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**Egocentric and Allocentric Spatial Reference Frames in Aging: A Systematic Review**

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## Highlights

- Aging does not affect egocentric navigational strategies, whereas allocentric and switching abilities show a gradual decline;
- A general age-related weakening of spatial memory has been observed, even if not frame-specific;
- Executive functions may play a critical role in age-related spatial difficulties.

## Abstract

Aging affects many aspects of everyday living, such as autonomy, security and quality of life. Among all, spatial memory and spatial navigation show a gradual but noticeable decline, as a result of both neurobiological changes and the general slowing down of cognitive functioning. We conducted a systematic review using the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) guidelines to identify studies that specifically investigated the role of allocentric and egocentric frames in healthy aging. Concerning spatial navigation, our results showed a preservation of egocentric strategies, along with specific impairments in the use of allocentric and switching abilities. Regarding spatial memory, instead, outcomes were more divergent and not frame-specific. With this perspective, spatial impairments were discussed considering the cognitive profile of mild cognitive impairment (MCI) and Alzheimer's Disease (AD).

**Keywords:** aging; egocentric reference frame; allocentric reference frame; navigation; spatial memory

## 1. Background

Spatial abilities play an important role in everyday life, as they allow individuals to navigate in familiar or unfamiliar environments, locate objects and interact with them, and memorize their position.

For the first time, Tolman (Tolman, 1948) introduced the idea that individuals use “cognitive maps” to represent spatial information and navigate in the environment. Specifically, it is traditionally accepted the distinction between two types of “frames” used to represent spatial information: The egocentric frame, which includes spatial information about the location of the individual in the environment, and the allocentric frame, which involves the spatial information about the position of objects relative to each other.

The egocentric frame is based on subject-to-object relations and leads to the creation of body-centered representations (self-centered representations). According to Goodale and Milner (Milner and Goodale, 1993), an egocentric frame is fundamental in visuomotor control, as the planning and execution of an action needs the representation of the target location in relation to the body. Differently, the allocentric frame is supposed to be acquired later in life (Bremner and Bryant, 1977; Burgess et al., 2004; Siegel and White, 1975) and is founded on world-based coordinates; within this reference, locations are described using object-to-object relationships, independently from the subject’s point of view (world-centered representations). Nowadays, an increasing number of cognitive models are focusing on the relation between egocentric and allocentric frames, trying to explain how these processes combine to provide healthy and efficient spatial abilities (Avraamides and Kelly, 2008).

Generally, most authors agree that both frames allow for the development of spatial representations necessary to accomplish navigation (Burgess, 2006). Successful navigation does not rely on one single frame, but requires the ability to switch and combine different spatial strategies flexibly, depending on the environmental requirements. Interestingly, a great variability has been observed, as individuals may differ in the way they preferentially use egocentric or allocentric strategies (Marchette et al., 2011).

As underlined by a growing number of studies, spatial abilities develop from childhood to adulthood, and then start to deteriorate with aging (Gazova et al., 2013; Ruggiero et al., 2016; Techentin et al., 2014). Indeed, older adults often report reduced spatial skills, with important consequences on quality of life, safety and autonomy. These spatial impairments can have negative repercussions, as the elderly may avoid navigating and exploring new environments (Burns, 1999), which in turn may further affect their lifestyle.

With these premises, the aim of this systematic review is to provide an overview of the current experiments investigating the role of allocentric and egocentric spatial abilities in aging.

### 1.1 Neurobiological underpinnings of allocentric and egocentric reference frames

An increasing number of studies have investigated the neurobiological correlates of egocentric and allocentric frames, pointing out both different specific neural circuits and a shared bilateral fronto-parietal network (Zaehle et al., 2007). The allocentric frame is supported mainly by hippocampus place cells (Ekstrom et al., 2003; O’Keefe and Dostrovsky, 1971; Ono et al., 1993), which fire in specific spatial locations independently from the subject’s orientation. Other brain areas supporting allocentric processing are the

parahippocampal (Aguirre et al., 1996; Committeri et al., 2004; Janzen and van Turenout, 2004; Rosenbaum et al., 2004; Wolbers and Buchel, 2005; Zhang and Ekstrom, 2013) and the retrosplenial cortex (RSC) (Auger and Maguire, 2013; Epstein and Higgins, 2007; Iaria et al., 2007; Takahashi et al., 1997; Wolbers and Buchel, 2005; Zhang and Ekstrom, 2013). Differently, the egocentric frame relies primarily on the caudate nucleus and, more generally, on the medial parietal lobe (Cook and Kesner, 1988; Potegal, 1972), with a major involvement of the posterior parietal area 7 in the integration of different egocentric representations (Burgess, 2008). Interestingly, subjective variances in strategy preference have been found to reflect neurobiological differences: Allocentric learners, for example, show more grey matter in the hippocampus compared to egocentric learners (Bohbot et al., 2011).

The ability to switch from one frame to another, specific of the environmental navigation, involves the posterior cingulate cortex (PCC) and the RSC (Byrne et al., 2007; Maguire, 2001; Vann et al., 2009; Wolbers and Hegarty, 2010). Consistently, Burgess and colleagues proposed the Boundary Vector Cells Model, defining white matter connections between hippocampus and neocortex as the main pathway for integration (Burgess et al., 2001) and, specifically, identifying the RSC as the main cortical structure involved in the combination of head-direction information with scene representations (Burgess et al., 2001). Recent evidence supported this model (Boccia et al., 2016a; Boccia et al., 2017; Kravitz et al., 2011) and confirmed the role of RSC in the allocentric coding of head directions (Sulpizio et al., 2016). In addition, some studies have pointed out cells that are supposed to be specific for analyzing and converting spatial information: Grid cells, mainly located in the entorhinal cortex, are involved in updating spatial information in relation to self-motion (Hafting et al., 2005), whereas head-direction cells, located in many brain areas like the RSC, dorsal thalamic nuclei and entorhinal cortex, are thought to update information on the basis of head direction (Taube et al., 1990).

## **1.2 The relation between spatial navigation and spatial memory**

Spatial navigation is the ability to find and maintain a route from one place to another. It represents a complex and multi-componential cognitive skill, as it involves the elaboration of different types of information, such as sensorimotor information about self-position or about self-motion. On the other hand, spatial memory is the ability to encode, store and retrieve spatial information through the construction and storage of spatial representations (O'keefe and Nadel, 1978; Tolman, 1948). These two spatial abilities are strictly connected. For instance, specific mnemonic impairments have been shown to affect navigational performances (Aguirre and D'Esposito, 1999; Claessen and van der Ham, 2016).

Spatial information is provided by the sensory organs and it is then collected based on the position of the body in the external space. As a consequence of head and body movements within an environment, egocentric spatial maps need to be continuously integrated and updated by proprioceptive, vestibular and motor signals in order to maintain accurate spatial representations. This process would serve as an egocentric frame, which corresponds to the concept of "body schema" (Galati et al., 2010), and it involves a parieto-frontal cortical network, with a major role played by the posterior parietal cortex and the premotor cortex (Galati et al., 2001; Galati et al., 2000; Neggers et al., 2006; Vallar et al., 1999). Beyond this "online" spatial update providing updated information about landmarks, objects and obstacles (Avraamides and Kelly, 2008), our brain is also

able to build and store stable representations based on the allocentric frame, responsible for the “offline” update of memorized spatial locations (Amorim et al., 1997; Avraamides and Kelly, 2008). The precuneus would play a critical role in this process (Wolbers et al., 2008).

Some cognitive models have been proposed to explain how spatial memory supports online and offline navigation. The “self-reference” model, for instance, postulates the existence of two systems: The first system is involved in the storage of orientation-free allocentric representations in long-term memory, while the second one plays a key role in encoding and updating spatial information by analyzing egocentric relations at two different levels – perceptual-motor and representational levels. In the perceptual-motor level, representations are created in order to guide movement at the immediate time; the representational level, instead, communicates with the allocentric system, in order to update and retrieve stored representations (Easton and Sholl, 1995).

Navigation occurs thanks to both allocentric (or survey) and egocentric (or route) strategies (Berthoz, 1997; Burgess, 2006; Maguire et al., 1998) and to the ability to flexibly shift between them (Aadland et al., 1985; Byrne et al., 2007). Conversely, the role of frames in spatial memory has been more debated: Although some models proposed that spatial memory is mainly supported by egocentric representations (Bennett, 1996; Filimon, 2015; Wang, 2002), many researches evidenced the existence of allocentric representations at the single-neuron level (Ekstrom et al., 2003; Hafting et al., 2005; O'keefe and Nadel, 1978; Ono et al., 1991; Rolls, 1999; Taube et al., 1990). Therefore, both systems of reference would be essential to structure spatial information in memory.

An increasing number of studies have investigated the neurobiological underpinnings of egocentric and allocentric navigation in humans. Egocentric navigation is supported by landmark knowledge (i.e. parahippocampal place area) (Epstein and Ward, 2010), egocentric representations in the parietal cortex (i.e. precuneus and cuneus, inferior parietal lobe) and heading information (i.e. head-direction cells in the RSC) (Nemmi et al., 2017). On the other hand, allocentric navigation is supposed to rely on the right hippocampus and, more specifically, on a neural network involving place cells (hippocampus) and grid cells (entorhinal cortex) (Maguire et al., 1998; O'keefe and Nadel, 1978; Tolman, 1948) together with the superior temporal gyrus, thought to be responsible for the formation and use of allocentric representations through the elaboration of spatial relations (Nemmi et al., 2017). Interestingly, a recent meta-analysis has investigated the neural correlates of navigation considering fMRI studies in healthy subjects (Boccia et al., 2014). Allocentric strategies activated the bilateral parahippocampal gyrus, precuneus, lingual gyrus, frontal cortex, right middle temporal gyrus, middle occipital gyrus, and the left superior temporal gyrus. This latter structure is supposed to be involved in the formation and use of allocentric representations through the elaboration of spatial relations (van Asselen et al., 2008). Conversely, egocentric strategies activated the parahippocampal gyrus, cerebellum, PCC, right caudate nucleus and the amygdala. Other clusters were observed in the left parahippocampal gyrus and posterior cingulate cortex, bilateral precuneus, and in the right superior and middle occipital gyrus, middle frontal gyrus and superior frontal gyrus. Confirming other studies (Committeri et al., 2004; Galati et al., 2000), contrast analysis revealed a partially overlapping neural network between egocentric and allocentric representations, including the fusiform gyrus, insula, lingual gyrus, precuneus, cuneus and superior frontal

lobe bilaterally: The allocentric frame recruited, indeed, a subset of areas which were also designated to the egocentric encoding. On the other hand, egocentric strategies showed more extended activations, involving the superior occipital gyrus, angular gyrus and the precuneus in the right hemisphere (Boccia et al., 2014).

The most important shared structure between memory and navigation is the hippocampus: Hippocampal formation is indeed supposed not to be space-specific, but to encode for different information. Specifically, representations of objects and events together with their spatio-temporal context would be integrated in this neural structure (Bergouignan et al., 2014; Glenberg and Hayes, 2016; Good, 2002). During both navigation and memory, hippocampal cells are thought to play a key role in the creation of mental maps (Milivojevic and Doeller, 2013). According to Eichenbaum and Cohen's model, the hippocampus is involved in a sort of "relational processing mechanism", that allows for the creation of relational representations that bind experiences and link memories (Eichenbaum and Cohen, 2014). Consistently, the hippocampus is supposed to play a role in navigation by detecting the spatial context and by creating spatially coherent scenes. Moreover, it encodes events as relational maps of objects and actions in a context, represents routes as episodes defined by sequences of places, and binds new representations with the pre-existent information. The hippocampus would not be involved in navigational computations per se, but it would play an important role in navigation by supporting spatial memory.

### **1.3 Physiological and pathological decline of spatial reference frames**

Depending on specific neural systems, spatial abilities and allocentric/egocentric computations undergo a physiological decline through life, reflecting the underlying changes in the aging brain.

By definition, aging is a physiological process affecting all aspects of everyday life. Post-mortem and neuroimaging studies have revealed important age-related neurobiological changes, with a general widespread reduction of white matter integrity and of grey matter volume, mainly due to loss of neuropil (Burke and Barnes, 2006; Raz and Rodrigue, 2006). Primary cortices seem to remain almost intact, whereas associative cortices are more vulnerable to aging deterioration: Above all, the prefrontal cortex (PFC) shows a higher decline (Raz and Rodrigue, 2006). Importantly, the hippocampus (Raz and Rodrigue, 2006) and caudate nucleus (Gunning-Dixon et al., 1998; Raz et al., 2003), two important structures in spatial cognition, show a great loss of volume. As a consequence, aging leads to an overall weakening of cognition: The elderly show difficulties in episodic memory (Tromp et al., 2015), working memory (Kirova et al., 2015), executive functions (Kirova et al., 2015) and, above all, in spatial skills, like spatial memory (Iachini et al., 2009; Nemmi et al., 2017; Wolbers et al., 2014) and spatial navigation (Lithfous et al., 2013; Moffat, 2009), especially regarding the creation of cognitive maps (Iaria et al., 2003; Moffat and Resnick, 2002) and path integration (Allen et al., 2004; Harris and Wolbers, 2012; Mahmood et al., 2009). This cognitive decline is usually shaped by many factors, including education (Cohen and Syme, 2013; Zahodne et al., 2015), cognitive reserve (Tucker and Stern, 2011), genetic factors (Deary et al., 2004) or, concerning navigation, even gender (Clint et al., 2012).

The relation between aging and spatial frames has been investigated using a great variety of cognitive tasks and focusing on different cognitive domains, like spatial memory, spatial navigation, mental rotation or

spatial encoding. Many studies have noted impaired allocentric computations, usually ascribed to hippocampal deterioration. On the other hand, the effect of aging on the egocentric frame is more controversial, especially depending on the considered cognitive domain. Nevertheless, age-related allocentric impairments have also been given a different interpretation, possibly reflecting a decline in the ability to switch from egocentric to allocentric frame.

Adding to the confusion in the literature, there is strong evidence pointing toward specific spatial deficits in certain pathological conditions, such as Mild Cognitive Impairment (MCI) and during the first stages of Alzheimer's Disease (AD) (Serino et al., 2014).

MCI patients are characterized by a slight but noticeable decline in cognitive abilities, specifically observable in memory. These patients usually report a higher risk of converting to AD, a neurodegenerative condition that leads to a gradual loss of memory, speech, movement and thinking skills. From a neurobiological point of view, these patients show an accumulation of plaque and tangles across many brain areas, mainly in the temporal lobe.

During the first stages, AD is primarily characterized by episodic memory impairments and, interestingly, by topographical disorientation, namely the inability of navigating in a familiar environment, learning new routes, recognizing places or using maps for navigation (Guariglia and Nitrini, 2009). As noted above, navigation requires a flexible adoption of both egocentric and allocentric strategies; consistently, MCI and AD patients have been reported to show both egocentric and allocentric spatial impairments (Hort et al., 2007; Laczó et al., 2011; Laczó et al., 2012; Laczó et al., 2010; Laczó et al., 2009), with a major decline of the allocentric hippocampal-dependent frame (Burgess et al., 2006). In addition, a specific impairment was evident in the translation of representations between the egocentric and allocentric frame (Morganti et al., 2013; Pai and Yang, 2013). These findings could reflect the progressive neurodegeneration of the medial temporal lobe and, especially, of two important spatial structures: Hippocampus and RSC (Pennanen et al., 2004). According to Serino and colleagues (Serino et al., 2014), such degeneration would lead to difficulties in the construction, storage and retrieval of spatial representations. Therefore, patients would no longer be able to define or remember what direction to go within an environment (heading disorientation). Consistently with these outcomes, Serino and colleagues have proposed spatial impairments as possible markers of AD onset (Serino et al., 2014).

This evidence raises an important question: Is navigation decline a specific disease-predictor or is it just a physiological consequence of age-related neurobiological and neuropsychological changes?

#### **1.4 Objectives**

To our best knowledge, no systematic review has focused on the role of spatial reference frames in age-related navigation. Thus, the aim of this paper is to provide an overview of current evidence concerning allocentric and egocentric spatial frames among older adults, taking into account two cognitive domains: spatial memory and spatial navigation. The two main objectives of this paper are: (1) Understand how aging affects allocentric and egocentric spatial abilities and (2) illustrate the current neuropsychological and neurobiological theories explaining such decline. To give a wider comprehension of age-related spatial



impairments, results will be discussed highlighting the current literature on navigational deficits observed during the first stages of AD.

## **2. Methods**

We followed the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) guidelines (Moher et al., 2009).

### **2.2 Search strategy**

To collect relevant publications, a computer-based research was performed (December, 2016). We searched in two high-order databases, PubMed and Web of Science (Web of Knowledge), by using the following strings: (“Aging”) OR (“Ageing”) AND (“Allocentric” OR “Egocentric” OR “Spatial Navigation” OR “Spatial Memory”). This search produced a total of 11099 articles. After removing duplicate papers, we made a first selection by reading titles and abstracts. A total of 145 articles were retrieved. We finally selected experimental publications by applying selection criteria. This procedure resulted in 21 experimental papers. The search was performed for publications in the English language. We provide more details in **Table 1** and in the flow diagram (**Figure 1**), with the purpose of making this search repeatable in future.

### **2.3 Selection criteria**

We included all the experimental studies on aging that investigated allocentric and/or egocentric impairments in two cognitive domains: Spatial navigation and spatial memory. We included only studies specifically highlighting the role of allocentric and egocentric abilities and clearly discussing results with frames’ theories. Moreover, we selected only studies in which the sample was composed of healthy elderly people, excluding mild cognitive impairment (MCI) and Alzheimer’s Disease (AD). We excluded studies comparing the healthy elderly to pathological samples, like MCI or AD, and included only studies in which healthy old and/or young subjects were compared.

We excluded from the analysis non-English papers and studies that omitted the inclusion criteria. We also excluded articles lacking experimental data or articles that did not have an available full-text. Moreover, we excluded the following types of manuscripts: Conference papers, rapid communications, brief reports, reviews, meeting abstracts, notes, case reports, letters to the editor, editor’s notes, extended abstracts, proceedings, patents, editorials and other editorial materials.

We tried to contact the corresponding authors of the included articles when needed, in order to obtain missing or supplementary data.

### **2.4 Quality assessment and data abstraction**

To control for the risk of bias, PRISMA recommendations for systematic literature analysis have been strictly followed. Studies were independently selected by two different authors (D.C. and C.T.), who first analyzed titles and abstracts and subsequently selected the full papers meeting the inclusion criteria, resolving

disagreements through consensus.

The data extracted from each included study were as follows: Author(s), Year, Sample(s), Primary spatial task(s), Cognitive domain and Primary outcomes (**table 2** and **table 3**).

### **3. Results**

To provide the state of the art, the role of allocentric and egocentric frames in navigation and spatial memory will be reviewed, taking into account the main outcomes and providing a brief description of the spatial tasks adopted. Considering that some studies investigated both cognitive domains, we classified papers based on their primary outcome. In light of the results of the listed studies, current neurobiological and neuropsychological theories on age-related spatial decline will be reported and discussed. A synthesis of results is reported in **Table 2** (spatial navigation) and **Table 3** (spatial memory).

#### **3.1 The effect of aging on allocentric and egocentric frames in spatial navigation tasks**

After applying the inclusion criteria, ten experimental studies focusing on spatial navigation have been included.

Two experimental studies pointed out an age-related preferential use for egocentric rather than allocentric strategies during navigation (Goeke et al., 2015; Rodgers et al., 2012). Rodgers and colleagues assessed aging effects on navigational abilities, adopting a virtual version of the Morris Water Maze Task (hMWM) (Rodgers et al., 2012). The Morris Water Maze Task, also called Morris Water Navigation Task, is one of the most used allocentric spatial tasks to assess spatial abilities in rodents. Rats are positioned in a circular pool and are required to find a visible or invisible podium lifting them out of the water. To assess spatial navigation, many human versions of this task have been developed, mainly adopting the use of virtual environments. In Rodgers' study, the virtual hMWM consisted of a circular pool with four objects located on its edge and two objects located more distally in the environment. Consistent with the classical version, participants were required to locate a hidden platform. After navigation trials, three different maps of the virtual environment were shown to all subjects (one with objects surrounding the pool, one with only room geometry, one with both cues), who were asked to exactly locate the hidden platform found before. In the hMWM, elderly people achieved worse results as they travelled longer distances before finding the hidden platform. Conversely, no differences were observed in the allocentric mapping test. Thus, aging may affect allocentric navigation, but not the retrieval of spatial information encoded through the use of an allocentric frame. In addition, participants were assessed on their preferential navigational strategy through a Virtual Y Maze task, consisting of a three-arm virtual road. After some training trials in which participants were asked to navigate toward different goal areas, strategy preference was assessed and participants were asked to move toward one of the previous goal areas. Egocentric preference was defined as the use of the same route learnt during training, regardless of absolute location. On the other hand, the allocentric category included participants who moved to the same absolute location, even if it required taking a different route. While younger participants were almost equally distributed between strategies (46% egocentric, 54% allocentric), older adults were more likely to adopt an egocentric strategy (82% egocentric, 18% allocentric). Interestingly, only young participants, who preferred allocentric strategies,

performed better on the cognitive mapping test and on the Morris Water Maze Task. Given these outcomes, authors have concluded that age-related alterations in the neural system supporting allocentric computations, especially in the medial temporal lobe, may drive the elderly to more frequent use of egocentric rather than allocentric strategies. With the same purpose, Goeke and colleagues adopted an online navigation task, using the tunnel paradigm (Goeke et al., 2015). After a visually presented path, participants were asked to choose one of the four arrow keys presented on a screen, which indicated the way back to the starting position. The difference between adopting an allocentric or egocentric frame depended on whether participants updated their heading along with the stimulus turn. Consistent with increasing literature pointing toward age-related navigation difficulties, results showed worse navigational performances in the elderly compared to younger participants. Interestingly, no significant effect of sex on preferential strategy was observed. Concerning age, older adults were more likely to adopt an egocentric strategy, even if such preference was not statistically significant. On the contrary, cultural background was the only significant factor influencing spatial strategies. North Americans, for instance, adopted more often an allocentric frame when compared to Europeans; on the other hand, South Americans clearly preferred navigation relying on an egocentric frame.

Three studies have specifically underlined age-related impairments in navigation depending on an allocentric frame (Gazova et al., 2013; Moffat et al., 2006; Wiener et al., 2012). However, no study has shown age-related impairments in egocentric navigation. To assess the progressive deterioration of spatial frames among different age samples, Gazova and colleagues used a real-space version of the hMWM (Gazova et al., 2013). The spatial setting was the Blue Velvet Arena, a cylindrical arena surrounded by a high dark blue velvet curtain. Two different subtests were performed: The egocentric subtest and the allocentric subtest. During the egocentric subtest, participants were asked to locate a target goal by using the starting position, as no other distal orientation cue was presented. In the allocentric condition, instead, participants could orientate in the virtual environment thanks to the use of two distal cues at the perimeter; in this condition, the starting position was no more related to the goal location. Finally, a training condition (the allocentric-egocentric condition) was performed, which required locating the goal by using both the starting position and the distal cues. Results showed that 71-84-year-old participants performed significantly worse in terms of accuracy during allocentric trials when compared to younger individuals or even to 60-70-year-old subjects. No differences were observed during egocentric tasks. Performing a linear regression analysis, the authors pointed out a quadratic effect of age on allocentric abilities, which were more likely to deteriorate very rapidly as age advanced; specifically, the allocentric decline was observable starting at about 70 years. No effect of aging on egocentric frame was observed. Confirming these results, Wiener and colleagues developed a virtual environment to assess navigation impairments in the elderly (Wiener et al., 2012). The virtual environment consisted of a virtual route with 11 four-way intersections, each marked by unique landmarks (the image of an object in a cube). During the training phase, participants were transported along the route and were asked to memorize as accurately as possible the surrounding environment. Successively, three different spatial tasks were performed: The Route Direction Task, the Intersection Direction Task and the Landmark Sequence Task. During the Route Direction Task, participants were transported either in the same (route repetition) or in the opposite (route retracing) direction and were asked to identify the travel direction. In the Intersection Direction Task,

participants were moved along the route and stopped at an intersection, where they had to indicate the right direction to reach the starting (route retracing) or the ending point (route learning). Finally, participants performed the Landmark Sequence Task, during which three images were presented. The task required indicating the next landmark that would have been met if the navigation had not been stopped. Compared to younger participants, the elderly performed worse on route retracing, whereas accuracy on route repetition between groups was the same. Moreover, older participants did not show a learning effect across retracing trials, while they did during repetition ones. Egocentric strategies are supposed to be adopted to solve route repetition tasks. Route retracing, instead, requires abstracting from viewpoint-dependent memory involving therefore the allocentric computation of landmarks in relation to the target (Lipman and Caplan, 1992; Trullier et al., 1997; Wiener et al., 2012). As suggested by authors, retracing impairments, thus, supported evidence toward specific allocentric impairments, possibly reflecting age-related hippocampal decline; moreover, the lower level of learning across trials may also explain why the elderly show greater difficulties when navigating in novel rather than familiar environments. Finally, one study has investigated the neurobiological underpinnings of allocentric navigation in a virtual environment (Moffat et al., 2006). Participants were asked to navigate using an allocentric frame in a virtual environment consisting of room and hallways and to memorize six different objects located along routes. As the control condition, participants were also assessed on a cognitive mapping test, in which they were asked to construct a map of the environment, and on a directional task, in which they were required to locate a specific object taking as short a time as possible. This condition was performed to make sure participants were maintaining high vigilance while navigating. Behavioural results highlighted a better navigational performance in younger compared to older subjects, in terms of both accuracy and time of execution. Concerning fMRI analysis, activations revealed a shift from more posterior and medial temporal areas toward a more anterior frontal system, perhaps reflecting the use of compensatory spatial strategies. Compared to their younger companions, the elderly showed reduced activation in the posterior hippocampus, parahippocampus gyrus, RSC and in many regions of the parietal lobe. These outcomes, then, point toward an age-related alteration of the neural system supporting allocentric navigation.

Two studies highlighted age-related switching deficits during navigation, specifically focusing on the ability to switch from an egocentric to an allocentric frame. In both their studies, Harris and colleagues adopted a computerized adaptation of the classic Plus Maze Task (Harris et al., 2012; Harris and Wolbers, 2014), consisting of a central plus maze composed of curbed paths and transparent walls, surrounded by mountains. No other landmarks to facilitate orientation were included in the environment. Trials started from one of the two opposing starting arms; participants reached the central junction and decided whether to turn left or right in order to find a reward, a yellow ball emerging from the well. During 320 trials, either reversal or switch conditions could occur: During switches, the rewarded strategy changed; during reversal, the strategy was unvaried but the rewarded place was changed. Reward was provided in two conditions: When participants chose the correct place (regardless of required response) or when they made the correct response (regardless of heading). Authors found that older adults systematically performed worse in terms of number of correct trials, strategy learning, number of blocks learned and learning speed (Harris et al., 2012). Specifically, the

elderly obtained lower scores on allocentric trials than on egocentric ones, and on trials following an egocentric-to-allocentric switch. Switching to egocentric strategy and reversal trials, instead, were both preserved. Comparing all the four conditions (allocentric, egocentric, reversal, switching), authors pointed out that aging had a major effect on allocentric-to-egocentric translation rather than on the allocentric strategy itself. According to the authors, thus, aging may have a deeper impact on switching abilities; these switching impairments may lead the elderly to worse allocentric performances and, more generally, to worse spatial skills. In their second study, a Spatial Shortcutting Task and a cognitive mapping test were added to the previous experimental design (Harris and Wolbers, 2014). During the Spatial Shortcutting Task, participants were instructed to use arrow keys to actively navigate in two different virtual environments consisting of routes and salient landmarks, in order to find a goal target. They were also required to develop possible shortcuts while navigating across roads. After training, participants were assessed on their ability to navigate in the same environment taking as short time as possible, observing the length of taken routes and the application of previously acquired shortcuts. What authors observed was that older participants were less likely to use novel shortcuts; indeed, they often took longer routes to reach the goal. Concerning the Plus Maze Task, none of the older adults switched to the allocentric strategy when required, whereas young subjects did it stably. No differences between younger and older participants were observed when switching occurred from egocentric to allocentric strategy. Moreover, worse results among the elderly were also shown on the cognitive mapping test. These results show that aging may lead to difficulties in switching abilities, but only when the translation from an egocentric to an allocentric frame is required. Furthermore, lower scores on the allocentric cognitive map test suggest that allocentric abilities may also be affected by aging, with a subsequent worsening of general navigational abilities.

Conversely, two studies identified age-related impairments in the opposite direction: When navigation requires switching from the allocentric to the egocentric frame (Carelli et al., 2011; Morganti and Riva, 2014). To specifically investigate allocentric-to-egocentric translational abilities, Carelli and colleagues adopted two spatial tasks (Carelli et al., 2011). Participants were first asked to complete the Wisc-R paper and pencil (P&P) mazes, consisting of eight different mazes during which participants had to trace the right route to the maze exit; virtual mazes differed in difficulty level, depending on the number of intersections faced. Successively, a virtual version of each maze was developed, in which participants were instructed to navigate and find the exit. To achieve the task efficiently, allocentric knowledge had to be translated into an egocentric frame; during navigation, participants could look at the paper mazes in order to use survey information. The overall performances positively correlated with Mini Mental scores, as higher cognitive functioning was associated with a higher number of correct trials. Regarding P&P mazes, 50-59-year-old subjects performed worse than both younger and older groups in terms of total execution time. During VR tasks, instead, accuracy and execution time were significantly worse in 60-71-year-old participants when compared to younger groups. In another study (Morganti and Riva, 2014), age-related spatial abilities on the same spatial tasks (P&P mazes and equivalent virtual environments) were investigated, along with the assessment of other neuropsychological measures. Older adults showed specific impairments when performing the virtual mazes, and this effect was strongly evident as age increased. Even if the elderly also performed worse on P&P mazes when compared to

younger companions, age-related effects were less evident. Finally, MMSE score, 15 Rey's Wordlist Immediate Repetition, 15 Rey's Wordlist Delayed Repetition, Tower of London, Manikin Test, Corsi's Span and Corsi's Supraspan positively correlated with VR maze performances. According to the authors, this result support evidence of a specific age-related impairment in switching abilities, highlighting how classical paper and pencil mazes are not really able to evaluate spatial impairments among the elderly. Indeed, P&P mazes assess allocentric abilities but not the flexible use of navigational strategies, which are indeed the key to healthy and efficient spatial skills in everyday life.

To conclude, one study pointed out almost all the previous spatial impairments, both regarding egocentric preference and allocentric / switching deficits, considering both navigation and spatial memory. Wiener and colleagues adopted a simplified version of the same virtual environment used in their previous study (Wiener et al., 2012); in this study, the virtual route was composed of four four-way intersections (Wiener et al., 2013). After the training phase, always involving a passive navigation through the virtual environment, participants were assessed on spatial memory: While being guided again through the same environment, participants were stopped at each landmark and were asked to indicate the right direction of the original route by pressing arrow keys. Routes could be approached in the same (repetition) or in a different direction (retracing) as during training. The main purpose of the authors was to investigate whether, beyond the allocentric decline, older adults were more likely to show a specific egocentric preference, i.e. associative-cue strategy or beacon-based strategy. On one hand, the associative-cue strategy requires landmarks to be associated with an explicit directional behavior ("Turn right at the city hall") (Waller and Lippa, 2007) and it is mainly supported by the dorsal and dorsolateral striatum (Featherstone and McDonald, 2004, 2005). On the other hand, the beacon-based strategy does not require an explicit encoding of the directional information ("Turn towards the city hall") (Waller and Lippa, 2007). This latter strategy involves the ventral and dorsomedial striatum (Devan and White, 1999). Older participants showed difficulties when required to approach a previously remembered route from a different direction, highlighting possible age-related impairments in the use of allocentric strategies. While younger participants showed improvements across trials in both tasks, their older companions were likely to improve their performance only when performing route repetition trials. Moreover, older adults showed a preference for egocentric strategies (specifically, beacon-based strategies) and were less likely to navigate flexibly by changing strategy, perhaps also reflecting decreased switching ability. Consistent with these results, the authors suggested that age-related hippocampal decline and, consequently, age-related allocentric impairments may lead the elderly to the preferential use of extrahippocampal strategies and, more specifically, to the adoption of beacon-based strategies: Associative cue strategies would therefore be as vulnerable as allocentric ones in the elderly. These outcomes may also point toward difficulties in switching between different strategies, as the elderly were less likely to change their navigational behavior across trials.

### **3.2 The effect of aging on allocentric and egocentric frames in spatial memory tasks**

Eleven selected studies investigating the role of allocentric and egocentric frames in spatial memory were included.

Six studies pointed out allocentric impairments in spatial memory (Antonova et al., 2009; Iaria et al.,

2009; Lemay et al., 2004; Lemay and Proteau, 2003; Moffat and Resnick, 2002; Montefinese et al., 2015). Two experimental studies assessed aging effects on spatial memory by focusing on spatial variability when pointing to remembered targets depending on allocentric or egocentric frames (Lemay et al., 2004; Lemay and Proteau, 2003). In both studies, participants were shown visual cues on a black screen and were asked to memorize their locations. After a short delay, they were instructed to move a pointer (a two-degrees-of-freedom manipulandum) from a fixed starting position toward each of the previous targets. In the first experimental study, only the allocentric condition was investigated (Lemay and Proteau, 2003). Four targets were presented on a black screen; after a short delay, three of the previous targets were presented again. Participants were first asked to point toward the missing cue, and then to move the manipulandum toward all the other visible targets. As they did not know where the target would have appeared on the screen, they were obliged to use an allocentric frame to retrieve its location. Using this task, Lemay and colleagues found that pointing variability was much higher in older compared to younger participants, especially when the remembered cue was presented on the right side of the screen. Moreover, participants also took longer to point toward the missing target. This pointing variability was not detected when pointing to the visible cues, suggesting that perceptual or motor causes were not influencing the allocentric performances. Given these outcomes, the authors have suggested that aging may lead to difficulties in maintaining and retrieving spatial representations encoded in an allocentric frame, even after a very short recall delay (10 s). Differently, in their second experimental study both allocentric and egocentric frames were assessed (Lemay et al., 2004). In that study, participants were asked to memorize one, two or four stimuli presented on a screen. During the egocentric condition, a single target was presented: Without other landmarks, subjects were obliged to use an egocentric frame to memorize and successively localize the cue. Subsequently, an allocentric frame was investigated by presenting one, two or four targets with a white square (allocentric condition with context) in the surroundings or just by presenting four targets (allocentric condition without context). Again, participants were asked to move the manipulandum toward the position of the cues after a short delay. Lemay and colleagues found age-related impairments when performing the allocentric task, but only in terms of movement time, as the elderly were slower when pointing to the remembered target. No other differences were found: Indeed, older participants were as accurate as their younger companions in remembering the right position of the target, regardless of the required frame. Given that no differences in movement time were observed in the egocentric condition, the authors concluded that allocentric computations may require a higher amount of time to be processed, with consequent higher age-related difficulties in elaborating static information from the surrounding context. Even if slower, these outcomes highlight how allocentric representations and, therefore, allocentric memory may be partially preserved in older adults. Consistent with these results, Moffat and colleagues investigated age-related mnemonic abilities through a virtual version of the Morris Water Maze Task (Moffat and Resnick, 2002). Authors developed a virtual environment consisting of a circular arena filled with water and surrounded by irregular walls, on which several objects were hung. Participants were instructed to localize and memorize as quickly as possible the position of a hidden platform; once participants crossed the square platform, the platform became visible and elevated from the water. After navigation, an allocentric cognitive mapping test was performed: Participants were instructed to draw a map of the previous environment from an overhead

perspective, trying to include as many landmarks as possible and trying to locate the hidden platform in its right position. Results showed that older participants performed worse in the Water Morris Maze task, travelling a longer distance and spending a longer time finding the hidden platform; reduced spatial abilities were already observable at about 65 years. The elderly were more likely to use proximal objects than room-geometry to orientate and navigate in the virtual environment. Finally, older adults also obtained poorer scores on the cognitive mapping test, pointing toward specific age-related allocentric impairments. Montefinese and colleagues assessed allocentric and egocentric spatial memory using viewpoint changes (Montefinese et al., 2015). Specifically, two different kinds of allocentric representations were assessed: An object-based allocentric representation and an environmental allocentric representation. Participants were instructed to encode snapshots of a virtual living room presented on a computer screen and memorize the location of a target (a plant), which could be positioned at different spots in the environment. After a short delay following the encoding phase, the virtual living room was presented again to participants from an unpredictable point of view. Indeed, a viewpoint change could occur, as the room could be either in the same position or rotated 45° or 135°. The task required indicating the spatial displacement of the main target occurring between the two sessions, by using three different frames: A viewer-dependent frame (egocentric: Changes relative to the viewer position), a room frame (an environmental allocentric frame: Changes in relation to an absolute spatial location) and an object frame (an object-based allocentric frame: Changes in relation to furniture on the central carpet). Interestingly, the elderly performed worse in both allocentric tasks, which were differently influenced by viewpoint changes. Greater impairments were observed in the environment-based allocentric condition, where the elderly obtained lower scores even with no viewpoint change. Differently, in the object-based allocentric condition, older participants performed worse only when a viewpoint change occurred. No differences were detected for the egocentric condition. These outcomes underlie three important results. First, the egocentric frame seems to be preserved in aging, whereas the allocentric one is more likely to show a higher age-related vulnerability. Secondly, this study evidences an important role for rotational abilities in spatial computations, as the elderly have shown greater difficulties when the viewpoint changed. Finally, older adults were more impaired in the environment-based allocentric condition than in the object-based allocentric condition: The first frame requires a greater amount of cognitive resources, as it depends on the creation of stable representations and cognitive maps of the environment, whereas the second does not (Iaria et al., 2009; Montefinese et al., 2015). The environment-based frame is supported mainly by the parahippocampal and RSC (Sulpizio et al., 2013); interestingly, animals studies have shown that hippocampal lesions cause difficulties in the use of distal but not proximal landmarks (Save and Poucet, 2000). Therefore, the specific allocentric impairments detected in this experimental study may be related to hippocampal age-related decline, mainly involving the CA3 region, driving the elderly to obtain more benefits from the use of proximal cues rather than distal ones (Yassa et al., 2011). Differently, Iaria and colleagues investigated the effect of aging on the formation and use of cognitive maps (Iaria et al., 2009). In their experimental design, participants were asked to navigate in a virtual environment presented on a computer display through the use of arrow keys. The environment was a small neighborhood composed of routes and buildings of different shapes and measures, but with the same texture. During the learning phase, subjects were asked to navigate and memorize the



location of six targets (a cinema, a restaurant, a bar, a hotel, a pharmacy and a flower shop). The learning condition was considered complete only when participants were able to correctly indicate where all the six landmarks were located. Subsequently, twelve retrieval trials were performed. Participants were asked to reach as quickly as possible a specific target location, always starting from a different position: Requiring to trace a different path for each trial, this design was intended to prevent the use of procedural memory. Interestingly, older subjects performed worse on both tasks: On one hand, they spent more time creating a cognitive map of the environment; on the other hand, they significantly made more mistakes and took longer to reach the target locations during the retrieval phase. According to the author, aging may therefore affect the ability of creating and using cognitive maps of the external environment, with subsequent important impairments in orientation and navigation abilities. Finally, only one study investigated age-related neurobiological correlates of spatial memory depending on allocentric frame (Antonova et al., 2009). Antonova and colleagues used a virtual reality analogue of the Morris Water Maze, the Arena Task (Antonova et al., 2009). The Arena is a test of spatial memory consisting of a circular arena surrounded by colored walls. During the first phase (encoding phase), participants were asked to navigate using a joystick from periphery toward a pole positioned on the top of a circular puck in the center of the space. After a short delay, the environment was accessible again, but without the pole: Participants were then asked to navigate trying to locate the exact target position, but starting from a different point of the Arena. Since navigation started from a different position, a viewer-independent knowledge of the scene was required to solve the task. fMRI acquisitions were recorded during both the encoding and the retrieval phase. Concerning behavioral results, older participants obtained lower scores during the spatial retrieval. Regarding encoding fMRI results, instead, younger subjects showed activations in the bilateral hippocampus, the dorsolateral PFC and in the left parahippocampal gyrus; these activations were not observed in the older group, who conversely showed activations in the striatum, thought to be involved in extrahippocampal strategies. During the retrieval phase, only young participants showed activations in the thalamus, putamen, right hippocampus, right dorsolateral PFC and left parahippocampus gyrus. Interestingly, older participants activated more strongly the left post-cingulate gyrus, right precuneus, bilateral visual cortex and bilateral cerebellum. Therefore, worse allocentric performances in the elderly were associated with reduced hippocampal and parahippocampal activations during both encoding and retrieval; no volumetric alteration was observed.

Three different studies underlined widespread impairments in spatial memory, involving both the allocentric and egocentric frame (Merriman et al., 2016a; Merriman et al., 2016b; Ruggiero et al., 2016). To comprehend how spatial memory develops throughout life, Ruggiero and colleagues designed a spatial task to investigate the maturation and deterioration of allocentric and egocentric frames among different age samples, from 6 to 89 years of age (Ruggiero et al., 2016). Geometrical 3D objects were shown in different sizes and colors on a plasterboard panel. During the learning phase, participants were instructed to memorize the position and the characteristic of each object. Successively, they were assessed on a task of spatial memory which was either egocentric (“Which objects was closest/farthest to/from you?”) or allocentric (“Which object was closest/farthest to/from the cone?”), depending on the frame. Considering response time, results showed that 6-7-year-old children and 80-89-year-old adults were generally significantly slower in giving allocentric

judgements, especially when involving the peripersonal space. This cognitive decline was already observable at about 50 years. Concerning accuracy, however, age impacted more on egocentric performances. Indeed, 6-7-year-old children and 80-89-year-old adults performed worse than all the other groups. This egocentric decline in accuracy was observable starting at about 60 years. The authors discussed the symmetry observed between 6-7-year-old children and 80-89-year-old adults in terms of neuropsychological and neurobiological similarities between very young individuals and older companions, namely the maturation and the deterioration of executive functions and, especially, the structural and functional maturation and deterioration of certain neural areas. With the same purpose, Merriman and colleagues (Merriman et al., 2016a) developed two virtual reality environments based on a real space, the Campus of the Trinity College in Dublin. The West end of the campus is a well-known and familiar place to inhabitants, thanks to the presence of important historical and cultural Irish statues; the East end of the campus, instead, is a more recent and modern area, and no cultural attractions are located over there. Starting from these two different places, participants were asked to navigate in two different virtual environments: A familiar environment, based on the West end of the campus, and a less familiar environment, based on the East end of the campus. Different objects were embedded along the routes. After the classical learning phase, five different tasks were performed: An objects recognition task, an egocentric direction judgment task (retrieve the right route direction after meeting an object), an allocentric proximity judgement task (judgements on the distances between objects), a target landmark location test (indicate on a map the locations of the remembered targets) and a target landmark naming (retrieve objects marked by “x” on a map). When assessed on the egocentric trials, the elderly obtained lower scores in terms of accuracy; in addition, a significant effect of familiarity was found in both groups, as higher scores were observed for familiar environments. Interestingly, during the allocentric task, older participants again performed worse but, unlike in the egocentric condition, no facilitating effect of familiarity was observed. Consistent with these outcomes, the elderly also obtained lower scores when assessed on the map tasks. Authors have concluded that both egocentric and allocentric spatial frames are affected by aging, even if with a general major decline of allocentric computations. Along with their results, familiarity constitutes a facilitating factor only when spatial memory relies on the egocentric frame. Another study investigated how the presence of distractors may influence allocentric and egocentric remote spatial memory (Merriman et al., 2016b). Two different virtual environments were created; each environment could be presented in three different conditions, according to the presence of human distractors: The “no crowd” condition, the “low density crowd” condition and the “high density crowd” condition. After the learning phase, during which participants had to navigate in these mazes, 18 video clip were shown, each composed of a recording of the original learned route, either in the same (route repetition) or in the opposite (route retracing) direction. Three different spatial memory tasks were performed: The route direction task, the intersection direction task and the landmark sequence task. Merriman and colleagues found that older adults obtained lower scores during all memory tasks, regardless of the frame of reference, even if with a major decline in allocentric spatial memory. Interestingly, the effect of distractors was observed just in the elderly, who performed significantly worse after navigating in crowded environments. Such effect was not observed in younger participants, suggesting that the presence of crowd distractors may make spatial tasks more demanding and thus more difficult, regardless of

the frame.

One study pointed out age-related impairments during the retrieval of locations encoded through an egocentric frame (Pouliot and Gagnon, 2005). Sixty drawings were presented on two monitors; all drawings depicted objects referring to different semantic categories. Participants were asked to encode locations in relation to their body; to prevent allocentric encoding, drawings appeared one at time on one of the two monitors, which were located on the right and on the left of the participants. While performing this task, they were also asked to answer questions (“Where can this object be found?”) by pressing the space bar, in order to maintain a high level of attention. After this learning phase, participants were assessed on spatial retrieval and had to indicate whether during training each drawing was located on their right or their left. Results revealed a lower accuracy in older participants compared to younger companions (respectively 78% and 86%). Their performance was amply above chance.

Investigating remote spatial memory, one experimental study did not find reduced abilities among the elderly (Rosenbaum et al., 2012). To comprehend the role of environment familiarity, Rosenbaum and colleagues investigated remote spatial memory depending on real navigation in familiar and unfamiliar environments. The familiar environment was an environment that had been experienced at least 2-3 times per week for a minimum of 10 years. Participants were assessed on three allocentric (proximity judgments task, distance judgement task and vector mapping) and two egocentric mnemonic tasks (landmark sequencing task and blocked routes). In addition, route learning in an unfamiliar environment was assessed. Strikingly, no differences in either allocentric or egocentric frames were observed between young and old participants when tasks depended on the familiar environment; the elderly sometimes even obtained better scores. However, the elderly performed significantly worse on the route learning task when navigation occurred in an unfamiliar environment. According to the literature, the hippocampus is not involved in remote spatial memory (Committeri et al., 2004; Galati et al., 2010; Hirshhorn et al., 2011; Murphy et al., 2009; Rosenbaum et al., 2007): Even if aging leads to important hippocampal alterations, allocentric and egocentric frames would not be affected when navigation occurs in a well-known environment; whereas, important age-related impairments would be observed when spatial memory is related to a new environment.

### **3.3 Neurobiological and neuropsychological theories on the decline of spatial frames**

In the current literature, different neurobiological and neuropsychological theories have been proposed to explain age-related allocentric decline and switching-strategy impairments. Neurobiological theories focus on neurobiological consequences of aging, trying to correlate behavioral observations with brain physiological alterations. Neuropsychological theories, instead, aim to explain spatial decline by analyzing the neuropsychological correlates of aging. Models do not exclude one another, and it is possible that spatial decline is related to many factors.

The more supported neurobiological theory is the hippocampus theory (O'Keefe and Dostrovsky, 1971). As previously described, the hippocampus plays an important role in allocentric computations, as it is involved in the creation of abstract cognitive maps and in the integration of egocentric information arriving from other cortical areas. An increasing number of studies pointed important hippocampal changes among the elderly,

such as hippocampal atrophy (Driscoll et al., 2003; Du et al., 2006; Du et al., 2003), reduced hippocampal volume (Raz et al., 2005) and alterations in hippocampus place cells (Knierim et al., 1995). Moreover, many studies evidenced reduced activations in the hippocampus, parahippocampal complex, medial temporal lobe and RSC during both mnemonic and navigational tasks in the elderly (Antonova et al., 2009; Meulenbroek et al., 2004; Moffat et al., 2006). Specifically, the parahippocampal complex, which also shows reduced grey matter during aging (Antonova et al., 2009), supports the encoding of landmarks and of their locations (Janzen et al., 2007), and the representation and geometrical analysis of spatial layouts (Epstein and Kanwisher, 1998; Weis et al., 2004). The detrimental effects of aging on these structures may contribute to allocentric impairments, which were consistently observed in almost all the selected studies.

Interestingly, allocentric difficulties may force the elderly to a wider application of extra-hippocampal strategies (Iachini et al., 2009; Moffat et al., 2006; Moffat et al., 2007; Rodgers et al., 2012; Wiener et al., 2013) and to the preference for egocentric strategies (Goeke et al., 2015; Rodgers et al., 2012; Wiener et al., 2013). Some studies support this hypothesis (Goodrich-Hunsaker et al., 2010; Voermans et al., 2004). As a matter of fact, impairments within the caudate nucleus can be compensated thanks to wider hippocampal activations (Voermans et al., 2004); differently, the striatum is not able to compensate for hippocampal lesions and, therefore, for allocentric deficits (Goodrich-Hunsaker et al., 2010). Consequently, egocentric preference may reflect the inability to successfully compensate for impaired hippocampal elaborations (Wiener et al., 2013). Alternatively, age-related reduced connectivity between the hippocampus and the PFC could affect the ability to switch to an allocentric strategy, forcing the elderly to rely primary on egocentric strategies (Antonova et al., 2009; Bai et al., 2009; Grady et al., 2003; Harris et al., 2012; Rodgers et al., 2012; Wang et al., 2006; Wiener et al., 2012).

The selective deterioration of the allocentric neural system has been also explained by the retrogenesis hypothesis. The retrogenesis theory argues that pathological and physiological cognitive decline is influenced by sequential cognitive development: Abilities that are acquired first during life are more rooted and therefore less vulnerable than those abilities that have taken longer to be developed (Reisberg et al., 1999). From a neurobiological point of view, this theory is supported by the fact that late-myelinating structures, like the parahippocampal cortex, are more susceptible to myelin breakdown (Rogalski et al., 2012). Concerning spatial abilities, the egocentric frame is thought to be developed first in life (Acredolo, 1978; Piaget and Inhelder, 1948; Siegel and White, 1975). This is consistent with the overall preferential adoption of egocentric strategies among different age groups, suggesting the body-centered frame as a more elementary way of representing and encoding the external environment. On the other hand, the allocentric frame is thought to reach full maturation during school ages, when executive functions (Belmonti et al., 2015; Purser et al., 2012) and sensorial integration (Nardini et al., 2008) are completely acquired. According to the retrogenesis hypothesis, the neural system supporting allocentric computations would be therefore more vulnerable to aging.

As previously discussed, some studies support the hypothesis of an age-related switching deficit rather than an allocentric impairment (Carelli et al., 2011; Harris et al., 2012; Harris and Wolbers, 2014; Morganti and Riva, 2014). Many studies, for instance, evidenced age-related impairments in set-shifting tasks (Gamboz et al., 2009; Moore et al., 2003; Young et al., 2010). According to the noradrenaline hypothesis, the ability of

strategy switching is strongly supported by executive function and it is then coordinated by the PFC, as mediated by the locus coeruleus-noradrenaline system (Harris et al., 2012; Harris and Wolbers, 2014). The locus coeruleus faces a biological deterioration with aging, with subsequent noradrenaline dysregulation (Allard et al., 2011; Grudzien et al., 2007; Manaye et al., 1995; Mouton et al., 1994). Interestingly, the depletion of prefrontal noradrenaline produces attentional deficits and difficulties in switching between different strategies (Tait et al., 2007) by preventing the engagement of new strategies (Harris et al., 2012). On the other hand, some studies underlined the detrimental effects of age on connections between PFC and the hippocampus (Bai et al., 2009; Wang et al., 2006), which are the key for strategy switching and frames integration. According to Harris and colleagues, the PFC would be no more able to select the right spatial strategy because of reduced connectivity and subsequent reduced inputs from the hippocampus (Harris et al., 2012).

Concerning neuropsychological studies, the limited resources theory and the processing speed hypothesis are among the more supported.

Along with the limited resources theory ( Craik and Fergus, 1986), the overall cognitive decline observed during aging may be more generally related to decreased attentional abilities and executive function. Therefore, navigational deficits would be the consequence of reduced cognitive resources (Klencklen et al., 2012; Lithfous et al., 2013; Moffat et al., 2007), leading to difficulties in creating cognitive maps (Iaria et al., 2009), during memory retrieval (Fastenau et al., 1996) and in extracting salient information from the external environment (Wilkniss et al., 1997). Comparing allocentric and egocentric computations, Wilson and colleagues showed that allocentric strategies require more attentional resources (Wilson et al., 2005). According to Pouillot, attentional resources are particularly fundamental when allocentric computations are required, whereas their role is less crucial during egocentric elaborations (Pouillot and Gagnon, 2005). Consistently, Lithfous and colleagues pointed out that worse allocentric performances in older individuals during spatial encoding are associated with P2 alterations (Lithfous et al., 2014), an important top-down component in the suppression of irrelevant features (Phillips et al., 2009). Being more demanding in terms of attentional resources, allocentric computations may therefore be more vulnerable to degeneration.

On the other hand, the processing speed hypothesis (Salthouse, 1996) focuses on the general slowing down of cognitive processes in aging, particularly related to the decline of working memory, rotation abilities and executive functions, which are fundamental to select, plan and monitor actions. Importantly, a decrease in processing speed can negatively influence spatial and memory abilities, but not verbal ability (Finkel et al., 2007). The egocentric frame has been defined as the more elementary and automatic way to represent and encode the external environment. Differently, allocentric elaborations require an active cognitive scanning of the external environment, depending on the continuous construction of relations between spatial representations and landmarks (Parkin et al., 1995; Pouillot and Gagnon, 2005). The cognitive slowing down may therefore specifically affect allocentric computations: One hypothesis is that earlier cognitive operations may not be more available even after a short time (Byrne et al., 2007; Wiener et al., 2012). According to Burgess and Byrne's model, spatial encoding and spatial retrieval require the translation over repeated top-down and bottom-up updating cycles of egocentric and allocentric representations (Burgess et al., 2001; Byrne et al., 2007). While the hippocampus would be involved in the reconstruction of distances and allocentric

directions of landmarks, the Papez's Circuit would translate allocentric representations into an egocentric frame. Consistently, impairments or slowing down in allocentric elaborations would break the reciprocal updating mechanism between the two reference frames

#### 4. Discussion

From the reviewed studies on egocentric and allocentric frames in aging, it is possible to draw two main pieces of evidence: a) As concerns spatial navigation, our results showed a preservation (and preference) of egocentric strategies (Goeke et al., 2015; Rodgers et al., 2012; Wiener et al., 2013), along with specific impairments in the use of allocentric (Gazova et al., 2013; Moffat et al., 2006; Wiener et al., 2012) and switching abilities (Carelli et al., 2011; Harris et al., 2012; Harris and Wolbers, 2014; Morganti and Riva, 2014); b) regarding spatial memory, outcomes were more divergent and not frame-specific. Six studies underlined a specific impairment in maintaining and retrieving allocentric information (Antonova et al., 2009; Iaria et al., 2009; Lemay et al., 2004; Lemay and Proteau, 2003; Moffat and Resnick, 2002; Montefinese et al., 2015), but just two of them compared the allocentric task to an egocentric one (Lemay et al., 2004; Montefinese et al., 2015). Moreover, one of these two studies pointed out allocentric impairments not in terms of accuracy but in terms of response time, suggesting at least a partial preservation of allocentric abilities (Lemay et al., 2004). Making results still more divergent, one study individualized reduced egocentric spatial memory (Pouliot and Gagnon, 2005), whereas three studies did not find specific impairments (Merriman et al., 2016a; Merriman et al., 2016b; Ruggiero et al., 2016).

According to the frontal aging hypothesis, the neurobiological decline of the PFC could explain most of the cognitive impairments observed in healthy aging (Pfefferbaum et al., 2005; West, 1996). Executive functions and working memory play a key role during navigation, like selecting the correct strategy, finding possible alternative strategies, maintaining navigational goals, computing directions and distances, and translating spatial representations (Gras et al., 2012; Wolbers and Hegarty, 2010). Moreover, executive function influences memory, as remembering requires strategic elaborations during both the encoding and the retrieval of information (Buckner, 2004). These cognitive abilities are mainly located in the PFC, one of the most affected areas in normal aging (Buckner, 2004; Raz and Rodrigue, 2006). For instance, age-related changes in frontal-striatal circuits like white matter abnormalities in frontal lobe and anterior callosal regions (Moseley, 2002), atrophy of frontal gray matter (Raz et al., 1997; Salat et al., 1999) and striatal volume loss (Raz et al., 2003) are characteristic of old non-demented subjects. Consistently, many studies evidenced a general age-related decline in executive and attentional functions (Iachini et al., 2009; Lithfous et al., 2013; Salthouse, 1996). Beyond the hippocampal decline affecting the creation of allocentric representations, the preferential use of egocentric strategies may constitute a less demanding approach to achieve navigation and may represent a strategic way to compensate for both allocentric deficits and age-related cognitive slowing down and decline, involving attentional and executive function weakening. This hypothesis is further supported by the observed age-related switching impairments: If impairments only involve switching from the egocentric to the allocentric frame, they may relate to dysfunctional connectivity between the PFC and hippocampus, and to hippocampal alterations (Harris and Wolbers, 2014). Conversely, our results pointed out shifting impairments

in both directions, suggesting a possible key role of executive functions in affecting such abilities.

We should recognize, however, that some limitations in the selected studies exist: The scale of space, and the type of interaction within the environment. In light of these limitations, a comparison between normal aging and MCI and AD will be proposed by briefly reviewing the current literature on pathological spatial decline and by considering the potentialities of virtual reality (VR) in the study and rehabilitation of spatial skills.

In the literature, the scale of space was proposed as a factor influencing the mechanisms recruited during spatial tasks (Montello, 1993; Wolbers and Wiener, 2014). Specifically, the adoption of environmental space (i.e. large environments requiring navigation to be explored) or vista space (i.e. environments that can be visually apprehended from a single position or with a little exploration) is particularly crucial (Wolbers and Wiener, 2014). When navigation occurs in large-scale environments, more cognitive resources are recruited: The targets are out of the sensory field, boundaries and geometrical layouts are not available and navigation requires moving through different vista spaces, integrating information, self-monitoring and planning more complicated paths (Wolbers and Wiener, 2014). During the retrieval of contextual information, for instance, older adults perform worse (Spencer and Raz, 1995) and show functional deficits in BA 10 (Ankudowich et al., 2016), that plays a key role in retrieval monitoring (McDonough et al., 2013) and in the selection/maintenance of targets (Mitchell and Johnson, 2009). While the majority of the studies selected on navigational abilities were located in environment space, just four protocols focusing on spatial memory were located in large-scale space (Iaria et al., 2009; Merriman et al., 2016a; Merriman et al., 2016b; Rosenbaum et al., 2012). Beyond the Rosenbaum's study analyzing remote spatial memory (Rosenbaum et al., 2012) and Iaria's study in which only allocentric memory was assessed (Iaria et al., 2009), the other two studies both showed a general reduction of spatial memory, regardless to the frame of reference (Merriman et al., 2016a; Merriman et al., 2016b). In light of the role of space scale, the adoption of large-scale environments may have increased the complexity of the tasks. Consistent with this hypothesis, Montefinese et al. found specific allocentric environment-based rather than allocentric object-based impairments, even when no viewpoint change occurred (Montefinese et al., 2015).

Moreover, the type of interaction between the subject and the environment may account for different pattern of results. Indeed, it has been shown that active navigation increases the recall of spatial information (Carassa, 2002; Plancher et al., 2012). In half of our selected studies on spatial memory, instead, participants passively observed the environment (Lemay et al., 2004; Lemay and Proteau, 2003; Montefinese et al., 2015; Pouliot and Gagnon, 2005; Ruggiero et al., 2016).

In addition, the interpretation and comparison of some of the most important spatial tasks is often critical. From a methodological point of view, the allocentric frame is difficult to operationalize and different definitions of this construct have been proposed. For example, it is often unclear whether the origin of the coordinate system is elaborated through allocentric vectors relative to the origine of the coordinate system or by their relations to other locations (Wolbers and Wiener, 2014). In addition, most of the allocentric tasks also involve egocentric components, as the planning and execution of a movement requires egocentric information (Wolbers and Wiener, 2014). The cognitive mapping tests, for instance, is supposed to evaluate the allocentric

frame; by the way, survey maps can be generated also from a quantitatively scaled route representation (Montello, 2004). Furthermore, the hMWM is considered as the gold standard for the investigation of the allocentric frame (Morris et al., 1982). As underlined by Wolbers and Wiener, however, the location of the pool can be either detected by an allocentric vector or by multiple allocentric vectors. During the retrieval phase, participants always start from the same location, raising the possibility to achieve the task through the use of procedural memory (Iaria et al., 2009). Moreover, the hMWM is uniquely able to assess spatial abilities in vista space, therefore not requiring a process of self localization (Wolbers and Wiener, 2014). The same observations should be considered for other classical spatial tasks, like the T-Maze (a simple maze shaped like a “t”), the Y-Maze (a simple maze shaped like a “y”) or the Plus Maze (a maze containing two open arms and two closed arms). As a consequence, it would be worthy to understand how far these results can be generalized to daily life navigation and spatial memory, occurring not only in delimited spaces but also in open environments.

Considering the observed spatial impairments in the elderly, one of the main challenges in the study of spatial decline is the comprehension of how normal aging and MCI or AD are differently affected.

As previously mentioned, a recent systematic review has investigated the role of allocentric and egocentric abilities in the first stages of MCI and AD (Serino et al., 2014). Compared to healthy elderly people, MCI and AD patients show greater navigational impairments (Bianchini et al., 2014; Boccia et al., 2016b; Caffo et al., 2012; Cushman et al., 2008; deIpolyi et al., 2007; Kalova et al., 2005; Rusconi et al., 2015), also reflecting specific deficits in the perception of optic flow (Tetewsky and Duffy, 1999). Unlike normal aging, stronger spatial impairments involving both egocentric and allocentric frames are observable in AD and MCI patients, with a major involvement of the allocentric frame (for a review see (Serino et al., 2014). Importantly, the decline of the egocentric spatial frame, related to parietal cortex atrophy and to the degeneration of the precuneus (Weniger et al., 2011), seems to be disease-specific. Such impairment can have great repercussions on navigation: Indeed, egocentric experience has been reported to be the main factor influencing spatial memory (Shelton and McNamara, 1997). In addition, switching deficits have been observed only in the translation of representations from allocentric to egocentric frame (Morganti et al., 2013; Pai and Yang, 2013).

Strategy switching is mainly supported by RSC, one of the earliest detectable hypometabolic regions in MCI (Nestor et al., 2003). RSC plays a fundamental role in strategy retrieval, in the allocentric coding of heading directions and in hippocampal-based mnemonic processes (Sulpizio et al., 2016). Moreover, the RSC and the PCC connect the parietal lobe with the medial temporal lobe structures and play a critical role in switching between the allocentric coding of space in the medial temporal lobe and the egocentric frame of reference in the posterior parietal lobe (and vice versa) (Boccia et al., 2017; Kravitz et al., 2011).

Regarding the hippocampus, AD is supposed to be characterized by reduced neuronal density in both CA1 and CA3 regions, with a major decrease in CA1 (Padurariu et al., 2012). Conversely, increased activity in CA3 and dentate gyrus has been found to support pattern separation deficits in normal aging (namely, the encoding of new information distinctly from previously learned information); according to the authors, this specific functional deficit would contribute to age-related memory difficulties (Yassa et al., 2011). CA3 receives input from the entorhinal cortex and is involved in the creation of allocentric representations of the



scene toward which we orient (allocentric viewer-dependent representations). The representations created by CA3 neurons are successively sent to CA1 through Schaffer's collateral, which in turn is involved in the creation of representations based on object-to-object relations (allocentric viewer-independent representations). According to the "mental frame syncing" hypothesis, difficulties in the synchronization between these two kinds of allocentric representations would lead to navigational impairments, mainly dependent on difficulties in creating a coherent cognitive map of the surrounding environment (Serino and Riva, 2013). Beyond hippocampal deterioration, spatial decline among AD patients was shown to be related to the degeneration of a larger neural network, involving the RSC, lateral parietal cortex, right medio-dorsal thalamus, right caudate nucleus and entorhinal cortex (Gomez-Isla et al., 1996; Pengas et al., 2012), an important interface between the hippocampus and the neocortex for the translation of sensory input into durable allocentric representations (Fyhn et al., 2004). Considering the "mental frame syncing" hypothesis, the allocentric frame could be more strongly affected in AD patients and at least partially preserved in normal aging. Specifically, we may hypothesize that whereas AD patients are more likely to show stronger difficulties in creating both the first representation of the scene and allocentric viewer-independent representations, aging may just affect creating representations of the general scene. I

Furthermore, while alterations within the frontal-striatal system and subsequent impaired executive functions and mild memory difficulties are typical of normal aging, AD patients are more likely to show important alterations in medial temporal lobe, especially in the hippocampus, PCC, RSC and entorhinal cortex (Buckner, 2004; Head et al., 2005; Ohnishi et al., 2001; Petkov et al., 2004). These abnormalities would result in stronger memory impairments and could lead to difficulties in creating maps, retrieving representations and remembering directions in the external environment. Unlike in AD, no specific switching deficit has been observed among the healthy elderly. Given also the partial preservation of RSC when compared to MCI (Nestor et al., 2003) and the age-related changes occurring in frontal-striatal circuits (Buckner, 2004), we suggest that age-related allocentric and switching impairments may be at least partially the consequence of reduced executive functions and decreased working memory. This would also explain the greater impairments on task adopting large-scale navigation (Merriman et al., 2016a; Merriman et al., 2016b) and the observation of age-related navigational impairments even after the first experimental trial, when memory is not necessary to accomplish the task (Moffat, 2009). As discussed before, allocentric computations are more demanding in terms of cognitive resources. Interestingly, Nemmi and colleagues developed egocentric and allocentric navigational training for the healthy elderly (Nemmi et al., 2017). Despite being more difficult, only the allocentric training was able to strengthen both egocentric and allocentric navigation. Allocentric training could have addressed not only spatial skills but also higher-order abilities, generally involved in the creation and manipulation of spatial representations.

To conclude, a brief consideration about VR should be reported. Indeed, in the last decade the use of VR in the psychological field has steeply increased. Consistently, half of our selected studies assessed spatial abilities through the adoption of virtual environments, while the remaining articles adopted classical behavioral or paper and pencil tests.

The study of spatial skills was considered a psychological challenge. Indeed, navigation is a complex

and multi-componential cognitive process that occurs in large-scale space. This last aspect poses the question whether it is possible to investigate navigation by using classical cognitive tests. Hegarty and colleagues, for instance, showed only partial correlation between paper-and-pencil tests and virtual or real spatial tests (Hegarty et al., 2006). The use of VR may therefore simulate real-space navigation while eliminating some of the limitations of classical cognitive tests.

More specifically, VR has caught the researchers' attention thanks to its advantages, such as ecologically valid and secure environments, standardization, multimodal stimulation and feedback about the performance (Morganti, 2004). Even if traditional measures for the assessment of spatial cognition are reliable and have adequate validity, more ecological tools should be developed. For instance, many traditional tests were not able to adequately capture the complexity of navigational behavior for a prompt assessment of topographical disorientation (Aguirre and D'Esposito, 1999). Specifically, VR is considered a useful tool to assess (Burgess et al., 2002) and rehabilitate (Serino et al., 2014) spatial memory: By providing an "egocentric space", the subject is able to interact and synchronize the spatial frames in a real-life environment (Serino and Riva, 2013). Thus, VR could be an effective and innovative technology to investigate spatial memory and navigation among the elderly, further increasing the ecological validity of current protocols. Virtual environments may indeed allow for an active participation within virtual but realistic spaces (Riva et al., 2004), together with several other advantages: Online feedback about the performance, repeated training and multimodal stimulation (Bohil et al., 2011; Riva et al., 2004). For instance, Kober et al. (Kober et al., 2013) found that also a passive navigation in VR was able to enhance spatial cognition in neurologic patients. Such improvements may also be obtained in the healthy elderly. The sense of presence (i.e., the sense of "being there") that arises from interaction and immersion in virtual environments could be exploited to discover new psychological resources that are crucial for rehabilitation (Riva, 2012, 2014, 2015).

Given the decline of allocentric strategies and switching abilities in the older population, VR would give neuropsychologists and researchers the opportunity to develop appropriate environments and rehabilitative tools. Nevertheless, VR rehabilitation needs to be further investigated. Findings in spatial cognition may shed new light and give better insight to develop virtual training to boost spatial memory and navigation.

### **Competing interests**

The authors declare that no competing interests exist.

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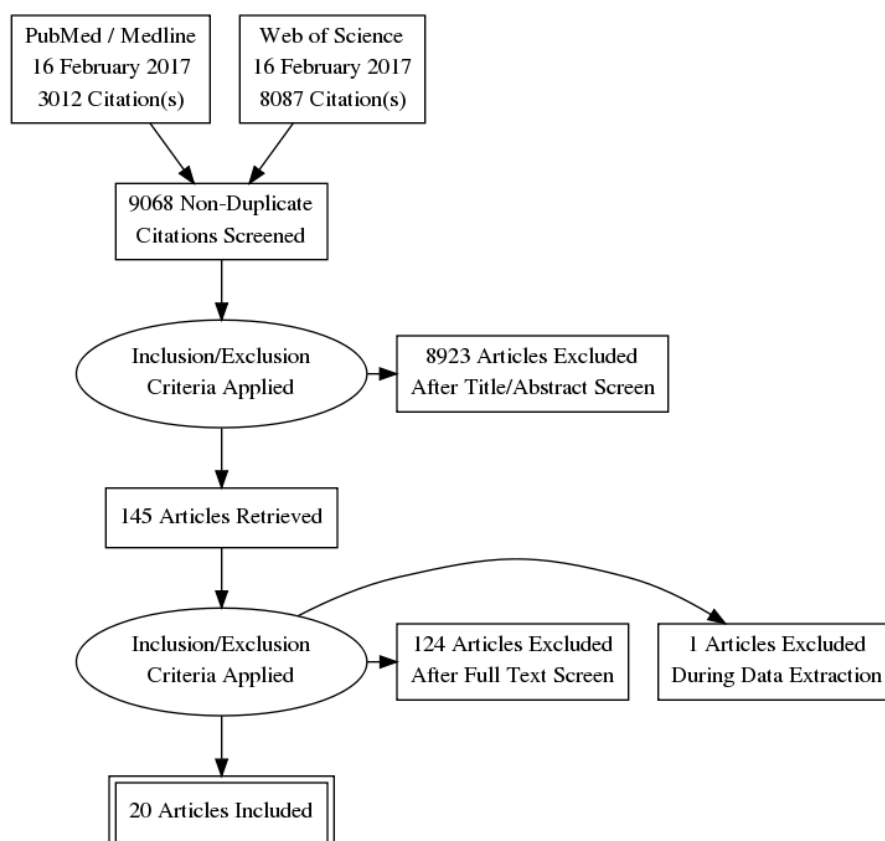


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*Figure 1: The flow chart of the systematic review*

*Table 1: Detailed search strategy*

<b>(Aging OR Ageing) AND</b>	<b>“Spatial Navigation”</b>	<b>“Spatial memory”</b>	<b>“Allocentric”</b>	<b>“Egocentric”</b>	<b>Total</b>
PubMed / Medline	245	2614	65	88	3012
Web of Science	675	6997	141	274	8087
Total	920	9611	206	362	11099
Not duplicated	771	7781	219	297	9068
Excluded (after reading title and abstract)					8923
Retrieved					145
Excluded (after applying inclusion criteria)					123
Excluded (missing experimental data)					1
Included					<b>21</b>

**Table 2:** More detailed information about the selected studies on spatial navigation

<b>AUTHORS(S)</b>	<b>Year</b>	<b>Sample(S) characteristics</b>	<b>Primary Spatial Task</b>	<b>Primary Outcomes</b>
Moffat, Elkins and Resnick	2006	30 younger (mean age: 27.07, SD=5.46) and 21 older participants (mean age: 68.43, SD=5.56)	A virtual spatial navigation task during MRI acquisition (only allocentric)	During the navigation task involving the use of the allocentric frame, reduced activations in the hippocampus, parahippocampal gyrus, RSC and medial temporal lobe were observed), together with increased activations in more anterior areas, including the anterior cingulate gyrus and the medial frontal lobe.
Carelli, Rusconi, Scarabelli, Stampatori, Mattioli and Riva	2011	40 healthy participants (mean age: 53.65) divided in 3 age groups: 40-49 years, 50-59 years and 60-71 years; 8 patients with brain lesions	Wisc-R Paper and Pencil (P&P), the Maze Task and correspondent Virtual Mazes	Older participants obtained lower scores on both tasks. Interestingly, they showed a specific impairment in the transfer from survey to route topographical representations.
Harris, Wiener and Wolbers	2012	18 younger (mean age: 22.22) and 20 older participants (mean age: 68.6)	A Virtual Plus Maze Task	Older participants showed worse performances when navigation required to switch from the egocentric to the allocentric frame. Conversely, no differences between young and old participants were observed in navigational performances depending on the egocentric frame.
Rodgers, Sindone III and Moffat	2012	54 younger (mean age: 21.13, SD=4.08) and 45 older participants (mean age: 62.16, SD=7.22)	Virtual Y maze strategy assessment, the Virtual Morris Water Task and the cognitive mapping test	Compared to younger individuals, older participants showed a preference for egocentric navigation. Interestingly, participants who preferred allocentric navigation were more likely to obtain better results during the cognitive mapping test.
Wiener, Kmecova and De Condappa	2012	20 younger (mean age: 20.53, SD=1.84) and 20 older participants (mean age: 69.45, SD=5.48)	A virtual navigational task	While no differences were observed in route repetition, older participants showed specific impairments in route retracing. Indeed, accuracy was lower and no learning effect was observed throughout trials.
Harris and Wolbers	2014	25 younger (mean age: 21.84) and 25 older participants (mean age: 68.68)	A virtual reality shortcutting task, a virtual adaptation of the Plus Maze Task and the cognitive mapping test	Older participants showed impairments in both allocentric and egocentric-to-allocentric strategies: Indeed, none of the older group stably switched to the allocentric frame when required.
Wiener, De Condappa, Harris and Wolbers	2013	23 younger (mean age: 20.8) and 24 older participants (mean age: 73.8)	A virtual navigational task	Young participants performed better both in route-knowledge and route-retracing tasks. Older participants preferentially used egocentric navigation and showed difficulties in approaching the remembered routes from a different viewpoint, suggesting impairments in allocentric frame.

Gazova, Laczò, Rubinova, Mokrisova, Hyncicova, Anđel, Vyhnašek, Sheardova, Coulson and Hort	2013	68 healthy participants, divided in 3 age groups: 18-26 years (24 subjects); 60-70 years (24 subjects); 71-84 years (20 subjects)	A real-space analog of the Morris Water Maze	71-84-year-old participants obtained lower scores during allocentric trials; no differences were observed during egocentric ones. This progressive allocentric decline was well represented by a quadratic function, indicating a rapid allocentric deterioration in older ages.
Morganti and Riva	2014	176 healthy participants ranging from 20 to 89 years (mean age: 52.04, SD=17.75)	Wisc-R Paper and Pencil (P&P) Maze Task and correspondent Virtual Mazes	Older participants were significantly impaired when performing the virtual Mazes; the effect of age on Paper and Pencil trials was less evident. These results point toward a higher effect of age on allocentric-to-egocentric switching abilities.
Goeke, Kornpetpanee, Koster, Fernandez-Revelles, Gramann and König	2015	1451 healthy participants, divided in 3 age groups: young adult (mean age: 21.54, SD=3.52), middle-aged (mean age: 37.05, SD=5.69) and elderly (mean age: 60.53, SD=10.54)	An online navigation task	Older participants showed a preference toward the use of the egocentric strategy during navigation; nevertheless, this result did not reach the statistical significance. Moreover, culture revealed a significant effect on the preferential use of allocentric or egocentric strategies.

*Table 3: More detailed information about the selected studies on spatial memory.*

<b>AUTHORS(S)</b>	<b>Year</b>	<b>Sample(S) characteristics</b>	<b>Primary Spatial Task</b>	<b>Primary Outcomes</b>
Moffat and Resnick	2002	86 participants (mean age: 61.35, SD= 17.25) divided in three groups: 25-45 years (mean age: 35.25), 45-65 years (mean age: 55.51), 65-93 years (mean age: 78.34)	The Virtual Morris Water Maze task and the cognitive mapping test (only allocentric)	Older participants showed reduced spatial abilities, spending longer time in completing the task, lower levels of learning through trials and lower accuracy in the cognitive mapping test. Aging may therefore affect the retrieval of allocentric representations.
Lemay and Proteau	2003	10 younger (mean age: 21.9, SD= 1.7) and 10 older participants (mean age: 73.8, SD=4.7)	A pointing task (only allocentric frame)	Older participants performed worse during the retrieval phase, showing a greater distance variability when pointing to the remembered target. This outcome suggests a specific effect of aging on allocentric memory.
Lemay, Bertram and Stelmach	2004	12 younger (mean age: 23.3, SD=2.6) and 12 older participants (mean age: 71.1, SD=5.2)	A pointing task	Older participants were as accurate as younger companions in spatial retrieval, regardless to the frame. By the way, they were significantly slower when pointing to the target across allocentric trials. These results suggest that both allocentric and egocentric frames are preserved; allocentric computations, instead, may be more demanding in terms of cognitive resources.
Pouliot and Gagnon	2005	20 younger (mean age: 22.15, SD= 3.86) and 20 older participants (mean age: 69, SD=3.35)	A computerized spatial memory task (only egocentric)	Older participants were significantly less accurate in retrieving locations encoded through an egocentric frame.
Antonova, Parslow, Brammer, Dawson, Jackson and Morris	2008	10 younger (mean age: 23.6, SD= 1.78) and 10 older participants (mean age: 72.14, SD=5.33)	A virtual reality analogue of the Morris Water Maze during MRI acquisition (only allocentric)	Older participants obtained lower scores during spatial retrieval. Neuroimaging results showed reduced activation of hippocampus, parahippocampus, right frontal pole and dorso-lateral PFC, along with reduced volumes in parahippocampus and PFC.
<b>IARIA, PALERMO, COMMITTERI AND BARTON</b>	2009	10 younger (mean age: 23.9) and 10 older participants (mean age: 55.8)	A virtual navigation task and spatial memory assessment (only allocentric)	Older participants required more time to learn the locations of the targets and to form a cognitive map of the virtual environment. In addition, they took longer and made more mistakes when required to use the cognitive map to orientate and reach the target locations.
Rosenbaum, Winocur, Binns and Moscovitch	2012	14 younger (mean age: 22.21, SD=4) and 14 older participants (mean age: 72.21, SD=6.31)	Two virtual navigation task (familiar and unfamiliar environment) and memory assessment	Regarding remote spatial memory, older participants performed as accurately as younger participants, or even better, during both allocentric and egocentric trials. Conversely, they were impaired when assessed after navigation in a less familiar environment.
Montefinese, Sulpizio, Galati and Committeri	2014	20 younger (mean age: 25.26, SD= 4.17) and 20 older participants (mean age: 54.40, SD=3.23)	A spatial memory task across viewpoint changes	A specific allocentric impairment was found in older participants, especially during the environment-based allocentric condition. No differences were observed during egocentric trials.



Ruggiero, D'errico and Iachini	2015	283 healthy participants, divided in 12 age groups: 6-7 years (22 subjects); 8-9 years (21 subjects); 10-12 years (25 subjects); 13-15 years (21 subjects); 16-19 years (23 subjects); 20-29 years (25 subjects); 30-39 years (27 subjects); 40-49 years (25 subjects); 50-59 years (23 subjects); 60-69 years (23 subjects); 70-79 years (24 subjects); 80-89 years (24 subjects)	A spatial memory task	Aging affected allocentric performances in terms of response time, and egocentric trials in terms of accuracy. Interestingly, a symmetry in spatial performances between children (6-7 years) and older participants (80-89 years) was observed.
Merriman, Ondrej, Roudaia, O'Sullivan and Newell	2016	48 younger (mean age: 24.48, SD=5.81) and 23 older participants (mean age: 69.87, SD=5.52)	A virtual spatial navigation task (familiar or unfamiliar environment) and spatial memory assessment	Older participants performed worse on both familiar and unfamiliar environments during egocentric and allocentric tasks. Familiarity improved performances of both samples on the egocentric task; no facilitating effect was observed during allocentric task.
Merriman, Ondrej, Rybicki, Roudaia, O'Sullivan and Newell	2016	30 younger (mean age: 24.83, SD=6.07) and 30 older participants (mean age: 71.23, SD=4.65)	A virtual spatial navigation task (crowded or uncrowded environments) and spatial memory assessment	Older participants performed worse on all spatial memory tasks; a major effect was observed on allocentric frame. The presence of distractors led to worse performances in old but not in young participants.