKoon, 2006; Ratcliff, Thapar, Gomez, & McKoon, 2004), we found an age-related decline in drift rate. Note, however, that the tasks used in earlier studies typically have only minimal memory demands and examine very different cognitive mechanism such as lexical decision making or perceptual discrimination. Given that the introduction of a perspective shift equally affects younger and older, age-related deficits in spatial perspective taking abilities are unlikely to explain lower drift rates in older adults. Instead, we interpret the lower drift rates in our study as evidence of a reduced ability of our older adults to extract useful information both from the test stimuli and the stored representation (obtained during encoding) required to solve the task. As drift rates in the current task are reflective of the quality of the stored representation, the ability to compare it to the test stimuli it is plausible that formation of an impoverished representation during encoding contributes to the observed lower drift rates. This idea is consistent with Ratcliff, Thapar, & McKoon (2004) who interpreted drift rates as evidence of the quality of the memory trace for studied items in a recognition memory task. Given this interpretation of drift rates, lower drift rates in ageing are indicative of a specific spatial processing deficit in ageing.

In line with previous research (Montefinese et al., 2015; Watanabe, 2011; Muffato et al., 2019), we observed performance declines with the introduction of a perspective shift in both age groups. These findings suggest that the 0° condition is qualitatively different from the conditions with a perspective shift. Specifically, the task in the 0° condition can be solved by accessing the learning scene from memory and using image matching to detect changes (Milner & Goodale, 2008; Nardini et al., 2009). However, when a perspective shift is introduced the task becomes a spatial perspective taking task that cannot be 'simply' solved by image matching. Instead, additional mental transformation of the stored spatial configuration to match the perspective at test with that of encoding (Hegarty & Waller, 2004) are required. These additional transformations are likely to recruit further brain regions, including the hippocampus circuit, which is associated with spatial processing (Mellet et al., 2000, Shelton & Gabrieli, 2002). Importantly, the performance and drift rate decline following the introduction of a perspective shift (i.e. from 0° to 45°) was almost three times larger than the decline observed when the perspective shift increased from 45° to 135°. These results suggest that it is the initiation of these mental transformations rather than the amount by which the spatial representations need to be transformed that produces the higher cognitive cost. Interestingly, this interpretation is inconsistent with findings from mental rotation research, which show that cognitive costs increase with increasing angular disparity, typically resulting in a linear increase in response times (Shepard & Metzler, 1971; Lohman, 1986). As we do not find a linear decrease in performance it is unlikely that our participants rotate the array to solve the tasks. Instead, they are more likely to imagine moving around the array to either match the test viewpoint with the encoded viewpoint or vice versa (King et al., 2001).

Participants in both age groups adopted a more conservative response strategy in trials in which the perspective shift was introduced and there was a trend for this increase to be higher in older adults. In addition, further increases in perspective shift resulted in adoption of an even more conservative response strategies across both age groups. It is not surprising that participants have wider decision boundaries when a perspective shift is introduced as they need to accumulate extra information to inform them about their new orientation. In addition, after participants accumulate information about the new orientation, they need to perform extra mental computations (Holmes, Newcombe & Shipley, 2018), that come with an increased cognitive cost, to transform their stored representation of object-locations to be consistent with that new perspective and this additional cognitive demand is reflected in lower drift rates. Those results highlight that the spatial perspective shift not only increases processing demands but that it induces changes in response strategies, which are differentially affected by ageing. This is particularly important for research on spatial perspective taking that frequently relies on measures of response times as marker of performance (i.e. Spatial Orientation Test; Guilford & Zimmerman, 1948; Hegarty & Waller, 2004).

Results of previous research on the effects of ageing on spatial perspective taking are mixed (Muffato et al., 2019; Montefinese et al., 2015; Watanabe, 2011). If there was an age-related spatial perspective taking deficit, we expected an age by perspective interaction. Although we did find an interaction, it was not of the form we expected. Specifically, we found that performance in older adults did not decline as much as it did in younger participants when perspective shift was increased from 45° to 135°, this is consistent with Montefinese et al. (2015) findings. We believe that this interaction was driven by older adults being more affected by the introduction of a perspective shift (interaction approaching significance). This contrasts with the performance of the younger group suggesting that the younger group was better able to deal with the introduction of a perspective shit as they showed a more linear decline in performance with the increasing size of the perspective shifts, which at 135° almost matched the performance of the older adults group. Therefore, the larger drop in performance in older adults with the introduction of the perspective shift and no decline in performance with the increase of the perspective shift suggests that ageing may be affecting the initiation of the extra mental computations that are required for spatial perspective taking. In addition, the age by perspective interaction may arise due to floor performance. That is, it is possible that older adults perform at floor levels when the perspective shift is introduced, and their performance thus remains unchanged with the increase in the perspective shift

Our results show that the Rotate condition was harder than the Swap condition. This was expected as the Swap condition, but not the Rotate condition, could be solved with only a coarse spatial representation. Specifically, the Swap condition can be solved by representing the spatial relationships between the object clusters or the coarse locations of the object clusters in the room. The Rotate condition, in contrast, also requires participants to encode the precise orientation of each object cluster either relative to the other clusters or relative to the room. This additional difficulty in the Rotate condition is reflected in substantially lower drift rates which suggests that participants found it more difficult to extract useful information to identify a change in object position when comparing the memory trace formulated during encoding to the position of objects at test. Surprisingly, we found that participants were more conservative in the Swap than in the Rotate condition. One possible explanation for this effect is that participants preferred to accumulate more information in the Swap condition, thus increasing the likelihood of producing correct answers. In contrast, in the Rotate condition, extracting useful information was harder (reflected in low drift rates), and spending additional time would not necessarily lead to any substantial information gain. This explanation may also apply to the Age Group and Condition interaction, in which older adults’ response boundaries were wider in the Swap condition.

One of the aims of this study was the examination of age-related differences in spatial encoding strategies using eye-tracking and how potential strategy differences are related to performance differences. We first examined general gaze patterns during encoding and found that older adults made more saccades than younger participants that were larger in amplitude and velocity (peak and average) and longer in duration. They also made more fixations that were consequently shorter in duration as they are bound by fixed encoding times. These patterns are not reflective of previous ageing research using other tasks which have reported that ageing is associated with reductions in saccade amplitudes, velocity and frequency (Dowiasch, Marx, Einhäuser & Bremmer, 2015; Williams et al., 2009; Porter et al., 2010). Consistent with our findings, Açık et al., (2010) found that older adults made more fixations when viewing complex visual stimuli. However, they also reported that saccade amplitudes were lower in older adults. One explanation for age-related declines in saccade amplitudes along with an increased fixation count is that the size of useful field of view declines in older age resulting in an increased number of fixations that are closer to each other (Sekuler, Bennett & Mamelak, 2000). This account does not, however, explain our findings as older adults produced saccades with larger amplitudes. We thus believe that the differences in these general parameters in this study reflect differences in encoding strategies rather than resulting from the general ageing of the oculomotor system.

In the current task, the environment contained room-based cues and room geometry. This contrasts with Muffato et al.'s (2019) study where objects were presented in an open-field and object locations could only be remembered by encoding the spatial relationships between the objects. Whilst, in our task participants could use different encoding strategies to encode object locations. Specifically, participants could either encode locations by focusing on the spatial relations among object clusters or by relating the object positions to other cues. Adoption of the latter strategy may be reflected in the gaze data as participants would presumably fixate on the layout objects as well as on the environmental cues.

To further explore how age differences in general gaze patterns might translate to differences in spatial encoding strategies we looked at the percentage of the stimulus attended to during encoding. Specifically, we found that older adults examined more of the stimuli. We interpret these findings as indicative of older adults employing an encoding strategy in which they tend to remember target object positions in relation to room-based cues while younger adults focus on the spatial relationship between object clusters.

An alternative explanation for why older adults were looking at room-based cues is that they were distracted by their presence. This is consistent with a prominent theory of cognitive ageing stating that older adults have difficulty in inhibiting attention to salient but task-irrelevant stimuli (Hasher & Zacks, 1988). The current design does not allow us to differentiate between those two alternative explanations as the stimulus set was not suited for interest area analyses. We are, however, currently running further experiments to distinguish between these alternative explanations. Preliminary analyses of these experiments suggest that older adults rely on extra cues to facilitate encoding (Segen et al., in preparation). To further investigate age-related differences in encoding strategies, future research could also make use of verbal reports during encoding or retrospective strategy reports. Such approaches may shed light on whether older adults explicitly adapt their encoding strategies to compensate for spatial memory deficits.

Interestingly, we found a negative correlation between the percentage of stimuli attended to and drift rate, but only in the Rotate condition. Our conjectures is that participants who explored a smaller proportion of the stimuli were more efficient at sampling the parts of stimuli which were most informative for formulating the fine-grained representations required to solve the task in this condition. The higher drift rate in the Rotate condition is in line with this explanation. However, in situations in which a coarser representation is sufficient, relating target objects to environmental cues is sufficient to solve the task. As already noted, older adults were more likely to look around more during encoding which could be indicative of coarser spatial encoding. Adoption of such encoding strategy would have enabled them to solve the Swap condition but not the Rotate, this interpretation is consistent with our diffusion modelling results as the drift rates are around zero for older adult in the Rotate and are slightly higher in the Swap condition. Drift rates around zero imply that older participants are sampling from largely uninformative representations in the Rotate condition whilst the positive drift rates in the Swap condition are indicative of ability to extract some useful information from the comparison between the stored representation formed during encoding and test stimuli to detect if the spatial arrangement has changed. In addition, we also found that in younger participants gaze became more focused over the course of the experiment whilst in older adults' gaze remained consistent throughout the experiment. We believe this adaptation of gaze behaviour in our young participants reflects their ability to improve their encoding strategy with practice.

Overall, our exploratory eye-tracking analyses suggest that spatial representations useful for the task presented here can be enhanced by adopting a visual encoding strategy that involves focusing on the to-be-encoded objects. This interpretation is consistent with research showing that focal shifts of spatial selective attention to the memorised locations is associated with active maintenance of location-specific representations within visuo-spatial working memory (Awh, Jonides, & Reuter-Lorenz, 1998; Shimi & Scerif, 2017; Smyth & Scholey, 1994). Thus, by focusing on to-be-remembered objects participants are more likely to maintain location specific representations within visuo-spatial working memory. This encoding behaviour is likely to contribute to the formation of a stronger long-term memory trace that participants can access at test (Ranganath, Cohen, & Brozinsky, 2005). Young participants were more likely to adopt this strategy during encoding which could explain higher performance in our younger adults' group. However, those interpretations would benefit from further investigation as the reported correlations were explorative in nature and yielded relatively small effects.

In summary, we have presented a novel task to investigate age-related differences in the ability to encode spatial relationships between objects and to recognize them across different viewpoints. As expected, we found that older adults performed worse than younger participants on the task and overall participants found the condition that required more fine-grained spatial representations harder than the condition that could be solved using a coarser representation. We also found that older adults' encoding strategies differed from those of younger participants. Moreover, the differences in encoding strategies identified via eye-movement behaviour were correlated with performance differences across different manipulations. This highlights the value of using eye movements to study tasks involving the memory of visual scenes. Our diffusion modelling analysis shows that declines in spatial memory are likely to be driven by specific declines in spatial processing rather than general age-related declines in cognition, whilst also highlighting that an age-related shift towards a more conservative response strategy appears to extend across a wide range of cognitive tasks.

2.5. Open practices statement

The data sets generated during and/or analyzed during the current study are available in the Open Science Framework repository (https://osf.io/xh5kd/). This experiment was not preregistered.

2.6. References

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Chapter 3: Age-related changes in visual encoding strategy preferences during a spatial memory task

The following chapter has been resubmitted submitted for publication following the first round of reviews as Segen, V., Avraamides, M. N., Slattery, T. J., & Wiener, J. M. (2020). Age-related changes in visual encoding strategy preferences during a spatial memory task. *Psychological Research*, 1-17

3.1. Introduction

Successful navigation and orientation depend on our ability to recognise familiar places across different perspectives (Waller & Nadel, 2013). In the lab, this ability is typically assessed with tasks in which participants first encode an array of objects or environmental features from one perspective and are then asked to indicate whether the array has changed when presented from a different perspective. Studies using such paradigms have reported age-related declines in performance (Hartley et al., 2007; Montefinese, Sulpizio, Galati, & Committeri, 2015; Muffato, Hilton, Meneghetti, De Beni & Wiener, 2019; Hilton, Muffato, Slattery, Miellet & Wiener, 2020; Segen, Avraamides, Slattery, Wiener, 2021). Building on these studies, and in an effort to gain a more detailed understanding of the factors that contribute to the performance decline, we use eye-tracking to investigate potential age-related differences in visual encoding strategies. Specifically, we are interested in whether young and older adults rely on the same or on different environmental cues during place recognition.

Recently, Muffato et al. (2019) and Hilton et al. (2020) investigated the effects of cognitive ageing on place recognition abilities using scenes defined by objects that were placed in an open field. After encoding a scene with four objects, participants were presented with another scene from a different perspective and had to decide whether or not it was identical to the one encoded. Results revealed the presence of object-location binding errors, particularly in older adults. That is, compared to younger participants, older adults found it harder to detect that two objects had swapped locations than when one of the objects was replaced with a new object.

In our previous work (Segen et al., 2021), we investigated age-related differences in the ability to recognise spatial configurations across different perspectives. The task required participants to encode the locations of an array of identical objects presented as an image on a computer screen. The objects were arranged in clusters of one, two and three objects, in a virtual room containing additional environmental cues such as windows and a door. Then, participants viewed a second image of the same room taken from the same (0°) or a different perspective (45° or 135°) and judged whether or not the objects were in the same locations. The positions of the objects were either changed by swapping two object clusters or by rotating one of the clusters. While with the former manipulation the task could be solved using a coarse categorical representation of the spatial relationships between object clusters (e.g. the cluster with two objects is to the left of the single object), the latter manipulation required a fine-grained spatial representation of the exact positions of the objects as the overall relationships between the clusters was maintained.

Consistent with previous research, we found that older adults had greater difficulty with the task than younger adults (Hartley et al., 2007; Montefinese et al., 2015; Muffato et al., 2019; Hilton et al., 2020). Diffusion modelling showed that older adults not only had greater difficulty in extracting useful information from the stimuli, but that they also adopted a more conservative response strategy, i.e. they accumulated more information prior to reaching a decision.

Furthermore, the analysis of gaze data in Segen et al. (2021) revealed that older adults attended to a larger proportion of the scenes compared to younger adults. We proposed two potential explanations for this. First, differences in gaze behaviour may reflect differences in encoding strategies with older adults encoding object locations relative to the landmarks available in the room (windows, door, etc), whilst young adults focus on the local arrangement of objects and on encoding the spatial relationships among them. The differences in encoding strategies may reflect a shift towards categorical spatial representations in older adults, driven by age-related hippocampal neurodegeneration (Antonova et al., 2009; Meulenbroek, Petersson, Voermans, Weber, & Fernández, 2004; Moffat, Kennedy, Rodrigue & Raz, 2007).

Second, older adults may have difficulties in focusing on the task-relevant information as they become distracted by salient features within the environment. This is in line with the attention inhibition deficit in ageing reported in past studies (e.g., Hasher & Zacks, 1988). According to this account, older adults exhibit top-down control difficulties, with attention orienting being more affected by stimulus properties rather than the task at hand (Olk & Kingstone, 2015; West, 1996). Lastly, older adults may have difficulties in selecting appropriate information required to solve the task. This is consistent with our findings that older adults have difficulties in extracting useful information from the stimuli (Segen et al., 2021).

In our earlier study (Segen et al., 2021), we could not distinguish between these explanations for several reasons. First, we did not systematically manipulate the availability of landmarks. Second, the landmarks used in the environment were all unique and informative and could, therefore, facilitate the encoding of the object locations, even if they distracted the older participants. Third, there was substantial overlap between the landmarks and the objects of the scene, which prevented a region of interest analysis. Finally, due to the large perspective shifts introduced in some trials (e.g. 135°), some landmarks were visible during encoding but not at test.

The current study was designed to disentangle the explanations for age-related differences in place recognition by examining gaze behaviour. To do so, we amended our original task (Segen et al., 2020) in a variety of ways to overcome the limitations of the earlier study. First, we reduced the size of the perspective shift between encoding and test which allowed us to present the same landmarks during learning and test, ensuring that participants could use the information they encoded during learning to solve the task at test. Decreasing the size of the perspective shift also made the task easier (Hegarty & Waller, 2004; Montefinese et al, 2015; Segen et al., 2020; Muffato et al.,2019; Hilton et al., 2020). Task difficulty was further reduced by including only the condition in which two object clusters were swapped with each other. Reducing task difficulty aimed at avoiding floor level performance in older adults, which would allow us to rule out that potential differences in gaze behaviour across groups are caused by participants' inability to carry out the task.

Generally, we predict a decline in performance in older adults consistent with age-related place recognition deficits (Hartley et al. 2007). Responding after a perspective shift requires additional and demanding mental manipulations of the stored representations (e.g., mentally rotating the new or the stored representation to match the other, imagining moving around the array; Holmes, Newcombe & Shipley, 2018; King et al., 2002; Hegarty & Waller, 2004). Therefore, we expect that the introduction of the perspective shift would impair performance in both groups. However, we predict a larger decrease in performance in older adults who seem to have difficulties with initiating those mental manipulations as reflected in past findings documenting larger impairments with the introduction rather than the increase of the perspective shift (Montofinesse et al., 2015; Muffato et al., 2019; Hilton et al., 2020; Segen et al., 2021).

To investigate the role of landmarks for encoding strategies and performance, we included trials in which landmarks (in the form of posters on the walls) were: 1) unique and could be used to encode object locations, 2) identical and thus uninformative or 3) absent from the scene. Varying the availability and utility of room-based landmarks allowed us to test whether age-related differences in gaze behaviour during spatial encoding were due to older adults encoding object positions by relating them to the landmarks or to older adults having difficulties in selecting and/or focusing on task-relevant information.

Since this part of the study is largely exploratory, we have formulated a series of predictions about results that we would expect to find depending on how older adults use additional landmarks during encoding of object locations. Given that the task can be solved either by focusing on the local arrangement of objects or by relating object positions to landmarks, we should not necessarily expect age-related differences in performance if older adults simply shift towards a particular encoding strategy depending on which information is available. However, if older adults select an encoding strategy that depends on the availability of landmarks as suggested by our previous research (Segen et al., 2021), we expect them to perform better when landmarks are informative than uninformative. Finally, if older adults have difficulties focusing on task-relevant information as a result of an attention inhibition deficit (Hasher & Zacks, 1988), and are therefore distracted by the presence of landmarks, we predict worse performance when landmarks are available (either informative or uninformative) than when they are not.

In terms of gaze behaviour, if older adults rely more on landmarks as part of their encoding strategy, compared to their younger counterparts, we expect them to spend more time gazing at informative landmarks than uninformative landmarks. If, however, older adults are distracted by the landmarks, we expected them to show similar gaze behaviour in conditions with informative and uninformative landmarks.

3.2. Method

3.2.1. Participants

Twenty-eight young (mean age = 21.00 years, SD = 2.27; age range = 18-27 years; 15 females and 13 males) and 32 older adults aged 60 years and over (mean age=68.80, SD=6.34, age range=60-85; 17 females and 15 males) took part in this study. Participants were recruited either through the participant recruitment system of Bournemouth University or through opportunity sampling in the community. Older adults received monetary compensation for their time whilst younger participants received course credits. Participants were screened for mild cognitive impairment using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005). Based on a threshold score of 23, no participants were excluded (Luis, Keegan & Mullan, 2009; Waldron-Perrine & Axelrod, 2012). All participants gave their written informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

3.2.2. Virtual environment

The virtual environment was designed with Adobe 3DS Max 2018 and depicted a 13.5 m x 14.6 m rectangular room. The room contained 6 identical objects; pink vases on metal stands that were arranged in three clusters of 1, 2 and 3 objects in the centre of the room (see Figure 3.1). In the No Landmarks condition, the walls contained no additional cues, in the Uninformative Landmarks condition eight identical posters of the Tower Bridge were presented, two on each wall. Finally, in the Informative Landmarks condition eight unique posters were presented, again two on each wall. These posters consisted of highly familiar and recognisable landmarks (Hamburger & Roser, 2014): the Leaning Tower of Pisa, Stonehenge, the Statue of Liberty, the Golden Gate Bridge, the Eiffel Tower, the White House, the Big Ben, and the Great Wall of China.

The experimental stimuli were renderings of the environment with a 70° horizontal field of view (FOV) with a 15% downward shift in the vertical FOV, yielding an asymmetric viewing frustum to simulate human vision. The virtual cameras from which the static images of the scenes were rendered were arranged on a circle (radius of 6.7 m) at 30° intervals, providing 12 possible camera positions and the object clusters were arranged in six unique layouts within the room (Figure 3.1A, C, & D). Six of those camera positions were used in the learning phase and in the 0° perspective shift condition. The remaining 6 viewpoints were used in the test phase in the 30° perspective shift condition. Stimuli were presented as static images on a desktop computer with OpenSesame 3.1.7 (Mathôt, Schreij, & Theeuwes, 2012) and a standard computer keyboard was used to collect responses.

3.2.3. Eye-tracking

Eye movements were recorded using an Eyelink II (SR Research) head-mounted eye tracker at a rate of 500 Hz. Calibrations were performed at least three times and drift correction was performed prior to each trial. The experiment was presented on a 102cm screen (diagonal) with an aspect ratio of 16:9 and a resolution of 1920x1080 pixels. Participants were seated 100 cm from the monitor resulting in a physical horizontal FOV of 47.9° and 28° vertical FOV.

3.2.4. Procedure

Each experimental trial started with a fixation cross and a scrambled stimuli mask presented for 1500 msec (Figure 3.1A). In the learning phase, participants were presented with a rendering of one of the 6 unique configurations of the target objects from one of the six possible viewpoints for 12 seconds. After this learning phase, participants were again presented with a fixation cross and a scrambled stimuli mask for 1500 msec. Then, in the test phase they were presented with a rendering of the room either from the same viewpoint (50% of trials) or a different viewpoint that was offset by 30° from the study viewpoint. Participants were asked to respond by pressing the x or m keys on the keyboard as to whether the target objects were in the same locations as during the training phase or not. In 50% of the trials, the target objects remained in the same locations (Same, Figure 3.1C) and in the other 50% of the trials two of the three object clusters swapped locations (Swap, Figure 3.1B & C). As a result, chance level performance for this task was 50%.

The experiment consisted of 144 experimental trials that were preceded by 6 practice trials. The entire study took around 90 minutes to complete and participants were allowed to take breaks when they wished.

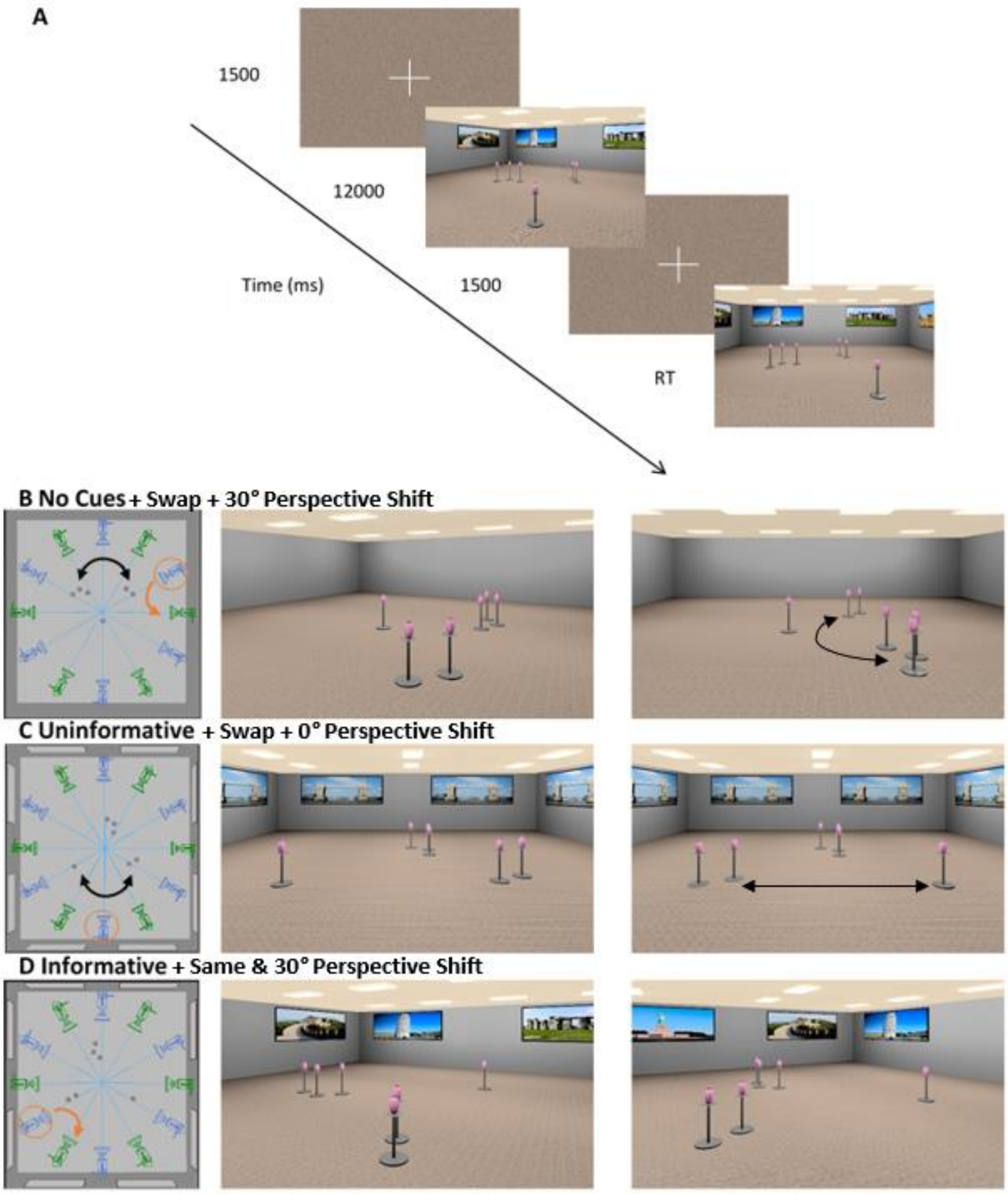

Figure 3.1 A Experimental protocol; B, C & D Virtual environment and stimuli for the experimental task, Blue and Green cameras represent the possible virtual cameras positions for the Learning and Test phase, respectively. Examples of possible object cluster layouts are shown

in B (No Landmarks), c (Uninformative Landmarks) and D (Informative Landmarks). The left panel shows a survey perspective of the example trials, indicating the rotation of the camera (Orange arrow) and swapping of the two object clusters (Black arrow) in Swap trials (B and C). The middle and right panels show the two corresponding snapshots for the learning and test phases, respectively. In B and D there is a 30° perspective shift, to the left and right respectively. In c there is no perspective shift. The black arrows in the right panel (B and C) indicate which clusters were swapped at test.

3.2.5. Design

The experiment followed a mixed 2 (Age Group: young vs. older adults) × 2 (Manipulation: Same, Swap, Figure 1B,C & D) x 2 (Perspective Shift: 0°, 30°) x 3 (Landmark Type: No Landmarks, Uninformative, Informative) design with Manipulation, Perspective Shift and Landmark Type manipulated within participants and Age Group between.

3.2.6. Data Analysis

Data from one older participant were excluded from all analyses due to chance level performance in the 0° Perspective Shift condition. The remaining data were analysed with linear mixed-effects models (LME) using LME4 (Bates et al. 2018) in R (R Core Team, 2013). Specifically, accuracy was analysed using generalized linear mixed-effects (GLME) models with the glmer function from LME4 package. The following contrasts were used in all (G)LMEs conducted: Age Group (Younger adults/Older adults), Perspective shift (0°/30°) and Manipulation (No Change/Swap) were coded using effect coding. This coding scheme compares the effect of a variable (i.e. Age Group) on performance averaged across all levels of other variables (i.e. Perspective Shift and Manipulation). Landmark Type was coded using treatment coding. Since we were interested in examining the difference between Informative and Uninformative Landmarks and the difference between No Landmarks and Uninformative Landmarks, we used the Uninfomative Landmark as the baseline. As a result, all of the effects for other factors are calculated with reference to the performance in the Uninformative Landmark, rather than the average of performance for all levels of Landmark Type. For the response time analysis, we included only the correct trials and we log transformed response times following the recommendations of Baayen, Davidson and Bates (2008) for dealing with the skewness of the response time distribution. Prior to transforming, response times below 200ms and over 20,000ms were removed.

3.3. Results

3.3.1. Accuracy

Accuracy estimates were obtained for each participant with Age Group, Perspective Shift, Landmark Type and Manipulation as fixed factors and a random by-subject and by-item intercept. Coefficients, standard errors and z-values (Table 3.1) indicate that Perspective Shift and Manipulation affected performance. Specifically, accuracy decreased with the introduction of a 30° Perspective Shift (Figure 3.2A) and in the Swap condition (Figure 3.2B). In addition, there was an interaction between Perspective Shift and Manipulation with a greater decline in performance in the No Change condition compared to the Swap condition following a 30° Perspective Shift (Figure 3.2C). Finally, we found a three-way interaction between Perspective Shift, Manipulation and Age Group with older adults showing a larger decline in performance than younger adults in the No Change condition when a 30° Perspective Shift was introduced, whilst displaying an increase in performance in the Swap condition when a 30° Perspective Shift was introduced (Figure 3.2D). Effect plots for significant main effects and interactions are reported in the Supplementary Materials.

Table 3.1 Coefficients from Accuracy GLME analysis

Predictors	Coefficients	Accuracy std. Error	z-value
(Intercept)	2.023	0.262	7.724
Age Group (Old)	0.145	0.112	1.293
Perspective Shift (30°)	-0.635	0.079	-8.049
Landmark Type (Informative)	-0.122	0.347	-0.350
Landmark Type (No Landmarks)	0.066	0.350	0.189
Manipulation (Swap)	-1.316	0.086	-15.216
Age Group (Old): Perspective Shift (30°)	-0.104	0.071	-1.468
Age Group (Old): Landmark Type (Informative)	-0.063	0.095	-0.659
Age Group (Old): Landmark Type (No Landmarks)	-0.138	0.105	-1.314
Perspective Shift (30°): Landmark Type (Informative)	0.176	0.106	1.659
Perspective Shift (30°): Landmark Type (No Landmarks)	-0.037	0.116	-0.319
Age Group (Old): Manipulation (Swap)	0.063	0.071	0.887
Perspective Shift (30°): Manipulation (Swap)	0.414	0.077	5.387
Landmark Type (Informative): Manipulation (Swap)	0.212	0.115	1.846
Landmark Type (No Landmarks): Manipulation (Swap)	-0.082	0.125	-0.656
Age Group (Old): Perspective Shift (30°): Landmark Type (Informative)	0.097	0.095	1.020
Age Group (Old): Perspective Shift (30°): Landmark Type (No Landmarks)	0.137	0.105	1.303
Age Group (Old): Perspective Shift (30°): Manipulation (Swap)	0.240	0.071	3.399
Age Group (Old): Landmark Type (Informative): Manipulation (Swap)	0.049	0.095	0.514
Age Group (Old): Landmark Type (No Landmarks): Manipulation (Swap)	0.054	0.105	0.512
Perspective Shift (30°): Landmark Type (Informative): Manipulation (Swap)	0.060	0.103	0.584

Perspective Shift (30°): Landmark Type (No Landmarks): Manipulation (Swap)	0.155	0.114	1.364
Age Group (Old): Perspective Shift (30°): Landmark Type (Informative): Manipulation (Swap)	-0.122	0.095	-1.277
Age Group (Old): Perspective Shift (30°): Landmark Type (No Landmarks): Manipulation (Swap)	-0.201	0.105	-1.916

Significant z values (|z|≥1.96) in bold

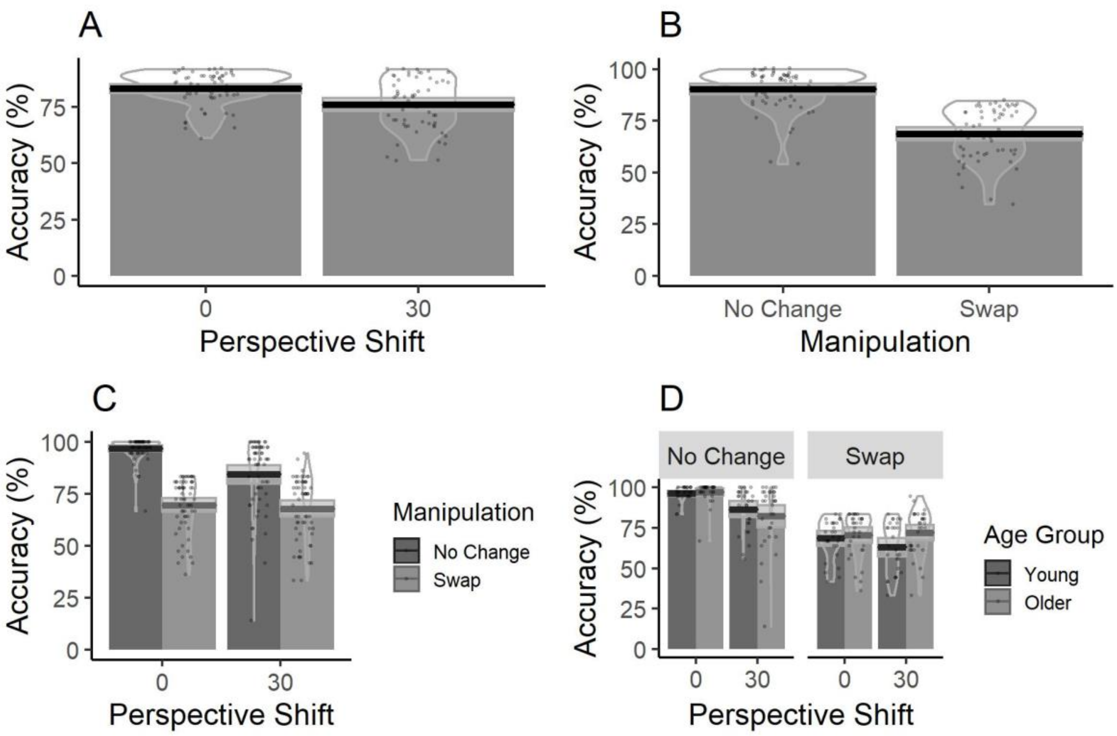

Figure 3.2 Bar plots of accuracy values for a significant main effect of A: Perspective Shift, B: Manipulation, and significant interactions C: between Manipulation and Perspective Shift and D: Interaction between Age Group, Manipulation and Perspective Shift with mean (solid line) and 95% CIs (grey shaded area) with individual data points and violin plots behind.

3.3.2. Response Time

As with accuracy, response time estimates were obtained for each participant with Age Group, Perspective Shift, Landmark Type and Manipulation as fixed factors and a random by-subject and by-item intercept with a random slope for Manipulation across participants. Coefficients, standard errors and t-values (Table 3.2) show that Age Group, Perspective Shift, Landmark Type and Manipulation were all reliable predictors of response time. Specifically, we found that older adults were slower to respond compared to younger adults (Figure 3.3A), and that response times increased with the introduction of a Perspective Shift (Figure 3.3B). In addition, response times were longer with Informative than Uninformative Landmarks condition (Figure 3.3C) and in the Swap condition compared to the No Change condition (Figure 3.3D). We also found a significant interaction between Age Group and Manipulation with a smaller increase in response times in the Swap condition in older than younger adults (Figure 3.3E). There was also a Perspective Shift and Manipulation interaction with a smaller increase in response times in the Swap condition than the No Change condition with the introduction of the Perspective Shift (Figure 3.3F). We also found an interaction between Landmark Type and Manipulation with a smaller increase in response times between the No Change and the Swap condition in the Informative Landmark Type (Figure 3.3G) compared to Uninformative Landmark Type condition. Finally, we found a three-way interaction between Age Group, Perspective Shift and Manipulation, with the Age Group and Perspective Shift interactions showing a different trend across No Change and Swap Manipulation. Specifically, there was a larger increase in response times in older adults than young adults, in the No Change condition with the introduction of the Perspective Shift (Figure 3.3). Whilst in the Swap condition, the increase in response times in older adults was smaller when a Perspective Shift was introduced compared to young adults. Effect plots for significant main effects and interactions are reported in the Supplementary Materials.

Table 3.2 Coefficients from Response Time LME analysis

	Log transformed Response Time		
Predictors	Estimates	std. Error	t-value
(Intercept)	7.834	0.041	190.067
Age Group	0.209	0.040	5.248
Perspective Shift (30°)	0.130	0.015	8.459
Landmark Type (Informative)	0.058	0.020	2.942
Landmark Type (No Landmarks)	-0.013	0.020	-0.640
Manipulation (Swap)	0.133	0.011	12.386
Age Group: Perspective Shift (30°)	0.006	0.014	0.451
Age Group: Landmark Type (Informative)	0.019	0.013	1.470
Age Group: Landmark Type (No Landmarks)	-0.019	0.013	-1.443
Perspective Shift (30°): Landmark Type (Informative)	0.012	0.015	0.813
Perspective Shift (30°): Landmark Type (No Landmarks)	-0.000	0.015	-0.007
Age Group: Manipulation (Swap)	-0.032	0.009	-3.474
Perspective Shift (30°): Manipulation (Swap)	-0.077	0.010	-7.542
Landmark Type (Informative): Manipulation (Swap)	-0.034	0.015	-2.259
Landmark Type (No Landmarks): Manipulation (Swap)	0.010	0.015	0.654
Age Group: Perspective Shift (30): Landmark Type (Informative)	-0.003	0.013	-0.239
Age Group: Perspective Shift (30°): Landmark Type (No Landmarks)	-0.013	0.013	-1.012
Age Group: Perspective Shift (30°): Manipulation (Swap)	-0.018	0.009	-1.960

Age Group: Landmark Type (Informative): Manipulation (Swap)	-0.008	0.013	-0.596
Age Age Group: Landmark Type (No Landmarks): Manipulation (Swap)	-0.024	0.013	-1.847
Perspective Shift (30°): Landmark Type (Informative): Manipulation (Swap)	0.019	0.014	1.312
Perspective Shift (30°): Landmark Type (No Landmarks): Manipulation (Swap)	0.002	0.014	0.162
Age Group: Perspective Shift (30°): Landmark Type (Informative): Manipulation (Swap)	0.005	0.013	0.406
Age Group: Perspective Shift (30°): Landmark Type (No Landmarks): Manipulation (Swap)	-0.004	0.013	-0.289

Significant t values (|t|≥1.96) in bold

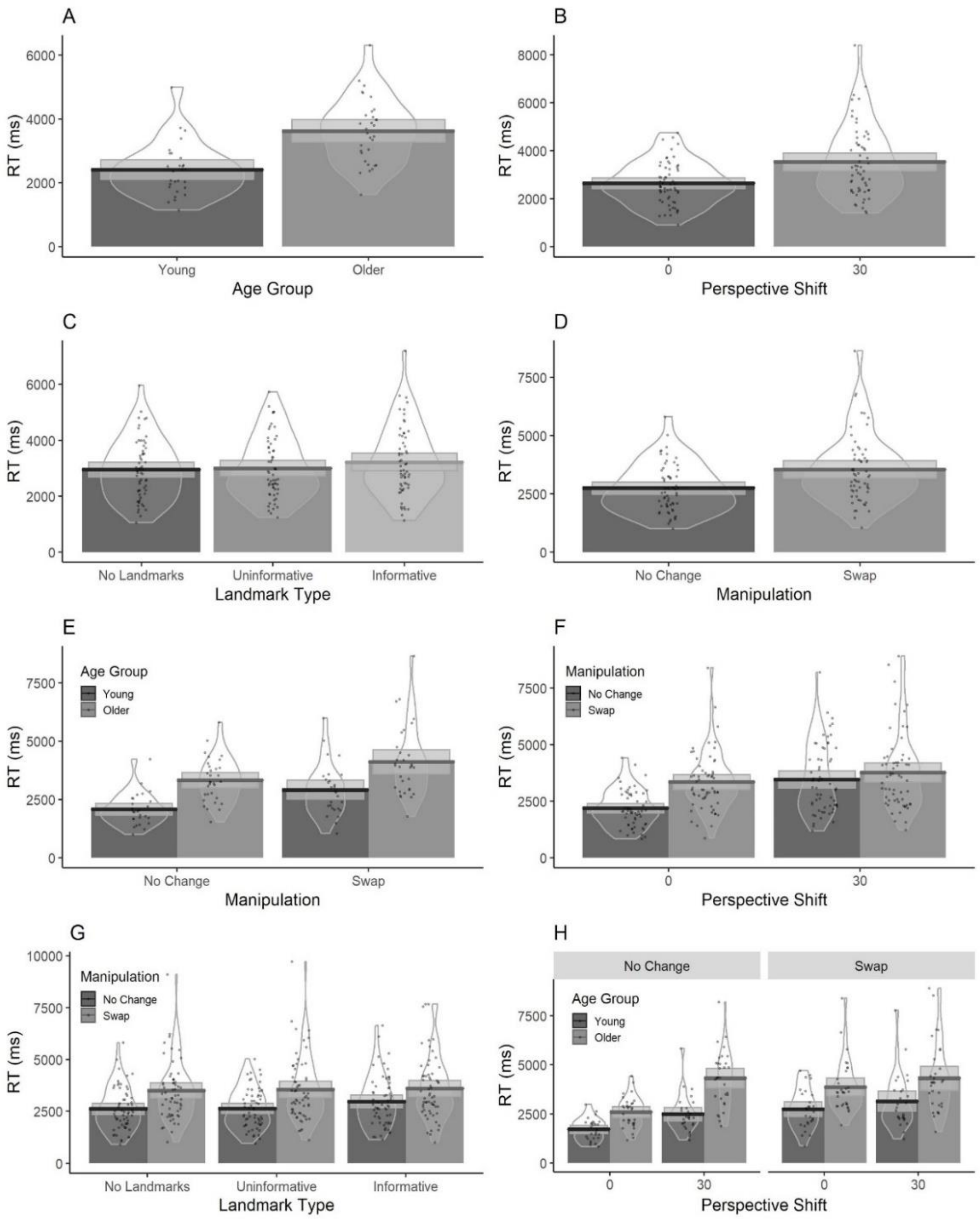

Figure 3.3 Bar plots of Response Times values for significant main effects of A: Age Group B: Perspective Shift C: Landmark Type (significant only for the Informative Landmark Type) D: Manipulation and interactions between E: Age Group and Manipulation F: Perspective Shift and Manipulation G: Landmark Type and Condition (significant only for the Landmark Type (Informative): Manipulation (Swap)) H: Age Group, Manipulation and Perspective shift with mean (solid line) and 95% CIs (grey shaded area) with individual data points and violin plots behind.

3.3.3. Response Bias

To examine if participants displayed a response bias, we carried out an analysis based on Signal Detection Theory (Harvey, 1992; Macmillan & Creelman, 1991) using the sdt.rmcs (Todorova, 2017) package in R. Signal Detection Theory evaluates sensitivity and response bias in situations that require decision making under uncertainty. It is applied when a binary decision about the presence or absence of a signal is made, comparing the response with the actual presence/absence of the signal. With Signal Detection Theory, the formula c = -0.5[z(hit rate) + z(false alarm rate) is used to compute response bias, where hit rate and false alarm rates refer to trials in which the signal was correctly or incorrectly, respectively, reported as present.

Overall, there was a positive response bias showing that participants were more likely to respond that nothing has changed than to respond that something had changed (Figure 3.4). LMM analysis (Table 3.3) with Age Group, Perspective Shift and Landmark Type as fixed factors and by-subject intercept with a random slope for Perspective Shift, indicated that the introduction of a Perspective Shift led to a decrease in response bias, which was larger in older adults than in younger adults. Furthermore, when a Perspective Shift was introduced, the response bias decreased more in the No Landmarks and the Informative Landmarks conditions compared to the Uninformative Landmarks condition.

Table 3.3 Coefficients from Response Bias LME analysis

	Response Bias (c)		
Predictors	Estimates	std. Error	t-value
(Intercept)	0.437	0.033	13.043
Age Group (Older Adults)	-0.047	0.033	-1.403
Perspective Shift (30°)	-0.069	0.029	-2.384
Landmark Type (Informative)	0.003	0.026	0.097

Landmark Type (No Landmarks)	-0.048	0.026	-1.826
Age Group: Perspective Shift (30°)	-0.072	0.029	-2.495
Age Group: Landmark Type (Informative)	0.007	0.026	0.264
Age Group: Landmark Type (No Landmarks)	-0.008	0.026	-0.306
Perspective Shift (30°): Landmark Type (Informative)	-0.052	0.026	-1.978
Perspective Shift (30°): Landmark Type (No Landmarks)	-0.058	0.026	-2.201
Age Group: Perspective Shift (30°): Landmark Type (Informative)	0.049	0.026	1.845
Age Group: Perspective Shift (30°): Landmark Type (No Landmarks)	0.028	0.026	1.043

Significant t values (|t|≥1.96) in bold

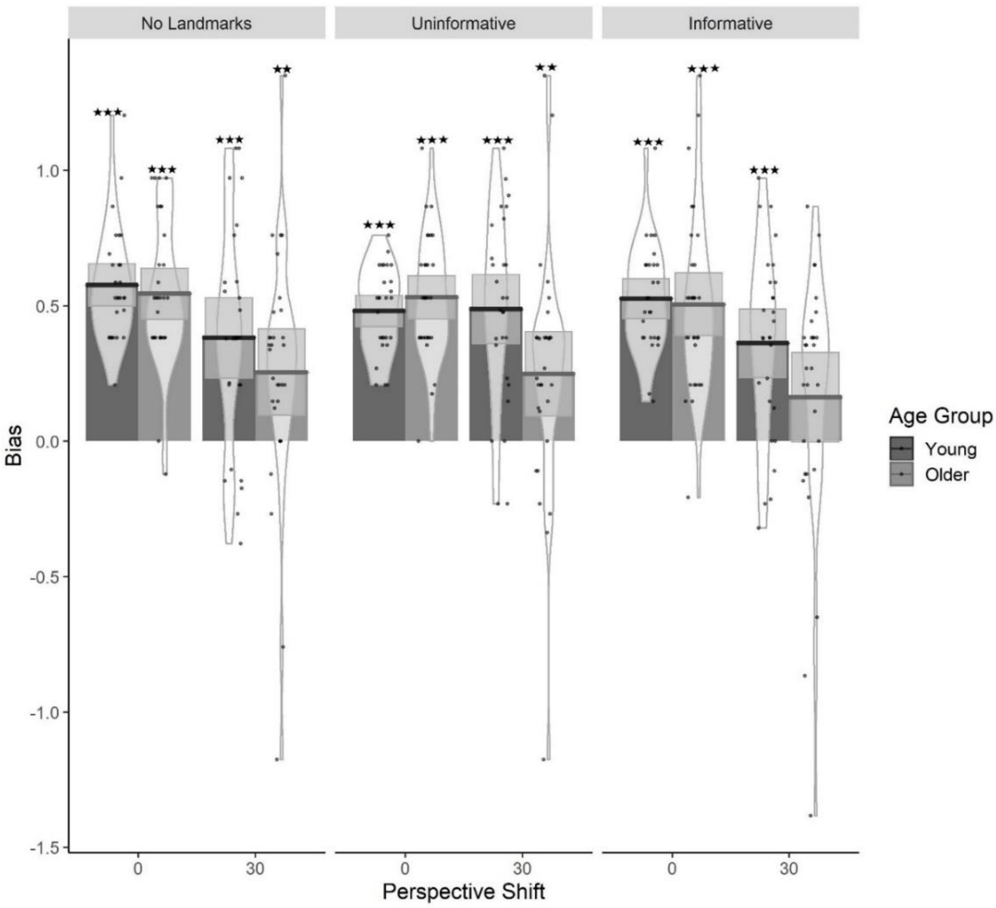

Figure 3.4 Bar plots for Response Bias as a function of Age Group, Landmark Type and Perspective Shift with mean (solid line) and 95% CIs (grey shaded area) with individual data

points and violin plots behind. Stars indicate response bias significantly different from 0 (1 star [p<0.05], 2 stars [p<0.01] and 3 stars [p<0.001]).

3.3.4. Gaze Analysis

Fixations and saccades were identified using the SR Research algorithms and were pre-processed as follows: First, we removed fixations that contained a blink, fell outside of the screen boundaries or were shorter than 80ms or longer than 1000ms (Inhoff & Radach, 1998; Nuthmann, 2017). Finally, we removed saccades with maximum amplitudes (41.35°va) or velocities (1,500°/s) larger than it should be possible based on the distance of the participant from the screen and the screen size.

The primary aim of the gaze analysis was to investigate age differences in encoding strategies and was therefore mainly focused on the analysis of gaze during the encoding phase. Analysis of differences in basic saccade and fixation parameters between young and older adults showed that during the 12 second encoding period, older adults made shorter and more frequent fixations as well as more frequent saccades. The results are reported in detail in the supplementary materials.

3.3.4.1. Gaze on Landmarks

As we were primarily interested in age-related differences in gaze as a function of Landmark Type, we split stimuli into two interest areas (See Figure 3.5) and compared the percentage of Dwell Time on the top interest area (IA) where Landmarks were located when available vs. the bottom area where the objects were located. To do so, we computed the total dwell time for each trial by adding up the durations of all fixations in the trial. Next, we calculated the proportion of dwell time that was spent fixating in the top IA. This approach allowed us to specifically focus on age-related differences in the use of room-based Landmarks during encoding with the increased Dwell Time on the upper part of the stimuli largely reflecting gaze on Landmarks (when available).

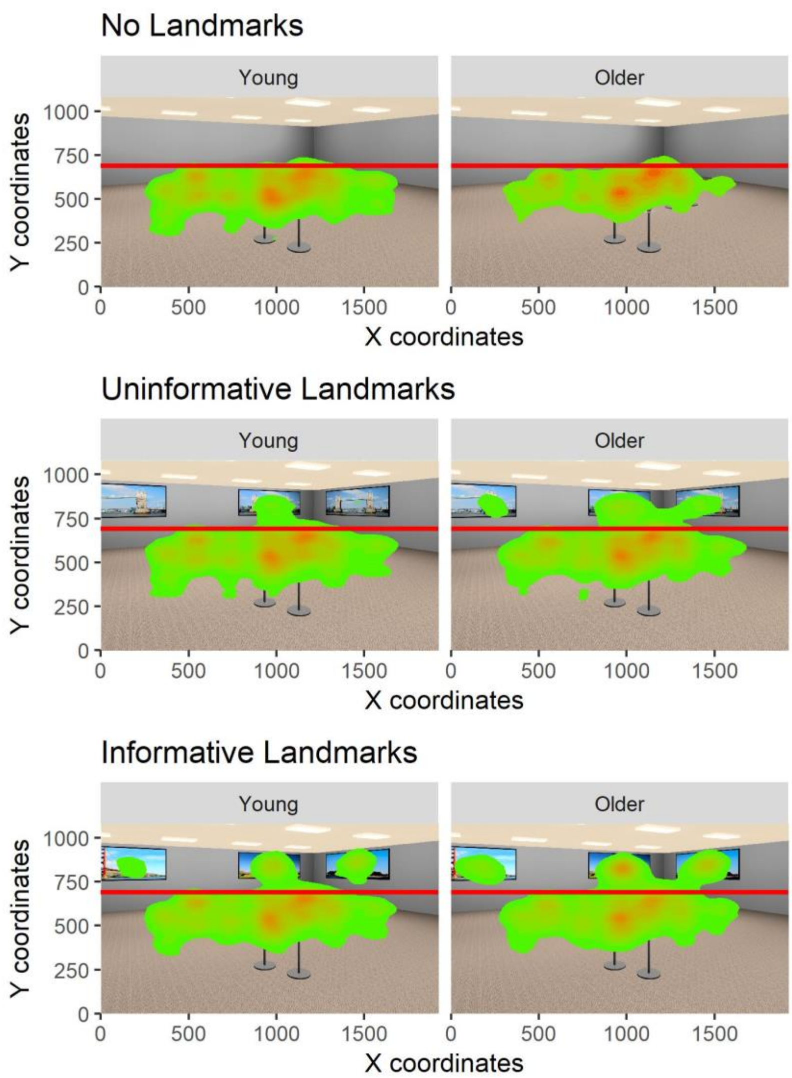

Figure 3.5 Heatmaps representing number of fixations as a function of Age Group and Landmark Type

LME analysis with Age Group and Landmark Type as fixed factors and a by-subject and by-item random intercept showed that Landmark Type and Age Group were reliable predictors of Dwell Time on the top IA. Specifically, we found that compared to the Uninformative Landmarks condition that was used as a baseline, there was a reduction in Dwell Time on the top IA in the No Landmarks and an increase in Dwell Time in the Informative Landmarks condition. We also found that older adults spent more time looking at the top IA compared to younger adults. In addition, there was a Landmark Type and Age Group interaction whereby older adults' Dwell Time on Landmarks decreased more than that of younger adults' in the No Landmarks condition compared to Uninformative Landmarks condition and showed a larger increase in the Informative Landmarks condition compared to the Uninformative Landmarks condition. A Dwell Time analysis on the top IA at test produced similar results to those of the learning phase, with the exception that the increase in Dwell Time in older adults and the Age Group by Landmark Type (No Landmarks) interaction were not significant. Results from this analysis are presented in the Supplementary Materials.

Table 3.4 Coefficients from Dwell Time on the top IA LME analysis

	Dwell Time on Landmarks		
Predictors	Estimates	std. Error	t-value
(Intercept)	13.054	1.503	8.684
Age Group (Older Adults)	2.99	1.457	2.058
Landmark Type (No Landmarks)	-8.108	0.644	-12.600
Landmark Type (Informative)	9.540	0.644	14.826
Age Group (Older Adults): Landmark Type (No Landmarks)	-1.804	0.375	-4.812
Age Group (Older Adults): Landmark Type (Informative)	1.171	0.375	3.124

Significant t values ($|t|\geq 1.96$) in bold

3.3.4.2. Relationship between Gaze and Performance

Dwell time on the top IA was not related to performance across any of the three Landmark Type conditions (Figure 3.6), suggesting that the task could be solved either by using Landmarks (when they are available) or by focusing primarily on the objects. Thus, the differences in gaze behaviour reported here are likely to represent differences in encoding strategy preferences that change with age.

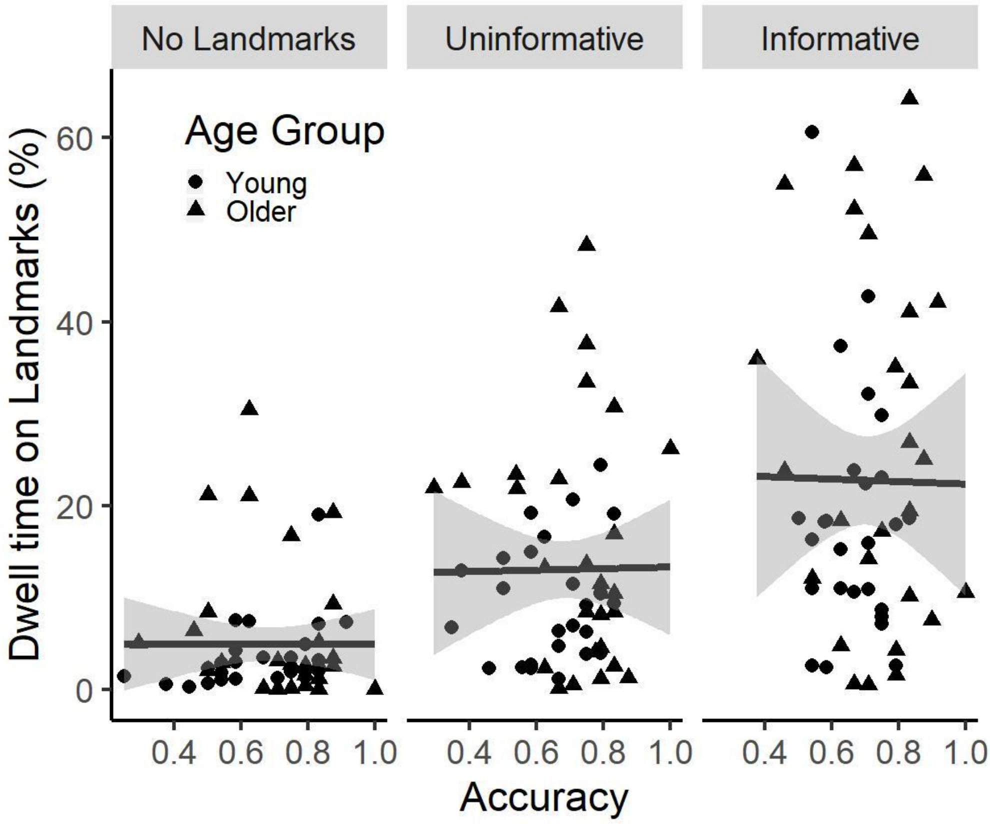

Figure 3.6 Scatter Plot between Dwell Time on the top IA and Accuracy as a function of Landmark Type with regression line and CI (shaded area)

3.3.4.3. Gaze behaviour across trials

We also investigated if gaze behaviour changes across time by correlating Dwell Time on landmarks with trial older for younger and older participants in the No Landmark, Uninformative and Informative Landmark conditions. We found that across both younger and older adults, Dwell Time remained consistent in the No Landmark condition throughout the experiment (Young: r=.011, p=.895, Older: r=-.09, p=.279). In the Uninformative Landmark condition, older adults spent less time fixating on landmarks over the course of the experiment (r=-.18, p=.032), whilst younger adults' gaze (r=-.05, p=.543) remained unchanged. In the Informative Landmark condition, an opposite pattern of results was found with younger adults spending less time fixating on Landmarks (r=-.20, p=.018) with older adults' gaze remaining unchanged (r=-.09, p=.266).

3.3.4.4. Consistency in gaze between learning and test

Finally, we examined if participants showed similar gaze behaviour during learning and test. To do so, we correlated the Dwell Time on the top IA across different Landmark Type conditions at learning and test. We found strong positive correlations across all Landmark Types (No Landmarks: $R2 = 0.67$, $p<.001$; Uninformative: $R2=0.88$, $p<.001$; Informative: $R2=0.94$, $p<.001$). Those correlations suggest that participants are highly consistent in which stimulus features they gaze at during encoding and test.

3.4. Discussion

In the present study, we used eye-tracking to investigate age-related differences in visual encoding strategies employed for memorizing the locations of objects in a room. To do so, we explored if participants were able to identify whether a spatial scene has changed following a perspective shift between encoding and test. The 30° perspective shift was introduced to ensure that participants relied on spatial representations instead of solving the task by matching the visual image with a stored visual snapshot from encoding (Nardini et al., 2009). To investigate the effect of landmarks on encoding strategies, we also manipulated the availability and informative value of landmarks within the environment.

We found that overall, older adults took longer to respond. This increase in response times is consistent with findings that are widely reported in the cognitive ageing literature (Choice reaction time task: Woods, Wyma, Yund, Herron, & Reed, 2015; Memory: Hertzog, Dixon, Hultsch, & MacDonald 2003; Language: Ratcliff, Thapar, Gomez, & McKoon, 2004), and is typically attributed to decrements in speed of processing (Salthouse, 1996; Salthouse, & Ferrer-Caja, 2003). We also found that the introduction of the perspective shift and the manipulation of object positions led to performance decrements in both age-groups. The availability and informativeness of the room-based landmarks did not affect task accuracy. Importantly, we found that when landmarks were presented, older participants spent more time than younger participants looking at the upper part of the display that contained the landmarks. This was particularly the case when the landmarks were informative.

Contrary to our expectations and to previous place recognition research (Muffato et al., 2019, Hilton et al., 2020; Segen et al., 2020; Harley et al., 2007), there were no age-related differences in accuracy. However, it should be noted that we used an easier task than those used in previous studies, which could yield fewer problems for older adults. For example, the perspective shift we introduced was smaller than that of previous studies (Muffato et al., 2019; Montefinese et al., 2015; Segen et al., 2021). In addition, the scene at test could differ from the encoded only in terms of a change in the categorical relationship between objects. That is, in contrast to Segen et al., (2021), in the current study no changes in fine-grained spatial relationships between objects occurred. That the easier task may be responsible for the lack of age-related deficits in task accuracy is in line with cognitive ageing research reporting greater age-related differences in performance with increasing task difficulty (Earles, Kersten, Berin Mas & Miccio, 2004; Angel et al., 2016; Verhaeghen, Cerella & Basak, 2006).

The lack of age-related performance accuracy differences in less demanding tasks can be explained by the compensation-related utilization of neural circuits hypothesis (Reuter-Lorenz & Cappell, 2008). This hypothesis posits that under low task demands older adults can perform the tasks as well as young adults, supported by increased neural activations. However, when task demands increase, older adults' cognitive limits are reached resulting in performance declines that are typically accompanied by a reduction in activation in the relevant neural networks (Morcom & Rugg, 2007; Angel et al., 2016). Thus, it is plausible that due to the relatively low task-demands in the current study, which are reflected in high performance across both age groups, older adults were able to carry out the task just as accurately as younger participants.

Consistent with our predictions, we found declines in accuracy in both age groups that were accompanied by an increase in response times when a perspective shift was introduced. This reduction in performance may have been driven by qualitative differences between trials that involved a perspective shift and those that did not. Specifically, without a perspective shift participant can refer to the representation of the learned scene from memory and use image matching to detect changes (Nardini et al., 2009). However, the introduction of the perspective shift required participants to engage in additional cognitive processing related to mental transformation in order to match the perspectives of the stored spatial configuration with the one presented at test (Hegarty & Waller, 2004). However, it should be noted that the effect of the perspective shift was small, which is likely due to the relatively small perspective shift that we introduced.

Interestingly, there was a much more nuanced (if any) decline in accuracy or increase in response time in the Swap compared to the No Change condition when a perspective shift was introduced. To explain such findings, we turn to the response bias analysis which suggested that the introduction of the perspective shift increased the likelihood of participants responding that the object positions were "different". Thus, when a perspective shift is introduced in the Swap condition, this leads to an increase in the number of correct responses albeit for the wrong reason. We believe that the increase of "different" responses after a perspective shift arises from the salient change in the visual input indicating that "something is different". However, if participants were solely responding to any change in the visual information between encoding and test, we expected them to perform below chance level in the No Change condition when a perspective shift was present. Yet, our participants were still able to perform well in this condition and their performance in the Swap condition with perspective shifts was not at ceiling. This pattern of results demonstrates that participants were not solely relying on basic visual change detection but were instead using a spatial strategy to perform the task. Yet, they might have found it hard to inhibit the immediate response that the image is “not the same” when the perspective shift was introduced. The increase in performance in older adults with the introduction of the perspective shift in the Swap condition may thus be due to older adults experiencing an even greater difficulty in inhibiting the response that the image is “not the same” when a perspective shift was present. Such difficulties are in line with age-related decline in executive functioning, in particular executive control (Treitz, Heyder, Daum, 2007; Schretlen et al., 2000; Braver & West, 2008).

Overall participants were more likely to make errors in the Swap condition than the No Change condition. In order to perform the task accurately participants in either condition had to bind an object's identity to its location (Postma, Kessels & van Asselen, 2004; Waller, 2006). Previous research has shown that this is a cognitively demanding and error-prone process. For example, in place recognition studies participants were shown to be less accurate in detecting that a change has occurred when two objects swapped places compared to when a previously shown object was replaced by a new one (Muffato et al., 2019; Hilton et al., 2020). Similar results are reported in visuospatial working memory studies in which participants were asked to encode positions of abstract objects on a blank display. Participants were more likely to make swap errors, that is to place objects in the positions that were previously occupied by a different object (Pertzov, Dong, Peich & Hussain, 2012; Pertzov, Heider, Liang, & Husain, 2015).

Thus, the lower performance in the Swap condition can be explained by difficulties with binding objects to their locations, which prevents participants from accumulating information signalling that a change has occurred (Muffato et al., 2019; Hilton et al., 2020). Specifically, in the current task, the objects within the scene and their general configuration remained the same between learning and test. The only change introduced in the Swap condition is the position that each cluster occupied within that general configuration. Therefore, participants needed to remember the specific locations of each object cluster within that configuration to detect that a change has occurred.

In addition to comparing the behavioural performance of older and younger adults, another aim of this study was to use eye-tracking to investigate age-related differences in spatial encoding strategies and to study if such differences are driven by the information available within the environment. Firstly, we focused on general gaze parameters and found that older adults made more fixations that were shorter in duration as well as shorter saccades than young adults. While these results are consistent with those from a recent study using a similar place recognition task (Hilton et al., 2020), relating these general gaze measures to encoding strategies is difficult. We thus performed IA analysis which showed that gaze behaviour differed as a function of room type. As expected, we found that both age groups spent the lowest amount of time looking at the upper part of the stimuli in the No Landmarks condition in which there were no images on the walls of the room, followed by the Uninformative Landmarks condition, in which the images on the walls were all identical, and the Informative Landmarks condition in which each image was unique. These findings are consistent with results reported by Livingstone-Lee et al. (2011) who showed that participants quickly learned to adapt their gaze distribution in a virtual Morris water maze task based on the information that was available in the environment. Importantly, we found that compared to younger adults, older adults spent more time looking at landmarks in the Uninformative and Informative landmarks conditions during encoding. A similar pattern was observed during the test phase in the Informative landmarks condition.

A possible explanation for these age-related-differences in gaze behaviour is that older adults simply look around more due to a lack of a systematic encoding strategy. This can arise as a result of difficulties in selecting task-relevant information (Raptis, Fidas & Avouris, 2017). Given our results, however, it appears unlikely that older adults were randomly scanning the environment without a clear encoding strategy for a number of reasons: first, older adults solved the task as accurately as younger participants, which would not be possible without a clear encoding strategy. Second, we found that older adults' gaze behaviour changed as a function of the landmarks used. Specifically, older adults spent significantly more time looking at the upper part of the stimuli when landmarks were present and when these landmarks were informative, i.e. when they could be used to encode the spatial locations of the objects by relating objects to these room-based landmarks. Third, both younger and older adults adapted their gaze behaviour over the course of the experiment such that older adults spent less time fixating on uninformative landmarks across trials. Younger participants, on the other hand, spent less time fixating on informative landmarks across the trial. These changes in gaze behaviour over time are likely to reflect adaptations of encoding strategies with older adults learning to inhibit attending to uninformative information and younger participants focusing on encoding the relationship between objects even in the presence of informative landmarks.

Finally, gaze behaviour was highly consistent between learning and test, which suggests that participants, both young and older, attended to the same information during learning and test. It is possible that low-level properties of the stimuli (i.e. colour, intensity and orientation) contributed to such similarities in gaze behaviour through bottom-up control of attention (Itti, 2005), as similar visual information was presented at both learning and test. However, given that participants performed well on the task and made very few fixations at test, it is unlikely that the consistency between gaze behaviour at learning and test was solely driven by bottom-up processes. Instead, we suggest that participants relied on the information they encoded at learning to make decisions regarding whether or not the objects have moved at test. Together, these results suggest that gaze behaviour, in both younger and older adults, represents task and stimuli-dependent visual strategies that participants employed to solve the task.

Age-related differences in gaze behaviour may also be driven by older adults being distracted by salient, but task-irrelevant landmarks as a result of attention inhibition deficits (Hasher & Zack, 1988; Healey et al., 2008, 2013). This account is partly supported by our findings as older adults spent more time than younger adults gazing at the uninformative landmarks. Notably, however, this did not affect their performance and can be explained by the relatively long encoding times that allowed participants to encode adequate task-relevant information even if they were briefly distracted.

An alternative explanation as to why older adults attended to uninformative landmarks (i.e. task-irrelevant information), is a more general age-related shift in the way they approach cognitive tasks. Zimmerman, Hasher & Goldstein (2011) suggested that older adults tend to implicitly encode all of the available information, regardless of its immediate utility. This is consistent with evidence showing that the inability to inhibit attention sometimes comes with benefits. Kim et al. (2007), for example, have shown that older adults display greater priming benefits when distractors on a previous task were used as primes in a problem-solving task. It is possible that the shift towards encoding irrelevant, as well as relevant information, stems from greater experience with real-world environments in which apparently task-irrelevant information often becomes relevant in the future (Zimmerman et al., 2011; Kim et al.,2007). For example, remembering extra landmarks in the environment could help to distinguish similar environments from each other. Such implicit shifts in encoding strategies may explain why older adults spent more time looking at extra information even if this information is not strictly necessary for solving the task at hand. However, such strategy shifts could lead to performance deficits in cognitively taxing situations, if older adults do not have enough resources to deal with the task at hand and if they are directing already limited resources to task-irrelevant information (Reuter-Lorenz & Cappell, 2008; Morcom et al., 2007; Angel et al., 2016).

The idea that older adults have a greater preference than young adults towards encoding strategies that incorporate all landmarks that are available is consistent with results from research that employs diffusion modelling. Several studies document an age-related shift towards a more conservative response strategy whereby, compared to young adults, older adults prefer to accumulate more information before making decisions (Segen et al, 2021; Spaniol, Madden, & Voss, 2006; Thapar, Ratcliff & McKoon, 2003; Ratcliff, Thapar, & McKoon, 2006; Ratcliff, McKoon & Gomez, 2004). This explanation is also supported by our findings of longer response times in older adults which could be indicative of greater cautiousness.

Alternatively, the preference for attending to landmarks during encoding could be indicative of age-related differences in spatial encoding strategies. Specifically, older adults' may be more reliant on an encoding strategy in which they relate the positions of objects to landmarks, while younger participants focus on the local arrangement of objects and encode the spatial relationships between them. This interpretation is in line with our findings that older adults spent more time than younger adults looking at the landmarks during encoding, especially when these were informative. The differences in encoding strategies may represent an age-related shift towards the use of a categorical encoding strategy whereby participants bind an object to the nearest cue/landmark without the need to encode the exact metric relationship between the two. This shift may arise from difficulties in forming precise spatial representations. For example, previous visuospatial working memory research has shown that older adults were less precise in estimating previous locations of objects compared to younger adults, despite positioning the objects in the correct region of the stimuli (Pertzov et al. 2015, Nilakantan, Bridge, VanHaerents, & Voss, 2018). Furthermore, in navigation, older adults show greater preference towards the use of beacon strategies (Wiener et al., 2013). Such strategies involve coarse categorical representations of locations in relation to environmental beacons or landmarks and may be preferred by older adults due to difficulties in formulating more precise representations.

Lastly, we did not find any relation between gaze behaviour and performance. This is not surprising as we found similar performance across different room types and across both age groups despite the presence of gaze differences. These results indicate that the current task can be solved equally well by focusing on objects and by relating the objects to landmarks (if they are available), with older adults showing a preference towards the latter. In addition, the lack of correlation between gaze and performance is consistent with our previous findings showing that the Swap condition could be solved either by looking around more or by having more focused gaze (Segen et al., 2021) outlining that coarse spatial representations can be formed using a wider range of encoding strategies and the available information.

To summarise, our results suggest that under specific conditions such as the presence of a relatively small perspective shift and the introduction of categorical changes within the scene, spatial memory is resistant to age-related changes as older adults perform the task as well as younger participants. Furthermore, we report an age-related shift in visual encoding strategy. Although we cannot completely rule out that these changes in gaze behaviour are driven by inhibitory control mechanisms, it seems highly plausible that older adults, who might be more distracted by the uninformative landmarks, employ an encoding strategy that relies on processing the categorical relationships between objects and room-based landmarks rather than forming fine-grain spatial representations.

3.5. Open practices statement

The data sets generated during and/or analyzed during the current study are available in the Open Science Framework repository (https://osf.io/v4mwe/). This experiment was not preregistered.

3.6. References

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Chapter 4: Perspective taking and systematic biases in object location memory

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4.1. General Introduction

Our ability to orient and navigate depends largely on forming spatial representations that maintain information about the locations of landmarks and other objects (Epstein, Harris, Stanley & Kanwisher, 1999; Postma, Kessels & van Asselen, 2004; Waller, 2006). Such representations can vary greatly in terms of the precision with which they hold information (Evensmoen et al., 2013). In the visual working memory literature, the precision of spatial representations has been investigated with tasks that involve memorizing first the position of an object presented in a 2D stimulus array on a blank screen, and then repositioning the object to its original position (Stevenson et al., 2018; Aagten-Murphy & Bays, 2019; Nilakantan, Bridge, VanHaerents & Voss, 2018; Pertzov, Dong, Peich, & Husain, 2012; Pertzov, Heider, Liang, & Husain, 2015). Moreover, psychophysical approaches with change detection tasks have also been used to quantify the precision of spatial representations (e.g., Brady & Alvarez, 2015; Luck & Vogel, 1997; Luck & Vogel, 2013). In these tasks, participants are asked to indicate whether an object has moved or changed between encoding and test, with the amount of movement/change systematically manipulated. Such tasks, which are primarily designed to investigate visuo-spatial working memory capacity, showed that increasing the number of to-be remembered items leads to a reduction in the quality of the representation for each of the items (Brady, Konkle & Alvarez, 2011). In addition, the precision of encoding was shown to be negatively affected by typical and atypical aging (Nilakantan et al., 2013; Pertzov, et al., 2015; Liang et al., 2016).

Although such approaches provide a detailed account of the precision with which object locations can be memorized, they typically focus on 2D spaces and do not investigate the precision of spatial representations in the three-dimensional (3D) space that is encountered during navigation and were the same environments/locations are viewed from different perspectives. In addition, tasks that use 2D spaces can often be solved by memorising the pixel positions of the objects on the screen and thus do not require participants to infer how space is structured (Nardini, Thomas, Knowland, Braddick, & Atkinson, 2009). In contrast, the use of virtual environments and the introduction of perspective shifts between encoding and test allows investigating the ability to encode 3D spatial locations. It also ensures that participants cannot simply memorize the position of the objects on the screen. Instead, participants must remember the position of the object in the virtual world and understand how the visual projections of the objects and the room would change following a perspective shift.

There are several virtual reality navigation tasks that allow assessing the precision of spatial representations. In some tasks participants have to learn the position of target locations within an environment (i.e. virtual Morris Water Maze (vMWM) tasks [e.g. Moffat et al. 2007; Daugherty et al, 2015; Woolley et al, 2010]; The flag localization task [Hartley, Trinkler & Burgess, 2004]; Object-location memory tasks [Doeller et al. 2008]), while in other tasks they have to memorize their own locations before being transported to a new location and asked to navigate back to the previous location (e.g. Gillner, Weiß, & Mallot, 2008). These experimental tasks provide rich data sets with a wide range of measures that allow assessing the precision with which spatial locations can be memorized, such as distances and angular differences between the estimated position of the target or own location and the correct locations, time spent searching in the vicinity of the correct location, and path trajectories amongst others.

These tasks have also been used to investigate spatial encoding strategies (e.g. Mueller, Jackson & Skelton, 2008) and reference frames (e.g. King et al., 2004; King et al., 2002) used during navigation as well as effects of (a)typical aging on spatial navigation (e.g. Moffat et al.,2007). More recently, the vMWM has also been applied to investigate the precision of spatial representations in patients with hippocampal lesions (Kolarik et al., 2016; 2018).

Despite their utility for studying the precision of spatial memory, these tasks often require specialized equipment, software, and skills, as well as prolonged training and familiarization with the task, the virtual environment, and the equipment. For example, a typical virtual Morris Water Maze task consists of training trials during which participants learn the position of the hidden platform by navigating within the environment (Kolarik et al., 2016, 2018; Moffat et al., 2007; Daugherty et al., 2015; Woolley et al., 2010) as well as control trials where participants navigate to a visible platform. In addition, those tasks require participants to navigate/move within the environment using a keyboard or a joystick, which can introduce unwanted confounds that depend on gaming and computing experience (Richardson, Powers & Bousquet., 2011; Murias, Kwork, Castillejo, Liu & Iaria, 2016). This becomes a particular challenge if testing involves patients and older adults, who are often less experienced in using such devices (Charness & Boot, 2009; Diersch & Wolbers, 2019). Difficulties in operating the testing apparatus can inflate differences in navigation performance (Waller, 2000; Richardson, Powers & Bousquet, 2011). Moreover, the in-depth analysis of performance on those virtual navigation tasks, which is needed to estimate the precision of spatial representations (Kolarik et al., 2016, 2018), can often be quite complex (Cooke et al., 2020)

Spatial memory and perspective taking tasks offer advantages for studying the precision of spatial representations over navigation tasks as they are easier to administer and require neither prolonged training nor specialised equipment. Typically, they involve an encoding stimulus portraying a place or an array of objects that participants have to memorized, followed by the presentation of a second stimulus presented from a different perspective with participants asked to judge whether it depicts the same place, or whether the objects have moved (Hartley et al., 2007; Montefinese, Sulpizio, Galati & Committeri, 2015; Muffato, Hilton, Meneghetti, De Beni & Wiener, 2019; Hilton et al., 2020; Segen, Avraamides, Slattery, Wiener, 2021).

A popular spatial memory task that follows this paradigm is the Four Mountains task (Hartley et al., 2007), which involves viewing an image of a place defined by four mountains, followed by four new images. One of these images depicts the same place but from a different perspective while the other images display a slightly different arrangement of the mountains. Participants are asked to select from the four, the image that corresponds to the same place they have seen during encoding. The Four Mountains task was specifically designed to provide a test that is quick and easy to administer, tapping into viewpoint independent spatial memory. What is more, the task has been successfully used to differentiate between healthy older adults and those with MCI as well as between MCI, AD and Frontotemporal Dementia patients (Chan et al., 2016; Bird et al., 2010).

The Four Mountains task, however, does not systematically manipulate the amount of change of the spatial information between encoding and test and is therefore not suited to assess the precision of spatial representations. Similarly, spatial memory tasks that focus on object location binding typically either move the object by a specific invariant amount (Montefinese et al., 2014) or swap two objects with each other (Muffato et al., 2019; Hilton et al., 2020; Segen et al., 2021a, 2021b). Again, such manipulations do not allow the assessment of the precision with which spatial locations are encoded.

Spatial memory precision has recently been associated with hippocampal functioning (Kolarik et al., 2016, 2018; Stevenson, 2018; Ekstrom & Yonelinas, 2020). For example, Stevenson (2018) reports that increased high-frequency activity in the hippocampus was associated with the precision of spatial memory retrieval in a task using 2D stimuli. Moreover, Kolarik et al. (2016, 2018) showed that hippocampal damage was associated with deficits in the ability to precisely remember the position of targets while coarse memory for the targets' approximate locations was not affected. Importantly, the hippocampus and related regions undergo functional and anatomical changes in typical and atypical aging which are often associated with declines in spatial memory (Hartley et al., 2007; Muffato et al., 2019; Hilton et al., 2020; Segen et al., 2021; Montefinese et al., 2015). However, the nature of those deficits is not well understood as the findings reporting deficits are often mixed, specifically in healthy older adults and those with very early MCI (Segen et al., 2020b; Moodley et al., 2015; Colombo et al., 2017). Quantifying the precision of spatial memory may offer a more sensitive tool, compared to studies focusing on coarse spatial changes (Hartley et al., 2007; Muffato et al, 2019; Hilton et al., 2020; Segen et al., 2021b; Montefinese et al., 2015), to investigate spatial memory deficits in those groups. As a result, a quick and accurate tool that taps into the precision of spatial representations would provide a more nuanced understanding of the nature of spatial deficits across those groups (i.e. (a)typically aged groups) that could be extended for early detection of MCI as well as differential dementia diagnosis in the future.

Here, we set out to develop a novel spatial memory task that aims to provide a quick and objective assessment of precision of spatial encoding, with minimal training requirements. To do so, we developed a two alternative forced choice (2AFC) task where participants had to judge the direction in which an object has moved in a 3D environment following a perspective shift. By systematically manipulating the distance by which the object was displaced, we estimated how accurately participants could detect the movement of objects in space following a perspective shift.

4.2. Experiment 1

4.2.1 Introduction

In this experiment we introduce a novel task that was designed to provide a quick assessment of the precision of object location representations in healthy younger adults. We employed psychophysics methods using an 2AFC task in which participants had to judge the direction in which an object moved in an environment following a perspective shift. A 2AFC approach was chosen as it is better suited to rapidly and reliably assess precision of spatial memory than change detection tasks (Heywood-Everett et al., 2020). To investigate the precision of participants' representations for object locations, we systematically manipulated the distance by which the object was displaced.

4.2.2 Method

4.2.2.1. Participants:

In total, 44 participants aged between 20-48 (Mean=25.5, SD=6.31) years of age took part in the study (29 females; 15 males). The majority of the participants (40) were right-handed. Participants were recruited through Bournemouth University’s participant recruitment system and received monetary compensation for their time. Written informed consent was obtained in accordance with the Declaration of Helsinki (World Medical Association, 2013).

4.2.2.2. Design:

The experiment followed a within 2 (Object Direction: Left/Right) × 2 (Camera Direction: Left/Right) × 6 (Object Displacement Distance (ODD): 5, 8, 13, 22, 37 & 61 cm) design.

4.2.2.3. Materials:

4.2.2.3.1. Virtual environment

The virtual environment was designed using 3DS Max 2018 (Autodesk Inc.) and consisted of a square room (9.8 m x 9.8 m), on the walls of which there were posters depicting highly familiar and recognisable landmarks (Hamburger & Roser, 2014). A teal plank was placed diagonally in the middle of the room (14 m long) and a target object was placed centrally on that plank with its position varied within a range of 65cm either to the left or right of the centre. The target object could only move along the plank.

The experimental stimuli were renderings of the environment with a 47.7° horizontal field of view and a 15% shift in the vertical field of view to simulate human vision (Figure 4.1A). Creating an asymmetric viewing frustum that resembles natural vision has been found to improve distance estimates in virtual environments (Franz, 2005). The experiment was presented on a 80.9 cm screen (diagonal) with an aspect ratio of 16:9 and a resolution of 1920x1080 pixels. Participants were seated 80 cm from the monitor with their head positioned on a chin rest. The physical vertical field of view (FOV) of the screen at this distance was 28° and the horizontal FOV was 47.7° and matched the horizontal FOV of the rendered stimuli

The cameras were arranged around an invisible diagonal line that was perpendicular to the plank. In both encoding and test stimuli participants would always see one corner of the room and two posters on either side of the corner (Figure 4.1A). There were two possible camera start and object start positions in encoding stimuli. The two possible camera start positions were 15° to the left (Position 1) or to the right (Position 2) of the diagonal line (Figure 4.1A). The target object was positioned on the plank, either 5cm to the left or to the right of the centre of the room. The camera always faced the centre of the room.

The test stimuli were rendered from a different viewpoint with a 20° perspective shift. If the stimuli at encoding was presented from Camera Position 1 the camera moved right and if the encoding was presented from Camera Position 2 it moved left (Figure 4.1A). The target object at test would move by 5, 8, 13, 22, 37 or 61cm from its start position either to the left or the right. Stimuli were presented with OpenSesame 3.1.7 (Mathôt, Schreij, & Theeuwes, 2012) and the left and right arrow keys on a standard computer keyboard were used to record responses.

A

B

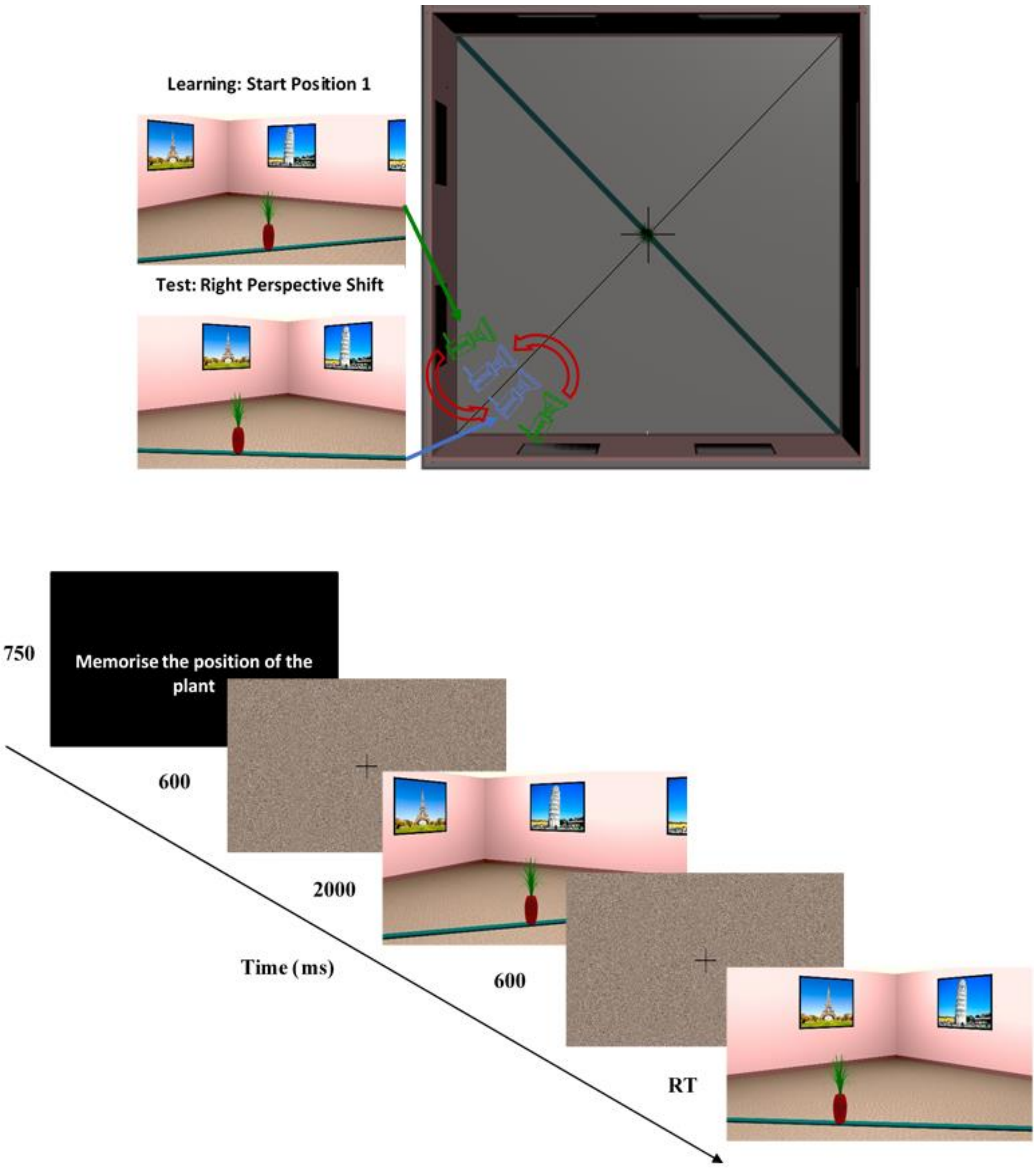

Figure 4.1 A: Top down schematic of the virtual environment used in the experiment with camera positions. Green cameras represent camera positions at encoding and the blue cameras represent the corresponding camera positions at test. Red arrows indicate the direction of perspective shift for each of the encoding cameras. Example renderings from the encoding (Start Position 1) and Test Camera are also provided; B: Trial structure

4.2.2.4. Procedure:

Each experimental trial started with a brief presentation of text instructing participants to remember the location of the target object (750 msec), followed by the presentation of a fixation cross and a scrambled stimuli mask (600 msec) (Figure 4.1B). In the subsequent encoding phase, participants were presented with a rendering of one of the two target object start positions either from camera Position 1 or Position 2 for 1.7 seconds. After the encoding phase, participants were again presented with a fixation cross and a scrambled stimuli mask for 600 msec. In the test phase, participants were presented with a rendering of the room following a 20° perspective shift. Their task was to decide whether the target object has moved to the left or to the right and respond by pressing the corresponding key on a standard computer keyboard. In 50% of the trials the target object moved left, and in the remaining 50% of the trials the target object moved right.

The experiment consisted of 72 experimental trials presented in randomised order, with each object displacement distance repeated 8 times. The task took around 10-15 minutes to complete and was administered as part of a larger study.

4.2.3. Results

4.2.3.1. Accuracy

Accuracy estimates were obtained using Generalised Linear Mixed Effects (GLME) models using the glmer function from LME4 package (Bates et al. 2018) in R (R Core Team, 2013) with ODD (Object Displacement Distance), Camera Direction and Object Direction as fixed factors and a random by-subject and by-stimuli intercept. We also estimated corresponding p-values using the lmerTest package (Kuznetsova, 2020). Both Camera Direction and Object Direction were effect coded and ODD was scaled and log transformed and used as a continuous variable. Our results (Table 4.1) showed that performance increased with an increase in the distance by which the target object was displaced between encoding and test. In addition, we found an interaction between Camera Direction and Object Direction, with lower performance in situations when the camera and the object moved in the same direction, e.g. the target object moves left, and the camera moves left. We also found a three-way interaction between Camera Direction, Object Direction and ODD, in which the effect of Camera and Object Direction was reduced with an increase in the ODD.

Table 4.1 Coefficients from Accuracy GLME analysis

	Accuracy			
Predictors	Coefficients	std. Error	z-value	p-values
(Intercept)	1.428	0.183	7.787	<0.001
Camera Direction (Left)	0.045	0.072	0.620	0.535
Object Direction (Left)	0.076	0.072	1.052	0.293
Log(ODD)	0.837	0.074	11.327	<0.001
Camera Direction * Object Direction	-1.965	0.078	-25.167	<0.001
Camera Direction * Log(ODD)	-0.062	0.072	-0.858	0.391
Object Direction * Log(ODD)	0.034	0.072	0.467	0.640
Object Direction (Left)*Camera Direction*Log(ODD)	0.393	0.074	5.335	<0.001

4.2.3.2. Reversed Congruency Effect

To further investigate the interaction between Camera and Object Direction we split data into Congruent and Incongruent trials. In Congruent trials the camera and the object moved in the same direction, whilst the camera and the object moved in opposite directions in Incongruent trials. We then ran a GLME to investigate the effect of Congruency and ODD on performance. The same random effect structure was used as in the previous analysis. The results (Table 4.2) show that participants performed significantly worse in Congruent than Incongruent trials, we termed this bias the Reversed Congruency Effect. We also found a two way-interaction with the reduction of the Reversed Congruency Effect with an increase in Distance (Figure 4.2). Specifically, our results show that in the Congruent trials participants consistently reported that the object has moved in the opposite direction of the actual movement for small displacements (i.e. 5cm - 22cm). Only once the object was moved by 37 cm or more (61 cm), participants began to perform above chance level in the Congruent trials (Figure 4.2). A different pattern of results was found in Incongruent trials with participants responding correctly on over 90% of the trials regardless of the ODD.

Table 4.2 GLME Analysis investigating the Congruency

	Accuracy			
Predictors	Coefficients	std. Error	z-value	p-values
(Intercept)	1.458	0.186	7.849	<0.001
Log(Distance)	.852	0.079	10.807	<0.001
Congruency (Congruent)	-1.910	0.082	-23.174	<0.001
Log(Distance) * Congruency (Congruent)	0.370	0.079	4.705	<0.001

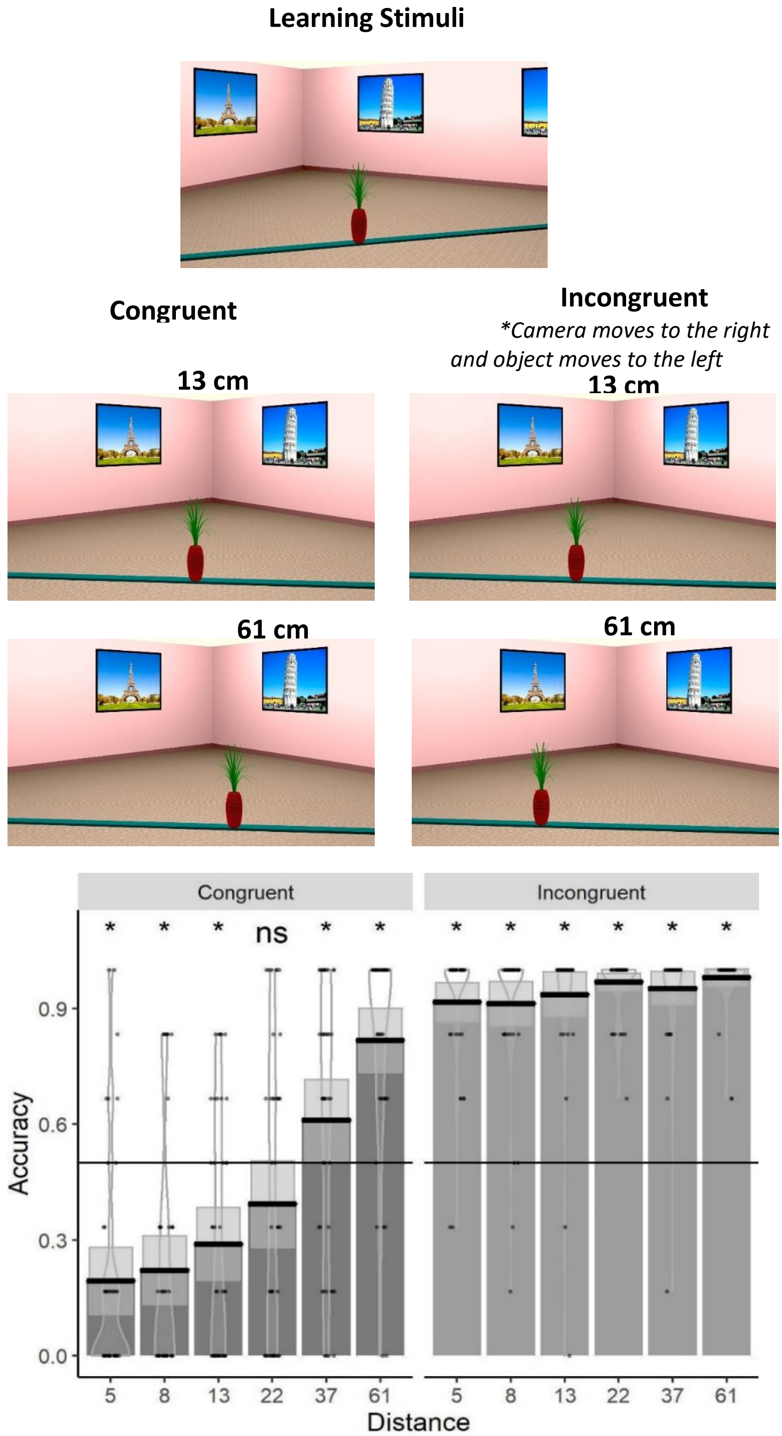

Figure 4.2 The upper panel shows example stimuli from the learning and the test phases for Congruent and Incongruent trials across 13 cm and 61 cm object movements. The bottom panel shows accuracy as a function of Distance (cm) and Congruency, with mean (solid line) and 95% CIs (grey shaded area) and individual data points and violin plots behind. Chance level performance is indicated by the solid horizontal line.

4.2.4. Discussion

This experiment set out to establish a new task that allowed for a quick and easy assessment of the precision of spatial representations. Unexpectedly, we found that the combination of object and camera movement direction systematically biased participants' responses. Specifically, if the object and the camera moved in the same direction, participants perceived the movement of the object to be in the opposite direction. This was most pronounced at smaller displacement distances. If, however, the object and the camera moved in the opposite directions, participants reliably detected movement direction even at the smallest displacement distances. We termed this the Reversed Congruency Effect.

It is not obvious how spatial cognition theories, including those differentiating between egocentric and allocentric spatial representations (Klatzky, 1998; Burgess, 2006; Shelton & McNamara, 2001), could explain this Reversed Congruency Effect. For example, if participants formed an allocentric representation of the environment (Burgess, 2008), they should reliably detect the direction of object movement regardless of whether the camera and the object moved in the same or opposite directions. This is because their representations of object locations are encoded relative to other features or landmarks in the environment and do not depend on the perspective from which the environment is viewed. Similarly, if participants encode the position of the object and other environmental cues in relation to their current position in space and engage in mental transformations to achieve spatial perspective taking (Holmes, Newcombe & Shipley, 2018; Klencklen, Despres & Dufour, 2012; King et al., 2002), we would expect them to adjust the expected positions of the objects in the environment based on their new position in the environment and perform the task without the systematic bias that we observed. Of course, neither the egocentric nor the allocentric strategy would guarantee that participants always responded correctly. Instead, performance would depend on the individual’s ability to generate precise spatial representations. Thus, we expected a linear increase in performance in both Congruent and Incongruent trials with increasing target object displacement, with the slope and intercept of the increase being determined by individual differences in precision.

If participants, as argued above, did not solve the task using a spatial strategy (i.e. ego- or allocentric strategy), it is possible that they used a heuristic that may have given rise to the systematic bias we have observed. We considered a number of such heuristics for the Reversed Congruency Effect (more information on those heuristics is available in the Supplementary materials). First, given the relatively small extent of the camera movement between encoding and test, participants may have found it difficult to understand the perspective shift and, therefore, essentially ignored it. As a result, they would have remembered the position of the target object on the screen (i.e. in screen coordinates) and used this position to judge whether the object has moved to the left or right. The screen-based strategy would be akin to participants using an egocentric strategy that would ignore the perspective shift and use the absolute relationships between their body and the object to judge the direction in which the object has moved. This screen-based strategy, however, predicts correct response for all trials, a pattern that we did not observe in the congruent trials. Second, participants could have encoded the position of the target object relative to other room-based cues - such as the room corner - but in the image, rather than in the 3D space. During test, they may have compared this memorized relationship to that in the test image in order to decide whether the object moved left or right. This “corner-based” strategy does predict correct responses in all incongruent trials, thus predicting participants’ performance well in these trials. However, the corner-based strategy predicts incorrect responses for all congruent trials, which does not match the empirical data.

We believe that the Reversed Congruency Effect is primarily driven by the movement of the camera in the real-world such that when the camera moves left participants expect that the object would appear to move left as well. As a result, even if the object remained stationary participants would experience “camera-induced object motion” to the right (as they expected that it would move to the left). This camera-induced object motion together with actual object movement direction would give rise to the Reversed Congruency Effect. Specifically, if the object moves in the opposite direction to the camera (incongruent trials), the camera-induced object motion amplifies the actual object movement. In contrast, when the object moves in the same direction as the camera (congruent trials), the camera-induced object motion effect may be greater than the actual object movement. In such cases, participants would incorrectly perceive the direction of object movement. However, when the object movement is large enough, it will eliminate the induced motion effect caused by the camera movement, and participants may perceive the object movement in the correct direction. This interpretation is in line with our empirical data, as participants consistently misjudged the direction of movement for small object displacements in congruent trials with performance improving for larger displacements. In incongruent trials, on the other hand, participants responded correctly across all object displacement distances.

To our knowledge, there have been no other reports that have described an “induced object motion effect” after a perspective shift in the spatial cognition literature. We did, however, find reports from studies with 2D stimuli that describe an induced object motion effect, called the Induced Roelofs Effect (IRE, Bridgeman, Peery & Anand, 1997). Specifically, when a dot and a surrounding rectangular frame move in opposite directions on the screen participants perceive the movement of the dot as larger than when the dot and the frame move in the same direction (Abrams & Landgraf (1990); see also, Bacon, Gordon & Schulman, 1982). The IRE has also been demonstrated using static stimuli showing that if the frame is shifted to the left, participants estimate the target object to be farther to the left (Bridgeman, Peery & Anand, 1997; Taghizadeh & Gail. 2014). Two explanations have been proposed for the IRE: (1) the frame biases the egocentric perceived midline in the direction of the frame shift, thus changing the location of the target relative to perceived midline (Bridgeman et al., 1997, Bridgeman, Gemmer, Forsman & Huemer, 2000); (2) the effect is induced by an allocentric influence with the relative relationship between the target and the frame directly affecting the perceived location of the target (de Grave et al. 2002; Taghizadeh & Gail, 2014). Importantly, both explanations suggest that the IRE stems from biased encoding as a result of the shift of the frame position on the screen. In our experiment, it is not clear what the frame would be as the stimuli were always presented full screen and thus did not move on the screen. Thus, the camera-induced object motion effect in our experiment is unlikely to be driven by the same mechanisms that describe the IRE. Instead, we propose that the camera-induced object motion is the product of the camera movement in the “real-world” (virtual environment) between encoding and test rather than by the movement of the object on the screen. While we do not have a firm explanation for the camera-induced object motion effect we observed, we speculate that it is driven by difficulties in precisely encoding the position of the object in the environment and difficulties in understanding how the perspective shift between encoding and test affects the projected position of the object in the two-dimensional image. It is also possible that the camera-induced object motion effect experienced by participants may arise due to naive theories that people hold about how the visual world works (for more in-depth discussion see Bertamini, Latto & Spooner, 2003). It is also worthwhile to note, that the encoding time was relatively short, as a result it is possible that this has contributed to difficulties in precisely encoding object position.

The primary aim of Experiment 1 was to introduce a new task to assess the precision with which participants can memorize the locations of objects in space. The Reversed Congruency Effect described above, however, demonstrates that the perspective shift between encoding and test had a significant impact on participants’ judgments. Therefore, Experiment 2 was designed to facilitate our understanding of the Reversed Congruency Effect. Specifically, we investigate whether the effect is driven by object movement on the screen or as a result of camera movement in the real-world. Experiment 2 aimed to provide a conceptual replication of the Reversed Congruency Effect but also aimed to investigate whether providing additional cues in the environment would eliminate or at least reduce the effect.

4.3. Experiment 2

4.3.1. Introduction

This experiment set out to further investigate the Reversed Congruency Effect observed in Experiment 1. We proposed that the effect is driven by movement of the camera in the virtual environment that induces object motion. However, in Experiment 1, the object position on the screen differed between encoding and test, thus the object moved both on the screen as well as in the virtual environment. In Experiment 2 we held the object position on the screen constant between encoding and test, thus allowing us to investigate whether the Reversed Congruency Effect described above was driven by the object movement in the virtual environment or on the screen.

Difficulties in forming a precise spatial representation of object positions in the environment are likely to increase susceptibility to the bias induced by camera movements that give rise to the Reversed Congruency Effect. To reduce both the proposed induced object movement based on the perspective shift and the susceptibility to the induced movement based on uncertainty in the memorized object location, we introduced additional objects in the environment both during encoding and test. We expected that enriching the spatial scene with these additional objects would help participants to better memorize the exact object location (Cánovas, Leon, Serrano, Roldan & Cimadevilla, 2011, Chamizo, Artigas & Banterla, 2011) and to understand the perspective shift.

In addition, we have increased the encoding time as we thought that the short encoding times in Experiment 1 could have prevented participants from formulating precise representations of object positions. Lastly, due to Covid-19 restrictions that prevented in-person laboratory testing, Experiment 2 was carried out online. Based on recent research indicating that online data collection can provide valid and reliable data on a variety of cognitive and perceptual experiments (Reinecke & Gajos, 2015; Komarov Reinecke & Gajos, 2013; Huber & Gajos, 2020), we expected to replicate the Reversed Congruency Effects of Experiment 1, in the condition without additional objects, as it was most similar to Experiment 1.

4.3.2. Method:

4.3.2.1. Participants

Forty-seven participants (40 female and 7 male) aged between 18-35 years old (Mean=21.94, SD=4.09) took part in the study. Participants were recruited through Bournemouth University's participant recruitment system and through online advertising. All participants provided their informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

4.3.2.2. Materials:

4.3.2.2.1. Virtual environment

We used the same virtual environment as in Experiment 1. However, in this version of the task the camera was always directed such that the target object was in the centre of the screen, regardless of the position of the camera and the target object within the environment. Thus, in order to solve the task participants were required to consider the movements of the object in the world rather than on the screen. In addition, the camera moved by 20 degrees between encoding and test either to the left or the right, regardless of the camera position during encoding. This ensured that the camera position during encoding could not be used to predict its movement, as was the case in Experiment 1. We also added the Additional Objects condition, in which two view-invariant columns were added to the environment (Figure 4.3). The columns were placed approximately halfway between the walls and the plank, such that they were closer to the target object than the posters that were available in Experiment 1 and the No Additional Object condition. The columns were positioned at equal distances either to the left or to the right of the centre of the room on the horizontal plane. The target object at test could move by either 8, 13, 22, 37 or 61cm from the start position, either in the left or right direction on the plank.

4.3.2.3. Design

The experiment followed a within 5 (Object Displacement Distance (ODD): 8, 13, 22, 37 & 61 cm) x 2 (Condition: Additional Objects/No Objects) x 2 (Congruency: Congruent/Incongruent) design

4.3.2.4. Procedure

Participants completed the task using an online testing platform Testable (testable.org). Prior to the experiment they were presented with instructions on how to calibrate their screen to ensure that the entire stimulus was visible during the experiment which was run in full screen mode. The experimental set up was similar to Experiment 1, however encoding times were increased from 1.7 sec in Experiment 1 to 5 sec.

The experiment began with four practice trials that preceded the 160 experimental trials. The Additional Object manipulation was blocked and counterbalanced such that half of the participants completed the No Object condition first and the other half completed the Additional Object condition first. Within each block, trials were presented in randomised order with the entire experimental procedure taking around 35 minutes to complete.

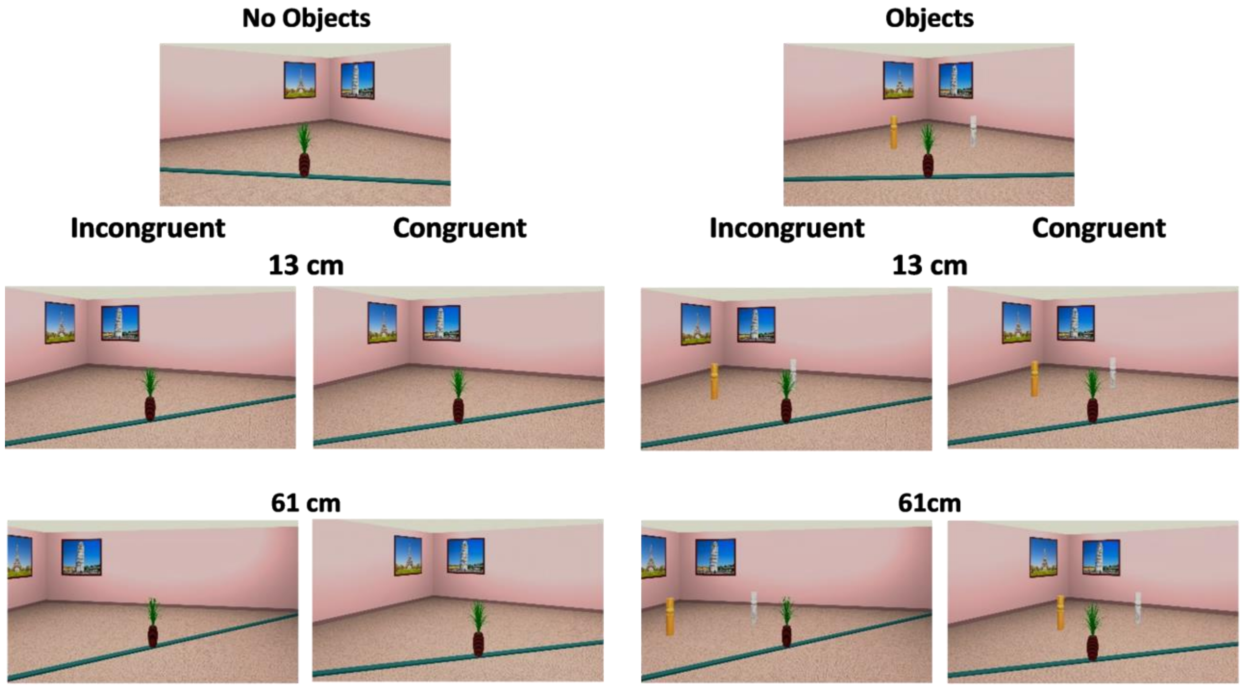

Figure 4.3 Stimuli examples for the No Objects and Additional Object in Incongruent and Congruent Trials for 13 and 61 cm Object Displacement Distances

4.3.3. Results

To investigate performance, we ran a GLME with Object Displacement Distance (ODD), Additional Objects and Congruency as fixed factors and random by subject and by-stimuli intercept and slope for Condition. Results showed that accuracy increased with the increase in the ODD (Table 4.3 and Figure 4.4). Consistent with our predictions we replicated the Reversed Congruency Effect reported in Experiment 1, with lower performance in Congruent compared to Incongruent trials. We also found that accuracy was lower in the No Objects condition than in the Additional Object condition. Importantly, we found an interaction between Congruency and Condition, whereby the Reversed Congruency Effect was no longer a reliable predictor of performance in the Additional Objects condition (See supplementary materials for follow-up analysis). Lastly, we found a two-way interaction between ODD and Condition, with a larger increase in performance in the Additional Object condition when ODD increased.

Table 4.3 Coefficients from Accuracy GLME analysis

	Accuracy			
Predictors	Coefficients	std. Error	z-value	p-value
(Intercept)	0.329	0.027	12.044	<0.001
Log(ODD)	0.256	0.027	9.344	<0.001
Congruency (Congruent)	-0.404	0.027	-14.799	<0.001
Condition (Additional Objects)	0.135	0.032	4.217	<0.001
Log(ODD) * Congruency (Congruent)	0.038	0.027	1.387	0.165
Log(ODD) * Condition (Additional Objects)	0.070	0.027	2.555	0.011
Congruency (Congruent) * Condition (Additional Objects)	0.239	0.027	8.773	<0.001
Log(ODD)*Congruency (Congruent) * Condition (Additional Objects)	0.023	0.027	0.842	0.400

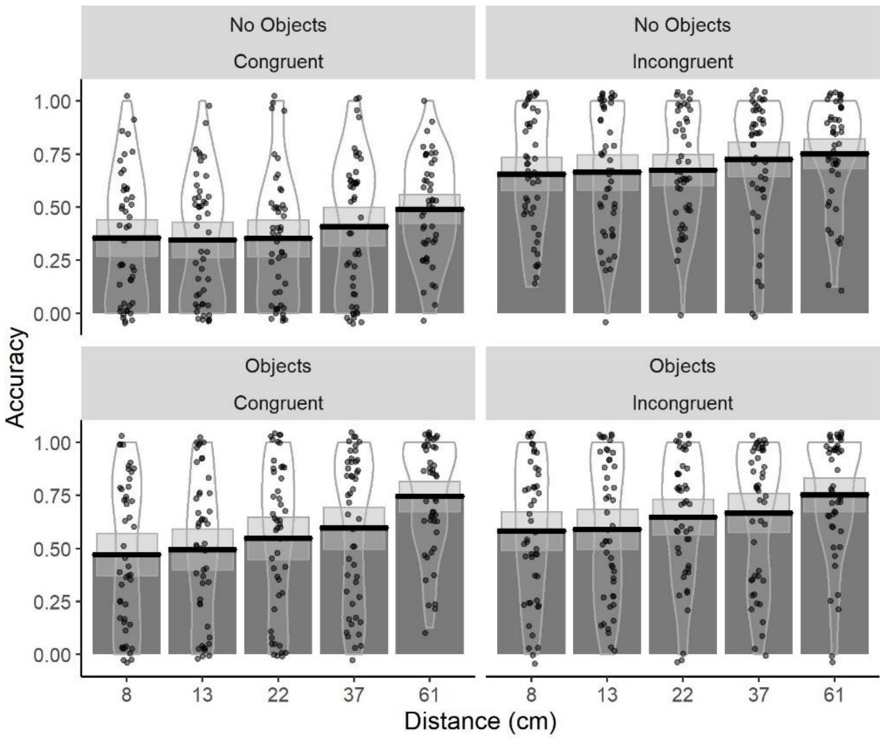

Figure 4.4 Bar plots for accuracy values as a function of Congruency (Incongruent/Congruent) and Condition (No Objects/Additional Objects) and age group with mean (solid line) and 95% CIs (grey shaded area) with individual data points and violin plots behind.

We also ran a GLME model with additional fixed effects (Block and Camera Rotation). We found some order effects such that the increase in performance in the Additional Objects condition was higher in those who have completed the Additional Objects condition first. This interaction was most likely driven by a larger increase in performance in Incongruent trials in the Additional Objects condition, when this condition was performed first. The complete model is reported in the supplementary materials.

4.3.4. Discussion

In Experiment 2, we replicated the Reversed Congruency Effect of Experiment 1, in the condition without additional objects in the environment. Thus, the Reversed Congruency Effect seems to be robust across different encoding times (1.7 sec vs 5.0 sec) and means of data collection (laboratory vs. online). Importantly, the replication of the Reversed Congruency Effect suggests that the effect was not driven by the movement of the object on the screen as the object always remained in the centre of the screen in Experiment 2. Instead, the bias likely arises from camera movements that results in an induced object motion in the virtual environment.

The use of additional objects in the environment reduced the Reversed Congruency Effect such that it no longer reliably predicted performance. We believe that the presence of additional objects in the environment helps to reduce the camera-induced object motion effect that gives rise to the Congruence Effect by doing two things. First, the addition of objects can improve the precision with which object positions are represented. Indeed, past studies show that increased availability of cues/landmarks is associated with more precise spatial encoding (Kamil & Cheng, 2001; Ekstrom & Yonelinas, 2020). This is also consistent with Ekstrom and Yonelinas (2020) who have proposed that the complexity of the environments is associated with the precision of representation, such that less complex environments are encoded using a coarser representation, whilst more complex environments with more features are encoded more precisely. Thus, the Additional Object condition may foster a more precise representation by increasing the complexity of the environment such that it contains enough detail that allows participants to understand the precise position the object occupies within the environment.

Furthermore, the additional objects in the current experiment were positioned closer to the target object, compared to the remaining cues (geometric cues and posters) that were available in Experiment 1 and the No Object condition. The proximity of the cues also makes it easier to anchor the target object to those cues. This is in line with previous reports suggesting that use of proximal cues improves memory for target locations (Cánovas et al, 2011; Chamizo et al., 2011).

Second, the addition of objects can also improve spatial perspective taking by providing 1) additional cues that can be used for self-localization following a perspective shift and 2) direct feedback on how perspective shifts affect the 2D projection of the positions that objects occupy on the screen. This feedback can be used to adjust the “expectations” that participants have about where objects are following a perspective shift. For example, if participants expect the objects to move more to the right when the camera moved to the right, but at test they see that the stable cues provided by the additional objects did not “move'' as they expected, they can use this information to adjust their expectations for the position of the target object. In addition, the objects in the environment act as additional monocular depth cues that improve depth perception (Luo, Kenyon, Kamper, Sandin & DeFanti, 2007). Improved depth perception is likely to facilitate the encoding of object positions as well as the understanding of perspective shifts.

4.4. Experiment 3

4.4.1. Introduction

One of our original aims that motivated Experiment 1 was to design a task that could be used with older adults as a quick measure of the precision of spatial encoding following perspective shifts. Given the results from Experiment 2 where the addition of objects in the scene substantially reduced the Reversed Congruency Effect, we created a shorter variant of the task with additional objects. The main aim of Experiment 3 was to investigate performance differences between younger and older adults and to examine if the task we designed is suitable to assess the precision of spatial encoding following perspective shifts in older adults.

Although previous research focusing on spatial memory across different viewpoints did not directly investigate precision of spatial representations in older adults. Nevertheless, such studies show age-related deficits in spatial memory across viewpoints (Hartley et al., 2007; Montefinese, et al., 2015; Muffato, et al. 2019; Hilton et al., 2020) and greater difficulties in older adults to extract useful information from the stimuli after perspective shifts when fine-grained spatial changes were introduced (Segen et al., 2021a).

Additional evidence for age-related declines in precision of spatial encoding comes from 2D tasks used in visuospatial working memory research (Pertzov et al. 2015, Nilakantan et al., 2018). It is plausible that those age-related difficulties in the formation of fine-grained spatial representations are caused by age-related changes in the anterior and posterior hippocampus. Indeed, a recent longitudinal study (Langnes et al., 2019) found that the posterior hippocampus, typically associated with fine-grained spatial processing, was more affected by aging than the anterior hippocampus, which is involved in the formation of coarser spatial representations (Røe Evensmoen et al., 2013; Nadel, Hoscheidt & Ryan, 2013).

Age-related functional and morphological changes (Antonova et al., 2009; Meulenbroek, Petersson, Voermans, Weber, & Fernández, 2004; Moffat, Kennedy, Rodrigue & Raz, 2007) in the hippocampal circuit and the retrosplenial cortex may also contribute to spatial perspective taking deficits (King et al., 2002; Vargha-Khadem et al., 1997). However, research investigating how aging affects spatial perspective taking renders mixed results with studies reporting similar effects of perspective shifts on performance in young and older adults on spatial memory tasks (e.g., Muffato et al., 2019; Hilton et al., 2020; Watanabe & Takamatsu, 2014). Other studies report specific age-related deficits in perspective-taking abilities (Inagaki et al., 2002; Montefinese et al., 2015; Watanabe, 2011; Segen et al., 2021a), with older adults being more affected by the presence of the perspective shift rather than its size (Montefinese et al., 2015; Segen et al., 2021a).

Given the age-related declines in spatial memory and precision of spatial encoding across 2D stimuli together with possible perspective-taking deficits, we predicted that older adults would form less precise spatial representations compared to younger adults which would be reflected in overall lower performance, particularly when the object displacement is small. However, given our current interpretation that the imprecise encoding of the target object position and difficulties in spatial perspective taking contribute to the Reversed Congruency Effect, it is possible that older adults will be more susceptible to the Reversed Congruency Effect.

4.4.2. Method

4.4.2.1. Participants

Forty young (mean age = 25.40 years, SD = 5.34; age range = 18-35 years; 24 females and 16 males) and forty older adults aged 55 years and over (mean age=63.60, SD=5.17, age range=55-74; 24 females and 16 males) took part in this study. All participants were recruited through Prolific (https://www.prolific.co), an online participant recruitment system. Participants received monetary compensation for their time. All participants gave their written informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

4.4.2.2. Materials and Procedure

This experiment was similar to Experiments 1 and 2. However, in the current experiment we only used the environment with additional objects (see “Additional Objects” condition in Experiment 2). Given the overall low performance in Experiment 2 and the prediction that older adults would have less precise spatial memory, we increased the Object Displacement Distance (ODD). Specifically, the target object could move in eight equally sized steps between 10-100cm (10, 23, 36, 49, 61, 74, 87 or 100cm) from the start position, either to the left or right. The camera and object positions were the same as in Experiment 2, however, instead of fixating on the target object as in Experiment 2, the camera always fixated at the centre of the room. This was done in order to allow larger ODD whilst ensuring that the same cues were visible at encoding and test.

The experiment consisted of 128 experimental trials presented in randomised order, with 16 trials per ODD. In addition, we included four vigilance trials at random intervals, to ensure that participants were paying attention. In these trials participants were asked to indicate the side of the screen in which the Eiffel Tower or the Leaning Tower of Pisa poster appeared on. Our criterion of including only data in which participants responded correctly to 3 out of the 4 vigilance trials resulted in no exclusions. The study took around 25 minutes to complete.

4.4.3. Results

The data was analysed using GLME with Age Group, Congruency and ODD as fixed factors and a random by-subject and by-item intercept. Age Group (Younger adults/Older adults) and Congruency (Incongruent/Congruent) were coded using effect coding. ODD was centred and scaled and used as a continuous variable. We found that Age Group, Congruency and ODD were all reliable predictors of performance (Table 4.4 and Figure 4.5). Specifically, performance increased with increasing ODD, performance was lower in older than younger adults and in Congruent compared to Incongruent trials. We also found a significant interaction between ODD and Age Group, with a lower increase in performance in our older adults with the increase in ODD. There was also an interaction between ODD and Congruency, with a larger increase in performance in Congruent trials with increasing ODD. In addition, we found an interaction between Age Group and Congruency, with lower performance in older than younger adults in Congruent trials. This demonstrates that the Reversed Congruency Effect was larger in the older age group. Lastly, we found a three-way interaction between ODD, Age Group and Congruency, with older adults showing a larger increase in performance in the Congruent trials with increasing ODD.

Table 4.4 GLME Coefficient for Accuracy Analysis

	Accuracy			
Predictors	Estimate	std. Error	z-value	p-values
(Intercept)	1.756	0.104	16.837	<0.001
ODD	0.963	0.049	19.683	<0.001
Age Group (Old)	-0.270	0.098	-2.775	0.006
Congruency (Congruent)	-0.391	0.048	-8.191	<0.001
ODD: Age Group (Old)	-0.113	0.032	-3.523	<0.001
ODD: Congruency (Congruent)	0.236	0.049	4.856	<0.001
Age Group (Old): Congruency (Congruent)	-0.224	0.032	-7.101	<0.001
ODD: Age Group (Old): Congruency (Congruent)	0.139	0.031	4.417	<0.001

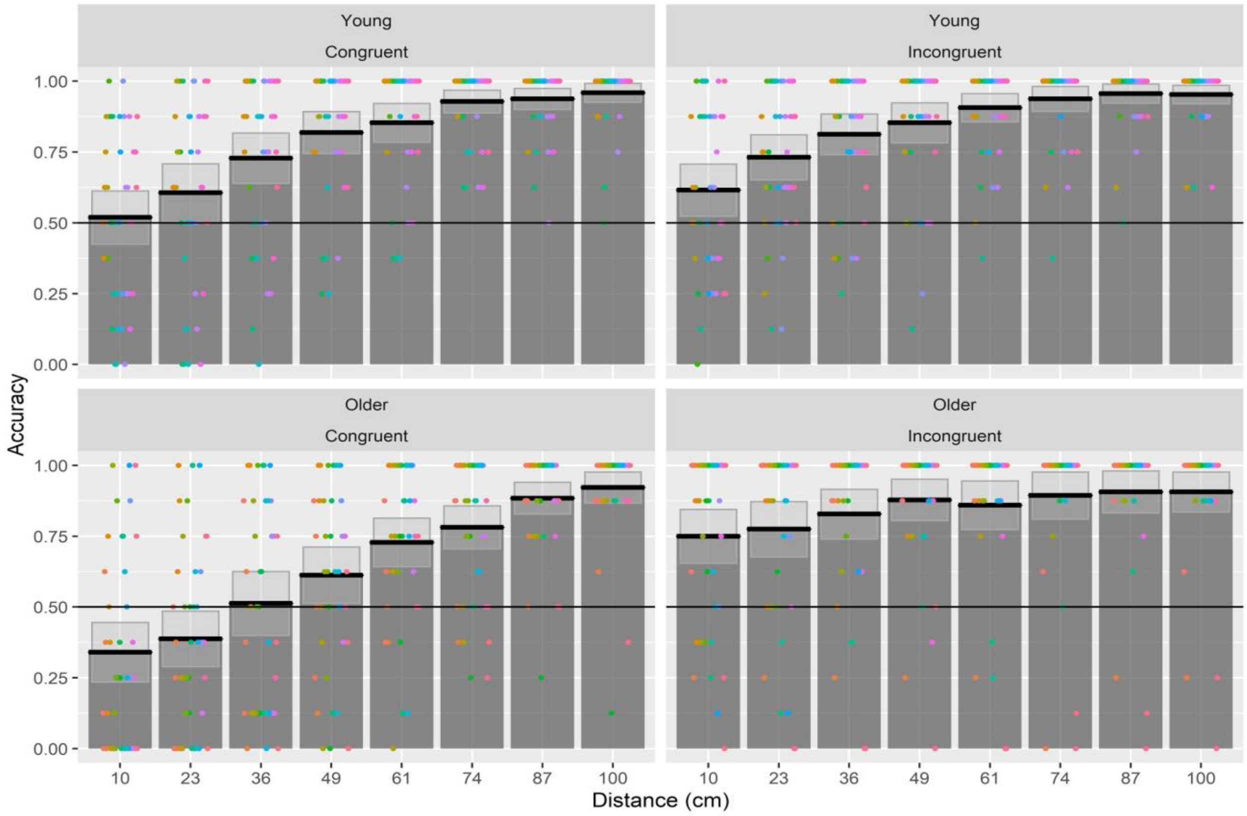

Figure 4.5 Bar plots for the accuracy as a function Age Group (*Young/Older Adults*) and Congruency (*Congruent/Incongruent*) with mean (solid line) and 95% CIs (grey shaded area) with individual data points. The solid horizontal black line indicates chance level performance

4.4.3.1. Clustering

Our results demonstrate a lot of variability in performance in both Congruent and Incongruent trials, which could be driven by individual differences in the strategies used to solve the task. To determine if there were separate groups of participants who show reliably different performance patterns, we performed a k-means cluster analysis. The cluster analysis was performed on the accuracy data which was averaged per participant separately for Congruent and Incongruent trials. To determine the optimal number of clusters, we used the fviz_nbclust function (from the factoextra package in R) which calculates the total within cluster sum of squares across a different number of clusters ranging from one to ten across

1000 iterations. The optimal number of clusters for this data set was 4, as indicated by the Elbow Method.

The largest group identified by the k-means cluster analysis (Cluster 1) contained 40% of our sample. They performed well across both Congruent and Incongruent trials (Figure 6A & B). Cluster 2 consists of participants whose performance closely resembles the Reversed Congruency Effect found in Experiment 1 and 2, with largest differences between Congruent and Incongruent trials at smaller ODD (Figure 4.6A & B). This group contained 36.25% of our sample. Cluster 3, made up of 20% of the sample, consisted of participants who showed the "opposite" Reversed Congruency Effect with higher performance in Congruent compared to Incongruent trials (Figure 4.6A & B). Finally, in the last cluster, there were only three older participants with low overall performance which was also not affected by ODD. It is likely that these participants did not understand the task.

Next, we focused on whether the distribution of participants in those clusters varies as a function of age group (exploratory analysis on sex differences presented in the supplementary materials). To investigate this, we conducted a Chi-Square test with simulated p-values based on 1000 iterations. We found that the distributions across clusters were not equal (p=.031). For example, almost half of our older participants fell within a cluster in which participants displayed the Reversed Congruency Effect (Cluster 2). On the other hand, half of our young participants fell within the cluster with overall high performance and minimal Reversed Congruency Effect (Cluster 1, Figure 4.6C).

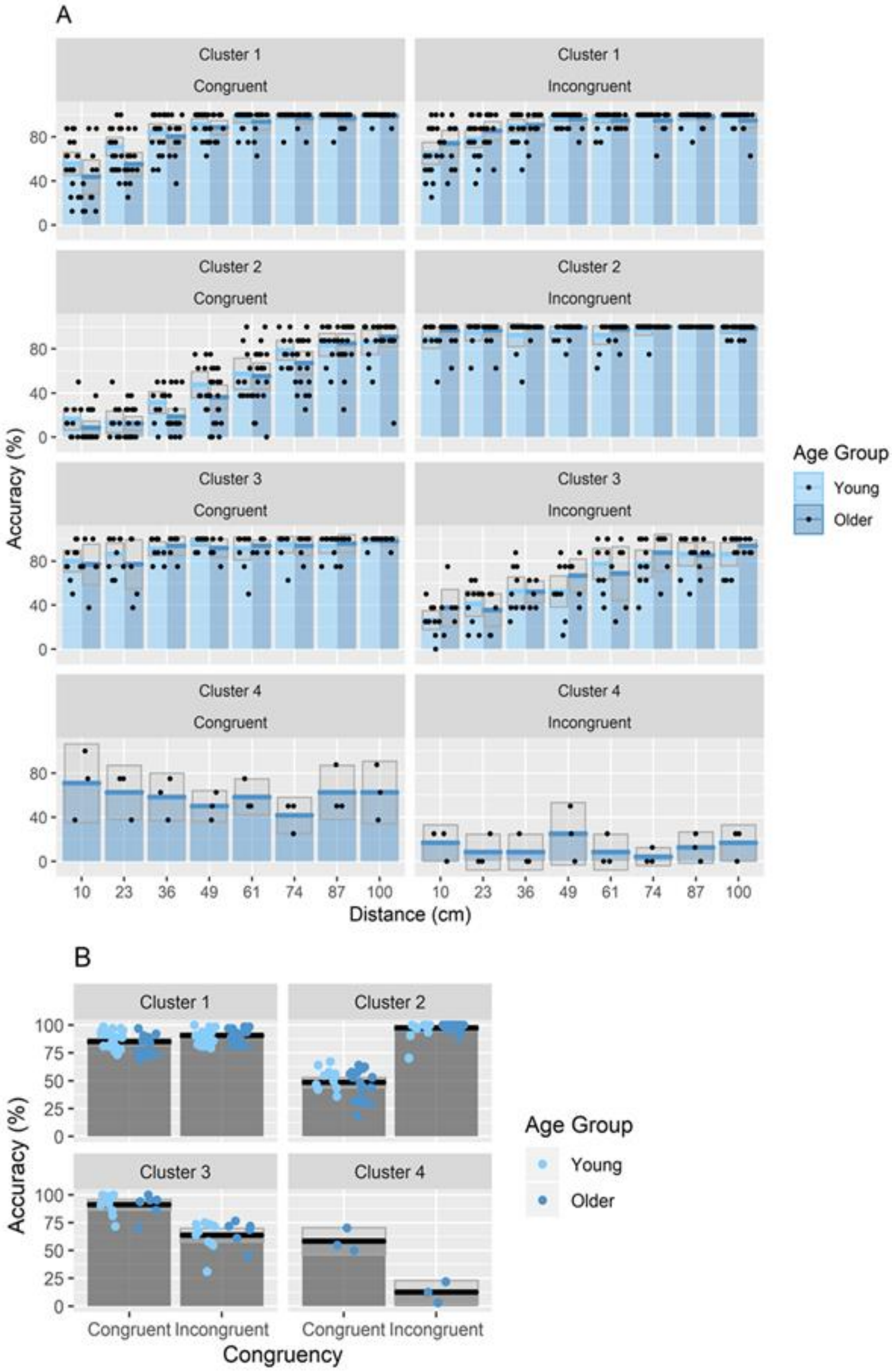

Figure 4.6 A Bar plots for the Accuracy for each Cluster as a function of Congruency and ODD with mean (solid line) and 95% CIs (grey shaded area) with individual data points; B Mean Accuracy in each Cluster in Congruent and Incongruent trials with individual data points

4.4.4. Discussion

In line with our predictions, we found overall better performance in younger than older adults as well as a larger Reversed Congruency Effect in older than younger adults. Importantly, our results demonstrated large variability in the pattern of performance for Congruent and Incongruent trials across participants. To further investigate these individual differences, we used a data-driven clustering approach that identified four distinct clusters of participants based on their performance in Congruent and Incongruent trials. Specifically, the cluster analysis identified a group that consisted of a large proportion of our sample (40% of participants) who did not show a Reversed Congruency Effect. The fact that this group showed very good overall performance (>80%) demonstrates that participants in this group formulated precise representations of object locations and understood the perspective shifts.

We also found a second large group of participants (~36% of participants) who displayed a reliable Reversed Congruency Effect. Specifically, having high performance in Incongruent trials and low performance for small object displacement distances in Congruent trials, that improved as the displacement distances increased. In line with our interpretation of the nature of the Reversed Congruency Effect in Experiments 1 and 2, we believe that this finding indicates that this group had greater difficulties with formulating precise spatial representations and understanding perspective shifts even when additional cues are available in the environment.

Lastly, our clustering analysis identified a group (consisting of 20% of participants) that showed the “opposite” Reversed Congruency Effect. We do not currently understand what may give rise to this performance pattern. Further investigation is needed to understand what drives this “opposite” effect.

Consistent with our prediction that older adults should be more susceptible to the Reversed Congruency Effect, there were more older adults in the group which showed the Reversed Congruency Effect, whilst the reverse pattern was found in the group that did not display the Reversed Congruency Effect, which contained more young adults. Specifically, we hypothesised that older adults would form less-precise representations of object locations as result of age-related functional and morphological hippocampal changes (Antonova et al., 2009; Meulenbroek et al., 2004; Moffat et al., 2007). It is also possible that older adults have more difficulties than young adults in understanding perspective shifts (Segen et al, 2021a; Montefinese et al., 2015). As a result of those difficulties, older adults should be more susceptible to the camera-induced object motion, which may give rise to the Reversed Congruency Effect.

In addition, younger and older adults may rely on different spatial strategies to solve the task as our previous research shows that older participants rely more on cues during spatial memory tasks than younger participants (Segen et al., 2021a, 2021b). Thus, it is possible that if we added even more landmarks/cues into the environment that age differences would be less pronounced

Overall, the greater tendency of older adults to display the Reversed Congruency Effect is in line with our interpretation that the effect is driven by difficulties in encoding spatial information and understanding the perspective shifts.

4.5. General Discussion

In this study we set out to create a quick and easy to administer task to assess the precision of spatial representations. However, in Experiment 1 we found strong influence of camera and object movement direction, that we termed the Reversed Congruency Effect. Specifically, we found that when the camera and object moved in the same direction (congruent movement), performance in identifying the direction of object movement was below chance level for small object displacements. In contrast, performance was at ceiling across all object displacement distances when the camera and the object moved in different directions (incongruent movement). This Reversed Congruency Effect was unexpected. In

Experiment 2 we established that the Reversed Congruency Effect was driven by the object and camera movement in the virtual world and was not an artefact of the object movement in screen coordinates. If indeed the effect is driven by object and camera movement in the virtual environment, this would demonstrate some egocentric influences in the current task. Specifically, if participants relied solely on an allocentric object-to-object representation, perspective shifts should not introduce any systematic biases in participants' responses that are related to the direction of the perspective shift. However, it should be noted that the current experiment was not designed to distinguish between egocentric and allocentric reference encoding.

We also demonstrated that the size of the Reversed Congruency Effect can be substantially reduced by adding objects into the environment, such that performance becomes similar across congruent and incongruent trials. In Experiment 3, we tested young and older participants with an environment containing additional objects. Our results showed that older adults were more likely to display the Reversed Congruency Effect. Finally, Experiments 2 and 3 were online studies and provided conceptual replications of the laboratory findings from Experiment 1, showing that online spatial memory and perspective taking studies using static stimuli can render reliable results.

In Experiment 2 we have shown that the Reversed Congruency Effect was driven by how the object and the camera moved in the environment. Our main explanation for the Reversed Congruency Effect is that camera movements between encoding and test create an induced object motion effect in the same direction as the camera movement. This camera-induced object motion amplifies perceived object movements in incongruent trials and contributes to incorrect responses at smaller object displacement distances in the congruent trials. While it is currently unclear why the movements of the camera lead to the perception of object movement in the same direction, we have shown that the Reversed Congruency Effect is reduced if we provide additional spatial cues by adding further objects to the environment. Increasing the number of cues/landmarks in the environment is associated with improvements in the precision with which object positions are encoded and better understanding of the perspective shifts (Cánovas et al, 2011; Chamizo et al., 2011; Kamil & Cheng, 2001; Luo et al., 2007; Ekstrom & Yonelinas, 2020). As a result, we argue that the camera-induced object motion that gives rise to the Reversed Congruency Effect is driven by difficulties in forming precise representation of object locations and difficulties with understanding perspective shifts can result in camera-induced object motion.

It is possible that the experimental set up that we used, and in particular the presentation of a three-dimensional virtual world using two-dimensional images (pictorial space), contributes to difficulties in understanding the position of the object in the environment across different viewpoints. As recently pointed out in other studies (Troje, 2019; Karimpur, Eftekharifar, Troje, & Fiehler, 2020), the location of the observer in pictorial space is ill-defined, because the observer is not actually present in the depicted space (Avraamides & Kelly, 2008). Observers may adopt the location of the (virtual) camera, which is what we asked our participants to do, but this process is challenging for a number of reasons: First, when viewing images, observers have access to monoscopic, but not stereoscopic, depth cues; second, the sensorimotor contingencies that link movements in the world to changes in the retinal image are different for images and for real world visual space; finally, when viewing pictures, we generally accept distortions of the geometry of the displayed space (Troje, 2019). Together, these factors are likely to contribute to a less reliable understanding of the exact nature of the perspective shift as well as less reliable estimates of the distances and directions to the objects in the stimuli (Troje, 2019; Karimpur, Eftekharifar, Troje, & Fiehler, 2020). As noted in discussion of Experiment 2, difficulties in depth perception can prevent participants from formulating a correct representation of object location and from understanding the perspective shifts correctly, which in turn may give rise to the camera-induced object motion.

Future research should, therefore, address if and how the result from our study using pictorial stimuli generalizes to real world setting or to a setting that makes use of immersive virtual reality.

In Experiment 3, we show that the Reversed Congruency Effect is more pronounced in older adults. Thus, even in situations when additional environment cues are available, older adults have greater difficulties in overcoming the camera-induced object motion. This is in line with our interpretation that susceptibility to camera-induced object motion is driven by difficulties in forming precise representations of object locations and in spatial perspective taking. Specifically, aging is associated with declines in the precision of memory for object locations (Pertzov et al., 2015, Nilakantan et al., 2018; Segen et al., 2020) as well as difficulties in perspective taking (Segen et al, 2020; Montefinese et al., 2015). These declines may be associated with age-related functional and morphological changes in the retrosplenial cortex and the hippocampal circuit (Antonova et al., 2009; Meulenbroek et al., 2004; Moffat et al., 2007; Langnes et al., 2019), which is crucial for the development of precise spatial memories (Røe Evensmoen et al., 2013; Nadel et al., 2013) and the manipulation of spatial memories to carry out perspective taking (King et al., 2002).

Our initial aim was to design and test a task that would allow us to study the precision of spatial memory for object locations. However, given the unexpected Reversed Congruency Effect that was observed, further experimentation with the task is necessary to be confident about its validity to serve as a diagnostic tool on spatial memory precision. Specifically, although we managed to substantially reduce the influence of the Reversed Congruency Effect has on performance by enriching the environment with additional spatial cues in Experiment 2, the effect was still present in a similar situation in Experiment 3, particularly in older adults. In addition, in Experiment 3 we also showed that individual differences greatly influence performance on our task. It is therefore important that the task is validated using a substantially larger sample and to relate performance on the tasks to spatial cognition tasks. This will allow us to achieve a better understanding of what abilities our task taps into, and to understand what individual differences in spatial abilities are contributing to the observed Reversed Congruency Effect.

Lastly, we should briefly discuss the differences in performance across the three experiments presented here. Firstly, although in Experiment 2 we replicated the Congruency Effect in the No Additional Objects condition, which most closely resembles Experiment 1, the difference between Incongruent and Congruent trials was smaller compared to Experiment 1. Secondly, performance in the Additional Objects condition was lower in Experiment 2 than in Experiment 3. We believe that the differences in performance and the manifestation of the Reversed Congruency Effect between Experiment 2 and Experiments 1 and 3 arise due to the camera always fixating on the target object in Experiment 2. This means that the amount of camera rotation between encoding and test depends on the position of the target object during encoding and the amount of object displacement. In other words, the position of the environmental features in the 2D image differed between trials, even if the camera was in the same position. In Experiments 1 and 3, on the other hand, the camera fixated on the same environmental location, and the positions of all of the environmental features in the image (apart from the target object) are always the same for the given camera positions. These differences in camera rotation may have introduced greater variance in participants' performance in Experiment 2 and led to overall lower performance compared to Experiments 1 and 3. Despite those fluctuations in performance and in the “size” of the Reversed Congruency Effect, our conjecture is that it is a robust effect that is present across different viewing conditions (e.g. different sizes of monitors used by participants in the online experiments, and relative positions to the monitor) as well as camera settings that are used to render experimental stimuli.

To conclude, in the present study we introduced a novel task to study the precision of spatial memory for object locations across perspective shifts and reported a novel systematic bias in participants' performance, the Reversed Congruency Effect that is likely to be driven by induced object motion introduced by camera movements in the “real-world”. We believe that this camera-induced object motion arises from difficulties in formulating precise spatial representations and understanding of perspective shifts. This is in line with our findings across all three experiments showing that the Reversed Congruency Effect is influenced by both environmental properties (i.e. presence of additional cues) and individual differences (age-related differences) that make it harder to understand the spatial perspective shift and the precise position of the objects in the environment. Importantly, our findings highlight that experimental paradigms employing static stimuli across different perspectives can be greatly affected by systematic biases. This has significant implications for the interpretations that can be made from such studies. Thus, researchers should be mindful that camera movements may introduce unwanted systematic biases and given our results, we suggest using environments that contain enough spatial information to enable the formation of precise spatial representations and understanding of the perspective shifts.

4.6. Open practices statement

The data sets generated during and/or analyzed during the current study are available in the Open Science Framework repository (https://osf.io/7n5vd/). This experiment was not preregistered.

4.7. Acknowledgements

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Chapter 5: The role of memory and perspective shifts in systematic biases during object location estimation

The following chapter has been submitted for publication as Segen, V., Colombo, G., Avraamides, M. N., Slattery, T. J., & Wiener, J. M. The role of memory and perspective shifts in systematic biases during object location estimation. *Journal of Experimental Psychology: Human Perception and Performance*.

5.1 Introduction

Successful orientation and navigation critically depend on our ability to formulate precise spatial representations of landmarks or objects and their locations (Epstein, Harris, Stanley & Kanwisher, 1999; Postma, Kessels & van Asselen, 2004; Waller, 2006). In the lab, memory for object locations is typically assessed with tasks in which participants first encode an array of objects or environmental features from one perspective and are then asked to indicate whether the array has changed when presented from a different perspective (Diwadkar & McNamara, 1997; Schmidt et al., 2007; Hartley et al., 2007; Sulpizio, Committeri, Lambrey, Berthoz, & Galati, 2013; Montefinese, Sulpizio, Galati & Committeri, 2015; Muffato, Hilton, Meneghetti, De Beni & Wiener, 2019; Hilton et al., 2020; Segen, Avraamides, Slattery, Wiener, 2021a, 2021b). Most previous studies employing such paradigms focus on the ability to remember object locations rather than on assessing the precision of those representations. However, spatial representations can greatly vary in terms of the precision with which they are encoded (Evensmoen et al., 2013). For example, you can remember that the car is parked in a car park, or you can formulate a more precise representation in which you remember the row in which the car is parked and the relative position in this row (back, centre, front).

In our previous work (Segen et al., 2021c) we designed a novel task to investigate the precision of spatial representations. The task required participants to memorise the position of an object within a room. At test, the scene would be presented from a different perspective, the object would be displaced to either the left or the right, and participants needed to decide in which direction the object had moved. To evaluate the precision of the object location representations we adopted a psychophysics approach and systematically manipulated the object displacement distances with the aim of identifying the distance at which participants would be able to reliably detect the direction of movement. Unexpectedly, we found a systematic bias that was associated with the combination of the directions of the perspective shift and object movement, which we termed Reversed Congruency Effect. Specifically, when the direction of the perspective shift and the object movement were congruent (e.g. the object moves to the right and the perspective shift is to the right) participants consistently misjudged the direction of the object movement for small object displacement distances. The opposite pattern was found in trials where the direction of the perspective shift and the object movement were incongruent (i.e. the perspective shift was in the opposite direction to the object movement direction). In this case, participants correctly identified the displacement direction regardless of the distance by which the object was moved.

Our conjecture is that the Reversed Congruency Effect (Segen et al., 2021c) is driven by biases introduced during perspective taking, with participants “dragging” the object in the same direction as the perspective shift (Figure 5.1). Thus, when the object remains stationary, participants would “perceive '' that the object as having moved in the opposite direction of the perspective shift. Together with the actual object movement, this expectation that the object “moves” in the same direction as the perspective shift would yield the observed Reversed Congruency Effect. Specifically, if the object moved in the opposite direction to the perspective shift, participants would perceive the object movement to be larger due to the expectation that the object follows the perspective shift.   Whilst, in situations when the object moves in the same direction as the perspective shift, participants may incorrectly perceive the object movement direction, as the change in the object position may not be large enough to overcome their expectation regarding the new object position following a perspective shift. Yet, in trials when object movement was large enough, the effect of the perspective shift related expectation of object movement is overcome allowing participants to correctly detect the direction in which the object moved.

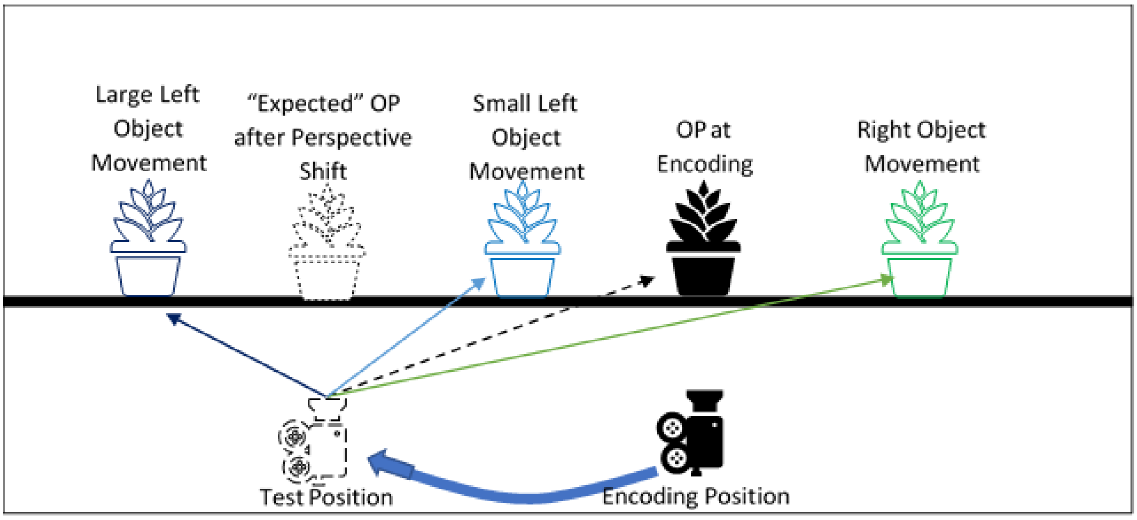

Figure 5.1 Schematic of the Reversed Congruency Effect: The black plant and camera represent the position of the object (OP) and camera at encoding. The dotted camera represents the position at test following a perspective shift to the left. The dotted plant represents the "expected" position of the object following a perspective shift if participants "drag" the object with them. Given the new position (dotted camera) it appears that even if the object was stationary (black plant) that the object has moved right i.e. perspective shift induced object motion. The green plant represents small movement to the right, which is perceived to be much larger due to the perspective shift induced object motion. Conversely, small left movements (light blue plant) are perceived as right movements due to being further to the right than the "expected" object position, conversely, and only when the movements to the left (congruent with the direction of the perspective shift) were large enough (i.e. dark blue plant) participants could correctly detect the movement direction.

Although this explanation is in line with our empirical data, our original study (Segen et al., 2021c) did not allow us to directly investigate if the Reversed Congruency Effect described above was primarily driven by the proposed perspective shift related bias in which participants drag the object in the same direction as the perspective shift. Alternatively, it is possible that the Reversed Congruency Effect relied on the presence of the object in both the encoding and test phase and that the comparison of the object locations across those stimuli gave rise to the observed bias.

Following up on our previous work, the first aim of the current study was to investigate whether perspective shifts lead to a systematic bias in the remembered object positions. This question is particularly important also because many studies investigating spatial memory and perspective taking ability present static images across different perspectives and could be subject to the same effect (Diwadkar & McNamara, 1997; Schmidt et al., 2007; Hartley et al., 2007; Sulpizio et al., 2013; Montefinese et al., 2015; Muffato et al., 2019; Hilton et al., 2020; Segen et al.,2021a,; Segen et al., 2021b). To address this question, we designed a task in which participants first encoded the position of an object. Then, they were presented with an image of the same scene but from a different perspective but without the object and had to indicate the position of the object. If, as argued above, the Reversed Congruency Effect was driven by a perspective shift related bias, we expect that participants will produce systematic errors in the same direction as the perspective shift. That is, if the perspective shift is to the left, participants would place the object further to the left of its actual position.

Our second aim was to investigate whether the potential perspective shift-related bias is related to memory processes. It is well known that spatial memory is prone to distortions. For example, when drawing sketch maps of environments from memory, participants often draw non-orthogonal junctions as 90° junctions and straighten the curved street segments

(Wang & Schwering, 2009). In addition, distance estimates are influenced by the presence of physical or geographical borders (Uttal, Friedman, Liu & Warren, 2010). Memories for object locations are also prone to systematic biases. That is, many studies have shown that object location estimates tend to “move” towards category prototypes (Huttenlocher, Newcombe, & Sandberg, 1994; Crawford & Duffy, 2010; Holden, Curby, Newcombe & Shipley, 2010; Huttenlocher, Hedges & Duncan, 1991). For example, when asked to memorise the location of a dot in a circle, participants divide the circle into quadrants and estimate the dot position closer to the centre of each quadrant (Huttenlocher et al., 1991).

Additionally, previous research suggests that spatial perspective taking is differently affected depending on whether the task needs to be solved by relying on spatial memory. Specifically, Hartley et al. (2007) showed that reliance on spatial memory leads to greater difficulties in spatial perspective taking. The authors suggested that this can be explained by the need to manipulate the whole scene to achieve perspective-taking if the representation is held in memory. In contrast, when participants can see the scenes from both perspectives simultaneously (perception condition) it is possible to use piecemeal rotation of each element in the scene to ensure that the positions between the two scenes match. Following this explanation, we would expect that the perspective-shift related bias would only be apparent in the memory condition, where perspective taking itself may be more complex.

We investigated whether memory contributes to the predicted perspective shift related bias in the object locations by creating two conditions: in the memory condition, participants first saw the image of a scene with the target object during encoding, and, following a short delay, the second image showing the same scene from a different perspective but without the object. Their task was to indicate, on the second image, the position of the object. In the perception condition, participants performed the same task but the two images were presented simultaneously on two adjoining computer screens. If memory contributes to the systematic bias introduced by the presence of a perspective shift, we expect a stronger bias in the memory condition than in the perception condition. However, if the effect is driven by the introduction of the perspective shift and is independent of memory, we expected similar biases in the two conditions.

5.2 Method

5.2.1. Participants

Seventy-seven participants took part in the experiment (Mean age=19.94 years, SD =2.35; age range = 18–32 years; 49 females and 28 males) with thirty-nine participants completing the Memory condition and thirty-eight the Perception condition. Participants were recruited through Bournemouth University's participant recruitment system and received course credit for their participation. All participants gave their written informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

5.2.2. Materials

5.2.2.1. Virtual environment

The virtual environment was designed with 3DS Max 2018 (Autodesk Inc) and consisted of a square room (9.8 m x 9.8 m) that contained famous and easily recognisable landmarks on its walls (Hamburger & Roser, 2014). A teal plank was placed diagonally in the middle of the room (14 m long). During encoding, an object was placed on that plank at one of 18 predefined positions that were 14, 28, 42, 84, 98, 112, 168, 182 and 192 cm to the left or to the right of the centre of the plank. The object was removed during testing and 37 markers appeared on the plank serving as possible response locations (Figure 5.2B).

To analyse participant responses, we created six groups containing the three object positions (Left, Mid-Left, Center-Left, Center-Right, Mid-Right, Right) that were close to each other, i.e. objects positions at 14, 28 and 42 cm to the left of the centre were grouped together (Figure 5.2A). From hereon we will refer to those object groups as Clusters.

A

B

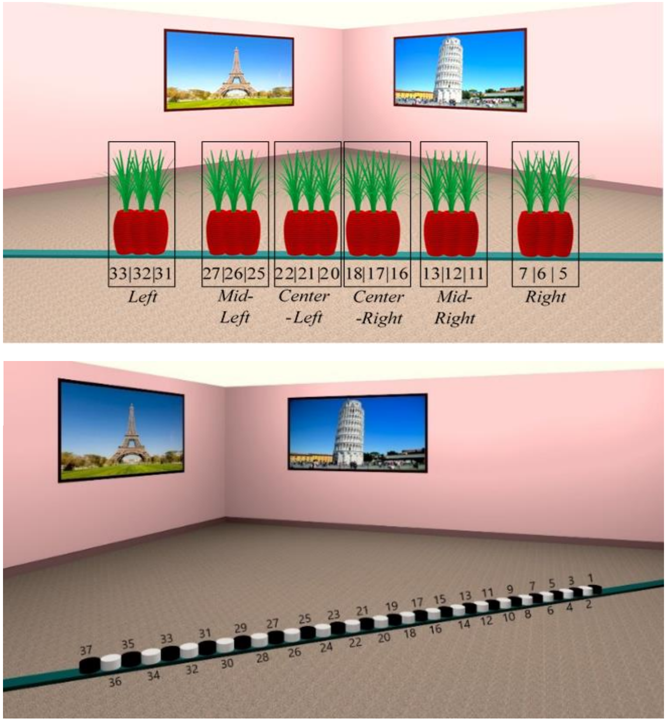

Figure 5.2 A: Example stimuli superimposing all of the possible object positions ranging between 5 to 33 (positional markers in Figure 5.2B) and the corresponding six Clusters (Left, Mid-Left, Center-Left,Center-Right, Mid-Right, Right); B: Example of Test stimuli containing the positional markers from 1 to 37 that participants needed to select to estimate object position

The visual stimuli were presented on a 40-inch screen at a resolution of 1920x1080px and subtended 47.7° x 28° at a viewing distance of 1 meter. The experimental stimuli were renderings of the environment with a 60° horizontal field of view (FOV), a custom asymmetric viewing frustum that resembles natural vision with a 15% shift in the vertical field of view was used (Franz, 2005; Figure 5.3).

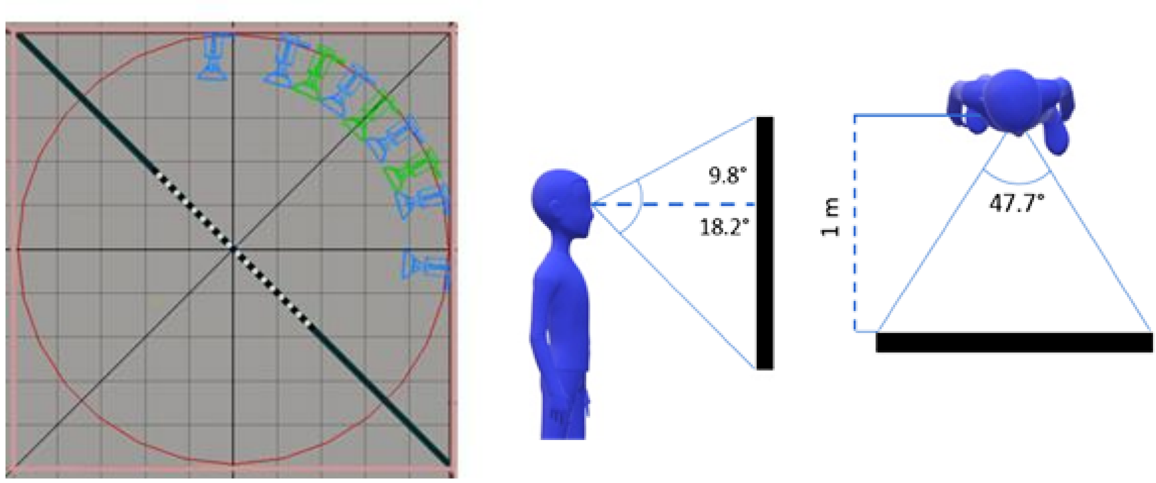

Figure 5.3 Left Schematic of encoding (green) and test (blue) camera positions arranged in an invisible circle in the environment; Right A representation of how participant position related to the stimulus display.

The cameras were arranged in an invisible circle around an invisible diagonal line that was perpendicular to the plank. The encoding stimuli were rendered from three possible camera positions (Figure 5.3). The test stimuli were rendered from a different viewpoint with a 30° perspective shift either to the left or to the right of the encoding viewpoint. In both encoding and test stimuli, the room corner and one poster at each side of the corner were visible.

Stimuli were presented with OpenSesame 3.1.7 (Mathôt, Schreij, & Theeuwes, 2012). In the Memory condition, the stimuli were presented on a single monitor and in the Perception condition stimuli were presented across two monitors. Responses were made with a standard keyboard that was labelled such that a different key corresponded to each of the 37 possible positional markers. Participants had to choose the marker that they thought corresponded to the position of the object during encoding, and to press the key that corresponded to that marker (Figure 5.2B).

5.2.3. Procedure

Each experimental trial started with the presentation of an instruction prompting participants to remember the location of the object (750 msec). This was followed by a display containing a fixation cross and a scrambled stimuli mask (500 msec). In the Memory condition, this was followed by the encoding phase, in which participants were presented for 5 seconds with an image of the scene that depicted the object in one of the 18 possible positions in the room, taken from one of three camera positions. After the encoding phase, participants were again presented with a fixation cross and a scrambled stimuli mask for 500 msec. In the test phase that followed, they were presented with another image that was taken after a 30° perspective shift. In this image, the object was removed, and 37 labelled markers appeared on the plank which participants used to indicate object locations (Figure 5.4A). In the perception condition, participants were presented with the encoding and test stimuli simultaneously across two screens (Figure 5.4B). In both conditions, participants were free to take as long as they needed to make a response.

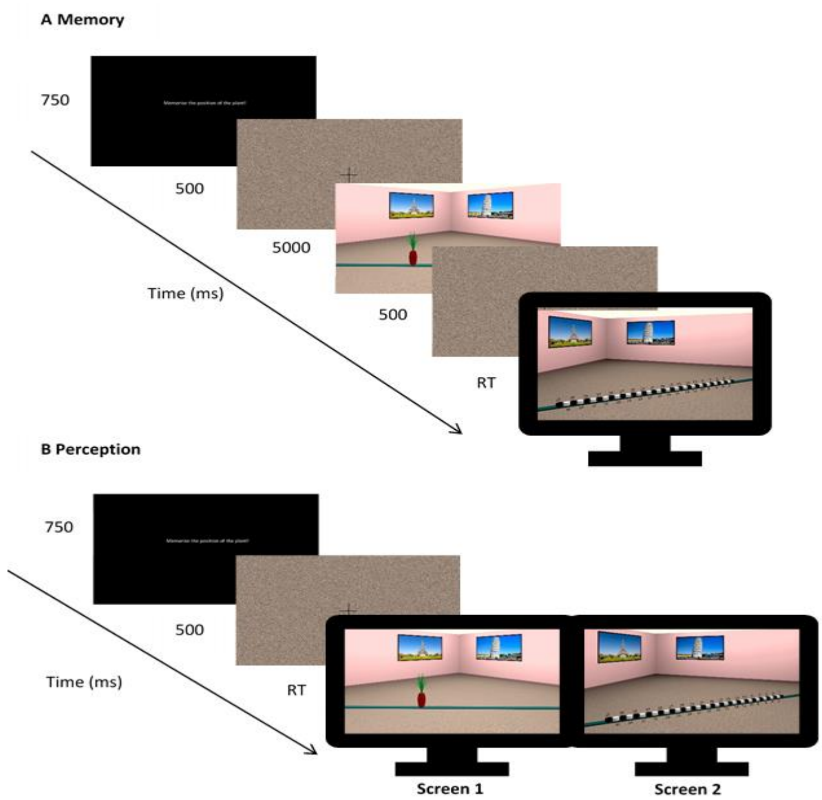

Figure 5.4 Trial structure in the Memory (A) and Perception (B) conditions

5.2.4. Design

A between-subject design was adopted, and block randomization was used to assign participants to the Memory or Perception condition. This ensured an approximately equal number of participants in each condition. Overall, the experiment included 108 experimental trials presented in randomised order with the experiment taking on average about 30 minutes.

5.2.5. Data Analysis

Statistical analyses were carried out using R (R Core Team, 2013). Data were analysed with linear mixed-effects models (LME) using LME4 (Bates et al. 2015) in R (R Core Team, 2013). Effect coding was used as contrasts for fixed factors, which were all categorical variables. The absolute error model included the by-item intercepts as well as a by-subject intercept and slope for Perspective Shift Direction (PSD). Prior to analysis, outlier responses were removed using the interquartile range method on individual absolute error (cm) distributions, which led to a total 3.3% data loss.

5.3. Results

5.3.1. Absolute error

We first examined the effect of Condition (Memory vs Perception), Cluster (Left, Mid-left, Centre-left, Center-right, Mid-right and Right) as well as the Perspective Shift Direction (PSD; Right vs Left) on absolute error (cm) (full results reported in supplementary materials). Interestingly, the results show that the absolute error was higher in the Perception compared to the Memory condition ($\beta=3.002$, $SE=1.052$, $t=2.854$) and there were no main effects of Cluster or Perspective Shift Direction. An interaction was found between Condition and Cluster, such that in the Memory condition errors in the Left cluster were lower than in the Perception condition ($\beta=1.862$, $SE=0.393$, $t=4.736$), no reliable differences between conditions was found for any of the other clusters. In addition, we found an interaction between Cluster and PSD, with higher errors in the Right cluster (β=3.271, SE=0.894, t=3.658) and lower errors in the Left cluster (β=-2.459, SE=0.895, t=-2.747) when the PSD was to the Left. This suggests that errors increased when perspective shifts resulted in movements away from the object cluster. This effect was amplified in the Perception compared to the Memory condition, with an even greater increase in errors in the Right (β=0.813, SE=0.393, t=2.068) and Mid-right (β=1.529, SE=0.395, t=3.870) cluster when the perspective shifted to the Left in the Perception condition and a greater decrease in errors in the Center-Left (β=-0.969, SE=0.393, t=-2.463) and Mid-Left (β=-1.936, SE=0.394, t=-4.918) clusters.

5.3.2. Signed Errors

We did not find differences in absolute errors as a function of PSD (Left and Right) and we have no reason to assume that perspective shifts to the left or the right would be qualitatively different. Errors to the left had a negative sign (i.e. -30 cm) and errors to the right had a positive sign (i.e. 30cm). However, since we are primarily interested in the direction of the errors as a function of the direction of the perspective shift, we multiplied (folded) all of the errors where the perspective shifted to the left by -1. As a result of this folding procedure, positive errors indicated errors in the direction of the perspective shift (i.e. perspective shift is to the left and the errors are to the left), conversely, negative errors indicate errors in the opposite direction (i.e. perspective shift is to the left and the errors are to the right). An LMM with Condition as a fixed effect revealed that overall, errors were positive (Intercept: β=10.927, SE=2.013, t=5.429). In other words, participant responses were biased towards the direction of the perspective shift (Figure 5.5). Signed errors did not differ between the Memory and the Perception conditions (β=-0.672, SE=1.551, t=-0.433).

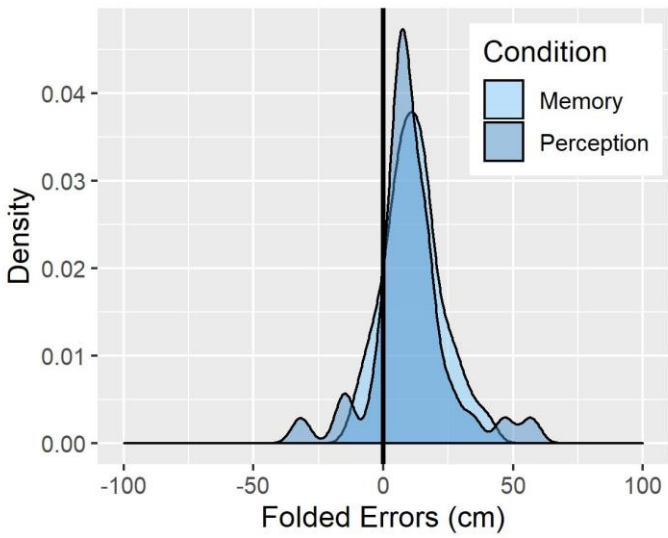

Figure 5.5 Density plot of Signed Errors (cm) across the Memory and Perception conditions

5.3.3. Role of Object position

Given previous reports of systematic biases in object location memory (Huttenlocher et al., 1991) towards a "category" prototype, we examined if object positions had an impact on participants' errors. To do so we calculated, using the response markers, the range of responses for each of the 18 object positions, such that the value of 0 corresponds to responses in which the participants placed the object in the correct position, negative values represent errors made to the left, and positive values indicate errors to the right. Figure 5.7 displays histograms of responses for each object position. To investigate if participants' responses for each object position were significantly different from zero, thus indicating a systematic bias, we ran one-sample t-tests for each object position separately for the Memory and Perception conditions.

As it is not clear what prototypes participants might have used in the current task, we evaluated different alternatives suggested by the previous literature. For example, one possibility is that participants remembered objects to be closer to the centre of the screen (conceptually similar to central tendency bias [Allred, Crawford, Duffy & Smith, 2015], Figure

5.6A). If participants indeed used the centre of the screen as the prototypical object position, we would expect them to make errors to the left for object positions 5 to 18, and to the right for object positions 20 to 33 (Figure 5.6A). Another possibility is that participants divided stimuli into the left and right half and used the centre of each half as prototypical locations (Huttenlocher, et al., 1994; Crawford & Duffy, 2010). If participants used the centre of those halves as prototypes we would expect a leftward bias in object positions 5-7 and a rightward bias for object positions 11 to 18 as this would bring objects positioned on the right closer to the centre of the right half of the plank. For the left half of the stimuli we would expect a leftward bias for object positions 20 to 27 and a rightward bias for object positions 31 to 33 (Figure 5.6B). Another possibility is that participants used more fine-grained categories in which the object in the centre of each of the six object clusters functioned as a category prototype (Figure 5.5C; Holden et al., 2010). This way, in the cluster consisting of object positions 31,32, and 33, participants would estimate the object positions to be closer to object position 32.

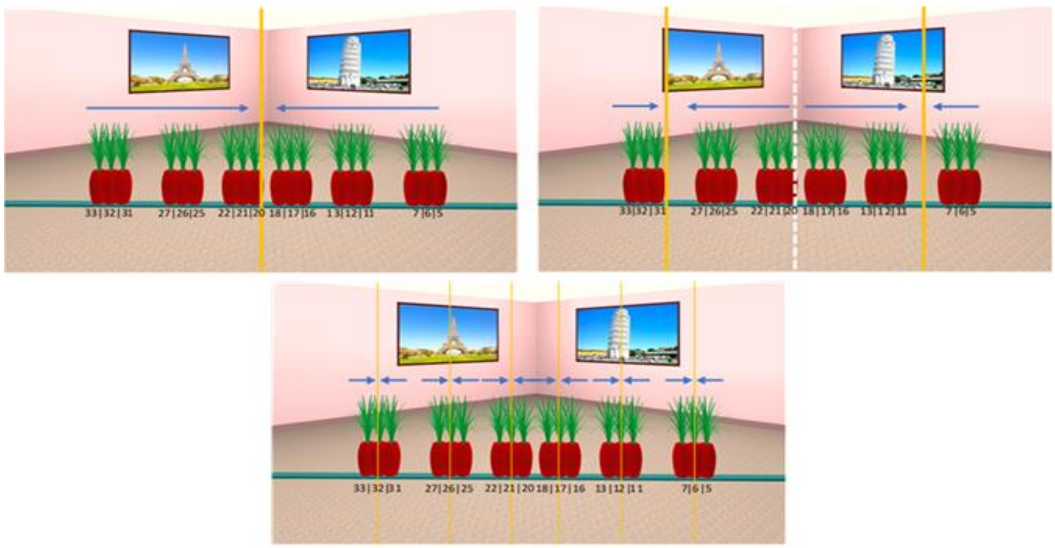

Figure 5.6 Examples of possible object location prototypes that participants may use with the blue arrows indicating the expected bias direction. Orange lines indicate prototype locations.

(A) Center of the screen, (B) center of the left and right side of the screen or (C) center of the cluster used as a category prototype.

Our results showed that for objects positioned at the extremes of the possible object positions (most leftward [i.e. 33,32,31] and most rightward [5, 6, 7] positions), participants made errors away from the extreme values (the positional markers on both ends) (Figure 5.7). For example, for object positions 33 and 32 which are on the left side of the plank, participants made more errors to the right, whilst for objects positions 5, 6 and 7 that are on the right, participants made more errors to the left. This result is partly in line with the category prototypes depicted in Figure 5.6A and B. However, for the more central object positions, we found a slight bias to the right that is not consistent with any of the possibilities we described (Figure 5.6).

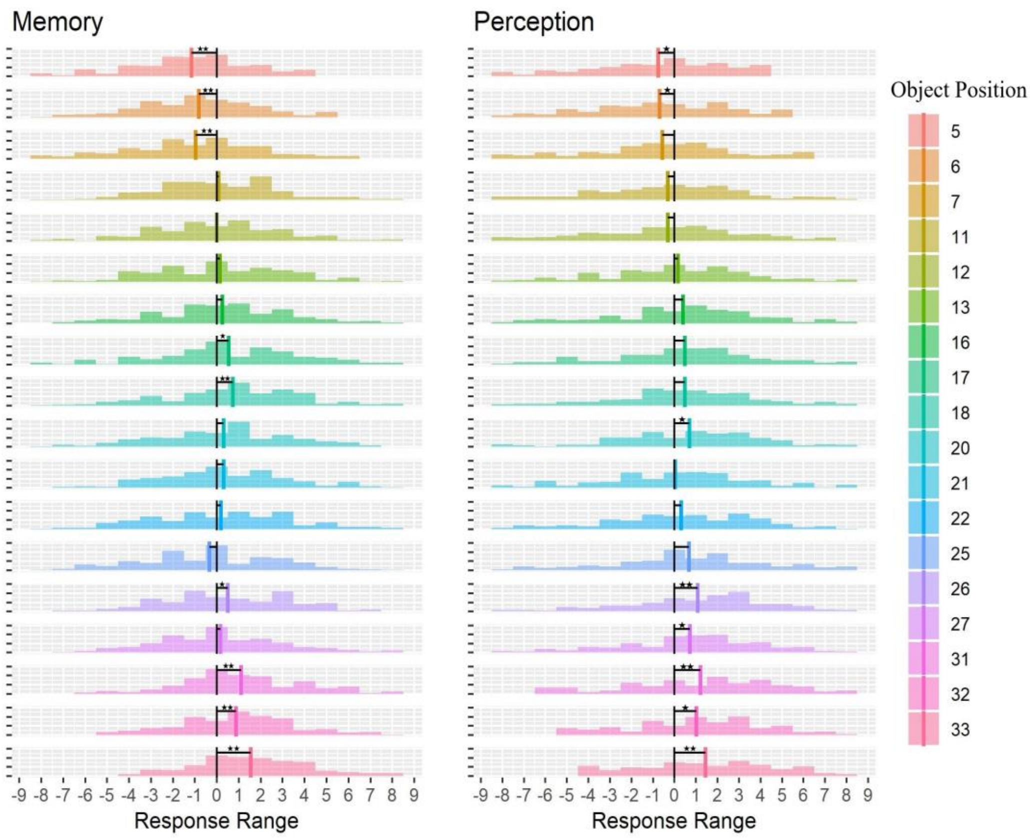

Figure 5.7 Distribution of the response range for each object position as a function of Condition (Memory and Perception)

We have also looked at directional errors with the complete model reported in the supplementary materials. As reported above, the direction of the perspective shift determined the direction of the errors. That is, if the perspective shift was to the right then the errors were to the right as well (positive errors). This was the case across all but the most leftward and rightward clusters, for which we found that participants made errors away from the extremes such that the direction of the perspective shift no longer determined the direction of the errors. Instead, participants made more errors to the right in the left cluster, with the opposite pattern of errors found for the most rightward cluster (Figure 5.8).

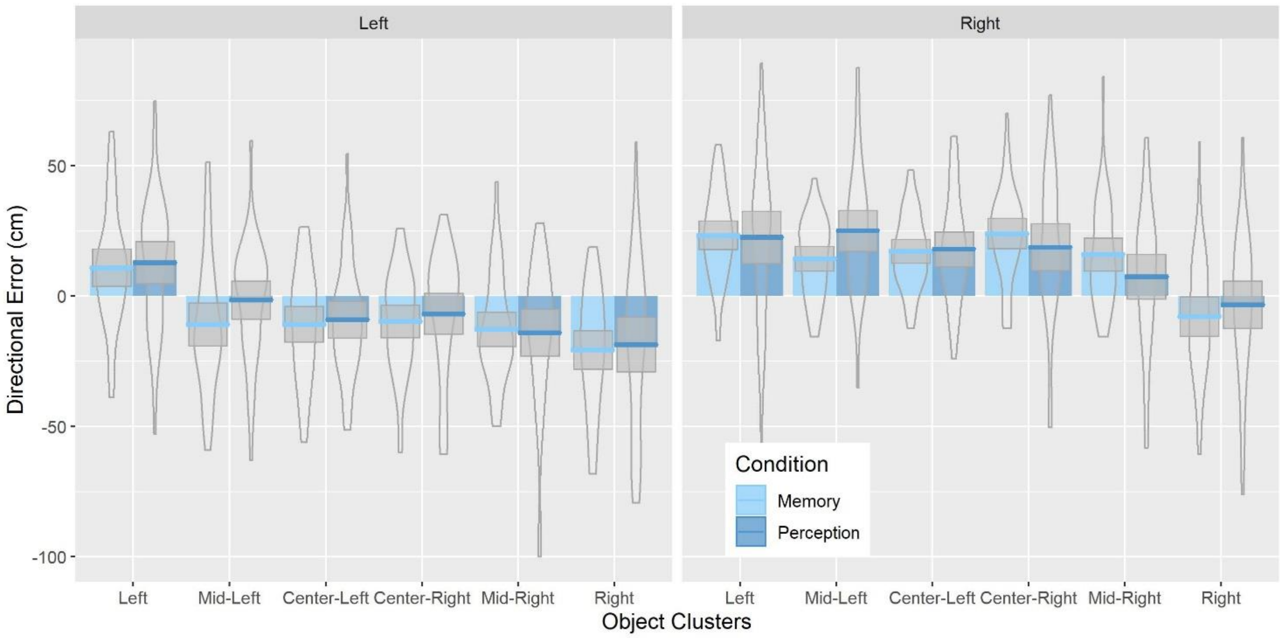

Figure 5.8 Bar plots for directional errors as a function of Perspective Shift Direction, Condition and Object Clusters with mean (solid line) and 95% CIs (grey shaded area) with violin plots behind

5.4. Discussion

The aims of the current study were twofold: the first aim was to investigate if perspective shifts systematically bias estimates for object positions. The second aim was to investigate if the proposed bias in object position estimates arises from distortions in spatial memory. To do so, we explored error patterns in a task in which participants estimated the position of an object following a perspective shift either with or without a memory delay. Consistent with our expectations, we found that participants' errors were systematically biased in the direction of the perspective shift, we termed this as the perspective shift related bias. Importantly, this perspective shift related bias was observed in both the Memory and Perception conditions, suggesting that it is not related to systematic distortions in memory.

But how can this systematic perspective shift related bias in object location estimation be explained? Spatial perspective taking can be achieved either by relying on an allocentric representation or by mentally transforming an egocentric representation (King et al, 2002; Hegarty & Waller, 2004). Yet, if participants relied solely on an allocentric representation in which the position of the object was encoded relative to other features in the environment, their own position and movement in the environment should not influence their responses and perspective shifts should not result in systematic biases (Ekstrom, Arnold & Iaria, 2014). Thus, the presence of the perspective shift related bias in the estimations of object locations in the direction of the perspective shift, suggests an egocentric influence on the estimates.

Specifically, we believe that uncertainty about the exact nature of the perspective shift leads to uncertainty about the exact object location, which in turn results in participants biasing their estimates towards the encoded egocentric location of the object. This idea is conceptually similar to the anchoring and adjustment heuristic proposed by Tversky and Kahneman, (1974), which posits that, when uncertain, people make decisions/responses using an initial estimation, an anchor that they then adjust to correct for errors. Interestingly, these anchors are often based on egocentric representations (Epley, Keysar, Van Boven, Gilovich, 2004; Gilovich, Medvec, & Savitsky, 2000; Keysar, Barr, Balin, & Brauner, 2000). For example, people often use their own experience as an anchor when estimating how their actions affect others (Gilovich et al., 2000) and when making judgements about how others perceive ambiguous stimuli (Epley et al., 2004). In the current task, participants may have used the original egocentric relation of self to object as an anchor, which would result in participants dragging the object with them following a perspective shift. Adjustments are then made, taking into account the available information about the perspective shift, i.e. changes in the position of other features in the environment. However, if participants are uncertain about the exact nature of the perspective shifts, these adjustments are not sufficient, resulting in estimates that are biased towards the anchor (Tversky & Kahneman, 1974; Quattrone, 1982). This leads to a systematic shift in object position estimates in the direction of the perspective shift giving rise to the perspective shift related bias.

We also found that when the perspective shift increased the distance to the object, participants were less accurate in estimating its position and displayed a larger perspective shift related bias. This pattern flipped in situations when the distance to objects decreased following a perspective shift, showing that participants were more accurate and less biased in estimating object positions when they were closer to them. One potential explanation for this is that there is greater compression of space for locations that are further away. Therefore, the difference between neighbouring object positions may become less pronounced the further away they are, making it harder to choose the appropriate position as the position markers are smaller and closer together. Given that the markers “appear” closer together for further away locations, it is also possible that a larger number of positional markers are considered as plausible estimates (as they are all close together), leading participants to accept positions that are further away from the actual object position but are closer to the original egocentric vector that is used as an anchor. This is in line with the idea that adjustments of the initial anchor are made until a plausible estimate is reached (Epley et al., 2004).

An alternative explanation for the *perspective shift related bias* relates to the specifics of the camera movement during the perspective shift. In our study, the camera moved on a circle such that a perspective shift to the left was realised by a camera translation to the left and a camera rotation to the right in order for the camera to remain directed towards the same point in the room. Such camera movements are typically used in spatial perspective taking tasks (Montefinese et al., 2015; Muffato et al., 2019; Hilton et al. 2020; Segen et al., 2021a; Segen et al., 2021b; Sulpizio et al., 2013). This combination of camera translation and rotation is chosen to ensure that the same part of the scene is visible in the images before and after the perspective shift. However, it produces images that can look surprisingly similar, and, as a result, may cause participants to underestimate the size of the perspective shift. Underestimation of the perspective shift may lead participants to think that the camera movement was smaller than it was, yielding a bias in responses to the direction of the perspective shift. While we cannot distinguish between this explanation and the anchoring heuristic in the current study, we recently ran a follow up experiment in which we systematically manipulated the way the camera moved during a perspective shift. Results from this follow-up experiment provides support for the anchoring hypothesis and suggests that the influence of camera rotations is marginal.

The second aim of this study was to investigate if the bias in object position estimates result from systematic distortions in spatial memory. Importantly, we did not find a difference in the perspective shift related bias between the memory condition and perception condition showing that the systematic bias in errors in the direction of the perspective shift is not introduced by memory. Additionally, we also found a small difference in absolute errors, with participants performing better in the memory than in the perception condition, thus further highlighting that the observed defects are unlikely to be driven by memory processes. Such findings contrast with previous research showing that biases in object location estimations are typically introduced by post-encoding processes (Crawford, Landy, & Salthouse, 2016). For example, when participants estimate city locations from memory they incorrectly place Montreal farther north than Seattle, influenced by their prior knowledge of Canada being to the north of the U.S (Friedman, Kerkman, Brown, Stea, & Cappello, 2005). In general, biases in object-location memory are typically explained by a post-encoding Bayesian combination of more uncertain fine-grained information with the more certain category knowledge (Huttenlocher et al., 1991).

Yet, given our interpretation that the systematic bias is driven by processes underlying the perception/understanding of the perspective shift, it is not entirely surprising that we do not find differences between the memory and perception conditions. It should be noted that participants need to engage in spatial perspective taking in both situations, with the only difference being that in the memory condition they need to rely on a stored representation which they should either manipulate to match the test viewpoint or use as a reference to which the test stimuli viewpoint is matched.

To further investigate the role of memory in object location estimation we focused on the positions of the objects in the environment, as object location memory has been shown to be biased towards category prototypes (i.e. centre of the screen, centre of the quadrant) (Huttenlocher et al., 1991; Crawford, Landy, & Salthouse, 2016). Consistent with the prominent models of object location memory i.e. the category adjustment model (Huttenlocher et al., 1991)/Dynamic Field Theory (Simmering, Spencer & Schöner, 2006; Spencer & Hund, 2002), we found that for the most leftward and rightward object positions, errors shifted away from the extremes towards the centre. However, we did not find a systematic shift away from the central positions towards category prototypes that would be expected based on these models. This is consistent with our findings that the systematic bias is not introduced by memory, as the bias towards a prototype is a phenomenon that relates specifically to object-location memory and increases with memory delay.

Notably, we did find a slight shift in errors to the right for the more central positions. A possible explanation for this bias is that the cameras were always directed towards the same spot in the environment that was slightly to the left of the center. If participants did not perceive this slight rotation and assumed that the camera faced the centre of the room, they may have remembered the object to be slightly to the right. However, even if this was the case, the effect is very minor and overall our results point to a systematic bias away from the extremes rather than towards a specific prototype and performance is mainly influenced by the perception/understanding of the perspective shift rather than distortions introduced in memory.

We also found that the absolute errors were lower in the memory condition than the perception condition. This was surprising as the requirement to memorise the encoding stimulus should have increased the cognitive demand which should have led to reductions in performance. However, the differences between the perception and memory condition were small and resulted from longer tails in the perception condition. We therefore believe that it is unlikely that there are fundamental differences between the memory and perception conditions.

Lastly, we turn our discussion to the relationship between the current findings of the perspective shift related bias and the Reversed Congruency Effect, which manifested itself in better performance in estimating object movements that are in the opposite direction to the perspective shift and misjudgement of smaller movements in the same direction as the perspective, that we found in our previous study (Segen et al., 2021c). The unexpected finding of the Reversed Congruency Effect was an important motivator for the current study as it was the first report of a systematic bias related to the direction of the perspective shift. We proposed that the Reversed Congruency Effect was driven by the perspective shift related bias. Specifically, if participants estimated the original object position to be shifted in the same direction as the perspective shift, as results from this study show, movement of an object in the opposite direction to the perspective shift would be perceived as larger and thus detected more easily. However, when the object moves in the direction of the perspective shift, the actual movement is attenuated by the expectation that the initial object position is "shifted" in the same direction. In such situations, smaller object movements may give rise to the impression of the object having moved in the opposite direction, as the expectation of original object position following a perspective shift may be shifted more in the direction of the perspective shift than the actual object movement.

Our findings of a reduced Reversed Congruency Effect with the use of additional information in the environment (i.e. columns that acted as environmental cues; Segen et al., 2021c) align with the anchor and adjustment explanation for the perspective shift related bias that we observe in the current study. Specifically, since adjustments are made on the basis of the information available (Northcraft & Neale, 1987; Tversky & Kahneman, 1974), and in our case this information is about the perspective shift, increasing the reliability of this information should reduce the biases introduced by the anchoring and adjustment heuristic. We contend that these additional cues result in a more precise understanding of the position of the object in space and a better understanding of the perspective shift. This reduces the uncertainty about the object position after the perspective shift and thus the weight given to the egocentric anchor while improving the adjustment process.

To conclude, the current study shows that participants make systematic errors in the same direction as the perspective shift when estimating object locations across different perspectives. This perspective shift related bias is present even in a perceptual version of the task and is likely driven by difficulties in understanding/perceiving the perspective shifts. We believe that the egocentric spatial relations between observer and target object acts as an anchor that participants fail to adequately adjust after the perspective shift. As a result, they make responses that are biased in the direction of the perspective shift. However, more research is needed to fully understand the mechanisms that give rise to the perspective shift driven bias in object location estimation. Importantly, the current findings are a conceptual replication of the *Reversed Congruency Effect* we reported in our previous study (Segen et al., 2021c). The presence of the perspective *shift related bias* across two different experimental paradigms (different sizes of perspective shifts, different tasks [determine direction of object movement vs estimate object positions]) suggests that this is a robust effect that may translate to other studies that rely on static stimuli and perspective shifts. Thus, it is paramount for researchers who use similar paradigms to be mindful of this bias as it can greatly influence the interpretation of their results.

5.5. Open practices statement

The data sets generated during and/or analyzed during the current study are available on figshare (https://doi.org/10.6084/m9.figshare.14701467.v1). This experiment was not preregistered.

5.6. References

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Chapter 6: Comparable performance on a spatial memory task in data collected in the lab and online

Introduction

In recent years, personal computers and the internet have become widely accessible to most people, from a wide range of socio-economic backgrounds. This, together with the development of user-friendly experimental presentation platforms, such as Gorilla (Anwyl-Irvine, Massonnié, Flitton, Kirkham & Evershed, 2018), Testable (testable.org) and), Pavlovia (pavlovia.org), JATOS (jatos.org) , and MindProbe (mindprobe.eu), that support data collection from a wide range of devices (i.e. phones, tablets and computers), has led to increased popularity of online behaviour data collection. In addition, recent widespread restrictions on in-person data collection because of the Covid-19 pandemic have encouraged many labs to consider switching to online research. The question we ask here is whether the data collected from online experiments are comparable to those obtained in the lab, at least in the context of spatial memory.

Running behavioural experiments online can offer many benefits including increased speed and reduced cost of collecting data (Nosek, Banaji, & Greenwald, 2002). This greatly reduces the time it takes from the initial theoretical conception of the experiment to obtaining the results. In addition, it frees up time that would have otherwise been spent on participant recruitment and testing and allows researchers to focus on other tasks including data analysis, writing and experimental design. Furthermore, recruitment platforms such as Prolific and Amazon Turk enable access to very large samples of participants with diverse backgrounds (socio-economic status, age, ethnicity and education levels amongst many others) (Komarov, Reinecke & Gajos, 2013; Huber & Gajos, 2020). Access to such diverse populations can greatly improve the generalizability of results, compared to typical psychological experiments that often rely on testing the WEIRD populations (Henrich et al., 2010).

Despite the advantages that online data collection offers, researchers may be reluctant to move their research online due to the limited control that online experimentation offers, especially about the context in which the experiment is conducted. This may impact the quality of the data as participants as both external and internal factors (e.g., noise, increased distraction, lower motivation etc) may influence performance on the task. In addition, ensuring informed consent, explaining the task, and conducting effective debriefings online can be more difficult than in traditional laboratory settings. Thus, online experiments might require more thorough piloting of instructions, manipulations, and data-collection instruments (Kraut, 2004; Sauter, Draschkow & Mack, 2020). Nevertheless, several studies have shown that online data collection does not compromise data quality (Dandurand, Shultz, Onishi, 2008; Gould, Cox, Brumby, & Wiseman, 2015; Leeuw & Motz, 2015; Armitage & Eerola, 2020; Bartneck, Duenser, Moltchanova, & Zawieska, 2015; Hilbig, 2015; Saunders, Bex, & Woods, 2013). Additionally, there are several steps that researchers can take to improve data quality (for a more comprehensive discussion see Sauter et al., 2020). For example, asking participants how they solved the task and if they had cheated, has been shown to capture a wide range of noise (Reinecke & Gajos, 2015). Using a progress bar and clear instructions also helps to increase motivation and engagement (Yentes et al., 2012)

Research in spatial cognition has widely adopted virtual reality as it allows the possibility of presenting realistic yet highly controlled environments (Hardiess, Mallot & Meilinger, 2015; Diersch & Wolbers, 2019). The ability to use highly controlled experiments lead to greater understanding of spatial cognition in humans. Despite technological advances, there are still barriers in running complex virtual reality experiments online as they often have specific software and hardware requirements. However, less technologically demanding spatial cognition experiments such as those used in spatial memory and perspective taking paradigms may be suited for online testing (Diwadkar & McNamara, 1997; Schmidt et al., 2007; Hartley et al., 2007; Sulpizio, Committeri, Lambrey, Berthoz, & Galati, 2013; Montefinese, Sulpizio, Galati

& Committeri, 2015; Muffato, Hilton, Meneghetti, De Beni & Wiener, 2019; Hilton, Muffato, Slattery Miellet & Wiener, 2020; Segen, Avraamides, Slattery & Wiener, 2021a; Segen, Avraamides, Slattery & Wiener, 2021b). Typically, such tasks consist of presentation of an encoding stimuli (on the computer or on paper) portraying a place or an array of objects that participants learn. This is followed by a presentation of a second image from a different perspective and participants judge whether both images display the same place or whether the objects in the array are in the same positions. Such studies do not require specialised software and have minimal hardware requirements as they often use renderings of virtual environments or short videos and rely on forced alternative responses (i.e. same/different) and thus can be implemented online with relative ease.

In this study, we assessed whether data collected online from a spatial memory task, in which participants viewed images of a virtual environment and memorised the position of the object, yielded comparable results to data collected in person in a lab. This was done by directly comparing the results from a controlled lab-based setting to data collected in an unsupervised online setting.

6.2. Method

6.2.1. Participants

The data from the lab-based version of the experiment were obtained from Segen et al., (2021c). It consists of 40 participants (Mean=19.9, SD=2.26, age-range=18-31, 27 females and 13 males). The online data were collected specifically for the investigation of differences between online and lab-based data collection. There were 40 participants who took part in the online variant of the experiment (Mean=23.02, SD=4.04, age-range=18-33, 27 females and 13 males). All participants for the lab-based version were recruited through Bournemouth University’s participant recruitment system and received course credits for their participation. Data for the online sample was obtained either through Bournemouth

University’s recruitment system, social media advertising and the online participant recruitment platform Prolific (https://www.prolific.co). All participants provided their informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

6.2.2. Materials:

The virtual environment was designed with 3DS Max 2018 (Autodesk) and consisted of a square room (9.8 m x 9.8 m). On the walls of the room there were posters depicting famous and easily recognisable landmarks. A teal plank was placed diagonally in the middle of the room (14 m long). In the encoding stimuli an object was placed on that plank along one of 18 predefined positions (14, 28, 42, 84, 98, 112, 168, 182 and 192 cm either to the left or to the right of the center of the plank). For analysis, we created six groups containing three object positions that were close to each other, i.e. objects positions at 14, 28 and 42 cm to the left of the center were grouped together (Figure 6.1). At test, we removed the object and instead placed 37 markers that marked the potential position of the object along the plank.

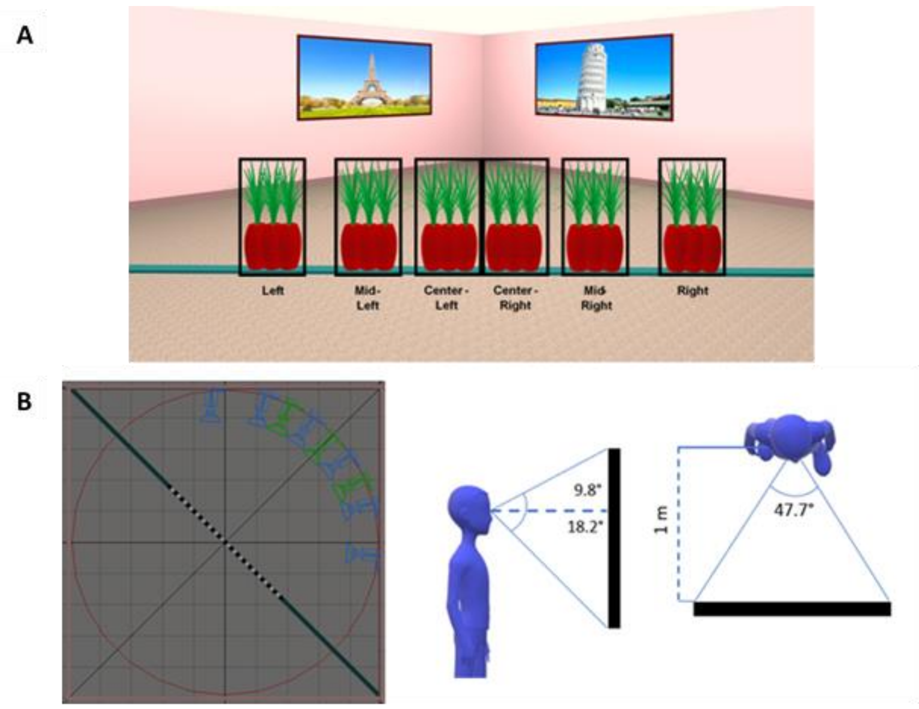

Figure 6.1 A Schematic of all possible Object Start Position groups; B Camera positions used to render encoding (green) and test (blue) stimuli

The experimental stimuli were renderings of the environment with a 60° horizontal field of view (FOV) and a 34° vertical FOV. A custom asymmetric viewing frustum that resembles natural vision with a 15% shift in the vertical field of view was used (Franz, 2005). The cameras were arranged in a circle with a radius around an invisible diagonal line that was perpendicular to the plank. The encoding stimuli were rendered from three possible camera positions (Figure 6.1B). The test stimuli were rendered from a different viewpoint with a 30° perspective shift that resulted in a ~2.5m camera displacement either to the left or to the right of the encoding viewpoint. In both encoding and test stimuli, the corner, and a poster on each side of the corner were visible.

In the lab-based version stimuli were presented with OpenSesame 3.1.7 (Mathôt, Schreij, & Theeuwes, 2012) on a monitor with 102cm diameter. Participants sat 1m away from the monitor(s) and gave their responses using a standard computer keyboard. The keyboard was labelled such that a separate key corresponded to a specific position marker.

In the online version, the task required a laptop or desktop computer. Testable (https://www.testable.org) was used to present the stimuli, and participants made responses by typing their responses into a text box. At the beginning of the experiment, participants were asked to adjust the screen zoom settings to ensure that the entire scene was visible during the experiment which was run in full-screen mode, however, screen parameters including monitor size and resolution were not controlled in the online version of the task.

6.2.3. Design

The experiment followed a mixed 6 (Object Position (OP): Left, Mid-Left, Center-Left, Center-Right, Mid-Right and Right) x 2 (Camera Direction: Left/Right) x 2 (Data Type: Lab-Based/Online) design. Data Type was a between subject factor and the rest were within-subject manipulations.

6.2.4. Procedure

Each experimental trial started with a brief presentation of a screen instructing participants to remember the location of the object (750 msec), this was followed by the presentation of a fixation cross and a scrambled stimuli mask (500 msec). In the learning phase, participants were presented with a rendering of the room containing a single object occupying one of the 18 object positions (Figure 6.1A) from one of three camera positions for five seconds (Figure 6.1B). After the encoding phase, participants were again presented with a fixation cross and a scrambled stimuli mask for 500 msec. In the test phase, participants were then presented with a rendering of the room following a 30° perspective shift with the plant removed and 37 markers placed on the plank which participants had to use to indicate the object position during learning.

Each version consisted of 108 experimental trials presented in randomised order with the experiment taking on average 30 minutes.

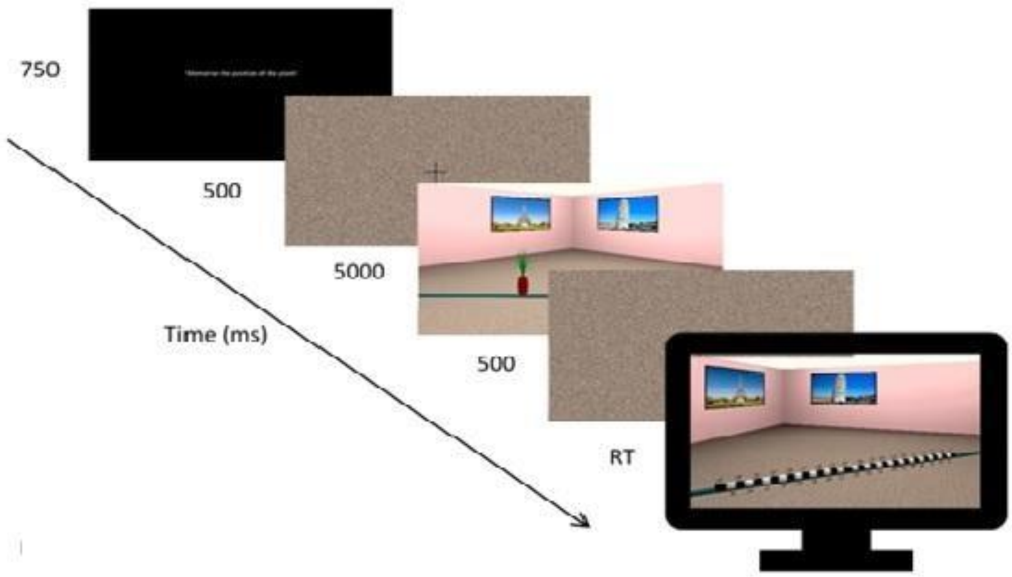

Figure 6.2 Experimental Trial Structure

6.3. Results

Prior to analysis outliers were removed from the individual absolute error distributions using the interquartile range method, for lab-based and online data separately. This resulted in 1.74% data loss for the lab-based data and 6.5% for the online data. Analysis was carried out using Linear Mixed Effects (LME) models utilizing the GLME4 package in R (R Studio) with by-subject and by-item intercept were included as random factors whilst fixed effects were effect coded.

6.3.1. Absolute Errors

Focusing on absolute (direction-free) errors, we ran an LME model with Data Type (Lab-Based/Online), Object Position (OP; Left, Mid-Left, Center-Left, Center-Right, Mid-Right and Right) and Camera Direction (Left/Right). Our results (Table 6.1 and Figure 6.3) show that absolute errors are larger in the Online data. We would like to note, that the difference in errors between the Online and Lab data is relatively small (β=2.796 cm) and constitutes less than 10% of the overall mean errors that participants made (intercept β=36.027 cm) during the performance of the task. We also found that OP influences absolute errors, specifically errors were smaller in the Left OP (and a trend for smaller errors in the Right OP). Whilst, OP closer to the center (Center-Left and Center-Right) yielded higher errors. The influence of OP was greater in the Online data as the decline in errors in the Left (and a trend in the Right OP) OP was larger in the Online vs Lab-Based data. There also was an interaction between OP and Camera Direction with greater errors in situations when the camera moved further away from the object (i.e. greater errors for the Right OP when the camera moves Left and smaller errors for the Left OP when the camera moves Left). Interestingly, the reverse pattern was found for Mid-Left OP as errors were larger for Left camera movements whilst smaller errors were found for Center-Right OP when the camera moved Left.

Table 6.1 Coefficients from Absolute Errors LME analysis

	Absolute Error (cm)		
Predictors	*Estimates*	*std. Error*	*t-value*
(Intercept)	36.027	1.037	**34.727**
Data Type (*Lab to Online*)	2.796	1.011	**2.766**
OP(*Right*)	-1.455	0.822	-1.769
OP(*Left*)	-3.574	0.822	**-4.346**
OP(*Mid-Left*)	0.805	0.820	0.982
OP(*Center-Left*)	1.932	0.823	**2.348**
OP(*Center-Right*)	2.044	0.824	**2.482**
Camera Direction (Right to *Left*)	0.323	0.368	0.880
Data Type (*Lab to Online*) * OP(*Right*)	-1.182	0.634	-1.863
Data Type (*Lab to Online*) * OP(*Left*)	-2.037	0.634	**-3.211**
Data Type (*Lab to Online*) * OP(*Mid-Left*)	0.763	0.631	1.209
Data Type (*Lab to Online*) * OP(*Center-Left*)	0.914	0.635	1.440
Data Type (*Lab to Online*) * OP(*Center-Right*)	0.816	0.636	1.282
Data Type (*Lab to Online*) * Camera Direction (*Right to Left*)	0.410	0.284	1.447
OP(*Right*) * Camera Direction (*Right to Left*)	2.633	0.822	**3.202**
OP(*Left*) * Camera Direction (*Right to Left*)	-2.646	0.822	**-3.218**
OP(*Mid-Left*) * Camera Direction (*Right to Left*)	2.300	0.820	**2.806**
OP(*Center-Left*) * Camera Direction (*Right-Left*)	1.314	0.823	1.598
OP(*Center-Right*) * Camera Direction (*Right to Left*)	-2.121	0.824	**-2.575**
Data Type (*Lab to Online*) * OP(*Right*) * Camera Direction (*Right to Left*)	-0.066	0.634	-0.104

Data Type (*Lab to Online*) * OP(Left) *Camera Direction (*Right to Left*)	-0.616	0.634	-0.971
Data Type (*Lab to Online*) * OP(*Mid-Left*) * Camera Direction (*Right to Left*)	0.853	0.631	1.352
Data Type (*Lab to Online*) * OP(*Centre-Left*) * Camera Direction (*Right to Left*)	0.619	0.635	0.975
Data Type (*Lab to Online*) * OP(*Centre-Right*) * Camera Direction (*Right to Left*)	0.874	0.636	1.374

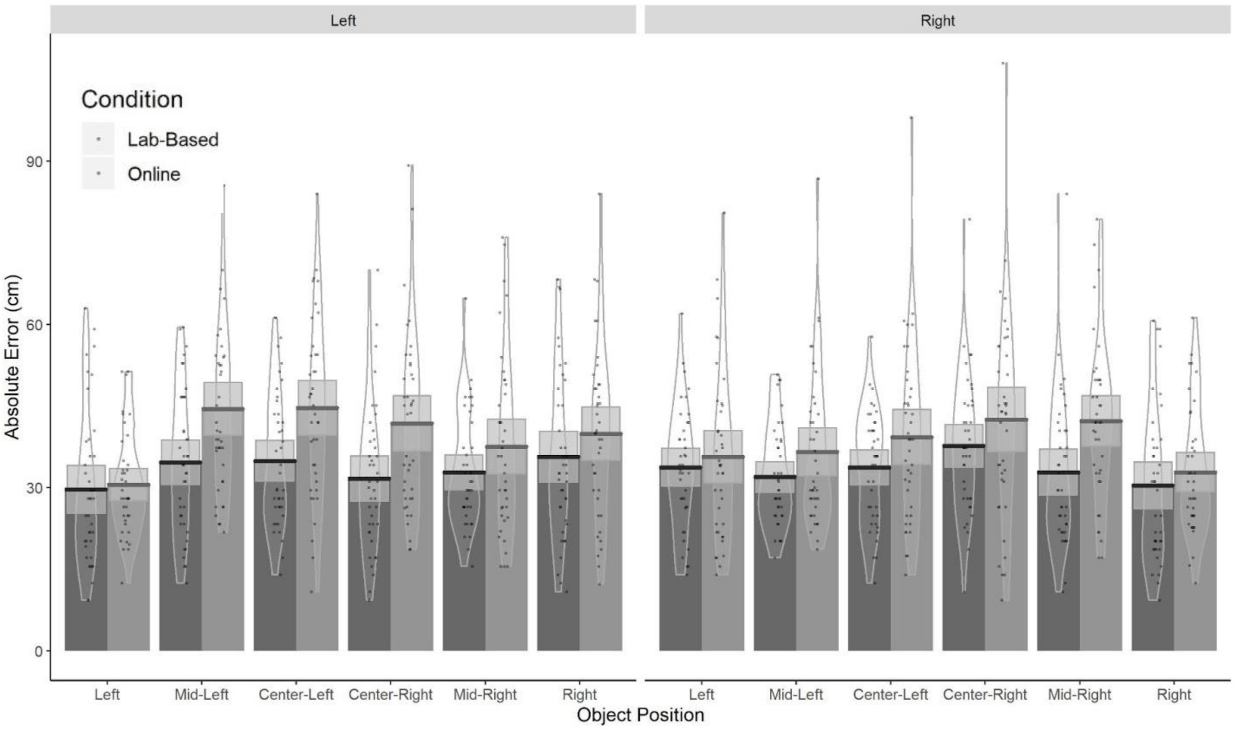

Figure 6.3 Absolute Errors as a function of Data Type, Object Position and Camera Direction

6.3.2. Signed Errors

Previous analysis of the lab-based data showed that participants' errors are systematically biased (Segen et al., 2021c). Specifically, we found that participants were more likely to make errors in the direction that is congruent with the camera movement direction at test i.e. if the camera moves left participants are more likely to make errors to the left. To investigate this bias, we multiplied (folded) all responses in trials where the camera moved to the left by -1. This folding procedure allowed us to collapse errors across left and right camera directions with positive errors denoting errors in the direction congruent with the perspective shift direction (i.e. camera moves Left, and participants make errors to the left) and negative errors indicating errors in the direction incongruent with the camera direction (i.e. camera moves left the errors are to the right). We ran an LME model with Data Type as a fixed factor. Overall, we found that participants' errors were positive (intercept; $\beta=14.13$, $SE=1.976$, $t=7.149$) highlighting that they were biased towards making errors congruent with the camera direction (Figure 6.4). Numerically, the magnitude of signed errors was larger in the Online compared to Lab-based data (Figure 6.4), however, this difference did not reach statistical significance ($\beta=2.426$, $SE=1.582$, $t=1.534$).

6.3.3. Variance

Given that online data is often associated with greater variance (Sauter, et al., 2020; Hubert & Gajos, 2020; Hilbig, 2016; Gould et al., 2015), we compared variance in absolute and signed errors in the Lab-based and Online data. To do so we sampled with replacement across 10000 samples the variance for each error type separately in the Lab-Based and Online datasets, then compared these variances with a t-test. Variance was significantly larger in the Online data for absolute errors (LabMean=678.17, OnlineMean=819.77, $p<.001$) as well as for signed errors (LabMean=1638.19, OnlineMean=2035.17, $p<.001$) (Figure 6.4).

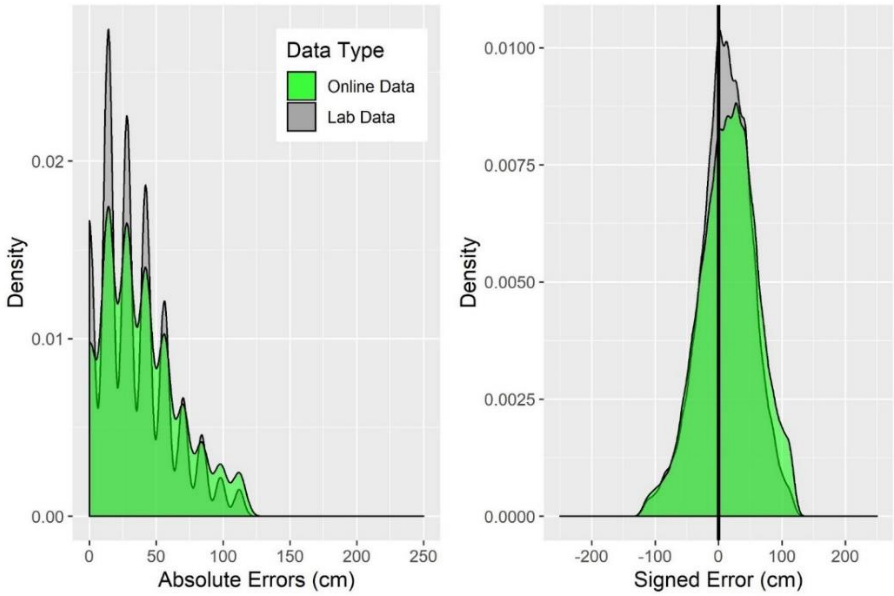

Figure 6.4 Distribution of Absolute (Left plot) and Signed Errors (Right plot) as a function of Data Type.

Lastly, we estimated the sample size that would be required in the online variant of the task in order to achieve the same standard errors (Table 6.2) as in the lab based setting for both the Absolute and Signed errors. Our results show that 48.33 and 49.69 participants would be needed to match the standard errors from the lab-based results for absolute and signed errors, respectively.

Table 6. 2 Mean, Standard Deviation and Standard Error of Absolute and Signed errors (cm)

	Absolute Errors (cm)			Signed Errors (cm)		
	Mean	SD	SE	Mean	SD	SE
Lab Data	33.08	26.05	4.12	11.58	40.48	6.40
Online Data	38.42	28.63	4.53	16.14	45.12	7.13

6.4. Discussion

The aim of this study was to compare performance in a spatial memory task between data collected in a lab-based setting and data collected online. Our results show that absolute errors are slightly larger (less than 10% of the overall mean error) in the online variant of the study. In a previous investigation of the lab-based data reported in the current study, we found that participants' errors were biased in the same direction as the perspective shift at test (Segen et al., 2021c). The comparison between lab-based and online data shows that this bias is present in both samples, and although the bias was numerically larger in the online group, the difference was not significant. We also found that for both the absolute and signed errors, the variance was greater in the online data compared to the data collected in the lab.

We propose that the bias in the direction of the perspective shift is driven by the uncertainty about the position of the object following the perspective shift due to difficulties in understanding/perceiving the perspective shifts as well as difficulties in precisely encoding the position of the object (Segen et al., 2021c; Segen et al. 2021d). The increased uncertainty about the position of the object following a perspective shift may lead participants to rely on an the egocentric self-to-object estimates derived during encoding (i.e. before the perspective shift) as an anchor that they then adjust to estimate the position of the object following a perspective shift (c.f. Anchor and Adjustment Heuristics, Tversky & Kahneman, 1974). Such adjustments are typically insufficient (Tversky & Kahneman, 1974; Quattrone, 1982) and in our case would result in the position estimates to be biased in the direction of the perspective shift (for a more detailed discussion see Segen et al., 2021c). The presence of this perspective shift related bias in both the online and lab based versions of the task suggest that participants are solving the task using the same strategy regardless of whether the experiment was conducted online or in the lab. Thus, highlighting that it is possible to study the same cognitive processes used during a spatial memory task in both a controlled lab setting and in data collected online.

Focusing on the more specific findings, the position of objects during encoding impacted errors. Errors were smaller for objects that were placed further away from the center of the room (left and right object positions), whilst greater errors were found for object positions that were closer to the center of the room. Interestingly, the decrease in errors for the left and right object positions was larger in the online data. Lastly, absolute errors were larger in situations where the camera moved further away from the objects. A reverse pattern was observed for objects that were placed closer to the center. These effects were similar for both online and lab-based data.

Consistent with previous research (Hubert & Gajos, 2020; Hilbig, 2016), we found greater variance in the online sample compared to lab data. This is not surprising, as the context in which participants complete the experiment is likely to vary between participants in the online setting. For example, there is a greater chance that there will be more background noise or other distractions. In addition, some variance may be introduced by differences in the monitor sizes that are used by participants who are completing the study online as well as the distance between participants and their monitor. In the lab-based version, we controlled for monitor size and viewing distance as stimuli were presented on the same large monitor and participants sat 1 m away from this screen. Those conditions resulted in a closer match between the virtual and participants field of view. In the online version, those things were not controlled as no constraints on monitor sizes were introduced and to ensure that the instructions are easy to follow, we also did not ask participants to adopt a particular viewing distance. In addition, more outliers were present in the online data set, which led to an exclusion of more data from the analysis (~6.5%) compared to the lab-based data (~1.7%). Given that online data is expected to be noisier (Sauter, et al., 2020) it is not surprising that more outliers were present in the online data set and our findings are consistent with previous studies suggesting that a larger proportion of data is excluded from online samples (Gould et al., 2015). However, given the relatively high number of excluded trials, it may be worthwhile to increase the number of trials that are used in online experiments, as this would ensure that enough data remains available for analysis following outlier removal.

Despite larger variance and larger number of outliers, we found comparable results in both online and lab-based data suggesting that the increased noise does not influence key effects, even in situations when a sample size common to offline studies is used (i.e. 40 participants were tested in each condition). However, previous research has shown that effect sizes decreased in an online variant of a virtual navigation task, due to increased noise associated with online data collection (Hubert & Gajos, 2020). As a result, and in line with previous research we suggest that larger sample sizes are used in online experiments. Specifically, based on our estimates, to achieve similar standard errors as those reported in the lab-based setting, the online sample size should be increased by 25% to 50 participants.

To conclude, we have shown that online data collection can be successfully used in the current task where we tested spatial memory across different perspectives using static image presentation as we were able to replicate the main findings from the lab experiment in an online version, albeit with greater variance. Our conjecture is that similar paradigms that investigate spatial memory using static images can be successfully run as online experiments. However, we recommend using a larger number of participants and trials to account for the increased variance that is found in data collected online.

6.5. Open practices statement

The data sets generated during and/or analyzed during the current study are available in the Open Science Framework repository (https://osf.io/y62sd/). This experiment was not preregistered.

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Chapter 7: Biases in object location estimation: the role of camera rotations and translation

7.1. General Introduction

Our ability to navigate and orient critically depends on our ability to recognize the place we are in. Place recognition requires memory for object locations as well as the ability to retrieve object locations from different perspectives (Epstein, Harris, Stanley & Kanwisher, 1999; Postma, Kessels & van Asselen, 2004). Typically, place recognition across different perspectives is studied using tasks in which participants are presented with static images depicting a scene, an array of objects or environmental features from one perspective and are then asked to indicate whether the array has changed when presented from a different perspective (Diwadkar & McNamara, 1997; Schmidt et al., 2007; Hartley et al., 2007; Sulpizio, Committeri, Lambrey, Berthoz, & Galati, 2013; Montefinese, Sulpizio, Galati & Committeri, 2015; Muffato, Hilton, Meneghetti, De Beni & Wiener, 2019; Hilton et al., 2020; Segen, Avraamides, Slattery, Wiener, 2021a, 2021b). Our recent research suggests that such paradigms may yield a systematic bias in reporting memorized locations (Segen, Colombo, Avraamides, Slattery, Wiener, 2021c, 2021d). Specifically, we found that when participants were asked to indicate where an object was positioned after a perspective shift (Segen et al., 2021d) or when asked to judge the direction in which an object has moved after a perspective shift (Segen et al., 2021c), they made systematic errors associated with the direction of the perspective shift. That is, participants appeared to "drag" the object with them during the perspective shift and as a result, shifted their responses further to the direction of the shift. Interestingly, this bias is not driven by distortions introduced in memory as participants also exhibited this bias in perception conditions that did not involve memory (Segen et al., 2021d).

It is not entirely clear what gives rise to this systematic bias. However, given that the direction of the bias is associated with the direction of the perspective shift, it is likely that the bias results from egocentric, rather than allocentric, influences on the estimates. Specifically, we believe that uncertainty about the exact nature of the perspective shift leads to uncertainty about the exact position of the object, which in turn results in participants biasing their estimates towards the egocentric self-to-object estimates derived during encoding (i.e. before the perspective shift). Henceforth, we will refer to this systematic shift in responses in the direction of the perspective shift as the *perspective shift related bias*. This idea aligns well with the anchoring and adjustment heuristic proposed by Tversky and Kahneman (1974). According to this heuristic, people base their responses on initial estimates (the anchor) that they adjust to correct for errors when they are uncertain. Often, these anchors are based on egocentric representations (Epley, Keysar, Van Boven, & Gilovich, 2004; Gilovich, Medvec, & Savitsky, 2000; Keysar, Barr, Balin, & Brauner, 2000). Epley et al. (2004), for example, found that participants used their previous experience (exposed either to positive or negative events) when making judgements about how others would perceive ambiguous stimuli (sarcastic or genuine).

In our task (Segen et al., 2021d), participants may use the egocentric vector between themselves and the object during encoding as an anchor for their response. Indeed, using the egocentric representation of the object location as an anchor would result in participants "dragging" the object with them following a perspective shift. In line with this possibility, previous research suggests that adjustments require time and cognitive effort (Epley et al., 2004) and are often insufficient and responses are therefore biased in the direction of the initial anchor, in part, because people stop adjusting once a plausible estimate is reached (Tversky & Kahneman, 1974; Quattrone, 1982). If participants in our previous experiments (Segen et al., 2021c, 2021d) also showed insufficient adjustments, this would explain why their estimates were systematically biased in the direction of the perspective shift.

Potential sources of uncertainty that may encourage the use of an anchor based on the egocentric self-to-object relations are: (1) uncertainty about the position of the object in the environment and (2) difficulties in understanding the exact nature of the perspective shift. The uncertainty about the object position could be reduced by enhancing the environment to include more spatial information i.e. by adding stable environmental cues that help to encode the position of the object more accurately (Cánovas, Leon, Serrano, Roldan & Cimadevilla, 2011; Chamizo, Artigas & Banterla, 2011; Kamil & Chen, 2001; Ekstrom & Yonelinas, 2020). In addition, stable environmental cues may also improve the understanding of the perspective shifts. For example, participants can use the change in the egocentric relations to those cues as well as the changes in the visual projection of those cues to understand how their position in space has changed following a perspective shift. Thus, we propose that enriching the environment with further spatial information will reduce the uncertainty about the object position after the perspective shift. If our conjecture about the role of uncertainty is correct, then reducing uncertainty by adding cues in the environment should reduce the perspective shift related bias by decreasing the weight given to the egocentric anchor as well as by improving the adjustment process.

It is possible that the uncertainty about the perspective shift may have also arisen from the way we introduced perspective shifts. For example, in our previous studies, the perspective shift consisted of both translation and rotation (Segen et al., 2021c, 2021d). Specifically, the camera moved on a circle such that it translated to one direction and at the same time rotated in the opposite direction. This combination of camera translation and rotation is typical for spatial perspective-taking tasks (Montefinese et al., 2015; Muffato et al., 2019; Hilton et al., 2020; Segen et al., 2021a, 2021b; Sulpizio et al., 2013; Schmidt et al., 2007) as it ensures that the same part of the environment is visible before and after the perspective shift. Given the small perspective shifts introduced in our studies (that involved small translations requiring only 20 to 30-degree rotations), the resulting images looked quite similar. This may have produced difficulties in understanding the perspective shifts, increasing participants' uncertainty regarding their movement within the environment. For example, if participants thought that the camera movement between encoding and test was smaller than it was, this could have caused a bias that is congruent with the direction of the perspective shift.

So far, the unique role of camera rotations and of translations during perspective taking has not been studied. Although our previous research suggests that the observed perspective shift related bias is linked to the introduction of camera movements during perspective shifts, it is not clear whether it is driven by camera translations or rotations separately or by the specific combination of the two. Therefore, the main aim of this study is to investigate the contribution of camera rotations and translations to the perspective shift related bias that we have observed in our previous studies (Segen et al., 2021c, 2021d).

Although no perspective-taking studies have investigated the role of translations and rotations separately, this has been done in tasks assessing spatial updating based on real or imagined body movements (Rieser, 1989, Wraga, 2003; Presson & Montello, 1994; Easton & Sholl, 1995). In such tasks, participants memorize an array of objects and are then either asked to move or to imagine moving to a different position in the array and point to one of the objects from that new position. Results show that, with physical movement, no differences in performance are present when the new position is reached by translation or rotation. However, when participants are asked to imagine moving to the new position, rotations lead to greater errors and longer response times than translations (Rieser, 1989; Presson & Montello, 1994; Sancaktar & Demirkan, 2008; Easton & Sholl, 1995). The difficulties in imagined rotations are also highlighted by difficulties in using maps that are misaligned with participants' orientation in space (Levine, Jankovic, & Palij, 1982; Presson & Hazelrigg, 1984; Roskos-Ewoldsen, McNamara, Shelton, & Carr, 1998). It is, however, not clear whether or how these results translate to spatial perspective taking tasks, as participants do not need to "imagine" rotations or translations, instead they need to use the available information to determine how they have moved in space. The current study aims to shed some light on this issue.

Another aim of the current study is to investigate potential ageing differences in object location memory. Previous research suggests that ageing is associated with difficulties in memorising and recognising object locations across different perspectives (Hartley et al., 2007; Montefinese, et al., 2015; Muffato, et al. 2019; Hilton et al., 2020; Segen et al., 2021a) with some studies reporting a specific deficit in spatial perspective taking abilities (e.g. Watanabe, 2011; Montefinese, et al., 2015; Segen et al., 2021a). Furthermore, there is evidence for age-related declines in the precision of encoding spatial locations. For example, in a number of studies, older adults were found to be less precise in estimating previous locations of objects presented on a computer screen compared to younger adults, despite positioning the objects in the correct region of the stimuli (Pertzov, Heider, Liang, & Husain, 2015; Nilakantan, Bridge, VanHaerents, & Voss, 2018). Additionally, a recent study reported age-related declines in precision of spatial memory in a virtual Morris water maze task (McAvan et al., 2021). In this study, participants physically navigated in a virtual environment presented via a head mounted display. Interestingly, older participants showed comparable performance for memory of object locations across different perspectives and displayed similar strategy use, yet their memory of object locations was less precise. These age-related declines in the precision of spatial representations may be caused by differential age-related changes in the anterior and posterior hippocampus. Indeed, a recent longitudinal study (Langnes et al., 2019) reported that the posterior hippocampus, typically associated with fine-grained spatial processing, was more affected by ageing than the anterior hippocampus, which is involved in the formation of coarser spatial representations (Røe Evensmoen et al., 2013; Nadel, Hoscheidt & Ryan, 2013).

7.1.1. Aims & Hypotheses

In the current study we present two experiments. The key aim of Experiment 1 is to provide a conceptual replication of Segen et al., (2021d) in which we found a perspective shift related bias during object position estimates. In the original task (Segen et al., 2021d), participants memorised the position of a target object that was always located on a plank in a virtual room. Then, following a short delay and a perspective shift, the target object disappeared, and participants were asked to indicate its position by selecting one of several predefined positions. In the current study, we introduced two key changes compared to the original task. First, we have removed the plank which may have acted as an influential cue that restricted the possible locations where the target object could be placed. Second, instead of presenting participants with predefined object positions that were overlaid on the plank during the test phase, participants' responses were unconstrained, and they could indicate the position of the target object anywhere in the environment. Removing the plank and the positional markers reduced the risk that participants relied on strategies we did not control for and which could be responsible for the perspective shift related bias.

The key aim of Experiment 2 was to investigate the contribution of camera rotations and translations to the perspective shift related bias. To do so, we manipulated camera rotation and the translations independently during the perspective shifts. We also investigated if enriching the environment by including additional objects that could be used as cues would improve participants' ability to remember the precise positions of the target object across different camera movements (rotations and translations). Furthermore, we examined the role ageing has on the precision with which participants estimate target object positions across different camera movements. Lastly, we investigated if older adults are differentially affected by camera rotations, translations, and the presence of additional cues in the environment compared to younger adults.

We postulate that the presence of the additional objects in the environment should improve the precision of participants' representations of the target object location (Cánovas et al, 2011; Chamizo et al., 2011; Kamil & Chen, 2001; Ekstrom & Yonelinas, 2020) as well as the understanding of the perspective shifts. Thus, we predicted smaller errors and a reduced perspective shift related bias when additional cues are present. Given the age-related declines in spatial memory (Hartley et al., 2007; Montefinese, et al., 2015; Muffato, et al. 2019; Hilton et al., 2020; Segen et al., 2021a, 2021b) and precision of spatial encoding across 2D stimuli (Pertzov et al. 2015; Nilakantan et al., 2018) together with possible perspective-taking deficits (Watanabe, 2011; Montefinese, et al., 2015; Segen et al., 2021b), we predicted that older adults would be less precise compared to younger adults and would display a larger bias related to camera movements in the environment. This prediction is based on our previous research that showed that older adults were more affected than younger adults by the direction of the perspective shift when estimating the direction in which the object has moved (Segen et al, 2021a). To our knowledge, this is the first study using spatial perspective-taking in which camera rotations and translations are decoupled. We therefore have no specific prediction on how the camera movements would contribute to performance and the perspective shift related bias. It is possible that participants will be more affected by camera rotations, as previous research on spatial updating shows that imagined rotations are harder than imagined translations (Rieser, 1989; Presson & Montello, 1994; Sancaktar & Demirkan, 2008; Easton & Sholl, 1995). Alternatively, if the perspective shift related bias that we reported in earlier studies was driven by the specific camera movements that we have used where the rotation is always in a different direction to the translation, we would expect the bias to be present only in such situations

7.2. Experiment 1

7.2.1. Introduction

In Experiment 1 we introduced a modified version of a task we used in Segen et al., (2021d) to investigate spatial memory across different perspectives. In this task participants memorised scenes containing a target object and then, following a short delay, they were presented with a second image showing the same scene from a different perspective but without the target object. When viewing the second scene, participants had to indicate the position of the target object.

The main aim of this experiment k was to provide a conceptual replication of the results reported in Segen et al. (2021d). Thus, we predict that participants' errors will be biased in the direction of the perspective shift.

7.2.2. Method

7.2.2.1. Participants

Twenty-eight participants aged between 18 to 35 years of age (mean age =24.04 years, SD = 4.69; age range = 18-33 years; 16 females and 12 males) took part in this study. Participants were recruited through the participant recruitment system of Bournemouth University and received course credit for their participation. All participants gave their informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

7.2.2.2. Materials

The virtual environment was designed with 3DS Max 2018 (Autodesk) and consisted of a square 9.8m x 9.8m room. Posters depicting famous landmarks were placed on the walls of the virtual room. The landmarks were chosen based on familiarity ratings obtained from previous research by Hamburger & Roser, (2014). The target object, a potted plant, was placed in one of 18 predefined positions and the scene for encoding was rendered from one of three camera positions (camera locations depicted in Figure 7.1). At test, the object was removed, and the scene was rendered from one of the six test camera positions (Figure 7.1) such that the camera either moved to the left or to the right of the encoding position. The experimental stimuli were renderings of the environment with a 58° horizontal field of view (FOV). A custom asymmetric viewing frustum that resembles natural vision with a 15% shift in the vertical FOV was used. This asymmetric viewing frustum resembles natural vision and has been found to improve distance perception in virtual environments (Franz, 2005).

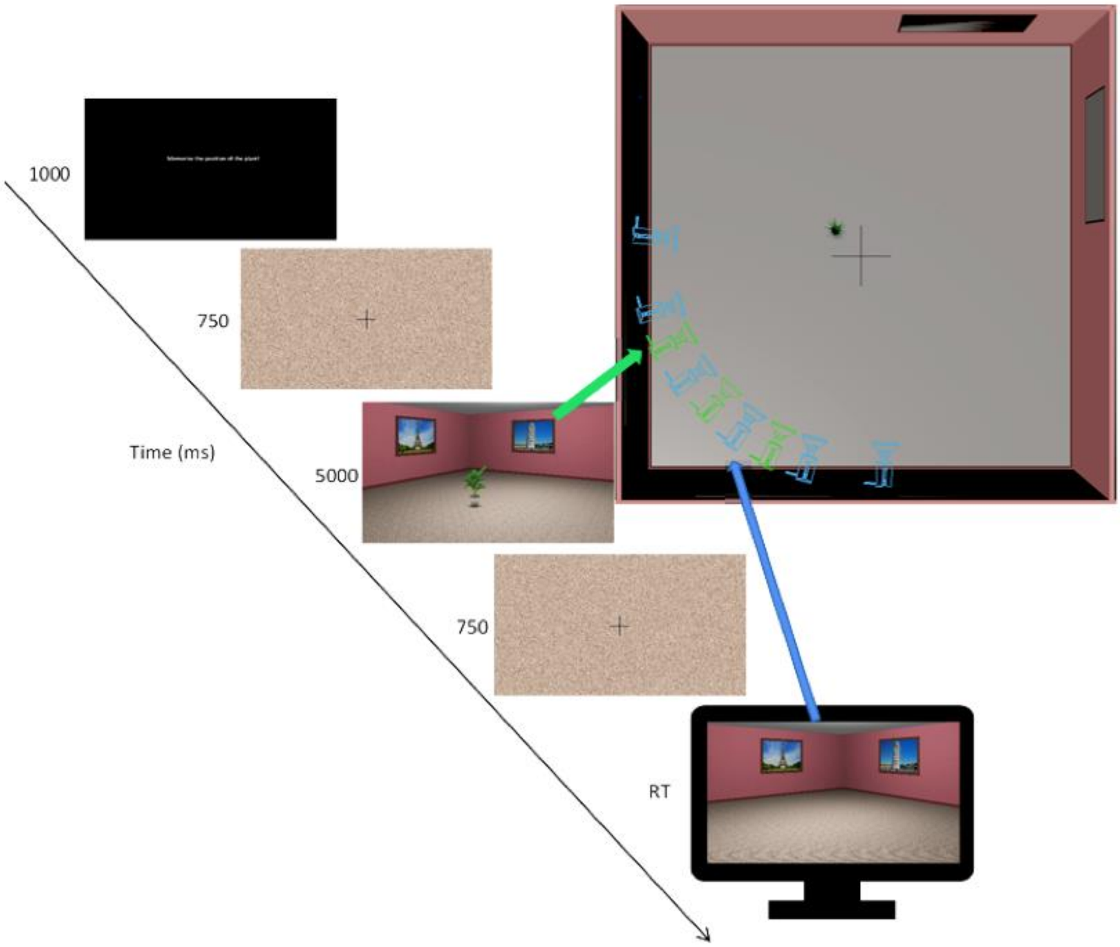

Figure 7.1 A top-down schematic of the virtual environment used in the experiment with camera positions. Green cameras represent camera positions at encoding and blue cameras represent the corresponding camera positions at test. B: Trial structure with green and blue arrows showing the encoding and test cameras used to render the encoding and test scenes

7.2.2.3. Procedure

The experiment was carried out online using Testable (testable.org). At the beginning of the experiment, participants were asked to adjust the screen zoom settings to ensure that the entire scene was visible during the experiment which was run in full-screen mode. Each experimental trial started with instructions to remember the position of the object (1000ms), this was followed by a fixation cross and a scrambled stimuli mask presented for 750 msec (Figure 1B). In the encoding phase, participants were presented with a rendering of the room with one of the 18 possible target object positions from one of three encoding camera positions for 5 seconds. This was followed by the presentation of a fixation cross and a scrambled stimuli mask for 750 msec. Finally, in the test phase, participants were presented with a rendering of the room without the target object from one of the six possible camera positions (Figure 7.1A). Participants had to indicate the position of the object taking into account the camera movements between encoding and test. Participants moved the mouse cursor to the position where they thought the object was during encoding and clicked to register their responses. They were instructed to use the base of the target object to estimate the position it occupied on the floor.

Each of the 18 possible target object positions was presented twice for each of the three encoding camera positions which resulted in 108 experimental trials that took around 25 minutes to complete.

7.2.3. Results

Since the main aim of the experiment is to investigate biases in the direction in which participants estimate object locations, only angular errors (i.e., the unsigned distance between the correct object location and participant's response) are reported, with distance errors (Euclidean distance between participants' estimate of the object's position and the object's actual position) presented in the supplementary materials.

To investigate if the direction of the perspective shift between encoding and test biased the direction of participants' position estimates for the object, we focused on signed angular error (Figure 7.2). Positive and negative errors indicate that the object was estimated to be to the right or the left (respectively) of the correct object position. We ran linear mixed-effects models (LME) using LME4 (Bates et al. 2015) in R (R Core Team, 2013) to investigate the role the Perspective Shift Direction (PSD) had on participants signed angular errors. PSD (Left/Right) was coded using sum contrasts such that left perspective shifts were compared to the average errors for the Left and Right PSD. We found that PSD (Left) influenced participants' errors (β= -6.712, SE=0.426, t=-15.743), with participants positioning the target object further to the left when the perspective shift was to the Left. If we reverse the contrasts such that Right PSD is compared to the grand average, a reverse pattern is found with participants' errors shifted to the right for Right PSD. In other words, participants exhibited a bias in their estimates that were in the same direction as that of the perspective shift between encoding and test (Figure 7.2).

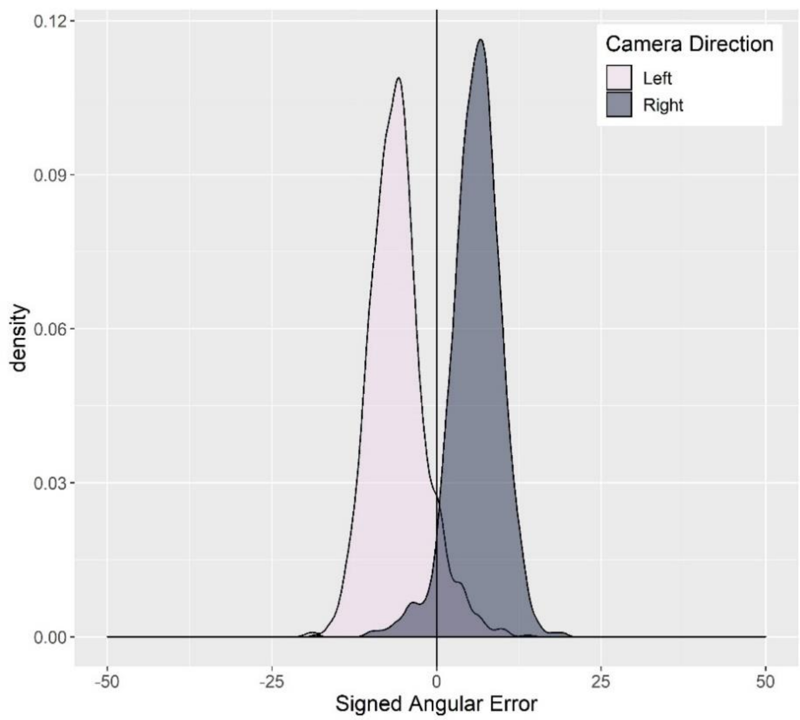

Figure 7.2 Distribution of Signed Angular Errors as a function of Camera Direction

7.2.4. Discussion

Experiment 1 showed that when indicating target object positions, participants systematically made errors in the same direction as the perspective shift. We also found that participants systematically overestimated the distance of the object as they had placed the object further than its actual position. The presence of a systematic shift in participants' estimates of the position of the target object in the same direction as the perspective shift provides a conceptual replication of our previous findings (Segen et al., 2021d). Notably, in the original task, the objects were always placed on a plank and participants were provided with a set of predefined positional markers on the plank and indicated the position of the target object by selecting one of the markers. In the current task, we removed both the plank and the positional markers to rule out the possibility that these cues were related to the perspective shift induced bias. Thus, the presence of a systematic influence of the perspective shift on participants' object location estimates in the current study suggests that the bias is more likely to be driven by camera movements in the environment. In Experiment 2, we further explore what may be driving the perspective shift induced bias.

7.3. Experiment 2

7.3.1. Introduction

It is possible that the camera movements used in Experiment 1 and in other studies with spatial perspective tasks (Montefinese et al., 2015; Muffato et al., 2019; Hilton et al., 2020; Segen et al., 2021a, 2021b ,2021c, 2021d; Sulpizio et al., 2013) contributed to the perspective shift related bias in target object position estimates. Specifically, we speculated that there might be something special about this combination of camera rotations and translations, where the camera translates in one direction and rotates in the opposite direction, that gives rise to the perspective shift related bias. For example, participants may have difficulties in correctly perceiving the size of the perspective shift since the images rendered from both perspectives look strikingly similar. This is because the rotation in the opposite direction to the translation ensured that the same features of the scene remained visible. This could lead participants to systematically underestimate the extent of the camera movement and lead to the systematic shift in the errors in direction of the camera shift.

The key aim of Experiment 2 was, therefore, to investigate the contribution of camera rotations and translations to the perspective shift related bias. To do so, we varied camera rotations and translations independently by creating situations with rotations but without translations and vice versa. In addition, we introduced camera movements that we and others have used in previous work (Segen et al., 2021a, 2021b ,2021c, 2021d; Montefinese et al, 2015; Muffato et al., 2019; Hilton et al., 2020; Sulpizio et al., 2013; Schmidt et al., 2007), in which the camera translates and rotates in opposite directions, to investigate if only this specific combination of camera movements gives rise to the perspective shift related bias. Lastly, we added a situation where the camera translates and rotates in the same direction.

We have argued that uncertainty about the location of the target object following perspective shift is likely to contribute to the perspective shift related bias (Segen et al., 2021c, 2021d). We expect that enriching the environment with additional stable environmental cues will help participants to better estimate the exact object location (Cánovas et al., 2011, Chamizo et al., 2011) and to understand the perspective shift, thereby reducing the uncertainty regarding the target position. The second aim of Experiment 2 was, therefore, to investigate if the introduction of stable environmental cues (two round pillars) would improve overall precision and reduce the effect of the perspective shift on participants' performance.

In addition, in Experiment 2 we investigated whether ageing mediates the effect of camera translations and rotations, as well as the effect that the additional cues may have on the ability to precisely encode and retrieve object positions and, specifically, on the perspective shift related bias. Since ageing is associated with declines in the precision of spatial memory (Pertzov et al. 2015; Nilakantan et al., 2018; Segen et al., 2021a, 2021c; McAvan et a., 2021) and has been linked with perspective taking deficits (Watanabe, 2011; Montefinese et al., 2015; Segen et al., 2021a), we expected that older adults would be less precise in estimating the position of the target object. Due to reduced precision, we expect that older adults would experience greater uncertainty about the exact position of the target object and therefore show a more pronounced error bias in positioning the target object in the direction of the perspective shift.

7.3.2. Method

7.3.2.1. Participants

Forty-five young adults (mean age =20.70 years, SD = 3.26; age range = 18-33 years; 25 females and 20 males) and forty-one older adults aged 60 years and over (mean age=68.00, SD=6.44, age range=60-86; 21 females and 20 males) took part in this study. Participants were recruited either through the participant recruitment system of Bournemouth University or Prolific (https://www.prolific.co), an online participant recruitment system. Older adults received monetary compensation for their time whilst younger participants received course credit. All participants gave their written informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

7.3.2.2. Design

The experiment followed a mixed 2 (Age Group: Young/Older) × 2 (Environment: No Columns/Additional Columns) × 3 (Camera Translation: Left Translation/No Translation/Right Translation) x 3 (Camera Rotation: Left Rotation/No Rotation/Right Rotation) design with Environment, Camera Translation and Camera Rotation manipulated within participants and Age Group manipulated between participants.

7.3.2.3. Materials

We used the same virtual environment as in Experiment 1. In this experiment, however, we only used 4 predefined target object positions and the encoding scenes were rendered only from the central camera position (Figure 7.1A). During encoding, the camera was oriented to always face the centre of the room. For the test stimuli, the target object was removed and the scenes were rendered from one of the three test camera positions such that the camera either remained in the same position, moved to the left, or moved to the right by 1m from the encoding position. The rotation of the camera was also manipulated at test such that the camera rotated by 10° to the left, 10°to the right, or did not rotate. This design yielded a total of nine possible combinations of camera position and rotation for the test stimuli (examples of stimuli shown in Figure 7.3A). In the Additional Columns condition, two round columns that differed in colour were added to the environment (Figure 7.3B).

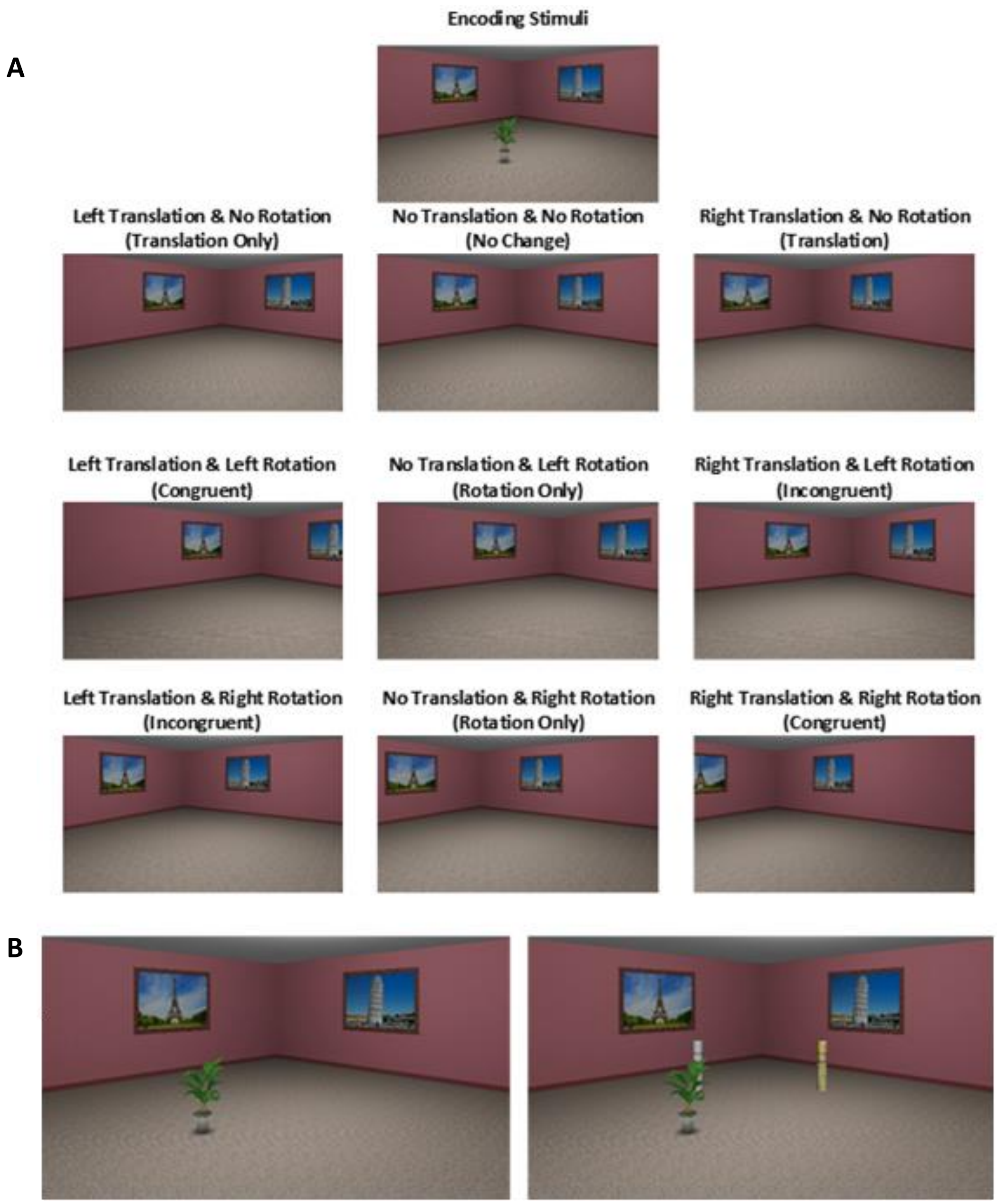

Figure 7.3 Sample scene during encoding. A Test scenes across different camera translation and rotation combinations; B Examples of scenes during encoding, depicting the No Columns and Additional Columns Environment conditions.

7.3.2.4. Procedure

The experimental procedure was identical to that of Experiment 1. Each of the 4 possible target object positions were presented twice for each Camera Translation, Camera Rotation and Environment combination. This resulted in a total of 144 experimental trials that were preceded by 2 practice trials. The entire study took approximately 30 minutes to complete and was run online using Testable (testable.org).

7.3.2.5. Data Analysis

Data were analysed with LMMs and included Age Group (Young/Older) and Environment (No Columns/Additional Columns) in all the models. Effect coding was used to set contrasts. To reduce the complexity of some of the models we combined Camera Translation and Camera Rotation into a single factor we refer to as Camera Movement (Figure 3B). This resulted in 5 levels, No Movement (No Translation and No Rotation), Rotation Only (No Translation and Left or Right Rotation), Translation Only (No Rotation and Left or Right Translation), Congruent movement (Left Translation and Left Rotation or Right Translation and Right Rotation) and Incongruent movement (Left Translation and Right Rotation or Right Translation and Left Rotation). Camera movement was used to analyse Absolute Angular Errors, contrasts were set using treatment coding with No Movement used as the baseline. In the analysis of Signed Angular Error, Camera Translation and Camera Rotation were used as separate fixed factors and were also coded using treatment coding with No Translation and No Rotation used as a baseline, respectively. All models included a random by-subject and by-item intercept. Prior to analysis, outlier responses were removed using the interquartile range method on individual absolute distance error (m) distributions, which led to a 3.6% data loss.

7.3.3. Results

7.3.3.1. Absolute angular errors

The LMM analysis showed that the absolute angular errors were larger with camera movements than without (Table 7.1 and Figure 7.4). Specifically, there was a small increase in angular errors when camera rotations were introduced (Rotation Only trials), a larger increase in errors was found for Incongruent trials, followed by an even larger increase for Translation Only trials and for Congruent trials. We also found a significant interaction between

Environment and Camera Direction, with a lower increase of error in the Additional Objects condition with the introduction of Congruent and Translation Only trials. In addition, we also found an interaction between Camera Movement and Age Group with a larger increase of error in the Incongruent and Translation Only trials in Older Adults.

Table 7. 1 Coefficients from Absolute Angular Error LME analysis

	Absolute Angular Error		
Predictors	Estimates	std. Error	t-value
(Intercept)	1.718	0.147	11.659
Environment (Additional Columns)	-0.137	0.126	-1.084
Camera Movement (Congruent)	3.373	0.155	21.753
Camera Movement (Incongruent)	2.024	0.155	13.079
Camera Movement (Rotation Only)	0.770	0.155	4.975
Camera Movement (Translation Only)	2.721	0.155	17.581
Age Group (Older)	0.033	0.104	0.318
Environment (Additional Columns)*Camera Movement (Congruent)	-0.563	0.155	-3.633
Environment (Additional Columns)*Camera Movement (Incongruent)	-0.258	0.155	-1.666
Environment (Additional Columns)*Camera Movement (Rotation Only)	-0.259	0.155	-1.676
Environment (Additional Columns)*Camera Movement (Translation Only)	-0.541	0.155	-3.494
Environment (Additional Columns)*Age Group (Older)	0.049	0.071	0.694

Camera Movement (Congruent)*Age Group (Older)	0.087	0.088	0.986
Camera Movement (Incongruent)*Age Group (Older)	0.263	0.087	3.005
Camera Movement (Rotation Only)*Age Group (Older)	-0.090	0.087	-1.030
Camera Movement (Translation Only)*Age Group (Older)	0.195	0.087	2.225
Environment (Additional Columns)*Camera Movement (Congruent) *Age Group (Older)	-0.045	0.088	-0.510
Environment (Additional Columns)*Camera Movement (Incongruent) *Age Group (Older)	-0.132	0.087	-1.507
Environment (Additional Columns)*Camera Movement (Rotation Only) * Age Group (Older)	-0.078	0.087	-0.893
Environment (Additional Columns)*Camera Movement (Translation Only)*Age Group (Older)	-0.091	0.087	-1.040

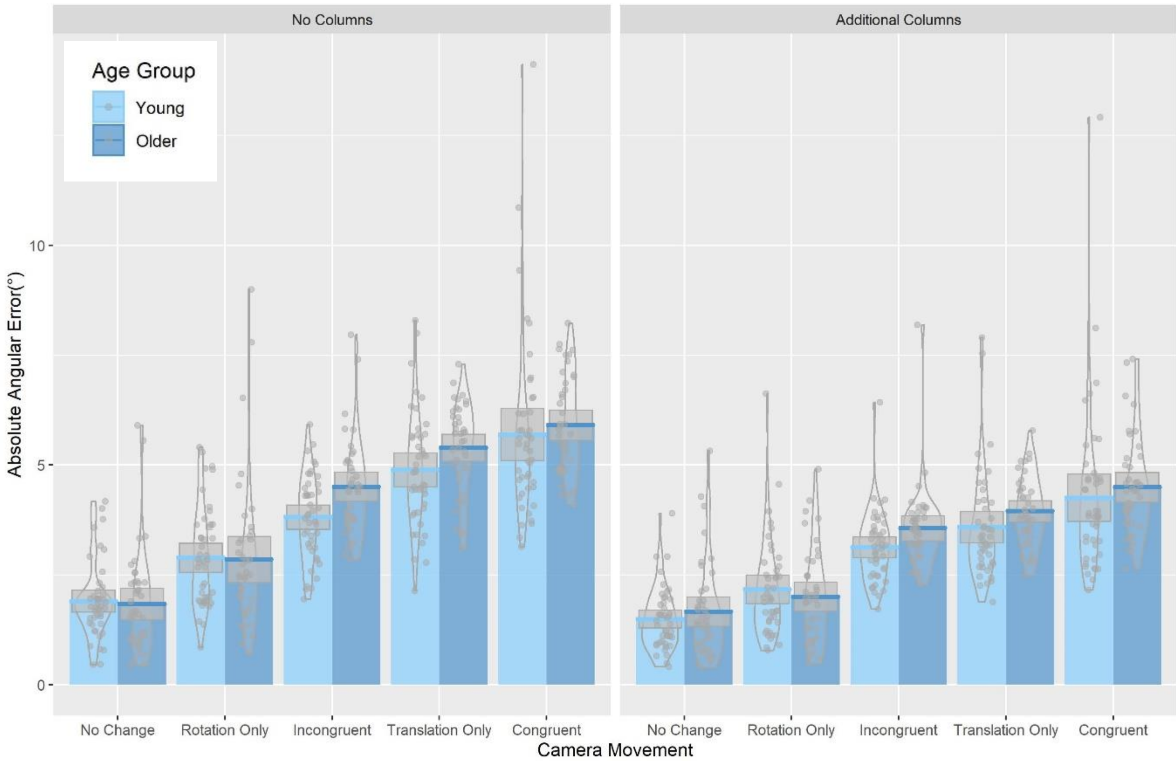

Figure 7.4 Absolute angular error as a function of Camera Movement, Environment and Age Group

7.3.3.2. Signed Angular Errors

To investigate which camera movements systematically bias the direction of object location estimates, we focused on signed angular error. Positive errors indicate that the target object was estimated to the right of the correct position and negative errors indicate errors to the left of the correct position. In this model we have included Camera Translations and Camera Rotations as separate fixed factors, as otherwise the errors for different directions of camera rotations and translations could cancel each other out.

The LMM analysis (see Table 7.2 and Figure 7.5) showed that Camera Rotations introduced a small bias in errors in the direction of the rotation. Camera Translations had a much larger effect on participants' signed angular errors, with participants' estimates of target object locations showing a large shift in the direction of the translation. We also found an Environment by Camera Translation interaction: errors were less biased when the camera translated to the left in the Additional Columns condition than in the No Columns condition. A similar trend (t=1.955) was also present when the camera translated to the right.

We also found an interaction between Camera Rotation and Age Group, with older adults showing smaller error bias when camera rotations were present compared to younger adults. This effect was only significant for rotations to the left, but the numerical trend is present also for rotations to the right. In contrast, older adults seem to be more affected than young adults by camera translations. This was corroborated by the presence of an Age Group by Camera Translation interaction with older adults showing a greater error bias in the direction of camera translations compared to young adults. Again, the interaction was only significant for camera translations to the right with a similar trend for camera translation to the left.

To quantify the differences between the effect of camera rotations and translations, we conducted linear hypothesis tests and found that the effect for each direction of the camera rotation were significantly different for the corresponding effect for each direction of camera translation, i.e. left translation vs left rotations (p <.001). Next, we compared the magnitude of that difference and found that the effect of camera translation on signed angular error is almost threefold (2.85) to that of camera rotations (p<.05).

Table 7.2 Coefficients Signed Angular Error LME analysis

	Signed Angular Error		
Predictors	Estimates	std. Error	t-value
(Intercept)	-0.211	0.193	-1.095
Environment (Additional Columns)	-0.117	0.181	-0.644
Rotation (Left)	-0.631	0.257	-2.459
Rotation (Right)	0.765	0.257	2.977
Translation (Left)	-3.647	0.257	-14.199
Translation (Right)	4.036	0.257	15.728
Age Group (Older)	-0.185	0.115	-1.607
Environment (Additional Columns)*Rotation (Left)	0.128	0.257	0.498
Environment (Additional Columns)*Rotation (Right)	-0.044	0.257	-0.171
Environment (Additional Columns)*Translation (Left)	0.502	0.257	1.955
Environment (Additional Columns)*Translation (Right)	-0.625	0.257	-2.435
Rotation (Left)*Translation (Left)	0.054	0.363	0.148
Rotation (Right)*Translation (Left)	0.192	0.363	0.530
Rotation (Left)*Translation (Right)	-0.360	0.363	-0.990
Rotation (Right)*Translation (Right)	0.042	0.364	0.116
Environment (Additional Columns)*Age Group (Older)	0.039	0.094	0.408
Rotation (Left)*Age Group (Older)	0.332	0.134	2.487

Rotation (Right)*Age Group (Older)	-0.207	0.134	-1.545
Translation (Left)*Age Group (Older)	-0.170	0.134	-1.266
Translation (Right)*Age Group (Older)	0.273	0.134	2.041
Environment (Additional Columns)*Rotation (Left)*Translation (Left)	0.148	0.363	0.408
Environment (Additional Columns)*Rotation (Right)*Translation (Left)	-0.113	0.363	-0.312
Environment (Additional Columns)*Rotation (Left)*Translation (Right)	0.173	0.363	0.476
Environment (Additional Columns)*Rotation (Right)*Translation (Right)	0.090	0.364	0.246
Environment (Additional Columns)*Rotation (Left)*Age Group (Older)	-0.021	0.134	-0.154
Environment (Additional Columns)*Rotation (Right)*Age Group (Older)	-0.017	0.134	-0.127
Environment (Additional Columns)*Translation (Left)*Age Group (Older)	-0.005	0.134	-0.035
Environment (Additional Columns)*Translation (Right)*Age Group (Older)	-0.121	0.134	-0.906
Rotation (Left)*Translation (Left)*Age Group (Older)	-0.116	0.190	-0.610
Rotation (Right)*Translation (Left)*Age Group (Older)	-0.013	0.190	-0.066
Rotation (Left)*Translation (Right)*Age Group (Older)	-0.169	0.189	-0.892
Rotation (Right)*Translation (Right)*Age Group (Older)	0.153	0.191	0.804
Environment (Additional Columns)*Rotation (Left)*Translation Left)* Age Group (Older)	-0.156	0.190	-0.822
Environment (Additional Columns)*Rotation (Right)*Translation (Left)*Age Group (Older)	0.108	0.190	0.570
Environment (Additional Columns)*Rotation (Left)*Translation (Right)* Age Group (Older)	-0.030	0.189	-0.157
Environment (Additional Columns)*Rotation (Right)*Translation (Right) * Age Group (Older)	0.207	0.191	1.083

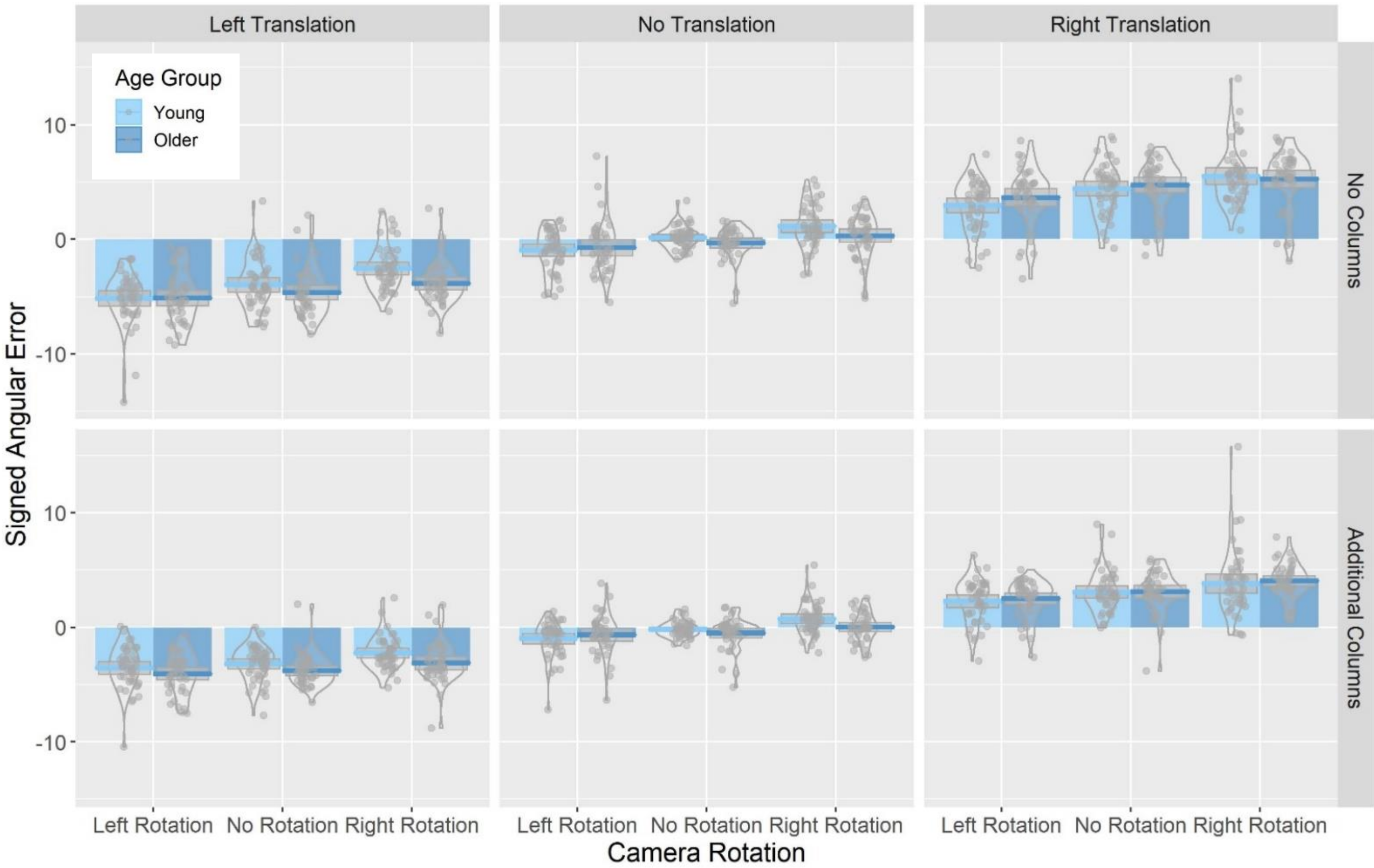

Figure 7.5 Signed angular error as a function of Camera Translations, Camera Rotations and Age Group in the No Columns condition (top panel) and Additional Columns (bottom panel)

7.3.3.3. Linear combination of errors for camera rotations and translations

To investigate how camera rotations and translations interact, we modelled predictions for combined movements based on rotation and translation data. Specifically, we created three models (Figure 7.6), one in which signed errors were solely affected by camera rotation (Rotation Only model), one in which signed errors were solely affected by camera translation (Translation Only model) and one which assumed an additive influence of camera rotation and translation (Additive Model). The predictions of the three models, along with the experimental data, are presented in Figure 8. It is apparent that participants' errors are unlikely to be driven solely by camera rotations, whilst both the Translation Only model and the Additive Model fit the experimental data well. However, the Additive Model provides a significantly better fit than the Translation Only model (Translation Only RSS=1677.5, Additive Model RSS=1146.1, F=35748, p<.001). The close fit of the predictions of the additive model for the combined camera movements with the actual data suggests that camera rotation and camera translation independently influence participants' performance.

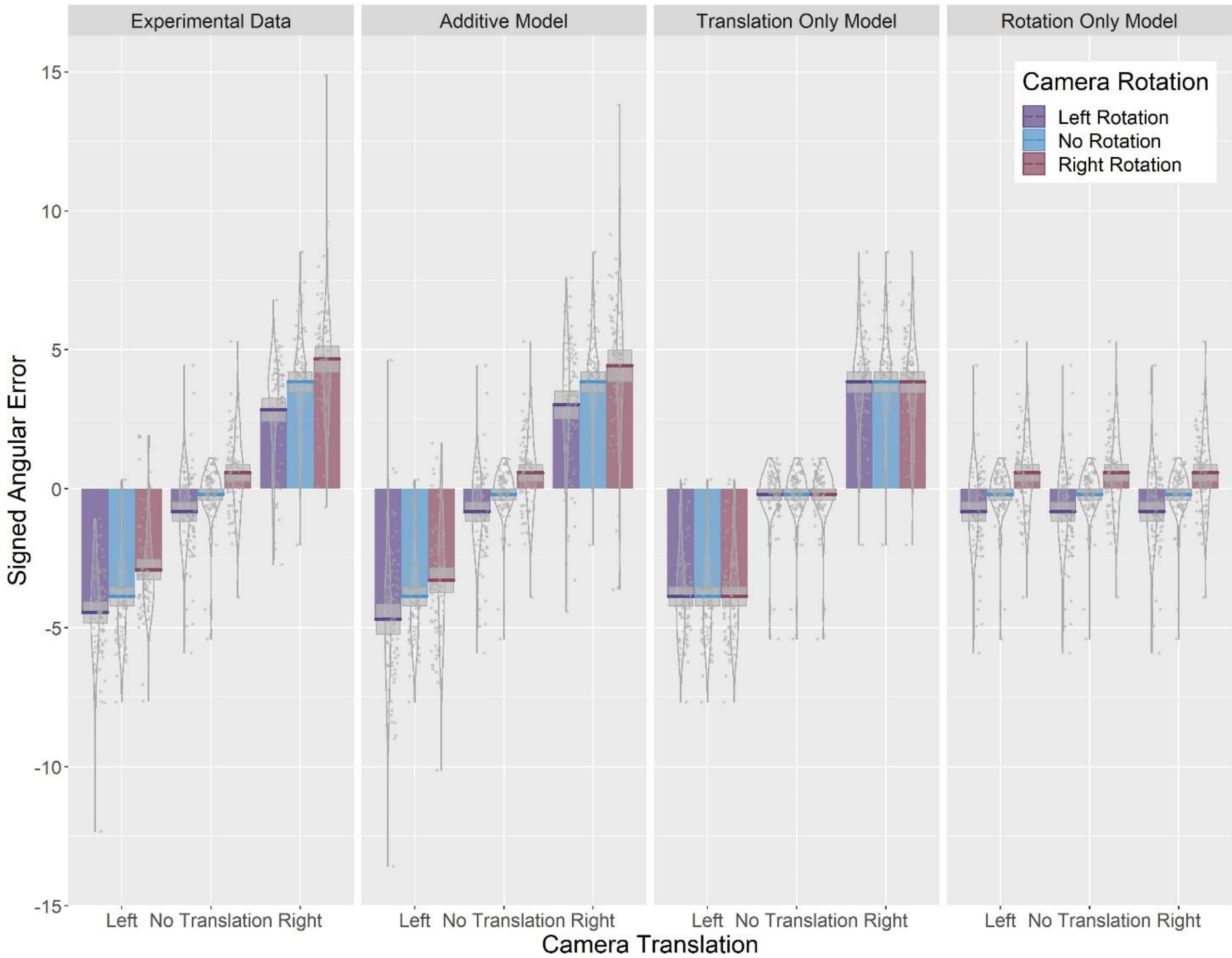

Figure 7.6 Experimental Data and predictions of the Additive, Translation Only and Rotation Only models

7.3.3.4 Absolute Distance Errors

Lastly, to investigate differences in the precision with which participants recalled the position of objects following a perspective shift, we focused on the Absolute Distance Errors The LMM analysis (complete results are presented in supplementary materials) showed that errors decreased in the Additional Columns Environment (β=-0.983, SE=0.013, t=-6.471). Moreover, the introduction of any camera movements increased participants' error when compared to the No Movement baseline. Notably, the increase was not uniform. The lowest increase in error occurred when camera rotations were introduced (Rotation Only; β=0.034, SE=0.016, t=2.134), followed by trials with Incongruent camera movements (camera translates and rotates in opposite directions; β= 0.074, SE=0.016, t=4.707). Error increased further in Translation Only trials (β=0.114, SE=0.016, t=7.268), with the largest errors observed in trials with Congruent camera movements (camera translates and rotates in the same direction; β=0.163, SE=0.016, t=10.298). We also found a significant interaction between Environment and Age Group (β=0.020, SE=0.009, t=2.167). Error was smaller in the Additional Columns condition than in the No Columns condition, but this difference was larger in younger compared to older adults. This finding suggests that older adults did not benefit from the availability of extra spatial information (extra columns) as much as younger adults did.

7.3.4. Discussion

In the present study we investigated the role camera rotations and translations have on the error's participants make when recalling object locations. We also examined if enriching the environment by providing additional spatial information influences the ability to precisely estimate the position of the target object following a perspective shift as well as the perspective shift related bias in the position estimates. We also investigated age-related differences in the precision with which people estimate target object locations. Lastly, we examined if older adults are differentially affected by camera rotations and translations as well as by the presence of additional cues when estimating target object locations.

We found that the introduction of any camera movements between encoding and test increased error in estimating the position of the target object. This was the case for both absolute angular deviations and absolute distance errors. Importantly though, the effect of translations was larger than the effect of rotations. Furthermore, we replicated the perspective shift related bias that we described in our previous studies (Segen et al., 2021c, 2021d). Specifically, we found that participants' responses were biased in the direction of camera movements for both rotations and translations, yet this bias was stronger with the introduction of translations.

There were age-related differences in the manifestation of the perspective shift related bias, as older adults were less affected by camera rotations compared to younger adults, whilst at the same time being more affected by camera translations than younger participants. Furthermore, we found that enriching the spatial information in the environment improved the precision with which participants estimated the position of the object following a perspective shift, yet older adults benefited less from the additional spatial information.

In line with our previous research (Segen et al., 2021c), we found that the presence of additional spatial information reduced the systematic bias in participants' object position estimates following a perspective shift, yet this was only true for perspective shifts containing camera translations.   Lastly, we showed that a linear additive model of errors for pure rotations and translations described our data well, suggesting that camera rotations and translations affected participants' errors independently.

We attribute the perspective shift related bias to egocentric influences on target object estimates. In the current task there were no self-motion cues that could support the automatic updating of egocentric representations of object locations during the perspective shift (Wang & Spelke, 2002). Instead, spatial perspective taking had to be achieved through more effortful processes (Easton & Sholl, 1995). Examples of those include using an allocentric representation that contains information of the object-to-object relations (which are independent from own/camera position in the environment) or by engaging in mental transformations of the egocentric representations to ensure that the encoding and test representations align (King et al, 2002; Hegarty & Waller, 2004). If participants relied solely on an allocentric representation in which the position of the target object was encoded relative to other features in the environment, their own position and movement in the environment should not have influenced their responses and perspective shifts would not have resulted in systematic biases in the same direction as the perspective shift (King et al, 2002; Hegarty & Waller, 2004). However, if participants relied on egocentric representations, their responses could be biased towards the egocentric estimates derived before the perspective shift (i.e., during encoding) which would result in the systematic shift in the direction of the camera movement.

In the current experiment, we decoupled camera rotations and translations and showed that translations resulted in a substantially larger angular bias in the direction of the camera movement than camera rotations. We propose that the differential effects of camera rotations and translations on participants' performance are driven by differences in how camera rotations and translations affect the egocentric self-to-object relations and on the 2D projections of object-to-object relations. We propose that in order to estimate the position of the target object following a perspective shift, participants need to first encode the position of the target object during encoding, then to compare the encoding and test stimulus to understand how they have moved through space (i.e. to understand the perspective shift which requires self-localization at both encoding and test), and finally to recompute the target object position given their new location in the environment.

When camera rotations are introduced, the distance to the object and other features in the environment remains the same but the location of the object and other features of the environment on the screen are uniformly offset by the rotation angle. Thus, the relative position of the target object in relation to other features in the environment on the image remains the same despite appearing at a different part of the image. As a result, participants do not really need to self-localize during camera rotations as they can rely on their memory for the object position relative to other nearby features in the environment. Alternatively, they can use the offset in the position of other features in the environment to estimate the position of the target object. However, when camera translations are introduced, the distance between one's own position and other objects changes. Notably, this change is not uniform and depends on the position of the objects. This leads to changes in the vectors and angles between the self and the environmental features, including the to-be-remembered object locations, and therefore to positions these features occupy on the screen. Participants need to consider this new information to understand how they moved through space, and to update the target object position accordingly.

Since camera translations are more difficult to resolve than camera rotations, they introduce more uncertainty about the position of the target object. Consistent with the anchor and adjustment heuristic (Tversky & Kahneman, 1974), we suggest that due to higher uncertainty following camera translations than rotations, participants exhibit greater reliance on an egocentric anchor (Epley et al., 2004; Gilovich et al., 2000; Keysar et al., 2000). According to the anchor and adjustment heuristic, the anchor is typically adjusted until a plausible response is reached, however, such adjustments are often insufficient (Tversky & Kahneman, 1974; Quattrone, 1982) such that the response remains biased in the direction of the initial estimate. In our task, the egocentric anchor is the self-to-object vector during encoding. Insufficient adjustment of this egocentric vector on basis of the perspective shift, would result in a systematic shift in object position estimates in the same direction as camera translations and rotations. Moreover, in line with our interpretation that camera translation results in greater uncertainty and consequently greater reliance on the anchor, the systematic shift is greater when camera translation rather than camera rotations are introduced.

The idea that uncertainty mediates the reliance on the egocentric anchor is in line with the reduction of the systematic bias introduced by camera translations when additional spatial information (stable environmental cues) was provided in the environment. Specifically, the addition of stable environmental cues is likely to improve the precision with which the object location can be encoded (Cánovas et al, 2011; Chamizo et al., 2011; Kamil & Chen, 2001; Ekstrom & Yonelinas, 2020). Consistent with this account, we found that participants are more precise when environmental cues are available. Additionally, the presence of these cues enriches the spatial structure of the environment and can therefore improve the understanding of the perspective shift. Improvements in the precision with which participants can encode the object location and the understanding of their own position following camera movements is bound to reduce the uncertainty that participants have about object positions at test. In turn, this is likely to reduce the weight that is given to the egocentric anchor during target object position estimation following a perspective shift.

Additional spatial information may not only help to reduce the uncertainty that participants have allowing them to rely less on an egocentric anchor but may also help them to improve the adjustment process. Specifically, additional cues may limit the range of plausible object positions. That is, if the object was between the two columns, then participants can use this information during adjustments to reduce errors as well as the systematic bias in the direction of camera movements.

The finding in our study of a greater detrimental effect of camera translations than rotations on overall performance and on the systematic bias in object position estimate, is inconsistent with the finding from the spatial updating literature that typically shows that imagined rotations have a more debilitating effect on performance than imagined translations (Klatzky et al., 1998; Rieser, 1989; Wraga, 2003; Presson & Montello, 1994). In spatial updating studies greater error is observed during imagined rotations than translations because the latter are less computationally demanding (Rieser, 1989; Presson & Montello, 1994). For example, Rieser (1989) argued that during imagined translations participants can simply retrieve the stored information from memory. However, for imagined rotations participants either need to recompute the object-to-object relations considering their new orientation or combine the signed self-to-target angle and the signed self-to-observation point angle. Both of those would require additional mental computations to transform the initial encoded representation of object locations.

Also, Presson and Montello (1994) suggested that differences between the imagined rotations and translations in a spatial updating task may be driven by a conflict between actual and imagined heading directions. Specifically, they proposed that humans have a strong tendency to use their immediate heading direction as a primary frame of reference. And in the imagined rotation condition participants need to override this primary frame of reference to adopt an alternative imagined heading direction. Such conflict between reference frames is not present in the translation condition as the actual and imagined heading always remain the same. The lack of conflict between reference frames is also likely to make the updating of self-to-object relations easier (Presson & Montello, 1994).

In our task, however, the impact of camera rotations and translations is different. Specifically, the object-to-object relations as they are projected on the screen change in the camera translation condition but not in the camera rotation condition. In addition, as noted earlier, the self-to-object relations are uniformly offset in the rotation condition, therefore the new self-to-target object relations can be calculated much easier in conditions when camera rotations are introduced. Conversely, in the translation condition participants need to engage in more demanding computations to estimate the new self-to-target object position. Furthermore, in our task, there is no conflict between heading directions. Participants are shown their new heading direction instead of imagining it. Therefore, their new heading is apparent at both encoding and test. Thus, in our view, the differential impact of rotations and translations between our task and the spatial updating paradigms is responsible for differences in the results.

The experimental design allowed us to investigate how the influence of camera rotations and translations combine during camera movements that include both rotation and translation components to influence participants' performance. We found that a simple linear model with additive inputs of pure rotation and pure translation errors closely matches the empirical data for combined camera movements and provides a significantly better fit than models that are based on errors associated with translations or rotations only. This result suggests that rotation and translation influences do not follow the winner-takes-it-all principle that has been used to explain higher-level cognitive phenomena such as visual attention (Itti and Koch, 2001; Walther & Koch, 2006) and decision making (Wang, 2002; Furman & Wang, 2008). Instead, we believe that performance on trials with combined camera translation and rotations results from independent influences of rotations and translations that are linearly combined to produce the observed errors. The linear additive model also explains the smaller errors observed after incongruent camera movements (camera rotates and translates in opposite direction) compared to congruent camera movements (camera rotates and translates in the same direction). Specifically, in incongruent movements, the errors have opposite signs since they are biased in the direction of movement for both camera rotations and translations. Therefore, when the errors are combined, they cancel each other out. In congruent movements the errors for rotations and translations are biased in the same direction and are therefore additive.

The final aim of Experiment 2 was to investigate how ageing affects the precision with which participants remember the position of objects following a perspective shift and whether older adults are differentially affected by camera rotations and translations as well as by the presence of additional cues in the environment compared to younger adults. Against our predictions, we found that, overall, older adults performed just as well as the younger participants. We did, however, find that older adults benefited less than younger adults from the addition of stable environmental cues. This is in line with our previous work (Segen et al, 2021c) in which we showed that older adults were more biased by the direction of the perspective shift when estimating object displacement directions than younger adults in whom the addition of extra spatial information substantially reduced the systematic bias related to the perspective shift.

One explanation for why older adults benefited less than younger adults from the presence of additional environmental cues is that the presentation of extra cues was not blocked. Instead, trials with and without additional environmental cues were randomly presented. This may have prevented older adults from utilising these additional cues due to problems in switching strategies to use additional information when it was available (for review on strategy switching in navigation and ageing see Colombo et al., 2017). Instead, older adults may have relied only on the information that was available across all trials. Additionally, our previous eye-tracking research using similar tasks suggests that older adults have a preference towards encoding object locations in a room using more distal room based cues such as posters, rather than encoding the spatial layout of more proximal object cues distributed in the room (Segen at al., 2021a, 2021b). This preference may further contribute to older adults not utilizing the additional spatial information in the room when it was available.

In line with our predictions, we found that older adults were more affected by camera translation than younger adults and displayed a greater bias in the direction of camera translations when estimating target object positions. Also, compared to younger participants, older adults exhibited larger absolute angular errors when camera translations were introduced. The larger bias in the direction of camera translation in older adults may be driven by greater uncertainty stemming from less precise encoding of object locations (Dai et al., 2016; Pertzov et al., 2015; Nilakantan et al., 2018; Segen et al., 2021a; McAvan et al., 2021) and difficulties in spatial perspective-taking in older adults (Segen et al., 2021a; Montefinese et al., 2015; Watanabe, 2011; Inagaki et al., 2002), which cause them to rely more on an egocentric anchor. Yet, contrary to our predictions, older adults did not display a bias in the direction of camera rotations, unlike younger adults who were affected by camera rotations. It is not clear from the current data why older participants were less affected by camera rotations than younger adults. This could be the focus of future studies.

The differential response to camera rotations and translation in older compared to younger adults may also explain the larger absolute angular errors in incongruent camera movements. Specifically, if errors for a specific rotation (i.e. right) are linearly combined with errors for a specific translation (i.e. left) then in younger adults, who are more biased by rotations, the rotation and translation errors are have different signs and when combined the angular errors are reduced in incongruent trials. However, since older adults show only very small systematic rotation errors, when combined with translation errors, the overall errors do not reduce as much as with younger participants in the incongruent trials. Note that the age-specific differences in angular errors related to camera rotations and translations are very small compared to the main effects of camera translation and rotations that we report in the current study. More research is needed to understand the role of ageing in mediating the effects camera rotations and translation have on memory for object locations.

7.4. General Summary

To summarise, in the present study we evaluated people's ability to estimate object positions following a perspective shift. In Experiment 1, we replicated (Segen et al., 2021d) a systematic shift in position estimates in the same direction as the perspective shift. In Experiment 2 we investigated the contribution of camera rotations and translations to this bias and showed that translations are largely responsible for causing a systematic bias in object location estimation. Camera translations introduced a greater change in the relations between own position and the object as well as other features in the environment compared to rotations. We believe that those greater changes lead to increased uncertainty regarding the position of an object in the environment which results in greater reliance on egocentric anchors leading to the systematic bias in errors in the same direction as translations. We also show that the influence of camera translations is influenced by both environmental properties and individual differences (age-related difference), such that the bias was larger in less informative environments and in older adults whose abilities to remember object locations have been shown to decline (Montefinese et al., 2015; Muffato et al., 2019; Hilton et al., 2020; Segen et al., 2021a). Lastly, this is the first study to show that the influence of camera rotations and translations on participants' performance is guided by a linear additive process.

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Chapter 8: General Discussion

8.1. Basic overview of research findings

In chapter 2 we used eye-tracking and diffusion modelling to investigate age-related changes in encoding and response strategies in a task requiring memory for object locations across different perspectives. In this task, we asked young and older participants to encode the locations of an array of objects in a virtual room from a 2D picture. Participants were then shown a second picture of the same room taken from the same or a different perspective and asked whether the objects occupied the same or different locations. Potential age-related differences in the resolution of spatial representations were investigated by introducing either coarse (two object clusters swapped places) or fine-grained (one object cluster rotated by 60 degrees) spatial changes.

In line with previous research, older adults had greater difficulties with the task than younger adults (c.f. Montefinese, Sulpizio, Galati, & Committeri, 2015; Muffato, Hilton, Meneghetti, De Beni & Wiener, 2019; Hilton, Muffato, Slattery, Miellet, & Wiener, 2020; Hartley et al., 2007), as reflected in lower performance and lower drift rates in older adults. Both age groups were negatively affected by the introduction and the increase in the perspective shift, with older adults showing a larger decrease in performance with the introduction of the perspective shift. In addition, across both age groups, performance and drift rates were lower in conditions with fine-grained spatial changes compared to coarse changes. Although no interactions between the type of spatial change and age group were found, drift rates in older adults were around zero in conditions with fine-grained spatial changes, suggesting that they struggled to extract useful information needed to solve this condition, documenting possible age-related deficits in the formation of fine-grained spatial representations.

Diffusion modelling revealed differences in decision making. For example, older adults were generally more conservative and needed to accumulate more information prior to making a decision. In addition, both age groups became more conservative with the introduction of perspective shifts and in the condition with a coarse spatial change, but this effect was more pronounced in older adults, highlighting that response strategies are adapted based on the type of task that participants need to solve.

Most importantly, gaze behaviour differed between younger and older adults with older adults examining a larger proportion of the stimuli during the encoding of object locations within the virtual room. These findings highlight differences in visual encoding strategies: older adults seemed to remember object positions in relation to room-based cues while younger adults focused on the spatial relationship between objects. However, it is also possible that more dispersed gaze in older adults arose due to difficulties in selecting and focusing on the task-relevant information. Interestingly, the inspection of a larger proportion of the stimuli was negatively associated with performance on the trials requiring fine-grained spatial processing, whilst no such association was found for the trials with a coarse spatial change. It is possible that participants who explored a smaller proportion of the stimuli focused on the spatial relationships between the objects, rather than the relationship between objects and room-based cues, which facilitated the formation of a more fine-grained spatial representation. Conversely, trials that included a coarser spatial change could be responded to either by focusing on the relationships between objects or by relating target objects to environmental cues, thus explaining why no association between gaze behaviour and performance was found in these trials. Overall, the results from Chapter 2 highlight that older adults have greater difficulties in remembering object locations across different perspectives and that they show a preference towards an encoding strategy that relies on room-based cues. It remains unclear, however, if the differences in encoding strategies are driven by older adults using room-based cues during encoding or by older adults having greater difficulties in inhibiting attention to the room-based cues or selecting task relevant information.

The experiment presented in Chapter 3 was designed to disentangle the potential explanations for the age-related differences in gaze behaviour reported in Chapter 2. To do so, the task used in Chapter 2 was slightly modified (incorporating smaller perspective shift which ensured that the same information was available both during encoding and test; only the coarse spatial manipulation was included [two objects swapped places]), and the availability and utility of room-based cues was manipulated such that the cues were 1) unique and could be used to encode object locations, 2) identical and thus uninformative or 3) absent from the scene. This allowed investigating whether age-related differences in gaze behaviour during spatial encoding were due to older adults encoding object positions by relating them to the room-based cues or to older adults having difficulties in selecting and/or focusing on task-relevant information. If the former explanation is true, then it would be expected that older adults use room-based cues when they are informative. However, if the latter explanation is true, then no differences in gaze behaviour across different types of room-based cues should be expected.

Overall, there were no differences in response accuracy between younger and older adults. In line with previous research, older adults took longer to respond, suggesting age-related decrements in the speed of processing (Salthouse, 1996; Salthouse, & Ferrer-Caja, 2003). The introduction of a perspective shift and swapping two object clusters with each other had a negative effect on performance in both age-groups. The availability and informativeness of the room-based cues did not affect task accuracy. However, as in Chapter 2, there were differences in gaze behaviour with older adults spending more time gazing at the room-based cues, particularly when the cues were informative and could be used to help solve the task. Furthermore, older adults adapted their gaze behaviour during the experiment and spent less time fixating on uninformative cues over the course of the experiment. Together, these results suggest that the explanation that older adults randomly scan the environment without a clear encoding strategy seems unlikely. Instead, it appears that they adjust their gaze behaviour in response to the type of information available in the environment and show a preference towards incorporating room-based cues into their encoding strategy.

The key aim of Experiment 1 in Chapter 4 was to design a quick and easy to administer task that would allow quantifying the precision of spatial memory for object locations. To do so, a two-alternative forced-choice task was developed in which participants first had to encode the position of an object in a room. Following a perspective shift, they then had to indicate the direction in which an object had moved. By systematically manipulating the distance by which the object was displaced, the accuracy with which participants could remember the position of the object following a perspective shift was evaluated. Surprisingly, a strong bias, that we termed the Reversed Congruency Effect, was found in participants' responses. The effect was linked to the direction of the perspective shift relative to the direction in which the object has moved. Participants performed worse, and often misjudged the distance in which the object had moved when the camera and the object moved in the same direction. Conversely, when the object and the camera moved in opposite directions, participants were able to correctly detect the object's movement direction with accuracy close to 100%.

The Reversed Congruency Effect was further investigated in Experiment 2. Results showed that this effect cannot be explained by the movement of the object on the screen, instead it relates to the perspective shift and the movement of the object in the virtual world. In addition, enriching the environment with additional objects reduced the Reversed Congruency Effect such that it no longer predicted performance. In Experiment 3, age-related changes in the precision of spatial representations and susceptibility to the Reversed

Congruency Effect were investigated. Overall, older adults performed worse than younger adults. In addition, older adults were more likely to display the Reversed Congruency Effect. Together, the findings across the three experiments reported in Chapter 4 suggest that the Reversed Congruency Effect is likely to be driven by difficulties in 1) the precise encoding of object locations in the environment and 2) understanding how perspective shifts affect the self-to-object relationships. It is possible that older adults had greater difficulties with formulating precise representations of object locations and with understanding perspective shifts leading to greater susceptibility to the Reversed Congruency Effect.

It is likely that the Reversed Congruency Effect was driven by the introduction of the perspective shift, with participants “dragging” the object in the same direction as the perspective shift. This was investigated in Chapter 5 by asking participants to encode the position of an object, and instead of judging the direction in which it has moved following the perspective shift, the object was removed and participants were asked to select the position of the object from a number of predefined positions. In addition, the role of memory in the systematic bias of object position estimates was investigated, as participants completed either a Memory or a Perception (no memory load) variant of the task. The results showed that participants indeed overestimated the position of the object in the same direction as the perspective shift, providing support for the interpretation that a perspective shift induces a systematic bias in object location estimates. In addition, there were no performance differences between the Memory and the Perception variants of the task, showing that the bias did not arise due to systematic distortions introduced by spatial memory. Instead, the bias appears to be linked to the understanding/perception of the perspective shift.

The experiment in Chapter 6, investigated if data collected online would yield comparable results to data collected in the lab. This study was largely motivated by the move to online data collection because of Covid-19 restrictions on in-person data collection. To do so, the Memory version of the experiment reported in Chapter 5 was adapted to an online experiment and performance on this task was compared with the data collected in Chapter 5 (Memory condition). Consistent with previous research (Hubert & Gajos, 2020), greater variance in performance was found in the online sample compared to the data collected in the lab. Despite the increased noise, comparable performance was observed in the lab-based and online data, suggesting that online data collection offers a viable method of behavioural data collection on tasks that assess object location memory across different perspectives using static images.

The first experiment in Chapter 7 provided a conceptual replication of the results reported in Chapter 5 using a modified version of the task. In this new task, participants were free to estimate the position of the object anywhere in the room. This allowed the estimation of both direction and distance errors in object location estimates. As in Chapter 5, participants systematically estimated the position of the object in the same direction as the perspective shift. The second experiment investigated this perspective shift related bias further by decomposing the influence of camera rotations and translations. The results showed that camera translations gave rise to larger systematic bias in object position estimates (in the direction of camera translations), compared to camera rotations. The greater bias in the direction of camera translations rather than camera rotations is likely to be driven by camera translations being difficult to resolve, leading to greater uncertainty about the position of the object. Increased uncertainty leads to greater reliance on the initial egocentric estimate of the object position thereby giving rise to the systematic bias in the direction of camera translations. In addition, the combined influence of camera rotations and translations on participants' performance appears to be guided by a linear additive process.

Experiment 2 in Chapter 7 also investigated if adding more information that could be used as stable cues in the environment would improve performance and reduce systematic biases in object position estimates. As predicted, the use of additional spatial information resulted in improved precision with which object locations were estimated as well as a reduction in the bias in the direction of camera translation. Lastly, age-related differences in the precision of object-location memory and susceptibility to the perspective shift related bias were also investigated with older adults displaying similar precision to younger adults when estimating object locations. However, older adults benefited less from additional spatial information and their responses were more biased in the direction of camera translations. Older adults may be more affected by camera translations, due to increased uncertainty about the position of the object due to deficits in spatial memory (Montefinese et al.,2015; Hilton et al., 2020; Muffato et al., 2019; Hartley et al., 2007) and spatial perspective taking (Montefinese et al.,2015; Inagaki et al., 2002; Watanabe, 2011).

8.2 Discussion of findings

To discuss the theoretical and methodological implications of the empirical chapters presented in the current thesis, this section is split into two parts. The first part focuses on the discussion of age-related changes in object-location memory across different perspectives with reference to the results of Chapters 3 and 4. This section also highlights the utility of eye-tracking and diffusion modelling in both cognitive ageing and spatial memory research.

In the second part, the discussion focuses primarily on the novel bias that was reported in Chapter 5, and further investigated in the remaining empirical chapters. In this section methodological consideration of presenting 3D information using 2D images as well as conducting experiments online are discussed.

8.2.1 Age-related changes in object-location memory across different perspectives

Eye-tracking is a widely established method that has been successfully and widely applied to study cognition (Rayner, 2009). Early research has shown that eye movements provide a dynamic trace of where attention is directed (Just and Carpenter 1980; Rayner, 1998) during complex information processing while reading, perceiving visual scenes , visual searching, music reading, and typing (for a detailed review see Radach & Kennedy, 2004, Rayner, 1998, Rayner, 2009). Broadly, attention can be viewed in terms of overt and covert attention, with the former involving selective processing of one location over the others by moving the eyes and fixating at that location and the latter involving direction of attention without eye-movements (Carrasco, 2011). Eye-tracking is particularly useful in studying overt attention (Brunyé, Drew, Weaver & Elmore, 2019). In addition, it can provide a rich and non-invasive index of high-level cognitive processing (Eckstein, Guerra-Carrilo, Singley, Bunge, 2017). For example, it has been used to explore learning processes across a variety of tasks (Hegarty, Mayer, & Green, 1992; Tsai et al., 2012, van Gog & Scheiter, 2010) as well as strategy differences in reasoning tasks (e.g. Chen, Ross & Murphy, 2016). Thus, eye-tracking can provide a window into key processes underlying complex human behaviour. It is with this view, that eye-tracking has been chosen as an appropriate method to investigate age-related differences in encoding strategies when remembering object locations within an environment.

Eye-tracking analysis in Chapter 2 and 3, revealed that older and younger adults gaze at different information during encoding of object locations within an environment. Those differences in gaze behaviour are interpreted in the context of differential preferences in encoding strategies between the age groups. In particular, results from both chapters indicate that older adults spent more time gazing at room-based cues, thus suggesting that they have a preference towards utilising room-based cues when encoding positions of an array of objects within a virtual room.

In contrast, younger adults showed a preference towards a strategy where they focused their gaze more on the array of objects instead of gazing at additional information in the environment i.e. room-based cues. Based on those results, it is likely that younger participants were more likely to utilize an encoding strategy where they encoded the configuration of the object array, whilst older adults were more likely to encode positions of objects with reference to room-based cues. From hereon, we will refer to the former strategy as *object-based* and to the latter as *cue-based*.

Why did younger and older adults use different encoding strategies during the task? One possible interpretation is that older adults attend to room-based cues due to using a coarser encoding strategy where they relate the position of a target object to an additional landmark. Conversely, the strategy of relating the positions of objects within an array to each other may facilitate more fine-grained spatial representations. This interpretation is supported by results in Chapter 2 where less spread-out gaze was associated with better performance on trials that required more precise representations of object positions within an environment. No such associations were found in trials where only categorical spatial changes were introduced by swapping two object clusters with each other in either Chapter 2 or in Chapter 3 where only such trials were used. The lack of a relation between the type of encoding strategy used and performance can be explained by the ability to resolve the coarse manipulation by either of the strategies (i.e. cue- and object-based). In contrast, it is insufficient to rely on the coarse representation to identify fine-grained spatial changes. Relating object positions to room-based cues is conceptually similar to a beacon strategy during navigation, where locations are encoded in relation to a prominent environmental beacon or landmarks. Interestingly, older adults show a preference towards such strategies (Wiener et al., 2013). Both the preference towards encoding object location in relation to room-based cues and the use of a beacon strategy during navigation in older adults may be a compensatory strategy to account for deficits in the ability to formulate fine-grained spatial representations (Pertzov, Heider, Liang, & Husain, 2015; Nilakantan, Bridge, VanHaerents, & Voss, 2018). And as shown in both Chapters 2 and 3, the cue-based strategy allows older adults to respond to the trials with coarse spatial changes fairly well, and in some situations (Chapter 3) on par with younger adults. A more comprehensive discussion of possible age-related deficits in the fine-grained spatial encoding is provided below.

Interestingly, Hilton et al. (2020) did not find age-related differences in encoding strategies using a similar task to the one used in Chapter 2 and 3 as participants were required to encode a place defined by a specific arrangement of objects, and then recognise those from different perspectives. However, the key difference between the tasks used in Chapter 2 and 3 with the task used by Hilton and colleagues is that there was no additional information present (i.e. geometrical or room-based cues). Given that the differences in gaze behaviour reported in this thesis are likely driven by differential use of additional cues (i.e. room-based cues), it is not surprising that Hilton et al. did not report age differences, as there were no additional cues to gaze at. Similarly, in Chapter 3, no differences in gaze behaviour were found between younger and older adults in conditions where no room-based cues were available. In addition, older adults were less likely to attend to uninformative compared to informative cues, this was particularly the case over the course of the experiment. These results highlight that older adults' gaze behaviour is sensitive to the type of information that is available, further supporting the argument that age-related differences in gaze behaviour reflect differences in encoding strategies rather than bottom-up influences or random scanning of the stimuli.

From a methodological point of view, it is important to discuss the implication of using eye-tracking to investigate both age-related differences during the performance of spatial tasks as well as the investigation of spatial cognition in general. As highlighted above, eye-tracking is an established technique to investigate cognitive tasks. However, despite the apparent utility of eye-tracking, it has not been widely applied to investigate performance on spatial tasks, with the majority of those studies focusing on navigation (e.g. Becu et al. 2020; Hilton et al., 2019; Livingstone-Lee et al., 2011, Andersen, Dahmani, Konishi & Bohbot, 2012; Grzeschik, et al., 2019).

The results from Chapters 2 and 3 highlight that relatively simple analyses of gaze behaviour can provide a window into the information that is used during the encoding of object locations, which typically would not be available from performance measures alone. In addition, results from Chapter 3 show that gaze behaviour can highlight that participants solve the tasks in a multitude of ways despite the absence of apparent differences in performance (as measured by reaction time and accuracy). The differences in strategy preference are in line with other research in spatial cognition and other cognitive domains reporting a lack of clear behavioural differences despite differences in encoding strategies. For example, a study examining sex differences during navigation reported that there were no apparent sex differences in navigation performance in the presence of landmarks, despite female participants spending more time fixating on landmarks than men (Andersen et al., 2012). Similarly, face processing research reports cultural differences in gaze behaviour when viewing faces with eastern participants attending to the nose and western participants attending more to the eye and lip areas without apparent performance differences (Kelly, Miellet & Caldara, 2010; Blais, Jack, Scheepers, Fiset & Caldara 2008). Collectively, those studies demonstrate that cognitive tasks can often be carried out using more than one strategy and that the preference for a given strategy is driven by individual differences such as age, culture and gender. Eye-tracking provides a window into these strategy differences, which would not be apparent from performance measures alone.

Eye-tracking is not the only tool that is available to assess spatial encoding strategies. For example, verbal reports have been successfully applied to study strategies used during spatial tasks (Kitchin, 1997; Hölscher, Tenbrink & Wiener, 2011; Bae & Montello, 2019). However, verbal reports are limited to quantifying explicit encoding strategies that often reflect what the participants think they are doing rather than what they are actually doing (Cohen, 1996; Newell & Shanks, 2014) Eye-tracking can capture explicit encoding strategies to which participants have conscious access to, as well as more unconscious "automatic" (e.g. bottom-up processes, such as visually salient environmental features capturing attention without having task-relevance) strategies. Nevertheless, combining both verbal reports and eye-tracking can offer a more detailed account of spatial encoding strategies (Spiers & Maguire, 2008). In the context of the current PhD it would shed more light on whether older adults explicitly adapt their encoding strategies to compensate for spatial memory deficits.

Another way to investigate encoding strategies is by combining neuroimaging techniques with eye-tracking. Such methods are becoming more commonly adopted, and have been successfully applied in other fields of cognition including language comprehension (Bonhage et al., 2015), and visual search (Manelis & Reder, 2012). Although neuroimaging techniques including EEG and fMRI cannot explicitly identify what information and in what temporal order this information has been attended to during a task, using them together with eye-tracking could provide a better understanding of how different brain activation relates to the strategies employed during spatial tasks (see Keskin et al., 2020 for an example of combined eye-tracking and EEG study). Such approaches may offer insight into the neural mechanisms implicated during spatial encoding, as well as provide potential explanations for age-related differences in encoding strategies.

In addition to investigating encoding strategies, diffusion modelling has been applied in Chapter 2 to investigate age-related differences in response strategies when making decisions on whether the object locations have changed or remained the same following a perspective shift. This was the first study to apply diffusion modelling to study age-related response strategies in a spatial task. Typically, diffusion modelling has been applied to investigating decision making in relatively fast and simple reaction time tasks, such as lexical decision or letter discrimination tasks (Ratcliff, Gomez, & McKoon, 2004; Thapar, Ratcliff & McKoon, 2003). Here, diffusion modelling was successfully applied to a more complex task, that likely involves multi-stage decision making, and substantially longer response times. Similar to eye-tracking, using diffusion modelling offers a more nuanced understanding of how participants solve the task over and above typical performance metrics (response times and accuracy). Specifically, by combining response time and accuracy data, diffusion modelling separately models task-specific information processing (indexed by drift rate parameter), decisional styles that depend on response conservativeness (indexed by boundary separation parameter) and non-decisional processes such as processing of low-level visual features and execution of the responses (Ratcliff, Smith,Brown & McKoon, 2016; Voss, Nagler, & Lerche, 2013).

By using diffusion modelling, it has been shown that ageing was associated not only with spatial processing deficits but also with changes in response strategies as older adults adopted more conservative response strategies (i.e. needed to accumulate more information before making a decision), which is consistent with research that used diffusion modelling to study cognitive ageing across a number of different domains, including memory (Ratcliff et al.,2004; Spaniol, Madden, & Voss, 2006), perceptual learning (Ratcliff, Thapar & McKoon, 2006) and language (Ratcliff et al., 2004). The need of older adults to accumulate more information to support their decisions is in concordance with their preference to look around (and as a result accumulate more information) more during encoding. Together, those results highlight that ageing has a more nuanced effect on how spatial tasks are solved then simply a reduction in performance, highlighting that older adults resolve the tasks differently and that those changes are not always associated with a reduction in performance (i.e. Chapter 3).

In line with this, previous diffusion modelling research in ageing, has also reported a shift towards more conservative response strategies (Spaniol et al., 2006; Thapar et al., 2003; Ratcliff et al, 2006; Ratcliff et al., 2004), indicating that this is likely to be a general artefact of cognitive ageing (cf. Starns & Ratcliff, 2010), with older adults placing greater importance on accuracy than speed. As discussed in section 3.6, it is possible that some of the changes in encoding and response strategies i.e. encoding of additional not necessary task relevant information which may be reflected in both more conservative response strategies and more spread out gaze behaviour, do not necessary reflect compensatory processes and are instead driven by knowledge that in the real world, often immediate irrelevant information, may become relevant in the future (Zimmerman, Hasher & Goldstein, 2011; Kim, Hasher, Zacks, 2007). This is, however, speculatory and future research into age-related changes in the way cognitive tasks are solved is needed.

Another advantage of using diffusion modelling in investigating age-related differences or differences between control and patient groups is that it separately models non-decisional processes that also often degrade in ageing (i.e. declines in visual function [Owsley, 2011] and reduced motor speed [Ren, Wu, Chan & Yan, 2013]) as well as patient groups (i.e. AD [see Albers et al., 2015 for a review]). This allows estimation of task-specific processing efficiency that is not contaminated by changes in the non-decisional processes. Such approaches shed light on the interpretations of response time differences between groups and prevent incorrect interpretations of processing deficits when the increases are driven by the degradation of non-decisional processes. For example, in Chapter 2, substantial differences (two-fold) between younger and older adults in non-decisional processes were found, thus, highlighting the importance of accounting for differences in non-decisional processes when evaluating performance differences using response time data.

Moreover, participants' response strategies were dependent on task demands. Specifically in Chapter 2 participants employed a more conservative response strategy in the trials which they are more likely to solve correctly (coarse spatial change), such that participants prioritised accuracy-over speed only in situations where they are more confident in their ability to respond correctly. This effect was more pronounced in older adults, who also displayed greater differences in the ability to solve trials with coarse vs more fine-grained spatial changes. In addition, participants were more conservative in all trials where a perspective shift was present. It is not surprising that participants have wider decision boundaries when a perspective shift is introduced, as they need to sample more information to inform them about their new orientation. Those findings highlight that spatial perspective taking is not only associated with increased processing demands but also changes in response strategies, which are differentially affected by ageing. This is particularly important for research on spatial-perspective taking that frequently relies on measures of response times as a marker of performance (i.e. Spatial Orientation Test; Guilford & Zimmerman, 1948; Hegarty & Waller, 2004), as it may lead to incorrect inference of less efficient performance on trials where perspective shifts are present, when the increase in response times may instead be representative of a shift towards more conservative response strategies.

It is noteworthy to briefly discuss the practical implications of applying diffusion modelling. In the last decade or so a number of freely available packages including those with GUIs (examples include: Fast-dm [Voss & Voss, 2007], E-Z Diffusion Model [Wagenmakers, van der Maas & Grasman, 2007], as well as several R packages [DstarM, van den Bergh, Tuerlinckx, & Verdonck, 2019; rtdist, Singmann et al., 2016]) have been developed that make diffusion modelling easily accessible to researchers from a wide range of backgrounds. It is also important to note that diffusion modelling requires a relatively large amount of trials and fairly rigid removal of response time outliers (Lerche, Voss & Nagler, 2017; Voss, Voss & Lerche, 2015), which can contribute to a fair amount of data loss. This may hinder between group comparisons if the number of outliers differs between age groups. In addition, there may also be model misfits for some participants, thereby reducing the number of participants that are used in the statistical analysis of the estimated diffusion parameters. Although this was not a major problem in Chapter 2, collective removal of outliers and model misfits have resulted in the loss of data from 8 participants for the statistical comparison of model parameters. In addition, due to the inability to satisfy the minimal number of trial requirements to fit the appreciated model, it was not possible to apply diffusion modelling in Chapter 3. Thus, experimenters need to plan in advance the minimum number of trials that are needed in order to fit the models successfully, taking into consideration that some trials may be lost during data pre-processing as well as model misfits.

Combining the results from Chapter 2 and 3, it is proposed that the reported age-related differences are driven by age-related changes in the resolution at which object locations are encoded, with older adults having greater difficulties in formulating fine-grained spatial representations. Such conjecture is consistent with older adults showing a preference towards an encoding strategy that is more suitable for the formation of more categorical spatial representations. Furthermore, older adults found it particularly difficult to extract useful information to make a decision of whether the objects have changed positions or not in trials where a fine-grained spatial change was introduced, as indexed by drift rates near zero, highlighting a possible deficit in the formation of fine-grained spatial representations. Additionally, the lack of age-related differences in Chapter 3 where only a categorical spatial change is introduced suggests that unlike the ability to formulate fine-grained spatial representation, the ability to formulate coarse spatial representations remains intact in older adults.

The current interpretation is consistent with research on visuospatial working memory in which participants encode multiple locations of objects presented on a computer screen and are then asked to reposition them back. Specifically, such studies found that older adults were less precise in estimating previous locations of objects compared to younger adults, despite positioning the objects in the correct region of the stimuli (Pertzov et al. 2015; Nilakantan et al., 2018). These difficulties in remembering the precise locations of objects, would explain both, very low drift rates for older adults in conditions requiring fine-grained spatial representation and the tendency to use the cue-based encoding strategy. Additionally, a recent study investigating age-related changes in spatial memory using virtual reality, found that the key difference between older and younger adults was driven by reduced precision of memory for object locations as both groups used similar strategies to solve the task and were similarly affected by changes in viewpoint (McAvan et al., 2021).

It is also worthwhile to note that age-related changes in precision are not only reported in relation to tasks requiring memory for object locations (in 2D or 3D environments). For example, previous research suggests that older adults tend to recall fewer specific details of past events (Luo & Craik, 2009; Addis, Wong, & Schacter, 2008; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). Additionally, older adults have greater difficulty in discriminating between previously seen items and perceptually similar lures (Stark, Yassa, Lacy, & Stark, 2013; Toner, Pirogovsky, Kirwan, & Gilbert, 2009; Yassa et al., 2011). Additionally, a recent study by Korkki, Richter, Jeyarathnarajah and Simons (2020) has shown that older adults were less precise when asked to recall the exact position, orientation or colour of previously presented objects. Collectively, those results suggest that older adults have a particular difficulty with encoding and retaining precise, highly detailed memories.

It is plausible that those age-related difficulties in the formation of fine-grained spatial representations are caused by age-related changes in the anterior and posterior hippocampus. The deficit in the ability to formulate precise spatial representations might be caused by age-related changes in the anterior and posterior hippocampus. Indeed, a recent longitudinal study

(Langnes et al., 2019) found that the posterior hippocampus, typically associated with fine-grained spatial processing, was more affected by ageing than the anterior hippocampus, which is involved in the formation of coarser spatial representations (Røe Evensmoen et al., 2013; Nadel, Hoscheidt & Ryan, 2013). In addition, Diersch, Valdes-Herrera, Tempelmann and Wolbers (2021) reported increased anterior hippocampus activation and less precise spatial learning in older adults. Interestingly, they found that older adults with greater activation in the posterior hippocampus performed better on the task and were able to generate a spatial representation of the environment quickly. Additionally, it has been suggested that a reduction in neural specificity in older adults (i.e. neural dedifferentiation, Abdulrahman, Fletcher, Bullmore, & Morcom, 2017; St-Laurent, Abdi, Bondad, & Buchsbaum, 2014; Zheng et al., 2018) may also be responsible for a more domain-general reduction in the precision with which older adults encode and store information (Korkki et al., 2020; McAvan et al., 2021).

Overall, given the findings from Chapter 2 and 3 and the previous research highlighted above, the key conclusion from the chapters discussed here is that ageing is likely to lead to deficits in the ability to formulate fine-grained spatial representations, whilst the ability to form coarser representation of object location remains intact.

8.2.2. Perspective taking and systematic biases in object location estimates

The possible age-related changes in the ability to formulate fine-grained spatial representations motivated the design of a new short and easy to administer experimental task to assess the precision of object location representations (Chapter 4). However, the unexpected discovery of the “Reversed Congruency Effect” shifted the focus of further research toward better understanding this bias. Further investigation of this bias led to the conclusion that it is most likely driven by the perspective shift, such that participants “drag” the objects with them during a perspective shift and that it is not a product of distortions introduced by memory. Particularly, it appears that the translational component of the perspective shift is largely responsible for this bias. The bias is mediated both by environmental properties, as it reduced when the environment was enriched through the use of additional spatial cues and by individual differences, as on average older adults were more affected by it.

The key explanation for the *perspective shift related bias* is that it arises in situations when there is greater uncertainty about the positions of the object following a perspective shift. This idea closely aligns with the anchor and adjustment heuristic introduced by Tversky and Kahneman (1974) to explain the decision-making process in situations when there is uncertainty. The key premise of the heuristic is that initial estimates are often used as anchors when making decisions in situations when uncertainty is present. The anchors are adjusted until a plausible response is reached. However, given that the adjustments are often insufficient, the final response is often biased in the direction of the initial estimate. For example, participants are more likely to think that Chicago is more sparsely populated when provided information that its population is more or less than 200,000. However, their estimates will be considerably higher if the initial anchor is 5 million instead of 200,000 (Jacowitz & Kahneman, 1995). Previously, the anchor and adjustment heuristic has been applied to numeric decision making, for example estimating event probabilities (Joyce & Biddle, 1981), values of objects (Northcraft & Neale, 1987) and future forecast generation (Switzer & Sniezek, 1991; Wright & Anderson, 1989). However, our results suggest that it may also be relevant in spatial tasks where participants have to estimate the locations of objects following a perspective shift.

Specifically, the anchor and adjustment heuristic may explain the perspective shift related bias whereby participants' estimates of object locations are biased to the direction of the perspective shift. Such bias may come around due to an uncertainty about the position of the object following a perspective shift, which causes participants to rely on the egocentric vector between the object and their own position during encoding (before the perspective shift) as their anchor on which they base their response after the perspective shift. In line with the anchor and adjustment heuristic, they then adjust this anchor to be more probable given the perspective shift and the changes in the position of other features in the environment following the perspective shift. These adjustments may not be enough, resulting in biased estimation of the object's position (Tversky & Kahneman, 1974; Quattrone, 1982), in the same direction as the perspective shift (particularly the translation component).

The results reported in the current thesis are also consistent with the idea that more weight is given to the egocentric anchor in situations when uncertainty is high (Epley, Keysar, Van Boven, Gilovich, 2004; Gilovich, Medvec, & Savitsky, 2000; Keysar, Barr, Balin, & Brauner, 2000). Specifically, the *perspective shift related bias* was substantially lower in situations where only camera rotations were present. In these trials the uncertainty is likely to be lower as the distance between the objects and their own position does not change and the self-to-object relationships change uniformly for all of the objects in the environment. However, when translations are introduced, distance between own position and other objects does not change uniformly and as a result the self-to-object relationships are differentially affected across the objects in the environment. Similarly, as evident in Chapter 4 and 7, the bias was reduced when additional spatial cues were added into the environment. This may be due to additional cues facilitating distance estimation (Kamil & Cheng, 2001), improving self-localization following a perspective shift, whilst also providing direct feedback on how perspective shifts affect the 2D projection of the positions that objects occupy on the screen. Lastly, the bias was more pronounced in older adults. These results are interpreted in the context of age-related degradation in spatial perspective taking (Montefinese et al., 2015; Inagaki et al., 2001; Watanabe, 2011) as well as the ability to formulate precise representation of object locations (Pertzov et al., 2015; Nilakantan et al., 2018). This may contribute to less reliable representations (higher uncertainty) about the position of an object following a perspective shift, making older adults more susceptible to the perspective shift related bias. Additionally, lower drift rates in older adults reported in Chapter 2 are also indicative of higher uncertainty in the older group as they are not obtaining as much useful information from the environment as younger participants.

Although not empirically evaluated in this thesis, the role that presenting 3D information in 2D images may have in the perspective shift related bias will be discussed here. The implications of using 2D images to present spatial information are important for interpreting the results presented in this thesis as well as other research relying on presentation of images. Two-dimensional images differ in a number of ways from the space we experience in the real world, and in some cases with immersive virtual reality. Most importantly, in the 3D world, the observer is internal to the scene, however, when experiencing a remote scene on a computer display, the participants' locations are ill-defined because the observer is not actually present in the depicted space. Instead, they are asked to adopt the location of the camera (that was used to render the stimuli), which can be challenging for several reasons (Troje, 2019; Karimpur, Eftekharifar, Troje, & Fiehler, 2020).

Firstly, when viewing images, observers have access to monoscopic, but not stereoscopic, depth cues. Stereoscopic depth cues provide additional information about the relative distance and direction of objects from the observer's standpoint (Troje, 2019; Karimpur et al., 2020) and have been found to improve distance estimates in virtual environments (Poyade, Reyes-Lecuona & Viciana-Abad, 2009; Jones, Swan, Singh, Kolstad & Ellis, 2008; Luo, Kenyon, Kamper, Sandin & DeFanti, 2007). That is, apart from having a clearly defined position in space in the real world, participants also have access to both monoscopic and stereoscopic cues including binocular disparity and relative movement at different depth planes (conceptually similar to motion parallax) that can be used for depth perception. This allows them to derive more accurate representations of the position of objects in the environment and the relationship between those objects.

Secondly, the need to adopt the location of the camera introduced a conflict between participants' actual positions/orientation in the real world and the positions and orientation they should imagine themselves in. This may increase the cognitive demands of the task, as participants need to inhibit the inputs about actual locations, and may lead to additional difficulties in particular in older adults who have greater difficulties with inhibitory control (Hasher & Zacks, 1988; Olk & Kingstone, 2015; West, 1996). The highlighted factors associated with perceiving locations of objects from 2D images can contribute to a less reliable understanding of the exact nature of the perspective shift and estimates of the distances and directions to the objects in the stimuli (Troje, 2019; Karimpur et al., 2020). As discussed above, such uncertainty can contribute to greater reliance on an egocentric anchor giving rise to the observed perspective shift related bias.

Finally, when viewing images, people are more accepting of distortions to the geometry of the displayed space (Troje, 2019), such tolerance of distortions is frequently exploited by filmmakers and artists. Partly related to that is the Venus Effect, which was first described by asking observers whether Venus depicted with a small mirror in which her face is visible, can see herself. Observers tend to say that Venus is admiring herself in a mirror, even when the location of the mirror makes this impossible (Bertamini, Latto, & Spooner, 2003; Croucher, Bertamini, & Hecht, 2002). It has been shown that this effect extends to photographs and largely originates with people misunderstanding how visibility is affected by the viewpoints of the observer (Bertamini, Lawson, Jones, & Winters, 2010) and holding "naive" theories of how vision works. The presence of such "naive" theories may also extend to tasks that are similar to those described in this thesis. For example, expecting the objects to move with them may be part of an incorrect "naive" theory about how the visual world works.

Note however, that this interpretation is speculative and future research is needed to investigate this idea further. Nevertheless, evidence for tolerance of distortions and possible influence of “naive” theories of vision during viewing of images/paintings, suggests that people treat real-world space differently compared to space depicted in images. Such differences raise concerns about whether the findings from image space extend to 3D settings where we experience space egocentrically.

The identification of the perspective shift-related bias in this thesis has implications for experimental paradigms which include the presentation of static images and the introduction of perspective shifts. Firstly, it appears that the reported bias is highly robust, as it has been replicated across seven experiments (reported in chapters 4 to 7), despite using different experimental tasks, means of data collection (online vs laboratory) and the populations that were tested (younger vs older adults as well as students and the general public recruited using online platforms). Based on those findings, there is no reason why the bias should not extend to other paradigms that involve static images and introduction of the perspective shift (e.g. Diwadkar & McNamara, 1997; Schmidt et al., 2007; Hartley et al., 2007; Sulpizio et al., 2013; Montefinese et al., 2015; Muffato et al., 2019; Hilton et al., 2020), including the work presented in Chapter 2 and 3. For example, participants may find it easier to detect object movements if they are in the opposite direction to the perspective shift, and conversely, they may have greater difficulty in detecting when something has changed if the object movement and the perspective shift are in the same direction.

It is possible that the studies reported in chapters 4 to 7 were particularly sensitive to the bias, as the tasks involved either small spatial displacements of objects or required participants to position the objects in the same positions, and small perspective shifts that always resulted in the scenes to be presented more or less from the same part of the environment. Those tasks require precise representation of object positions, and as a result small biases i.e. perspective shift related bias, are more likely to be apparent. In addition, the presence of small perspective shifts makes the self-to-object vectors encoded before the perspective shift fairly informative about the possible position of the object, making them a good candidate for an initial anchor for making judgements about the location of the object after the perspective shift.

Yet in tasks where object positions were swapped with each other (i.e. Chapter 2 and 3), even if participants "experienced" perspective shift related bias, they are still likely to identify that the positions of the objects have swapped places as the spatial change is larger than the effect of the perspective shift related bias. In addition, tasks that involve larger perspective shifts i.e. those where the scene is depicted from a different side (north to the north-west), can lead to use of different anchors when making decisions about the position of the object following a perspective shift, instead of reliance on an egocentric anchor. For example, a recent study reported that for larger perspective shifts, participants are more likely to rely on allocentric representations (Heywood-Everett et al., 2020), and therefore they are unlikely to use the initial egocentric estimation of object positions and adjust those until a plausible response is reached. This is likely to reduce the manifestation of the perspective shift related bias reported here, as the primary assumption is that it is driven by egocentric representations of object locations. It is possible that in tasks that involve both small and larger perspective shifts, as well as fine grained and categorial changes, the perspective shift related bias will affect trials that involve small perspective shifts and fine-grained spatial changes. If that is the case, disentangling the influence of the bias and the experimental manipulation could become very difficult and researchers should at least be cautious that such biases may also affect their results.

Before moving to the discussion of future implications, it is worthwhile to briefly comment on online data collection. Due to coronavirus related restrictions, several studies reported in Chapters 4,6 and 7 were conducted online. Overall, data collected in a laboratory setting and data collected online rendered very similar results although the online data was more variable. It is important to note that designing online studies requires more stringent preparations to ensure that good quality data is obtained. This requires piloting of the experimental paradigms, with a particular focus on instruction clarity, as the experimenter is unable to clarify any questions the participant may have. Implementation of "check" trials where participants are asked to perform simple tasks or respond to a set of questions, can help to identify when participants are not paying attention to the task at hand, which is particularly important in the online setting. Additionally, allowing participants to provide feedback at the end of the experiment, would help with identification of any technical (or other) issues that have arisen during the experiment. Use of the aforementioned steps have contributed to collection of good quality data that rendered results comparable to the data collected in the laboratory. It is hoped that the experience of transitioning to online data collection in the current thesis will be informative to other researchers who are considering running online studies using paradigms similar to the ones reported in this thesis as online data collection offers many advantages including fast data collection and the potential to reach a more diverse population.

8.3. Avenues for future research

One of the key findings in this thesis relates to age-related differences in gaze behaviour during encoding of object locations. Specifically, older adults were more likely to gaze at room-based cues than younger adults, whilst, younger adults focused more on the to-be-encoded objects. These findings are interpreted as evidence for the use of different encoding strategies by younger and older adults with the latter showing a greater preference toward encoding object locations in relation to room-based cues and the former encoding the position of objects relative to each other. However, it is also possible that older adults do not use the room-based cues to encode the positions of objects, and gaze at those objects for other reasons including inability to inhibit attention towards relatively salient room-based cues. In chapter 3, this possibility was investigated in greater detail, however since no performance differences were observed it remains unclear what role room-based cues play in the encoding strategies used by older adults. Therefore, future research should investigate this further. For example, swapping the locations of room-based cues at test, and asking participants to either respond if the target objects are in the same positions or by asking them to reposition the objects back into the environment would allow a more direct investigation into how older adults use room-based cues. It is possible that if older adults indeed use the room-based cues during encoding, they would be more likely to respond that object locations have changed even if the objects remained in the same position but the room-based cue position was manipulated. Similarly, in situations when the room-based cue position is changed, older adults might place the object in a different location, such that the relationship between the cue and the object remains the same. Conversely, younger participants who are more inclined to focus on the relative position between the objects, would be unaffected by such a manipulation. Similar manipulations have been previously applied to investigate preferences towards the use of geometric or landmark cues during navigation in younger and older adults (Becu et al., 2020).

Future research could incorporate qualitative elements and use verbal reports to assess if older adults use the room-based cues during encoding. Since it has been proposed that older adults may be more reliant on the cue-based strategy due to difficulties in formulating precise spatial representations, verbal reports may shine a light on whether older adults explicitly adapt their encoding strategies to compensate for spatial memory deficits.

Interestingly, the strategy adopted by younger adults where they encoded the position of objects in relation to each other correlated with better performance in the conditions where more fine-grained spatial representations were required. This result suggests that this strategy facilitates the formation of a more fine-grained representation of object locations. Future research may investigate this more directly by getting participants to adopt a particular encoding strategy by guiding their gaze behaviour. Such approaches have been previously used in gaze-training interventions where participants are exposed to "expert" gaze behaviour by highlighting the key locations on the monitor screen. For example, this approach has been shown to improve performance of trainee laparoscopic surgeons (Wilson et al., 2011; Vine et al., 2012). This approach would not only provide a more definitive account of whether encoding object locations in relation to each other results in more precise spatial representations, but it may also allow for development of interventions in which older adults are trained to use an encoding strategy that facilitates the formation of more fine-grained representations.

As noted above, a shift in encoding strategies in older adults may be driven by age-related declines in the ability to formulate fine-grained spatial representations. In fact, this is a key theme/message that is featured throughout this thesis. However, the results from Chapter 2 where this was directly investigated, are inconclusive as no specific-age related deficits in the trials where a fine-grained spatial change was introduced were found. The interpretation for age-related degradation in the precision of spatial memory is largely driven by older adults displaying drift rates around zero during trials where fine-grained spatial changes were introduced, which are typically indicative of inability to extract useful information needed to solve the task. However, in situations when coarser spatial changes were introduced, older adult's drift rates were above zero, implying that they were more likely to extract useful information in those situations. In addition, as noted above, more investigation is needed to understand whether the encoding strategy that is more dependent on relating object locations to room-based cues is related to coarser encoding, and whether older adults show a preference towards this strategy due to difficulties in formulating more precise representations. Attempts to conduct a more systematic investigation of the precision of object location memory undertaken in the current PhD project, were confounded by the presence of the *perspective shift related bias*, thereby limiting the ability to draw conclusions regarding how ageing affects precision of object location memory. As a result, further research into age-related changes in the precision of object location memory is needed.

Declines in precision of spatial representations can provide a sensitive marker of cognitive decline that cannot be captured by spatial memory tasks which focus on more coarse spatial changes, i.e. the 4 Mountains Task (Hartley et al., 2007). Given the emerging evidence that the hippocampus may be associated with the precision of spatial memory (Kolarik et al., 2016, 2018) quantifying the precision of spatial memory may be particularly important in the context of early pre-symptomatic diagnosis of Alzheimer's Disease, which is associated with hippocampal neuropathy at early stages of the disease progression (Braak, Alafuzoff, Arzberger, Kretzschmar & Del Tredici, 2006; Pennanen et al., 2004) as well as pronounced spatial deficits as the disease progresses (for reviews see Coughlan et al., 2018; Lithfous, Dufour & Depres, 2013; Lester et al., 2017). Longitudinal research, focusing on the link between declines in the precision of spatial representation and development of AD later on, would provide an evaluation of the utility of spatial precision as a biomarker for AD.

A potential avenue for future research is to assess the precision of object location memory across different perspectives in a 3D setting. It would be hard to introduce perspective shifts without asking participants to move, thereby allowing them to use self-motion information to update the locations of the objects within the environment (Bulthoff & Christou, 2000; Waller, Montello, Richardson & Hegarty, 2002). An alternative that would allow a more comparable investigation of perspective taking processes is to use immersive virtual reality. In such settings, it would still be possible to “teleport” participants to new positions within the environment without self-motion, yet participants' position in the environment would be more clearly defined, as they would be “present” in the environment rather than having to adopt the position of the camera (see Discussion in Section 8.2.2.). Participants would also have access to stereoscopic cues that are likely to facilitate the understanding of egocentric distances and direction to the objects within the environment. This approach is likely to achieve two things: Firstly, it would allow us to investigate if the perspective shift related bias reported in the current thesis generalizes to memory for object locations in situations where participants' position in the environment is clearly defined and has access to both stereoscopic and monoscopic cues, or whether it is a phenomena that emerges due to use of static images. Secondly, if the results do indeed show that performance is no longer affected by the perspective-shift related bias, then this would allow a systematic investigation of age-related change in the precision of memory for object locations. A direct comparison of results obtained using 2D images and immersive virtual reality settings will inform a wider field of cognitive and vision research, as it would add to the understanding of how results obtained from studies that involve viewing of 2D stimuli translate into a 3D setting, where space is experienced egocentrically (Troje, 2019).

Lastly, the presence of the perspective shift related bias has been explained within the framework of the anchor and adjustment heuristic (Tversky & Kahelman, 1974). However, the ability of the heuristic to explain the effect has not been directly investigated. One possible way to investigate this, is to model specific predictions based on where participants would place the object if they rely on an egocentric vector as an initial anchor and then adjust it until a plausible response is reached. Such an approach would probably require systematic manipulation of the size of the perspective shift, as this would directly impact the initial starting point of the anchor following the perspective shift (if participants rely on an egocentric anchor), that participants then adjust when estimating object position. Modelling the adjustments that participants make is likely to be a non-trivial endeavour, one possible avenue to achieve this is to manipulate the range of plausible object positions, as this would have a direct effect on the adjustments that participants make. This may be possible through the use of additional objects in the environment. Specifically, the target object may be placed in between two cues, whose distance to each other is systematically manipulated. When the objects are closer to each other, the range of possible responses would be reduced. Furthermore, it is not clear how the perspective bias would translate to studies where larger perspective shifts are introduced, and whether participants would still rely on egocentric vectors as their anchors, or whether they will use different anchors.

8.4 Concluding statement

In conclusion, by combining eye-tracking and diffusion modelling the current thesis sheds light on age-related changes in memory for object locations across different perspectives, showing that ageing is associated with changes in the type of information that is used to encode object locations. It has also been shown that memory for object locations is not uniformly affected as in situations when coarse spatial representations are sufficient, older adults do not show any impairments, thereby highlighting a more specific impairment in the formation of fine-grained spatial representations. Furthermore, by applying psychophysics methods, a novel bias that is related to the introduction of perspective shift has been reported during tasks where participants are either asked to judge the direction in which objects have moved or when estimating the location of an object following a perspective shift. The presence of this bias is likely to be driven by uncertainty regarding the position of the object following the perspective shift, and may partly stem from the use of static images, which make it harder to infer distance and direction information to the object.

8. 5. References

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A Supplementary Materials for Chapter 2

A.1 LME Analysis with Sex as a Factor

Table A.1 Coefficients from d' LME analysis

	dPrime		
Predictors	Estimates	std. Error	t-value
Intercept	-0.155	0.120	-1.289
Age Group	0.400	0.169	2.373
Condition (Rotate)	-0.274	0.039	-7.043
Perspective (0° to 45°)	-0.800	0.093	-8.630
Perspective (45° to 135°)	-0.315	0.092	-3.442
Sex (Female)	-0.092	0.120	-0.769
Age Group: Condition (Rotate)	0.049	0.055	0.887
Age Group: Perspective (0° to 45°)	0.238	0.130	1.828
Age Group: Perspective (45° to 135°)	-0.279	0.129	-2.168
Condition (Rotate): Perspective (0° to 45°)	0.196	0.059	3.318
Condition (Rotate): Perspective (45° to 135°)	0.091	0.059	1.539
Age Group: Sex (Female)	-0.224	0.169	-1.326
Condition (Rotate): Sex (Female)	0.065	0.039	1.671
Perspective (0° to 45°): Sex (Female)	-0.072	0.093	-0.779
Perspective (45° to 135°): Sex (Female)	0.036	0.092	0.397
Age Group: Condition (Rotate): Perspective (0° to 45°)	-0.090	0.083	-1.086
Age Group: Condition (Rotate): Perspective (45° to 135°)	0.103	0.083	1.238

Age Group: Condition (Rotate): Sex (Female)	-0.077	0.055	-1.404
Age Group: Perspective (0° to 45°): Sex (Female)	-0.064	0.130	-0.491
Age Group: Perspective (45° to 135°): Sex (Female)	-0.038	0.129	-0.292
Condition (Rotate): Perspective (0° to 45°): Sex (Female)	0.010	0.059	0.168
Condition (Rotate): Perspective (45° to 135°): Sex (Female)	0.037	0.059	0.627
Age Group: Condition (Rotate): Perspective (0° to 45°): Sex (Female)	0.013	0.083	0.153
Age Group: Condition (Rotate): Perspective (45° to 135°): Sex (Female)	-0.055	0.083	-0.660

Significant t values (|t|≥1.96) in bold

A.2 LME analysis for Bias

Table A.2 Coefficients from Bias LME analysis

	Bias		
Predictors	Estimates	std. Error	t-value
Intercept	0.026	0.047	0.558
Age Group	-0.053	0.067	-0.789
Condition (Rotate)	0.129	0.019	6.805
Perspective (0° to 45°)	-0.358	0.055	-6.544
Perspective (45° to 135°)	-0.185	0.050	-3.702
Age Group: Condition (Rotate)	-0.014	0.027	-0.542
Age Group: Perspective (0° to 45°)	0.217	0.077	2.806
Age Group: Perspective (45° to 135°)	0.127	0.071	1.797
Condition (Rotate): Perspective (0° to 45°)	-0.099	0.028	-3.522

Condition (Rotate): Perspective (45° to 135°)	-0.050	0.028	-1.784
Age Group: Condition (Rotate): Perspective (0° to 45°)	0.044	0.040	1.103
Age Group: Condition (Rotate): Perspective (45° to 135°)	-0.045	0.040	-1.119

Significant t values (|t|≥1.96) in bold

A.3. Gaze parameter analysis

Table A.3 Means and t-test results for saccade and fixation parameters between younger and older adults from the Learning Phase

Gaze measure	Mean Young	Mean Older	Confidence Interval	t-value	p-value
Correct trials					
Saccade Frequency	2.93	3.79	[-1.16,-0.56]	-5.65	<.001
Average velocity	100.61	110.47	[-16.44, -3.27]	-2.83	.006
Peak velocity	180.03	213.69	[-54.11, -13.20]	-3.29	.003
Amplitude	3.85	4.47	[-1.05, -0.20]	-2.80	.008
Saccade duration (ms)	32.42	34.93	[-4.89, -0.12]	-2.08	.041
Fixation Frequency	3.14	4.08	[-1.23, -0.65]	-6.49	<.001
Fixation Duration (ms)	325.85	270.17	[33.26, 78.09]	5.01	<.001
Blink Frequency	0.38	0.43	[-0.06, 0.18]	-0.96	.326
Incorrect Trials					
Saccade Frequency	2.98	3.82	[-1.21, -0.48]	-4.66	<.001
Average velocity	102.09	111.43	[-17.22, -1.47]	-2.29	.020
Peak velocity	182.80	217.53	[-53.33, -16.13]	-3.75	.001
Amplitude	3.90	4.56	[-1.30, -0.18]	-2.65	.011
Saccade duration (ms)	32.60	35.06	[-1.13, -.018]	-2.65	.011
Fixation Frequency	3.16	4,10	[-1.24, -0.63]	-6.01	<.001
Fixation Duration (ms)	323.37	268.93	[31.78, 77.15]	4.89	<.001
Blink Frequency	0.39	0.45	[-0.19, 0.07]	-0.98	.315

Note: significant p values are in bold

B Supplementary Materials for Chapter 3

B.1. Effect Plots for Accuracy Analysis

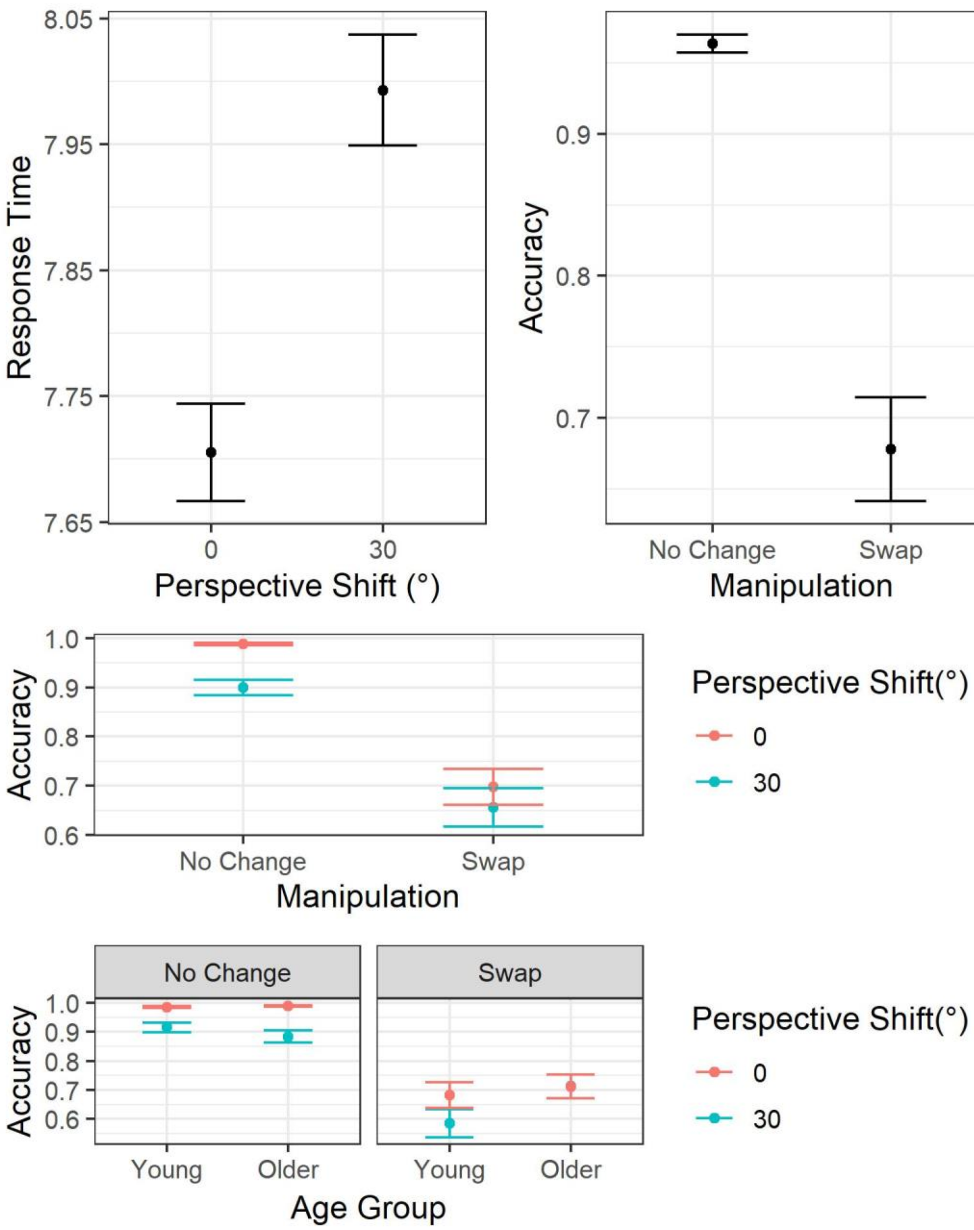

Figure B.1. LMM Effect plots for significant main effects and interactions for performance accuracy

B.2. Effect Plots for Response Time Analysis

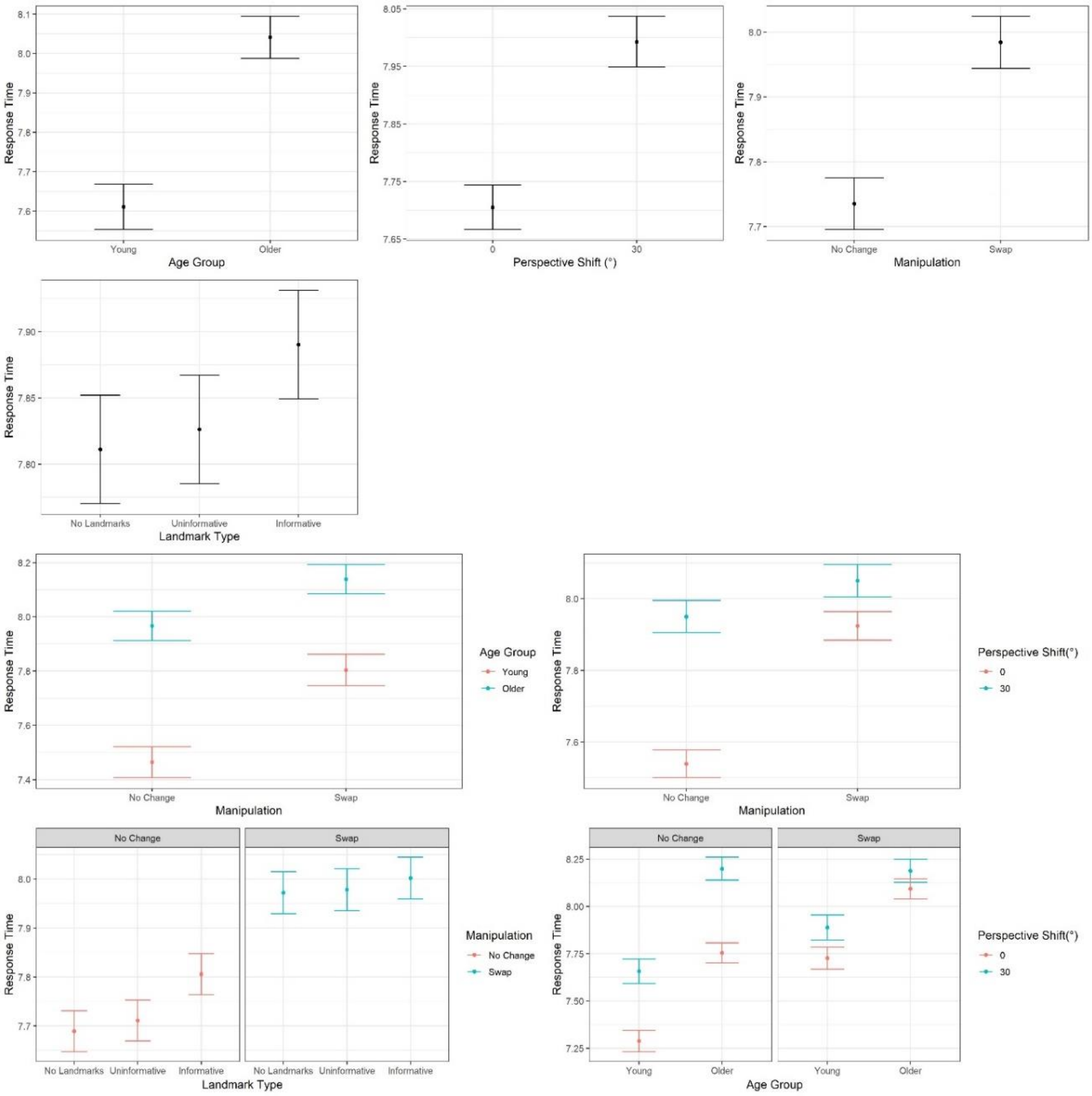

Figure B.2. LMM Effect plots for significant main effects and interactions for response times

B.3. Basic Fixation and Saccade Parameters.

Differences in basic fixation and saccade parameters were examined using the Bootstrap-t method (5000 resampling) with 20% trimmed means (Wilcox & Keselman, 2003). This method provides a robust estimation of central tendency as it reduces the probability of Type 1 error and bias and does not compromise power as median-based methods do (Wilcox & Keselman, 2003). During the 12 second encoding period, older adults made shorter and more frequent fixations as well as more frequent saccades (see Table B.1). Note however that these variables are not independent of each other especially in a fixed time interval.

Table B.1 Means and t-test results for saccade and fixation parameters between younger and older adults from the Learning Phase

Gaze measure	Mean Young	Mean Old	Confidence Interval	t-value	p-value
Saccade Frequency	2.51	2.84	[-0.55, -0.11]	-2.94	.004
Average velocity	138.98	134.85	[-9.51, 17.77]	-0.62	.524
Peak velocity	252.01	246.81	[-21.23, 31.63]	0.40	.697
Amplitude	6.81	6.41	[0.46, 1.25]	0.94	.337
Saccade duration (ms)	39.36	39.58	[-2.59, 2.13]	-0.20	.844
Fixation Frequency	2.67	3.11	[-0.67, -0.21]	-3.74	.001
Fixation Duration (ms)	286.23	255.88	[10.98, 50.77]	3.10	.005

Note: significant p values are in bold type

B.4. Gaze Behaviour at Test

As in the encoding phase of trials, an LME analysis with Age Group and landmark Type as fixed factors and by-subject and by-item random intercepts in the test phase showed that landmark Type was predictive of Dwell Time on landmarks (Table B.2). Specifically, we also found an Age Group and landmark Type interaction with older adults showing a larger increase in Dwell time on Informative compared to Uninformative landmarks compared to younger adults. Interestingly, at test older adults no longer displayed a larger increase in Dwell Time compared to younger adults between the No landmarks and Uninformative landmarks conditions, suggesting that they may have realised that Uninformative landmarks were not useful for solving the task.

Table B.2 Coefficients from Dwell Time on the top IA at Test LME analysis

	Dwell Time		
Predictors	Estimates	std. Error	t-value
(Intercept)	7.939	1.311	6.058
Age Group (Older Adults)	1.899	1.262	1.505
landmark Type (No landmarks)	-4.002	0.682	-5.868
landmark Type (Informative)	10.798	0.682	15.839
Age Group (Older Adults): landmark Type (No landmarks)	-0.872	0.462	-1.889
Age Group (Older Adults): landmark Type (Informative)	3.132	0.461	6.791

Significant t values (|t|≥1.96) in bold

C Supplementary Materials for Chapter 4

C.1. Additional information on 2D strategies

C.1.1. Screen-based strategy description

The screen-based strategy involves participants memorising the exact pixel position of the target object on the screen and comparing it to the screen position of the object at test (Figure C.1A). If participants have relied on this strategy, they would respond correctly on all trials (Figure C.1B). However, in situations when the target object moves by small distances, participants would need to be very precise in encoding the position of the target object on the screen as the smallest change in the position of the target object on the screen between encoding and test is 0.49 cm on the horizontal axis of the screen with the widths of 70.5 cm. As a result, it is possible that in such cases participants would not be able to reliably detect the direction in which the target object has moved on the screen. This does not explain the Congruency effect as even when the target object moves by a similar distance on the screen, performance is still higher for Incongruent compared to Congruent trials, particularly at smaller distances (Figure C.2).

C.1.2. Corner-Based Strategy

In this strategy participants memorise the 2D flattened relationship between the target object and the corner at encoding, and then comparing the same relationship at test i.e. the target object was to the left of the corner at encoding and now appears to be to the right of the corner (in the 2D plain) at test (Figure C.1A). If participants solely rely on this strategy, we would expect “maximal” Congruency Effect with ceiling level performance in the Incongruent trials and consistent incorrect responses on all (or most depending on which cue participants use i.e. if use poster would make correct responses at 61cm) Congruent trials Figure C.1B).

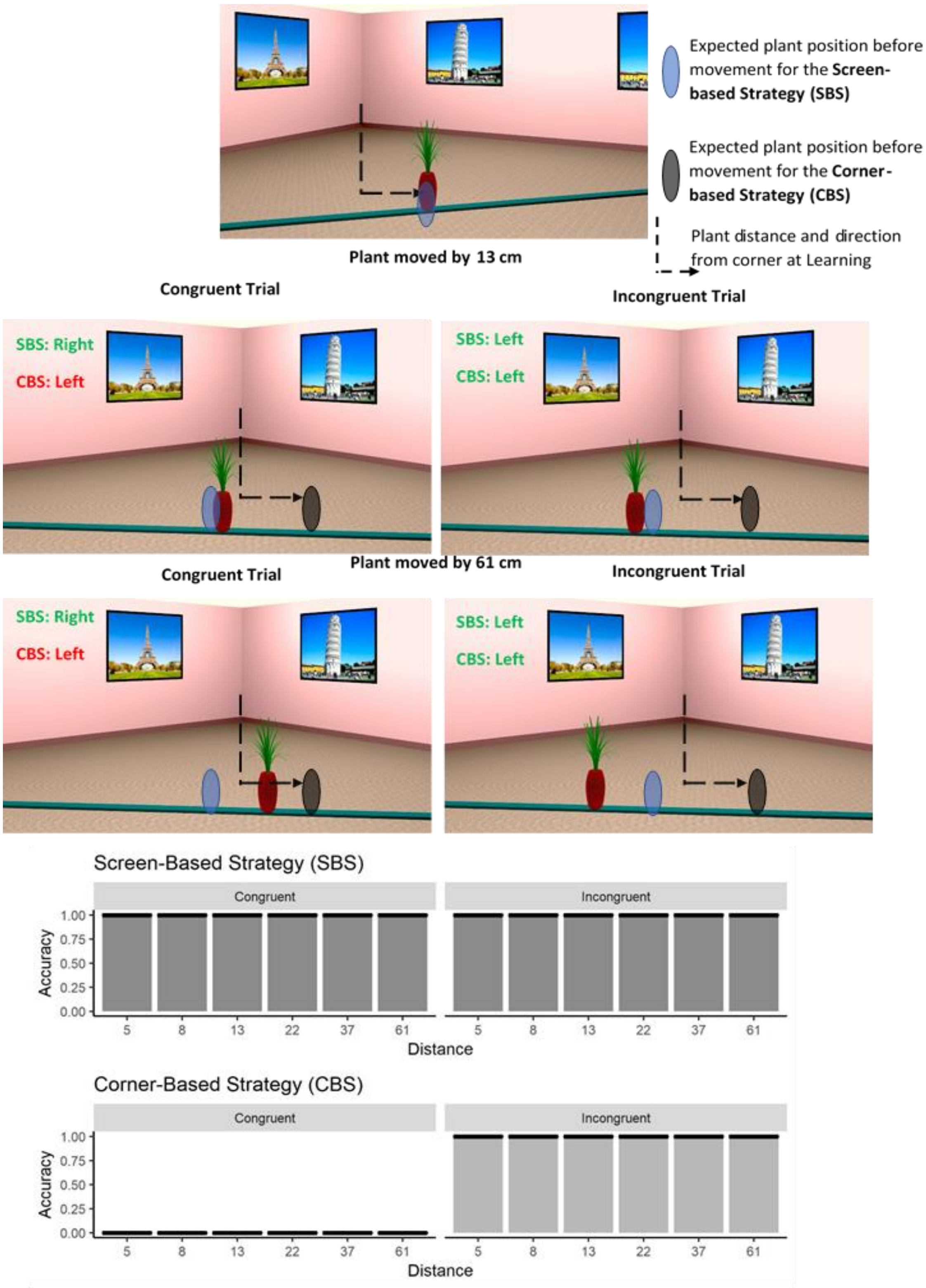

Figure C.1 A Schematic representing the Screen-Based Strategy (SBS) and the Corner-based Strategy (CBS); B Predicting performance for the SBS (upper panel) and CBS (lower panel) on Congruent and Incongruent trials.

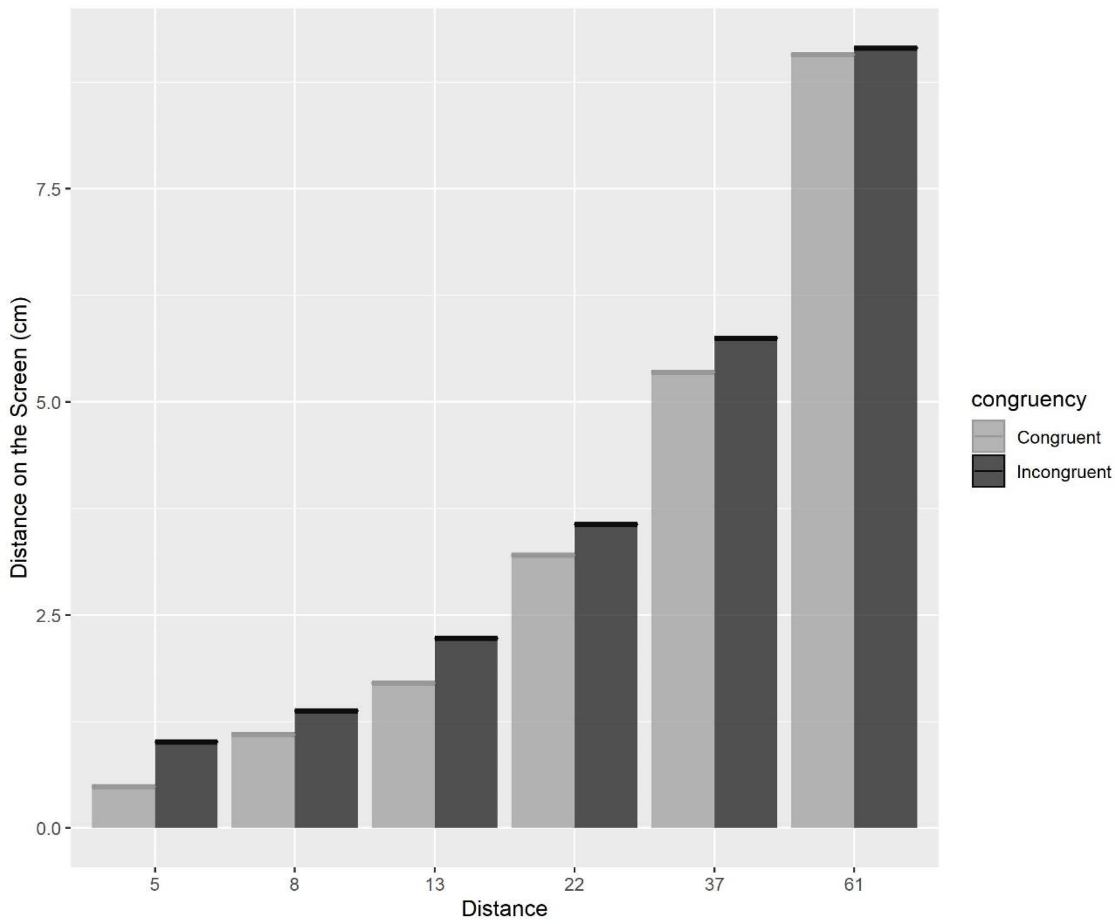

Figure C.2 Movement of the object on the screen for Congruent and Incongruent trials as a function of object displacement distance.

C.2. Follow up analysis in Experiment 2

To assess the extent to which the addition of objects helped to reduce the Congruency Effect, we split up the data to look at the No Object and Additional Objects conditions separately. A GLME analysis with Object displacement distance (ODD) and Congruency as fixed effects and a by-item and by-subject intercept and slope for Congruency showed main effects of ODD and Congruency in the No Object condition but only a main effect of ODD was found in the Additional Object condition. This analysis confirms that the addition of objects eliminated the congruency effect.

Table C.1 GLME Coefficient separately for No Objects and Additional Object conditions

	Accuracy		
Predictors	Coefficients	std. Error	z-value
No Objects			
(Intercept)	0.281	0.066	4.280
log(ODD)	0.251	0.052	4.858
Congruency (Congruent)	-1.019	0.244	-4.176
log(ODD) * Congruency (Congruent)	0.026	0.052	0.496
Additional Objects			
(Intercept)	0.784	0.095	8.240
log(ODD)	0.521	0.062	8.344
Congruency (Congruent)	-0.345	0.299	-1.152
log(ODD) * Congruency (Congruent)	0.110	0.062	1.767

Experiment 2 GLME model with ODD, Congruency, Condition, Rotation and Block as fixed effects

Table C.2 Coefficients from Accuracy GLME analysis

	Accuracy		
Predictors	Odds Ratios	std. Error	z-value
(Intercept)	1.397	0.039	8.665
Log(ODD)	1.295	0.025	10.317
Congruency (Congruent)	0.667	0.025	-16.207
Condition (Additional Objects)	0.872	0.029	-4.687
Block (Additional Objects 1st)	1.055	0.038	1.396
Rotation (High)	1.028	0.025	1.116
Log(ODD)* Congruency (Congruent)	1.038	0.025	1.497
Log(ODD)* Condition (Additional Objects)	0.929	0.025	-2.929
Congruency (Congruent) * Condition (Additional Objects)	0.788	0.025	-9.558
Log(ODD) * Block (Additional Objects 1st)	1.031	0.025	1.243
Congruency (Congruent) * Block (Additional Objects 1st)	0.947	0.025	-2.213
Condition (Additional Objects) * Block (Additional Objects 1st)	0.945	0.029	-1.946
Log(ODD) * Rotation (High)	1.013	0.025	0.522
Congruency (Congruent) * Rotation (High)	0.852	0.025	-6.443
Condition (Additional Objects) * Rotation (High)	1.047	0.025	1.825
Block (Additional Objects 1st) * Rotation (High)	1.003	0.025	0.139
Log(ODD) * Congruency (Congruent) * Condition (Additional Objects)	0.978	0.025	-0.882
Log(ODD)* Congruency (Congruent) * Block (Additional Objects 1st)	1.010	0.025	0.390
Log(ODD) * Condition (Additional Objects) * Block (Additional Objects 1st)	0.992	0.025	-0.327

Congruency (Congruent) * Condition (Additional Objects) * Block (Additional Objects 1st)	1.051	0.025	2.034
Log(ODD)* Congruency (Congruent) * Rotation (High)	1.000	0.025	-0.003
Log(ODD)* Condition (Additional Objects) * Rotation (High)	0.998	0.025	-0.095
Congruency (Congruent) * Condition (Additional Objects) * Rotation (High)	1.048	0.025	1.869
Log(ODD) * Block (Additional Objects 1st) * Rotation (High)	1.023	0.025	0.906
Congruency (Congruent) * Block (Additional Objects 1st) *Rotation (High)	0.962	0.025	-1.559
Condition (Additional Objects) * Block (Additional Objects 1st) * Rotation (High)	0.988	0.025	-0.489
Log(ODD) * Congruency (Congruent) * Condition (Additional Objects) * Block (Additional Objects 1st)	0.976	0.025	-0.991
Log(ODD)* Congruency (Congruent) * Condition (Additional Objects) * Rotation (High)	1.007	0.025	0.265
Log(ODD) * Congruency (Congruent) * Block (Additional Objects 1st) * Rotation (High)	1.008	0.025	0.303
Log(ODD)* Condition (Additional Objects) * Block (Additional Objects 1st) * Rotation (High)	1.010	0.025	0.384
Congruency (Congruent) * Condition (Additional Objects) * Block (Additional Objects 1st) * Rotation (High)	1.036	0.025	1.434
Log(ODD) * Congruency (Congruent) * Condition (Additional Objects) * Block (Additional Objects 1st) * Rotation (High)	0.973	0.025	-1.086

C.3. Follow-up analysis Experiment 3

We have separated younger and older adult's data to investigate the nature of the interaction between Age Group and Congruency as well as the interaction between Distance, Age Group and Congruency. To do so we ran two separate GLME models, one for each age group. The key differences between younger and older adults were that older adults showed a greater congruency effect, particularly at smaller distances (Table 3). This suggests that older adults may be more reliant on using 2D strategies at smaller distances when the task demands are higher and greater spatial precision is required.

Table C.3 GLME coefficients for younger and older adults

	Accuracy		
Predictors	Estimates	std. Error	z-value
Younger Adults			
(Intercept)	2.023	0.130	15.598
Distance	1.071	0.064	16.788
Congruency (Incongruent-Congruent)	-0.178	0.062	-2.877
Distance* Congruency (Incongruent-Congruent)	0.084	0.063	1.275
Older Adults			
(Intercept)	1.474	0.152	9.711
Distance	0.852	0.050	16.972
Congruency (Incongruent-Congruent)	-0.611	0.049	-12.575
Distance* Congruency (Incongruent-Congruent)	0.365	0.049	7.382

D Supplementary Materials for Chapter 5

D.1. Absolute error analysis

Table D.1 Coefficients from Absolute Errors (cm) LMM analysis

	Absolute Error		
Predictors	Estimates	std. Error	t-value
(Intercept)	36.076	1.112	32.452
Condition (Perception)	3.002	1.052	2.854
Cluster (Right)	-0.661	0.894	-0.739
Cluster (Mid-right)	0.038	0.895	0.043
Cluster (Centre-left)	0.087	0.895	0.097
Cluster (Left)	0.327	0.895	0.365
Cluster(Mid-left)	0.089	0.895	0.099
PSD (Left)	-0.391	0.573	-0.682
Condition (Perception)* Cluster (Right)	-0.632	0.393	-1.608
Condition (Perception)* Cluster (Mid-right)	0.209	0.395	0.530
Condition (Perception)* Cluster (Centre-left)	-0.244	0.393	-0.620
Condition (Perception)*Cluster (Left)	1.862	0.393	4.736
Condition (Perception)* Cluster (Mid-left)	0.105	0.394	0.266
Condition (Perception)* PSD(Left)	-0.486	0.446	-1.089

Cluster (Right)*PSD (Left)	3.271	0.894	3.658
Cluster (Mid-right)*PSD (Left)	1.401	0.895	1.565
Cluster (Centre-left)*PSD(Left)	0.413	0.895	0.462
Cluster (Left)*PSD (Left)	-2.459	0.895	-2.747
Cluster (Mid-left)*PSD(Left)	-0.452	0.895	-0.505
Condition (Perception)* Cluster (Right)*PSD(Left)	0.813	0.393	2.068
Condition (Perception)* Cluster (Mid-right)*PSD (Left)	1.529	0.395	3.870
Condition (Perception)* Cluster (Centre-left)*PSD (Left)	-0.969	0.393	-2.463
Condition (Perception)* Cluster (Left)*PSD (Left)	-0.399	0.393	-1.015
Condition (Perception)*Cluster(Mid-left)*PSD(Left)	-1.936	0.394	-4.918

D.2. Signed Errors Analysis

D.2.1. Signed errors

Signed errors were used to investigate if Condition, Start Position and Perspective Shift Direction (PSD) have an effect on the direction of the errors. Negative errors indicate errors to the left and positive errors are errors to the left.

Table D.2 Coefficients from Signed Errors (cm) LMM analysis

	Signed Errors (cm)		
Predictors	Estimates	std. Error	t-value
(Intercept)	3.355	1.480	2.267
Condition (Memory-Perception)	0.815	1.181	0.690
Cluster (Right)	-15.594	2.081	-7.493
Cluster (Mid-right)	-4.406	2.082	-2.116
Cluster(Centre-left)	0.111	2.082	0.053
Cluster(Left)	13.861	2.082	6.658
Cluster(Mid-left)	3.140	2.082	1.508
PSD (Right-Left)	-10.944	1.796	-6.093
Condition (Memory-Perception)* Cluster (Right)	0.748	0.595	1.257
Condition (Memory- Perception)* Cluster (Mid-right)	-3.206	0.598	-5.360
Condition (Memory- Perception)* Cluster(Centre-left)	-0.269	0.596	-0.452
Condition (Memory-Perception)* Cluster(Left)	-0.091	0.595	-0.153
Condition (Memory-Perception)* Cluster(Mid-left)	4.614	0.596	7.741
Condition (Memory-Perception)* PSD (Right-Left)	0.569	1.559	0.365
Cluster (Right)*PSD (Right-Left)	3.942	2.081	1.894
Cluster (Mid-right)*PSD (Right-Left)	-1.412	2.082	-0.678
Cluster(Centre-left)*PSD (Right-Left)	-2.342	2.082	-1.125

Cluster(Left)*PSD (Right-Left)	-5.245	2.082	-2.519
Cluster(Mid-left)*PSD (Right-Left)	-1.875	2.082	-0.901
Condition (Memory-Perception)* Cluster (Right)*PSD (Right-Left)	-0.897	0.595	-1.508
Condition (Memory-Perception)* Cluster (Mid-right)*PSD (Right-Left)	1.434	0.598	2.397
Condition (Memory-Perception)* Cluster(Centre-left)*PSD (Right-Left)	-0.629	0.596	-1.056
Condition (Memory-Perception)* Cluster(Left)*PSD (Right-Left)	-0.354	0.595	-0.594
Condition (Memory-Perception)*Cluster(Mid-left)* PSD (Right-Left)	-1.436	0.596	-2.409

E Supplementary Materials for Chapter 7

E.1. Absolute Distance Error analysis for Experiment 1

In addition to directional errors, the current design also allowed us to investigate distance errors. We calculated the absolute distance between the correct object position and the position that participants chose. An LMM analysis with PSD and Object Position as a fixed effect revealed that overall the distance between the location participants chose and the correct position was 1.00m (*Intercept*: β=1.003, SE=0.031, t=32.637). These distance errors were not affected by PSD or Object Position.

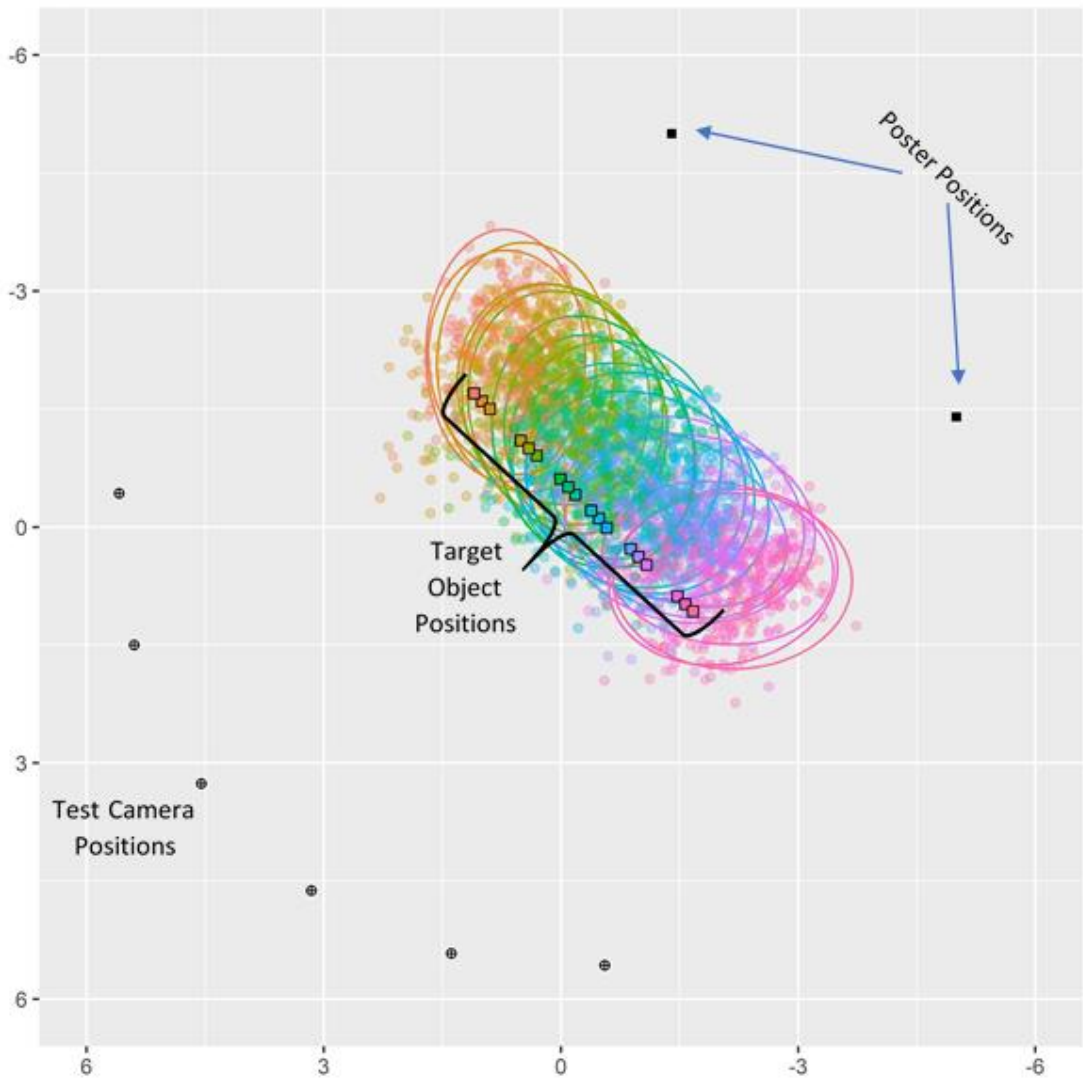

Figure E.1 Scatter plot of participants responses as a function of target object positions. Target object positions are depicted using multi-coloured squares, with each colour representing a different target object position, points that correspond in colour to the squares represent participants' responses for the given target object with error ellipses.

As apparent from Figure 1 participants’ systematically overestimated the distance of the object. To quantify this effect we subtracted the distance between the correct object position and camera position (i.e. the position from which the stimulus was rendered) from the distance between the chosen position and the camera position. An LMM analysis with PSD and Object Position as a fixed effect revealed that participants overestimated the distance of the object thereby placing it further away from the correct position (*Intercept*: $\beta=0.452$, $SE=0.050$, $t=9.088$). This overestimation was not affected by Camera Direction or Object Position.

We believe that this overestimation is driven by participants not using the base of the target object when reporting its position i.e. they might be using a higher part of the object as their reference point. To test that, we calculated predicted responses if participants used the centre of the plant pot as their reference point for the target object, and found that the average distance overestimation was 43.17 cm which is very similar to the amount of overestimation we observed in our results (45.20 cm).

Consequently, we propose that the systematic distance overestimation arose because participants did not use the base of the object when encoding and then estimating its position after the perspective shift. Specifically, during the analysis, we assume that participants indicate the position of the object using the base as a reference point and by clicking on the floor where the base would be. However, if participants do not use the base of the object but instead use a part of the object that is higher up, such as the centre of the plant pot, this would lead participants to click on a floor location that is systematically further away from the position of the virtual camera.

E.2. Absolute Distance Error analysis for Experiment 2

Table E.1 LMM coefficients for participants Absolute Distance Errors (m)

	Absolute Distance Error (m)		
Predictors	*Estimates*	*std. Error*	*t-value*
(Intercept)	0.658	0.029	22.556
Environment (Additional Columns)	-0.083	0.013	**-6.471**
Camera Movement (Congruent)	0.163	0.016	**10.298**
Camera Movement (Incongruent)	0.074	0.016	**4.707**
Camera Movement (Rotation Only)	0.034	0.016	**2.134**
Camera Movement (Translation Only)	0.114	0.016	**7.268**
Age Group (Older)	0.010	0.028	0.372
Environment (Additional Columns)*Camera Movement (Congruent)	-0.003	0.016	-0.181
Environment (Additional Columns)*Camera Movement (Incongruent)	0.006	0.016	0.413
Environment (Additional Columns)*Camera Movement (Rotation Only)	0.007	0.016	0.459

Environment (Additional Columns)*Camera Movement (Translation Only)	-0.006	0.016	-0.388
Environment (Additional Columns)*Age Group (Older)	0.020	0.009	**2.167**
Camera Movement (Congruent)*Age Group (Older)	0.001	0.011	0.084
Camera Movement (Incongruent)*Age Group (Older)	-0.005	0.011	-0.459
Camera Movement (Rotation Only)*Age Group (Older)	-0.016	0.011	-1.386
Camera Movement (Translation Only)*Age Group (Older)	-0.004	0.011	-0.332
Environment (Additional Columns)*Camera Movement (Congruent)*Age Group (Older)	0.013	0.011	1.181
Environment (Additional Columns)*Camera Movement (Incongruent)*Age Group (Older)	0.010	0.011	0.895
Environment (Additional Columns)*Camera Movement (Rotation Only)*Age Group (Older)	0.007	0.011	0.598
Environment (Additional Columns)*Camera Movement(Translation Only)*Age Group (Older)	0.004	0.011	0.331

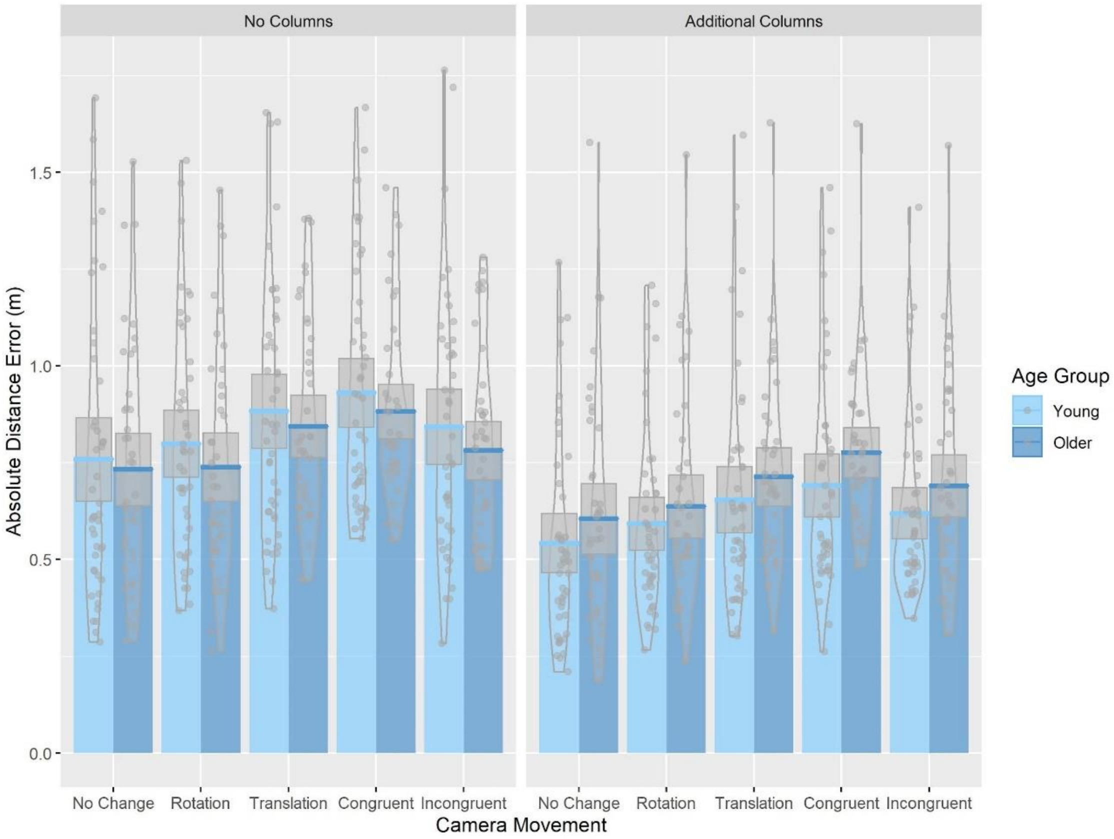

Figure E.2 Absolute distance error as a function of Camera Movement and Age Group in the No Columns condition (left panel) and Additional Columns (right panel)