Investigating Spatial Working Memory and Saccadic Remapping Processes in Healthy Young and Elderly Participants

by

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Abstract

Additional cognitive deficits, including impairments in spatial working memory and/or saccadic remapping processes, have recently been implicated in unilateral neglect – a neurological condition classically characterized as a disorder of attention. The interactions between saccadic remapping and three memory processes (position memory, object memory and object-location binding) were investigated in healthy young (n=27) and elderly (n=20) participants to establish a baseline of comparison for future use with neglect patients and to study the effects of aging on these processes. In a computerized task, participants were instructed to first detect a target, and then hold in memory either its position, identity or both over a delay period. Subsequently, participants were tested on their memory for that particular task. The saccadic remapping component was introduced at the onset of the delay period with the fixation cross shifting either to the left, or right, requiring participants to remap the visual array into either right or left space, or remaining in the centre of the screen (i.e., no remapping condition). In the position memory and object-location binding task, a consistent cost to memory performance was found when remapping right only for the young participants. Overall the elderly did not perform any of the tasks involving a position memory component as well as the young participants and showed spatial asymmetries in the target detection task. The lack of an effect of remapping in the elderly group may be due to a general decrement in performance. These results are discussed in terms of hemispheric asymmetries and cognitive theories of aging.

Acknowledgements

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Introduction

Unilateral neglect is a neurological condition that most commonly arises following right parietal damage. Classically, the disorder has been defined as a failure to orient towards or respond to stimuli in contralesional, left space (Danckert & Ferber, 2006; Driver & Mattingley, 1998; Halligan & Marshall, 1993; Heilman, Watson & Valenstein, 2003). In severe cases, the patient may act as though the left side of space has ceased to exist (e.g., they may leave food uneaten on the left side of a plate, bump into objects on the left side of space, etc.; Danckert & Ferber, 2006). The classic conceptualization of neglect focuses on the most salient impairment – a deficit in spatial attention. Two interacting components have been implicated: an attentional bias towards ipsilesional space (Kinsbourne, 1993) and difficulty orienting away from ipsilesional space towards contralesional space – the so-called disengage deficit (Posner, Walker, Friedrich & Rafal, 1984).

More recent models of neglect have suggested that the disorder cannot be fully explained by an attentional deficit (Pisella & Mattingley, 2004; Danckert & Ferber, 2006). Instead, it has been suggested that several component deficits, including spatial and non-spatial impairments of attention, poor spatial working memory and impaired saccadic remapping, comprise what may be more appropriately termed the “neglect syndrome” (Danckert & Ferber, 2006; Pisella & Mattingley, 2004). Impairments in spatial working memory (SWM) have been recently demonstrated on both clinical and experimental tasks. For example, on cancellation tasks, neglect patients may cancel targets in ipsilesional space multiple times, indicating that the patient is treating a previously viewed or ‘old’ target, as if it were ‘new’ (Parton et al., 2006; note, patients are often unaware they have made multiple cancellations). In addition, while there is an obvious spatial deficit on cancellation tasks (i.e., contralesional targets are omitted more frequently than ipsilesional targets) it is still true that patients often fail to cancel targets in right, putatively ‘non-neglected’ space. In experimental studies exploring SWM it has been shown that patients fail to recall a relatively small number of locations over very brief delays (Malhotra et al., 2005; Mannan et al., 2005; Husain et al., 2001; Wojciulik, Husain, Clarke & Driver, 2001; Ferber & Danckert, 2006). Perhaps the most important facet of these demonstrations is that impaired SWM has been observed for stimuli presented in central or right space – putatively non-neglected regions (Malhotra et al., 2005; Ferber & Danckert, 2006).

Re-visiting behaviour has also been observed in several studies utilizing visual search tasks (Husain et al., 2001; Mannan et al., 2005; Wojciulik et al., 2001). In one study, one neglect patients was asked to search for targets on a computer while eye movements were monitored (Husain et al., 2001). He was instructed to click a response button only when he was looking at a 'new' (i.e., previously unexplored) target and to avoid looking at previously viewed targets. The patient repeatedly re-fixated previously viewed targets in right space and often failed to remember that he had already visited these targets (Husain et al., 2001). In contrast, healthy age-matched controls rarely re-fixated already viewed targets and when they did so, they infrequently misjudged old locations as new. Moreover, there was a positive correlation between the patient's frequency of re-visiting behaviours and the severity of his neglect based on standard clinical tests. This re-visiting behaviour is thought to reflect an impairment in maintaining (or updating) spatial locations across saccades (i.e., a SWM and/or saccadic remapping (SR) deficit). In addition, Wojciulik and colleagues (2001) found that neglect patients showed more neglect on a cancellation task in which their cancellation marks were invisible to them, forcing them to rely solely on SWM to remember which targets were cancelled. Again, it has been suggested that the combination of the lateralized deficits in spatial attention and SWM and/or SR deficits together result in the classic symptom of neglect – the loss of awareness for contralesional space (Husain et al., 2001; Danckert & Ferber, 2006; Pisella , Berberovic & Mattingley, 2004). Moreover, the SWM deficit may exacerbate the lateral attentional bias if patients forget that they have already searched rightward targets and continually return to them, hence, contributing to the neglect of left space (Wojciulik et al., 2001).

While the studies cited above make it clear that neglect is not just a disorder of attention, the nature of these additional cognitive deficits is not fully understood. While the re-visiting behaviour may be driven by a spatial working memory deficit (i.e., an inability to keep in mind visited locations), it is possible that the problem may relate to a deficit in programming successive eye movements (Pisella & Mattingley, 2004; Duhamel, Goldberg, Fitzgibbon, Sirigu & Grafman, 1992; Heide, Blankenburg, Zimmermann & Kompf, 1995). Considering that many of the aforementioned studies use paradigms requiring multiple eye movements, it is possible that the observed impairments result from a deficit in remapping space as a consequence of previously executed saccades (i.e., saccadic remapping; Pisella & Mattingley, 2004).

Saccadic remapping is the process of updating the internal representation of space in anticipation of the sensory consequences of intended eye movements (Duhamel, Colby & Goldberg, 1992; Colby & Goldberg, 1999**).** Early studies on this process come from monkey neurophysiology literature and have employed the double step saccade task (Duhamel, Colby et al., 1992). In this task, participants direct successive eye movements to two targets that are briefly presented one after the other and are extinguished in under 200ms thereby preventing the monkey from making a saccade to the first target while it is still visible. To accurately acquire both targets then, the monkey could employ two strategies; first, he could rely on the retinal coordinates of the target locations. This would lead to an erroneous saccade to the second target as the retinal position of that target is no longer relevant once the monkey has already executed the saccade to the first target. Instead, the monkey could anticipate the sensory outcomes of the first saccade and use this information to plan the subsequent eye movement to the second target. In other words, an accurate saccade to the second target cannot be based solely on retinal coordinates. This is precisely what the monkey does, with saccadic remapping taking into account the intended eye movement to the first target (via corollary discharge) and updating the internal representation of space allowing for accurate programming of the saccade to the second target. The lateral intraparietal region (LIP) of the monkey has been implicated as the neural substrate for these remapping processes (Colby, Duhamel & Goldberg, 1995). Enhanced neural firing occurs in the LIP in anticipation of a saccade to a visual stimulus (i.e., even before the eye movement is initiated: pre-saccadic remapping).

In addition to the monkey neurophysiology evidence discussed above, human patients with parietal lesions also demonstrate impairments in saccadic remapping (Duhamel, Goldberg, et al., 1992; Heide et al., 1995; Vuilleumier et al., 2007). In one study, the double step saccade task was performed by a patient with a right frontoparietal lesion resulting in unilateral neglect (Duhamel, Goldberg et al., 1992). The patient showed no impairment when the first target was presented in right visual space and the second target in left visual space. However, when the first target was presented in left, contralesional space and the second in right space, the patient never acquired the second target. The authors suggest that this represents an inability to anticipate the sensory consequences of a contralesional saccade – a process that is critical for then accurately updating the internal representation of space such that the second target in ipsilesional space can be accurately acquired. This finding has been replicated in a larger sample of patients with parietal lesions (Heide et al., 1995). In this study, patients with left and right parietal lesions demonstrated impaired saccadic remapping on the double step saccade task when the second saccade was presented to either hemifield, although the deficit was more marked when the first saccade was made to contralesional space as was the case for Duhamel, Goldberg et al.'s (1992) patient, and was especially true for the right parietal group. Patients with right parietal damage also showed impairment when both targets were presented solely in the contralesional hemifield, whereas patients with left parietal damage showed no such within-hemifield impairment (Heide et al., 1995). Note that these deficits in remapping are independent of the impaired initiation of contralesional saccades that has previously been demonstrated in neglect (Behrmann, Ghiselli-Crippa, & Dimatteo, 2001/2002; Behrmann, Ghiselli-Crippa, Sweeney, Dimatteo, & Kass, 2002).

Pisella and Mattingley (2004) postulate that a deficit in spatial remapping (not just saccadic remapping) in combination with a pathological attentional gradient favouring ipsilesional space, leads to the classic loss of awareness for contralesional space in neglect. In their model, a 'salience map' codes and prioritizes salient or relevant stimuli in the environment, which may be subsequently selected for further attentional processing (i.e., brought to a conscious level of visual representation). This salience map is essentially an internal representation of space that is continually updated (i.e., remapped) to take into account changes in the environment, as well as overt (i.e., eye movements) and covert shifts of attention. The authors claim that visual space on the level of the salience map is represented contralaterally in the superior parietal lobe (SPL) of each hemisphere (i.e., the left SPL represents the right visual field, and vice versa) and that the right inferior parietal lobule (IPL) is thought to represent both the left and right visual fields (Corbetta, Miezin, Schulman & Petersen, 1993; Corbetta, Kincade, Ollinger, McAvoy & Shulman, 2000). In other words, Pisella and Mattingley (2004) posit that the right hemisphere maintains a salience map for the whole visual field. They claim that leftward saccades in patients with damage to the right parietal cortex (encompassing the IPL) will result in an 'overwriting' of the salience map (i.e., a deficit in remapping) that will affect the entire visual field. This hypothesis is consistent with neglect patients with right-hemisphere damage showing deficits not limited to contralateral space (e.g., the re-visiting behaviour and omission of targets in cancellation tasks in ipsilesional space).

Though many of the aforementioned studies have implicated SWM and/or SR deficits in neglect, the relationship between the two processes warrants further exploration. Both SWM and saccadic remapping involve the ability to keep in mind spatial locations of stimuli and their relationship to one another, however, the two processes operate on vastly different time scales (milliseconds for SR and seconds to minutes for SWM). Moreover, SR processes occur in response to overt and covert shifts of attention in any direction, whereas SWM processes are enhanced by attention directed towards the to-be-remembered target location (Awh, Jonides, & Reuter-Lorenz, 1998). In other words, spatial attention plays a functional role in the active maintenance of information in SWM by directing focal shifts of attention towards the to-be-remembered location (Smyth, 1996; Awh et al., 1998; Postle, Awh, Jonides, Smith, D'Esposito, 2004). In addition, SWM and spatial attention processes are subserved by a right-hemisphere dominant circuit of frontal and parietal sites, which are involved in the rehearsal of spatial information for SWM (Awh & Jonides, 2001), as well as the medial temporal lobe which is involved in the encoding and storage of SWM (Campo et al., 2005; O'Keefe & Nadel, 1978).

It may be the case that deficits in SWM and SR interact in neglect patients to exacerbate the disorder. Thus, it is of interest to understand how the two processes interact in healthy individuals and in patients with neglect. The effects of SR on SWM were investigated with neglect patients in a perceptual discrimination study (Vuilleumier et al., 2007). In this task, participants initially fixated a central cross, then directed attention to a target that was either on the left or right of fixation and identified whether it was green or red. A delay period followed in which the screen was either blank (i.e., the no remapping condition) or a single letter appeared at either the far-left or far-right of the screen inducing a gaze shift that would then require the initial target location to be remapped (i.e., rightward remapping is required following a leftward gaze shift and vice versa). Subsequently, a probe appeared (i.e., the previously presented coloured target) and participants made a SWM judgement indicating whether or not the probe was in the same location as the target (i.e., a same/different verbal judgement). It was found that remapping influenced spatial working memory in the neglect patients such that remapping left space (i.e., following rightward gaze shifts) resulted in large decrements in SWM performance whereas remapping right space (i.e., following leftward gaze shifts) resulted in no such costs to SWM performance (Vuilleumier et al., 2007).

While this study shows an interaction between SWM and SR it also contradicts previous work in neglect patients in that rightward (i.e., ipsilesional) gaze shifts led to the greatest impairment in contrast to previous demonstrations of impaired remapping following contralesional gaze shifts (Duhamel, Goldberg et al., 1992; Heide et al., 1995). This discrepancy between studies may be explained, in part, by the notion that deficits in remapping do not just arise due to initial saccade direction; they are also dependent on the location of the second target for a saccade (Heide et al., 1995; Pisella & Mattingley, 2004). Unfortunately, Vuilleumier and colleagues did not produce separate results for the different manipulations of initial and subsequent target locations making a direct comparison between the two studies impossible. In addition, several methodological issues make the data somewhat difficult to interpret. First, the task performed required a fine grained discrimination of location (targets moved only 2° of visual angle), making this an extremely difficult task for neglect patients to perform. Second, and perhaps more importantly, the task required several eye movements (and thus requiring space to be remapped several times within a trial commonly in opposite directions). Finally, during the delay in the no remapping condition participants were not instructed to fixate on any particular location. Therefore, one could keep their eyes fixed on the location of the initial target awaiting the probe to appear, thereby minimising the SWM component of the task.

In an attempt to address some of these issues, Vasquez and Danckert (2008) explored the effect of SR on SWM in which the locations of targets and probes were clearly distinguishable and only one gaze shift was required on individual trials. This study investigated the effects of saccadic remapping on SWM performance in healthy, young controls (note that healthy controls exhibited no remapping deficits in the study by Vuilleumier and colleagues, 2007). In addition, this study explored both saccadic and spatial (covert) remapping processes for horizontal and vertical gaze shifts. Participants initially fixated centrally with an array of five open circles presented around fixation. Participants were first asked to detect whether or not one of the five circles had a gap in it to ensure that there were no systematic perceptual biases across different target locations that would subsequently influence SWM performance. Targets were present for 500 ms. After a delay of 1500 ms, a probe stimulus (i.e., a filled circle) appeared in any of the five previous target locations. Participants then indicated whether the probe was presented in the location previously occupied by the gapped circle. Saccadic remapping was introduced in some instances at the onset of the delay period in which the fixation cross could either remain in the same location (no remapping), or shift left, right, up or down (remapping conditions). Participants were instructed to keep their eyes fixed on the cross at all times and to re-fixate on the new location of the cross after a shift. A decrement to SWM performance was found when participants were required to remap the visual array into right space (following a leftward saccade) for both overt and covert shifts (there was also a cost to SWM for saccadic remapping in the downward direction and for upward covert remapping; Vasquez & Danckert, 2008). Thus, remapping had a clear directional influence on the accuracy of SWM. Hemispheric differences in spatial processing might account for this finding as the right hemisphere has been found to be more adept at processing specific metric information (i.e., position memory) than the left hemisphere (Hellige & Michimata, 1989; Kessels, Kappelle, de Haan & Postma, 2002; Kosslyn et al., 1989). Such differences might explain why remapping right space (which presumably relies on the less spatially adept left parietal cortex) results in a significant decrement to SWM. Moreover, hemispheric differences may exist in the control of attention with the right hemisphere controlling attention to both left and right space, whereas the left hemisphere directs attention only towards contralateral (right) space (Heilman & Van Den Abell, 1980; Weintraub & Mesulam, 1987).

Vasquez and Danckert (2008) studied the effects of saccadic remapping on one particular type of spatial memory process, (i.e., positional memory). However, spatial memory can be divided into two types of processes: memory for locations and memory for routes and paths (De Renzi, Faglioni & Villa, 1977). Memory for locations can be further subdivided into categorical spatial memory (often referred to as object-location binding) and co-ordinate spatial memory (commonly referred to as position memory). Object-location binding occurs through the association of object-identities and the positions they occupy relative to one another (i.e., the ability to remember the positions occupied by objects with reference to one another; Chalfonte, Johnson, Verfaillie & Reiss, 1996). Position memory refers to the ability to remember the specific metric coordinate information about a location occupied by an object (McNamara, Hardy & Hirtle, 1989).

The current study sought to replicate the influence of saccadic remapping on position memory performance seen in healthy young participants in the Vasquez and Danckert (2008) study, and to extend this by examining the influence of saccadic remapping on memory for object identity (hereafter referred to as ‘object memory’) and object-location binding. We also decided to investigate how position memory and these additional memory processes are affected by aging in a group of healthy, elderly adults. The elderly participants were also included to provide an age-appropriate control group for future studies with neglect patients. Moreover, it has been shown that older individuals have difficulty with memory for object position and object-location binding (Chalfonte & Johnson, 1996). These experimenters carried out separate experiments in young and elderly individuals to investigate how aging affects memory for feature information (i.e., location, color, item) and the processes responsible for binding features together. Participants were independently assigned to study a particular feature (location only, color only, or item only) or a combination of features in the bound memory condition (location and item, or color and item) of 30 common objects presented on a grid. Participants were informed that they would be subjected to a recognition test shortly thereafter. When tested on memory for particular features, older adults had equivalent recognition memory for items and for colours with young adults, but had a disproportionate deficit in memory specifically for the feature of location. With regard to bound information, older adults showed poorer recognition memory than the young group for both bound item and location information and bound item and color information. This impairment in remembering bound information regardless of which features were bound together suggests that older adults experience difficulty in the ability to bind features together, and not in memory for the particular features themselves with the possible exception of position memory. Also, in a separate task, the elderly performed more poorly than the young adults when acquisition of bound information was intentional vs. incidental (at least for bound items and colors).

The authors linked the poor memory for locations to age-related changes in the hippocampus and surrounding areas (Davis & Bernstein, 1992; Selkoe, 1992; regions implicated in the computation and storage of spatial location information; O'Keefe & Nadel, 1978). Moreover, the authors make mention of a particular cognitive process critical to the binding process: reactivation. Presumably reactivation brings no longer active information back to a more 'active state' through internally generated repetition and is thought to promote binding and strengthen already-bound features (Johnson & Hirst, 1991). The hippocampal region is also implicated in reactivation and, as mentioned above, has been shown to be affected by aging. Therefore, this might help explain elderly adults' impairments in memory for bound information. In addition, the frontal lobes have been implicated in the reactivation processing and are also sensitive to the effects of aging (Craik & Grady, 2002). In light of the above findings on the effects of aging on memory, we were interested in observing the performance of the elderly participants on the memory tasks in the current study.

For the position memory task, we hypothesized that both the young and elderly groups would show a cost in performance when remapping right space based on the results of the study by Vasquez and Danckert (2008). We also expected that there would be no effect of remapping on memory for objects' identities (i.e., object memory). This hypothesis was based on the finding of impaired working memory for object position but spared memory for other features of objects, such as colour and shape, that can be considered to be more critical to determining an object's identity in a group of patients with neglect (Pisella et al., 2004). Presumably memory for positions (as well as SR) relies, at least in part, on parietal structures (i.e., the dorsal visual stream) and memory for object identities relies predominantly on the ventral visual stream (Owen, Milner, Petrides & Evans, 1996; Goodale & Milner, 1992; Milner & Goodale, 2006). Thus, we did not anticipate any directional effects of remapping on memory for object identities. For the object-location binding task, we expected a decrement for remapping right space (since this task involves a position memory component) though to a lesser extent than the cost expected in the position memory task. This hypothesis is based on the possibility that in the object-location binding task, individuals may be capable of 'bootstrapping' superior identity memory skills onto the positional components of the task to improve overall performance. We also speculated that performance on the position and object-location binding memory tasks may be worse for the elderly compared to the young group based on the research discussed above suggesting age-related deficits in memory for spatial locations and object-location binding (Chalfonte & Johnson, 1996).

Methods

The current study set out to examine the interactions between saccadic remapping and three related memory processes (i.e., position memory, object memory, and object-location binding) in healthy younger and older individuals.

Participants

Twenty-seven healthy young participants (12 females; mean age=20 years, ±SD=2.18; range=18–26; 1 left handed) participated in this experiment. These participants were undergraduate students recruited from the University of Waterloo. Two participants were excluded from analysis for failing to follow task instructions. Twenty healthy elderly participants were recruited from the Waterloo Research in Aging Pool (WRAP; 15 females; mean age=69 years, ±SD=5.31; range=61–82; 3 left handed). Two participants were excluded from analysis due to technical issues with the experiment resulting in unusable data. All participants had either normal or corrected to normal vision, were free from any neuropsychological conditions and provided written informed consent prior to commencing the study. Participants from the undergraduate population received research credit in their introductory psychology course for participation and WRAP participants received $10.00 in compensation for their time and reimbursement for any parking fees.

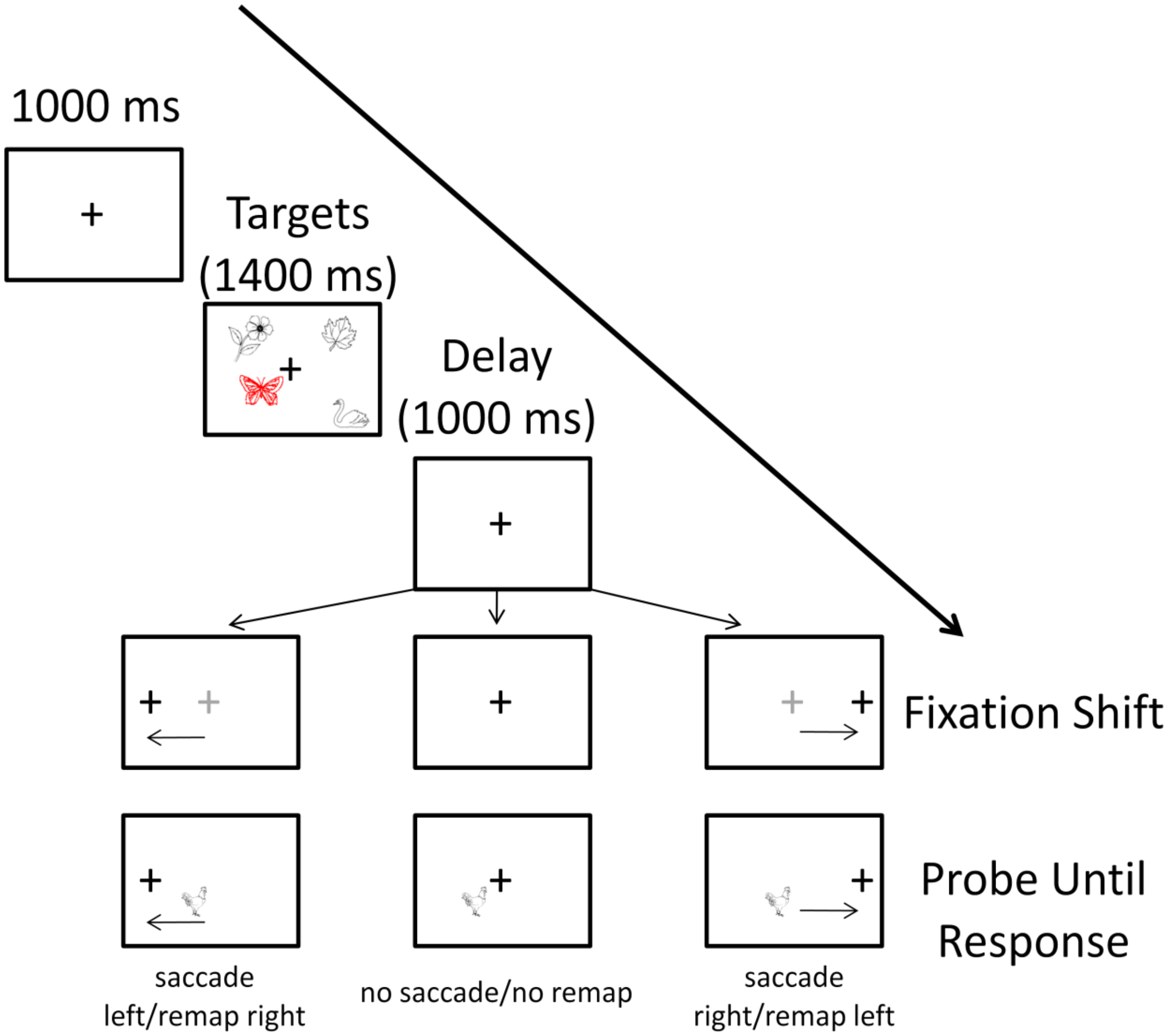
Procedure

Participants were seated before a 15.4-inch computer screen at a distance of approximately 57 cm with their head placed in a chin rest. The task was designed using E-Prime software and ran on a Dell Optiplex GX260 computer. All stimuli were black line drawings of common objects (e.g., scissors, a banana) derived from a standardized set (Snodgrass &Vanderwart, 1980). An equal proportion of animate and inanimate objects were included in the set and stimuli were sampled from a random pool across trials. Each stimulus had either the width or height of 162 pixels with the other side varying in size but all under 162 pixels. Each participant completed 30 practice trials (i.e., 10 practice trials per memory condition – position memory, object memory and object-location binding). Two blocks of 84 trials were allocated for each of the three memory conditions comprising a total of 504 experimental trials. A short break was provided between each block and between memory conditions. The order in which memory conditions were presented was randomized across participants.

Each trial began with central fixation followed 1 s later by four target stimuli surrounding the fixation cross in pseudorandom locations. Participants were instructed to press a button labeled “YES” with their left index finger if an oddball stimulus appeared in the array or to press “NO” with their right index finger if an oddball was not present. Responses were made on a Cedrus RB-530 response pad. An oddball was defined as a red object (as it would stand out from the other objects in the array which were all black) and appeared on 80% of trials. As in the Vasquez and Danckert (2007) study, the oddball (a gapped circle in their case) was intended to determine whether or not there were systematic biases in perception across different regions of the display. That is, if participants were more accurate in detecting oddballs in left versus right space this would obviously have an impact on their subsequent memory performance. Thus, this component of the task allowed us to first determine if such biases existed and second, to control for the impact of biases, where they exist, on subsequent memory performance. The array of targets remained on screen for 1400ms during which participants indicated whether or not an oddball was present. Participants were also instructed to keep in mind, over a 1 s delay period, a certain aspect of the oddball depending on the instructions given for that particular memory task (i.e., its absolute position on the display screen for the position memory task, the object’s identity for the object memory task, or both its position and identity for the object-location binding task). After the delay, a probe appeared (a randomly selected single black object) in one of sixteen possible locations. Probes remained on screen until participants responded based on instructions they had been given earlier pertaining to a particular memory condition. Thus, in the position memory task, participants were instructed to determine whether or not the probe appeared in the same position as the oddball, regardless of its identity. In the object memory task, participants were instructed to determine whether or not the identity of the probe matched that of the oddball, regardless of its position. Finally, in the object-location binding condition, participants were instructed to determine whether or not the probe's location and identity both matched that of the oddball stimulus (Figure 1).

Figure 1.

Schematic representation of the time course for a single trial. The control condition in which the fixation cross remains in the center is shown (i.e., no remapping required), along with the two saccadic remapping conditions. Note that remapping of the stimulus array was in the opposite direction to the gaze shift. Participants were asked to identify the presence of an ‘oddball’ (i.e., a red object) and to keep in mind either the spatial location, identity or both. Following the delay, participants responded to a probe indicating whether it was in the same position, had the same identity, or both depending on the task. In this example, the probe is in the same location as the target but does not have the same identity.



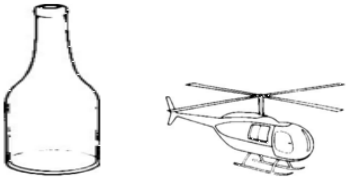
The saccadic remapping component of the task was initiated at the onset of the delay period with the fixation cross shifting either to the left, right or remaining in the centre of the screen (i.e., no remapping condition). Participants were instructed to keep their eyes fixated on the cross at all times and to re-fixate the new location of the cross when it shifted. Eye movements were monitored in a subset of participants using a Canon ZR500A camcorder to ensure fixations were accurate throughout the task. None of the participants had any difficulty following the instructions to fixate in this task.

The stimulus array was designed with certain characteristics to ensure that any effects of saccadic remapping on the memory tasks were not dependent on the potential effects of the initial eccentricity of targets. Targets positions were chosen from regions that surrounded the fixation point along two concentric circles (note that no actual circles existed in the stimulus array; Figure 1). The outer rim of the first circle was 7° from fixation and the outer rim of the second circle was 15° from fixation. This design allowed for the presentation of oddballs (i.e., red objects) to appear close to or further away from fixation. Thus, initial target detection served to inform us of any differences in perceptual ability for detecting targets based on their location (i.e., visual quadrant and distance from fixation) that could later affect performance on the tasks requiring a position memory component. The appearance of an oddball close to or further away from fixation was randomly distributed across trials. On trials in which the fixation point shifted at the onset of the delay period, the proximity of the fixation point to the location in which the target appeared (i.e., whether it was now closer to the target position or further away) was also randomized across trials. All individual stimuli subtended a visual angle that ranged from 2.19° to 6.22°. The range is due to the assortment of stimuli used in the study which vary in their dimensions (though recall the constraint of at least one side of the stimulus measuring 162 pixels; Figure 2).

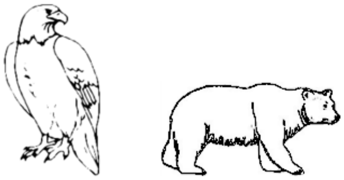
Figure 2.

Examples of stimuli: a) two inanimate objects and b) two animate objects. The first of each pair is longer than it is wide, the second of each is wider than it is long.

a) Inanimate objects



b) Animate objects



The four stimuli could appear in sixteen possible locations on the screen with the constraint that each quadrant must occupy one stimulus. The fixation cross would remain in the centre of the screen or shift to the left or right an equal number of times (56 trials each per memory task). When the fixation cross shifted left or right the visual angle of the displacement was 16.2°. Probes occupied the same location as the previously presented oddball (i.e., the target) on 50% of trials, had the same object identity on 50% of trials, and were in both the same location and of the same identity as the oddball in 25% of trials. Instructions explicitly pertaining to each memory task were provided prior to the initiation of each block of trials for that task.

Data Analysis

First, we investigated the accuracy with which participants were able to detect the target (i.e., the oddball) based on its location in the array (prior to any memory component of the task). This was carried out using an omnibus mixed ANOVA with the between-subjects factor of group (young, old) and within-subject factors of distance from fixation (near, far) and visual quadrant (lower right, upper right, upper left, lower left). Subsequently, responses to the probe stimulus were examined to assess performance in the memory tasks (i.e., position memory, object memory and object-location binding). Accuracy scores were calculated by subtracting the proportion of false alarms (e.g., in the position memory task, indicating that the probe was in the same position as the target when it was not) from the proportion of hits (e.g., accurately indicating that the probe was in the same position as the target). Accuracy scores were compiled for each individual for each of the three memory tasks from which group means were calculated. Separate mixed 2 x 3 ANOVAs were carried out for each memory task with the between-subjects factor of group (young, elderly) and the within-subjects factor of remapping direction (remapping right, no remapping, remapping left). In addition, the current design allowed for further analysis of performance related to the irrelevant stimulus attribute. That is, when performing a position memory task, the probe stimulus had the same identity as the oddball on half the trials in which the probe was presented at the same location. Thus, we could explore whether or not memory performance was improved for position memory when the object's identity, although irrelevant to the task, was also the same (and vice versa for the object memory condition). This was assessed for both the position memory and the object memory tasks by calculating accuracy scores (number of hits out of total number of possible hits for trials in which the target and probe matched vs. mismatched on the irrelevant attribute) in the remapping right and remapping left conditions. Paired *t*-tests were then used comparing accuracy in the matched vs. mismatched trials for remapping right and remapping left. Performance on the three memory tasks was only analyzed for trials in which the oddball had been accurately detected.

Results

Oddball Detection

A 2 (group; old vs. young) x 2 (distance from fixation; near vs. far) x 4 (quadrant; upper left, upper right, lower left, lower right) mixed ANOVA showed a main effect for distance from fixation with both groups demonstrating more accurate target detection in locations near (*M*=.97, *SD*=.01) vs. far (*M*=.94, *SD*=.01) from fixation (*F*(1,41)=86.37, *p*<.001; see Table 1a for group means). This result yielded a large effect size (1.28) as calculated by Cohen's D. While there was no main effect of group (*F*(1, 41)=1.91, *p*=.18), a significant main effect of quadrant (*F*(2.14, 87.92)=8.20, *p*<.001) was subsumed by a significant group by quadrant interaction (*F*(2.14, 87.92)=3.87, *p*<.05).

To investigate the interaction, a simple repeated measures ANOVA was conducted for each group separately**.** The analysis for the young participants yielded no significant effect of visual quadrant on accuracy in target detection (*F*(3, 72)=2.01, *p*=.12). For the elderly group, there was a significant effect of quadrant (*F*(3, 51)=5.76, *p*<.01) with pairwise contrasts revealing enhanced target detection in the upper left vs. upper right quadrant and the lower left vs. lower right quadrant (Table 1b). A paired *t*-test comparing difference scores between the upper left vs. upper right quadrant contrast and the lower left vs. lower right quadrant contrast found no significant difference (*t*(17)=.408, *p*=.69). Thus, while the elderly clearly show a left hemifield advantage for oddball detection (*t*(17)=3.29, *p*=.01), they did not show a difference in target detection accuracy between upper and lower space. Finally, the upper left vs. upper right quadrant contrast showed a large effect size (.89) and the lower left vs. lower right quadrant contrast showed a more moderate effect size (.52) as calculated by Cohen's D.

Table 1.

Comparison of mean accuracy % (±S.D.) for detection of an oddball a) close to (near) and further away from (far) fixation and b) between the four visual quadrants.

a)

Target Location	Group	
	Young	Elderly
Near	.984 (.02)	.961 (.07)
Far	.956 (.02)	.931 (.09)
p-value	.000	.000

b)

Quadrant Comparison	Group	
	Young	Elderly
Upper right	.969(.02)	.931 (.09)
Lower right	.963 (.03)	.928 (.11)
p-value	.323	.611

Target Location	Group	
	Young	Elderly
Near	.984 (.02)	.961 (.07)
Far	.956 (.02)	.931 (.09)
p-value	.000	.000
Upper left	.975 (.02)	.959 (.08)
Lower left	.969 (.02)	.962 (.06)
p-value	.150	.748
Upper right	.969(.02)	.931 (.09)
Upper left	.975 (.02)	.959 (.08)
p-value	.212	.002
Lower right	.963 (.03)	.928 (.11)
Lower left	.969 (.02)	.962 (.06)
p-value	.315	.041
Overall (whole display)	.969 (.005)	.945 (.02)

Note: Two comparisons are not presented in this table –upper left vs. lower right and upper right vs. lower left – because they were not considered meaningful.

We compared the lateral asymmetry discovered in the elderly group directly with the young group via difference scores. Difference scores were calculated for the upper left vs. upper right quadrant contrast (i.e., upper left – upper right accuracy scores) and the lower left vs. lower right quadrant contrast (i.e., lower left – lower right accuracy scores) for both groups and were then analyzed using independent samples *t*-tests. No difference was found between groups for the lower quadrant difference scores (*t*(20.83)=-1.75, *p*=.10). In contrast, a significant difference between groups was found for the upper quadrant comparison, (*t*(41)=-2.61, *p*<.05), with elderly participants showing an upper left quadrant advantage for target detection compared to the upper right quadrant, whereas no such difference was found in the young controls. Moreover, when performance on the left side of the display (collapsed across upper and lower space) was compared to performance on the right side, elderly individuals showed a significantly larger hemispheric asymmetry than the young group with enhanced target detection in left vs. right space (*t*(20.49)=-2.55, *p*<.05).

Order Effects

We examined whether the order in which memory tasks were presented to participants had an effect on performance and found that order had no effect on accuracy in the position memory task (*F*(2, 22)=.83, *p*=.45), the object memory task (*F*(2, 21)=1.39, *p*=.27) and the object-location binding task (*F*(2, 22)=1.03, *p*=.38) in the young group. Order also had no effect on memory performance in the elderly group (position memory, (*F*(2, 14)=.53, *p*=.60), object memory (*F*(2, 14)=.03, *p*=.97), and object-location binding, (*F*(2, 15)=.023, *p*=.98)).

Position Memory Analysis

Position memory was initially analyzed in the no remapping condition to determine whether there were any biases in memory performance relative to the position of the to-be-remembered target. Repeated measures ANOVA examined position memory in each of the four quadrants and found no significant differences in the young group (*F*(3, 72)=.034, *p*=.99), and a trend for a significant effect in the elderly group, (*F*(3, 48)=2.62, *p*=.06). This trend was examined using paired *t*-tests with Bonferroni corrections accounting for the number of comparisons made setting alpha at .05/4 = .0125. These analyses revealed no significant effect of quadrant on positional memory in the no remapping condition for the elderly group (Table 2). Thus, despite the fact that oddballs themselves were detected slightly more accurately when they appeared closer to fixation (and in left space for the elderly participants), this did not lead to any inherent biases in subsequent position memory performance.

Table 2.

Between-quadrant comparison of the elderly group's mean accuracy % (±S.D.) in the no remapping condition of the position memory task.

Quadrant Comparison	
Upper right	.766 (.15)
Lower right	.790 (.23)
p-value	.731
Upper left	.887 (.15)
Lower left	.880 (.16)
p-value	.865
Upper right	.766 (.15)
Upper left	.887 (.15)
p-value	.048
Lower right	790 (.23)
Lower left	.880 (.16)
p-value	.124

Note: Two comparisons are not presented in this table –upper left vs. lower right and upper right vs. lower left – because they were not considered meaningful.

$\alpha = .05/4 = .0125$

An omnibus 2 x 3 mixed repeated measures ANOVA examined the effect of group (young, elderly) and saccadic remapping direction (remap left, no remapping, remap right) on position memory performance. Note that the direction of remapping is opposite to that of the direction in which the fixation cross was shifted. For example, in the remapping right condition, the fixation cross was shifted to the left requiring the participant to remap the visual array into right space. This analysis revealed a trend for a group effect with a higher position memory accuracy score in the young group (M=.84, SE=.02) than the elderly group (M=.78, SE=.02; $F(1, 40)=3.13$, $p=.085$). A main effect of remapping ($F(2, 80)=5.41$, $p<.01$) was found with paired t-tests collapsed across group showing a higher position memory accuracy score in the no remapping condition (M=.86, SD=.11) compared to both the right (M=.78, SD=.13) and left remapping conditions (M=.81, SD=.14; $t(41)=-3.44$, $p<.01$, and, $t(41)=-2.27$, $p<.05$, respectively). Difference scores were calculated (i.e., no remapping condition minus the remapping condition of interest) and paired t-tests were ran between the two difference scores so that the direct cost associated with each remapping direction could be compared. There was no difference in the cost to position memory performance when remapping right vs. remapping left ($t(41)=1.37$, $p=.18$). No interaction was found between remapping and group ($F(2, 80)=.47$, $p=.62$).

Within-Group Analyses

The trend above towards a main effect of group warranted further investigation of each group separately.

Young Controls

Repeated measures ANOVA was carried out with the factor of saccadic remapping direction (no remapping, remap right, remap left). A significant effect of remapping direction was found, ($F(2, 48)=6.60$, $p<.01$) with a cost to memory performance in the remapping right condition relative to the no remapping condition (*t*(24)=-3.46, *p*<.01; Figure 3). Pairwise *t*-tests revealed a trend for a significant cost in memory for positions in the remapping left vs. no remapping condition, (*t*(24)=2.01, *p*=.06). A paired samples *t*-test between the costs of each specific remapping direction (i.e., difference scores calculated by subtracting the remapping condition of interest from the no remapping condition) on position memory performance revealed a trend for a greater cost associated with remapping right vs. remapping left (*t*(24)=1.73, *p*=.09).

Elderly Controls

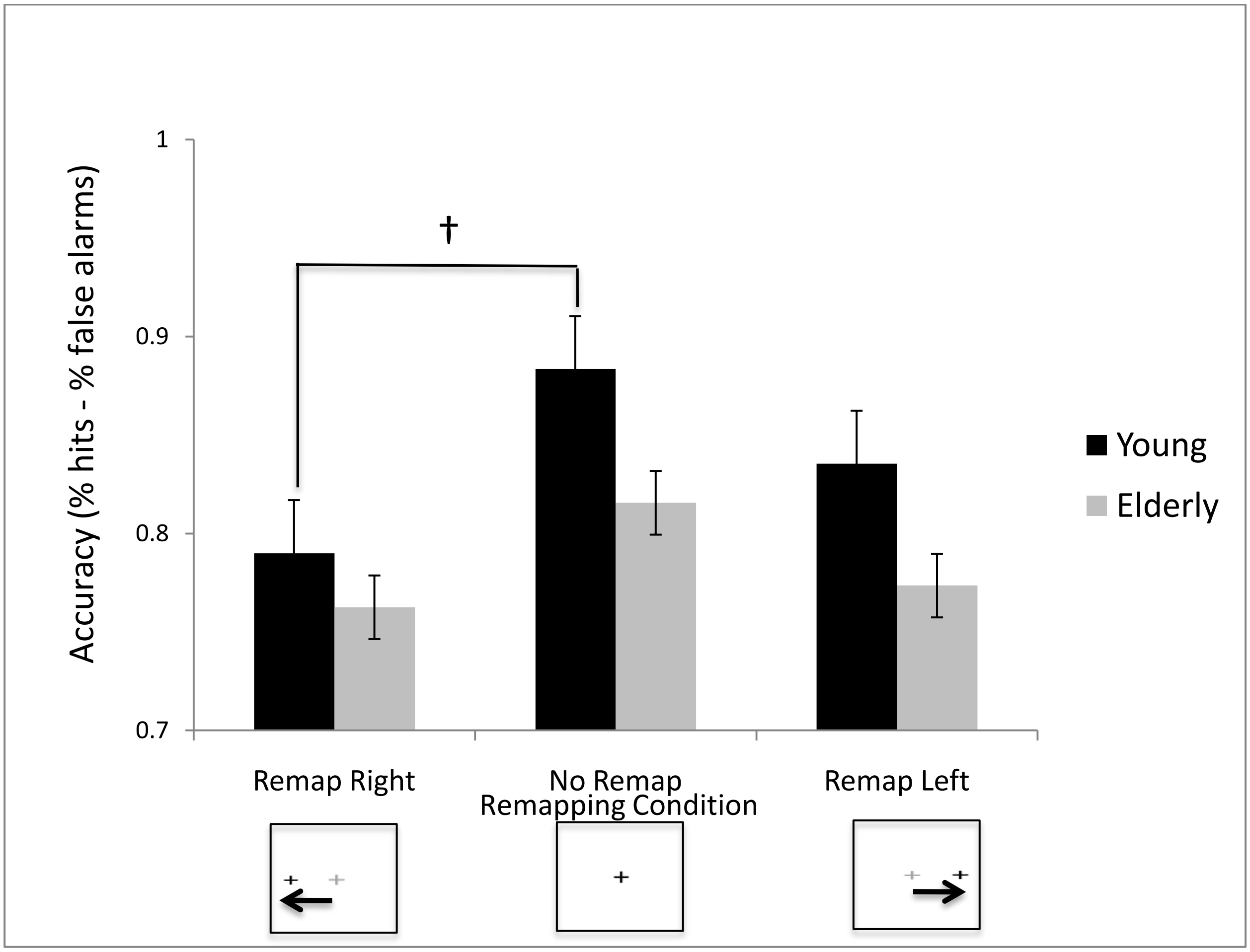
The same analysis for the elderly controls yielded no significant effect of remapping direction on position memory performance, (*F*(2, 32)=1.02, *p*=.37; Figure 3).

Between-Group Post-hoc Tests

We ran post-hoc independent samples *t*-tests between the young and elderly groups to examine whether there were age differences in position memory performance in any of the remapping conditions (though we were primarily interested in determining whether there were any age differences in position memory performance independent of remapping (i.e., in the no remapping condition) since older adults have been known to perform more poorly than young adults in tests of spatial memory; Chalfonte & Johnson, 1996). Bonferroni corrections accounting for the number of comparisons made set alpha at 0.05/5 = .01. These *t*-tests were not significant (remap left, *t*(40)=1.43, *p*=.16; remap right *t*(24.06)=.625, *p*=.54) however, there was a trend for a higher position memory accuracy score in the no remapping condition for the young group (*M*=.88, *SD*=.09) compared to the elderly group (*M*=.82, *SD*=.13; *t*(40)=1.978, *p*=.06; Figure 3).

Figure 3.

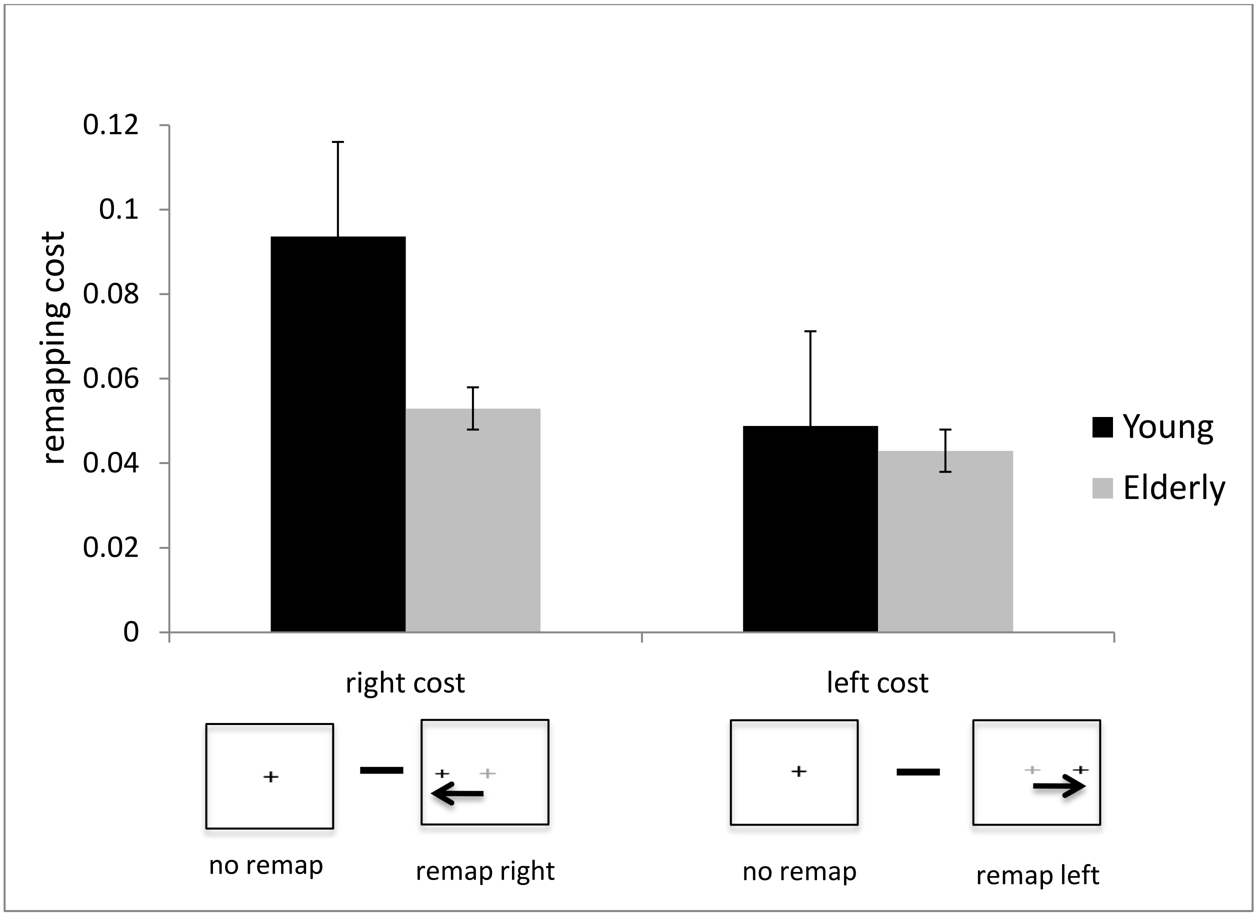
Mean accuracy (±SE) in young (black bars) and elderly (grey bars) participants as a function of remapping direction. † represents a significant difference between conditions at $p < .01$.



It is of interest to note that Levene’s test for equality of variances was significant between groups for position memory when remapping right (*p*<.01). In this case, the elderly group showed more variability in terms of mean standard deviation than the young group (.162 vs. 098 for elderly versus young respectively). We also examined whether the directional costs of saccadic remapping for position memory (i.e., difference scores calculated by subtracting the remapping condition of interest from the no remapping condition) were significantly different between age groups. There was no difference between young and elderly adults in the costs to position memory performance associated with remapping right (*t*(40)=.882, *p*=.38) and remapping left (*t*(40)=.145, *p*=.89; Figure 4).

Figure 4.

Remapping cost represented as difference scores for position memory accuracy contrasting remapping right and left each with the no remapping condition. A difference score approaching zero indicates no significant cost to position memory performance. The schematic below the data illustrates the method used to calculate each cost.



Matching on the Irrelevant Attribute

Young Controls

Next we explored whether participants had a higher position memory accuracy score in trials in which the probe matched the target in position and on the irrelevant attribute (i.e., object identity) compared to trials in which the target and probe matched in terms of position only (i.e., the probe was mismatched on the irrelevant attribute). Paired *t*-tests for the remapping right condition revealed a significantly higher accuracy score in trials in which probes matched the target on the irrelevant attribute (i.e., identity) compared to trials in which probes differed on the irrelevant attribute, (*t*(24)=3.17, *p*<.01), however no significant difference was found when participants were required to remap left, (*t*(24)=1.53, *p*=.14; Figure 5). A *t*-test between remapping right and remapping left when identity did not match revealed higher accuracy scores in position memory performance for remapping left, (*t*(24)=-2.50, *p*<.05) but no such difference was found between remapping conditions when target and probe matched on the irrelevant attribute, (*t*(24)=-.469, *p*=.64). This analysis suggests that remapping left does not incur a significant decrement to SWM performance when the probe and target are not matched on the irrelevant dimension. In contrast, when remapping right, performance is enhanced when the probe matches the target on the irrelevant condition.

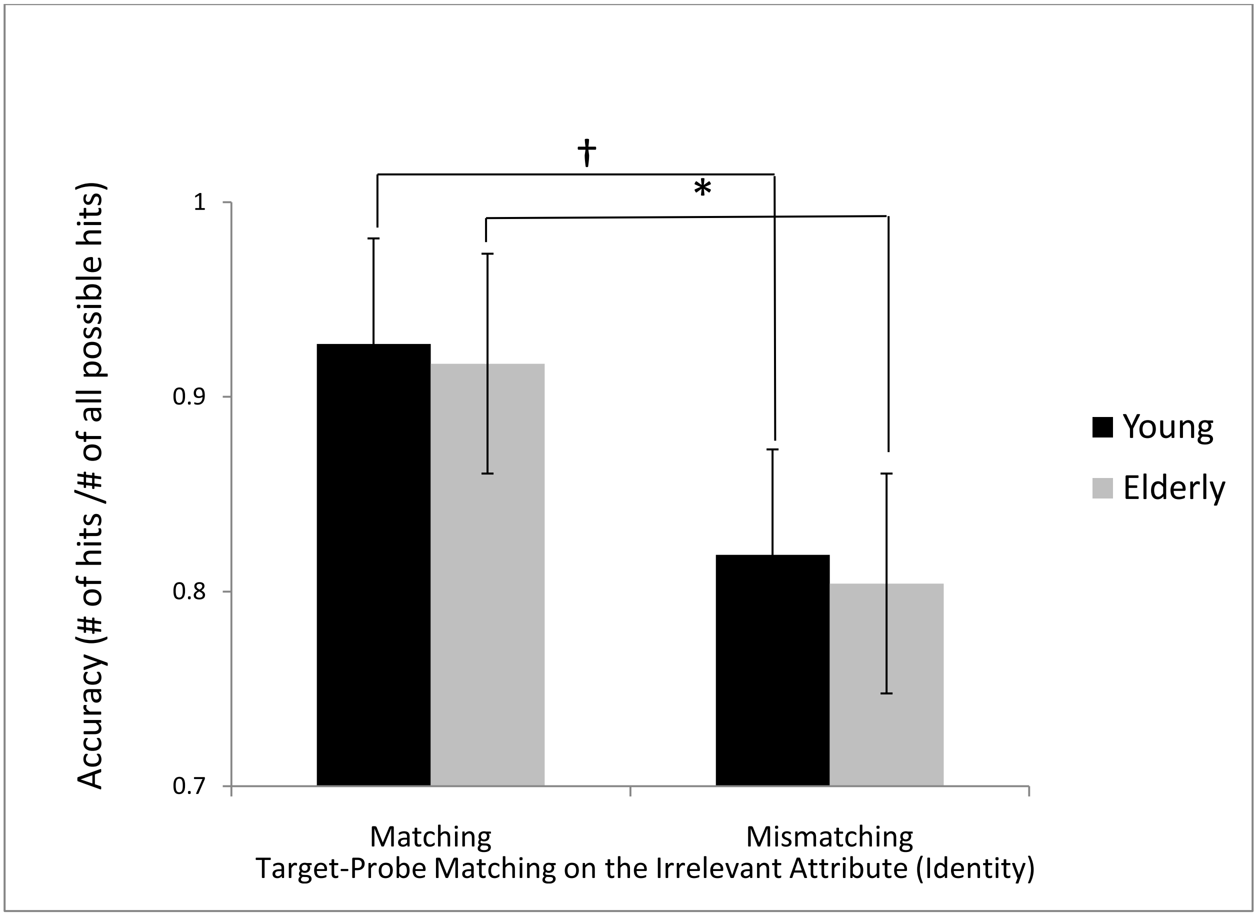
Elderly Controls

As with the young group, target-probe matching on the irrelevant attribute was examined to determine whether a boost in accuracy occurs when the position and identities are matched compared to when the same position is occupied but identities mismatch. Paired *t*-tests revealed significantly higher accuracy scores in the matched vs. mismatched trials in both the remapping right (*t*(16)=2.94, *p*<.05) and remapping left (*t*(16)=5.03, *p*<.001) conditions (Figure 5).

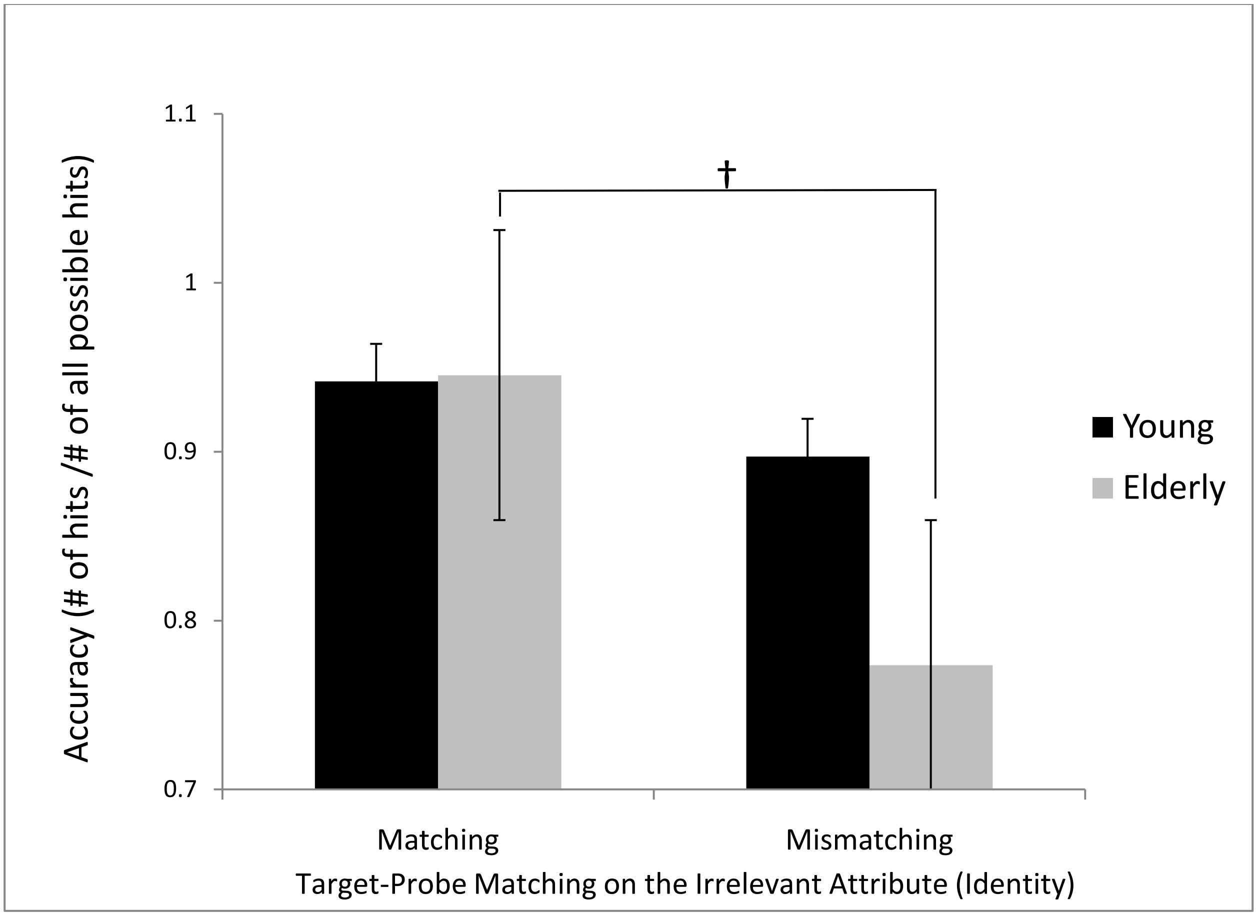
Figure 5.

Effect of matching on the irrelevant feature (i.e., identity) on position memory performance in young and elderly participants in the a) remapping right condition and b) remapping left condition. Same position, same identity = matching; same position, different identity = mismatching. Performance is measured as an accuracy score by dividing the number of hits for a specific scenario (e.g., when the target and probe matched in object identity) by the total number of possible hits one could have made for that particular scenario.* represents a significant difference at $p < .05$, and † represents a significant difference at $p < .01$.

a)



b)


1.1
1
0.9
0.8
0.7
Accuracy (# of hits /# of all possible hits)
†
Young
Elderly
Matching
Mismatching
Target-Probe Matching on the Irrelevant Attribute (Identity)

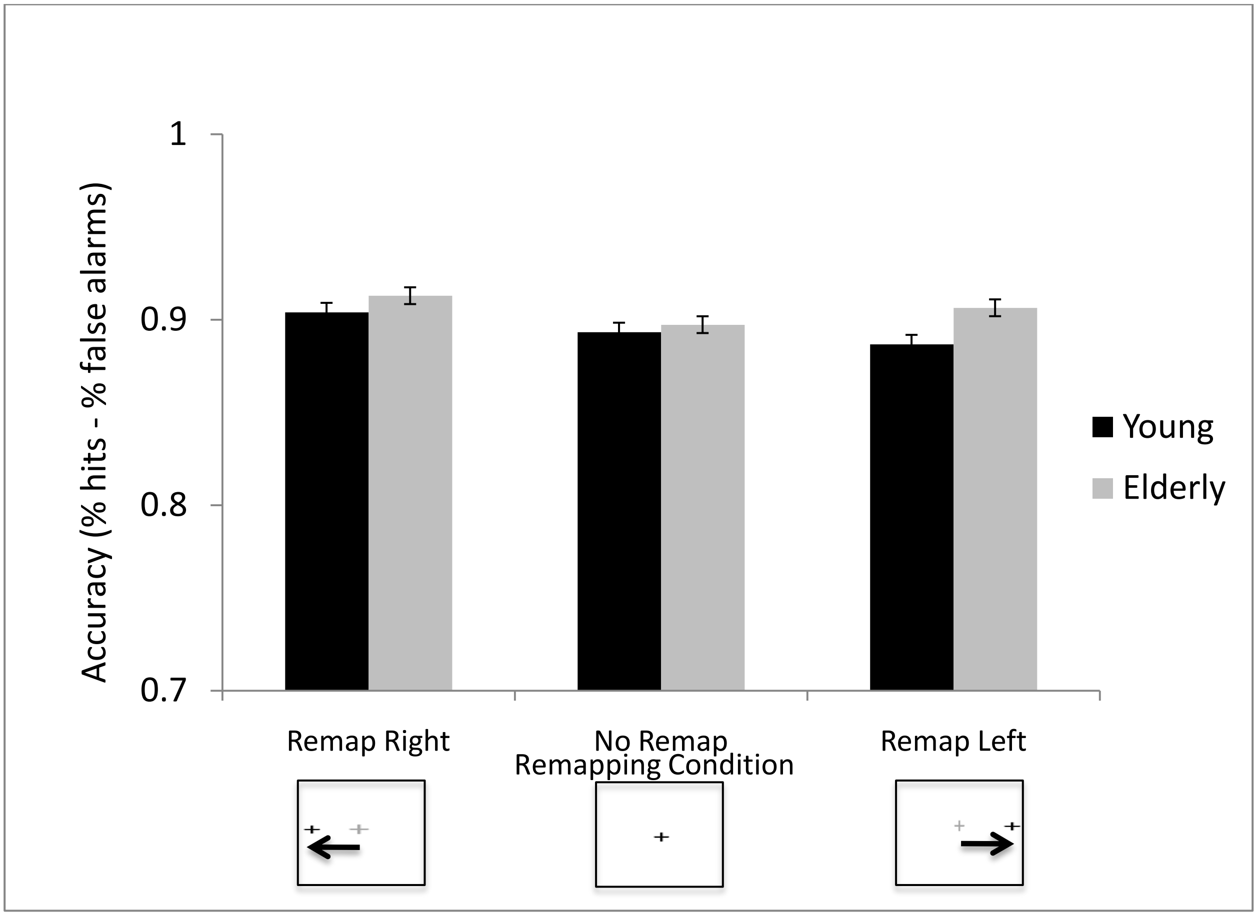
Object Memory Analysis

Object memory was initially analyzed in the no remapping condition to determine whether there were any biases in memory performance relative to the position of the to-be-remembered target. Repeated measures ANOVA examined object memory in each of the four quadrants and found no significant differences in the young group (*F*(1.67, 38.32)=1.27, *p*=.29) and the elderly group (*F*(2.13, 34.01)=.93, *p*=.41).

A 2 (group; young vs. elderly) x 3 (remapping condition; remap right, no remap vs. remap left) repeated measures mixed ANOVA showed no main effects of group (*F*(1, 39)=.11, *p*=.74) or remapping (*F*(2, 78)=.60, *p*=.55), and no interaction between group and remapping (*F*(2, 78)=.18, *p*=.83). Nevertheless, the mean accuracy scores for both groups are presented in Figure 6.

Figure 6.

Mean accuracy (± SE) performance in young (black bars) and elderly (grey bars) participants as a function of remapping direction.



Matching on the Irrelevant Attribute

Young Controls

As with the position memory task, we examined whether accuracy was higher when the target and probe matched in terms of identity and position vs. when the identities were the same but the positions differed. Paired *t*-tests revealed a significantly higher accuracy score when the irrelevant feature was matched vs. mismatched between target and probe for remapping right ($t(23)=2.76$, $p<.05$), and a trend in the same direction was found for remapping left ($t(23)=1.74$, $p=.10$; Figure 7).

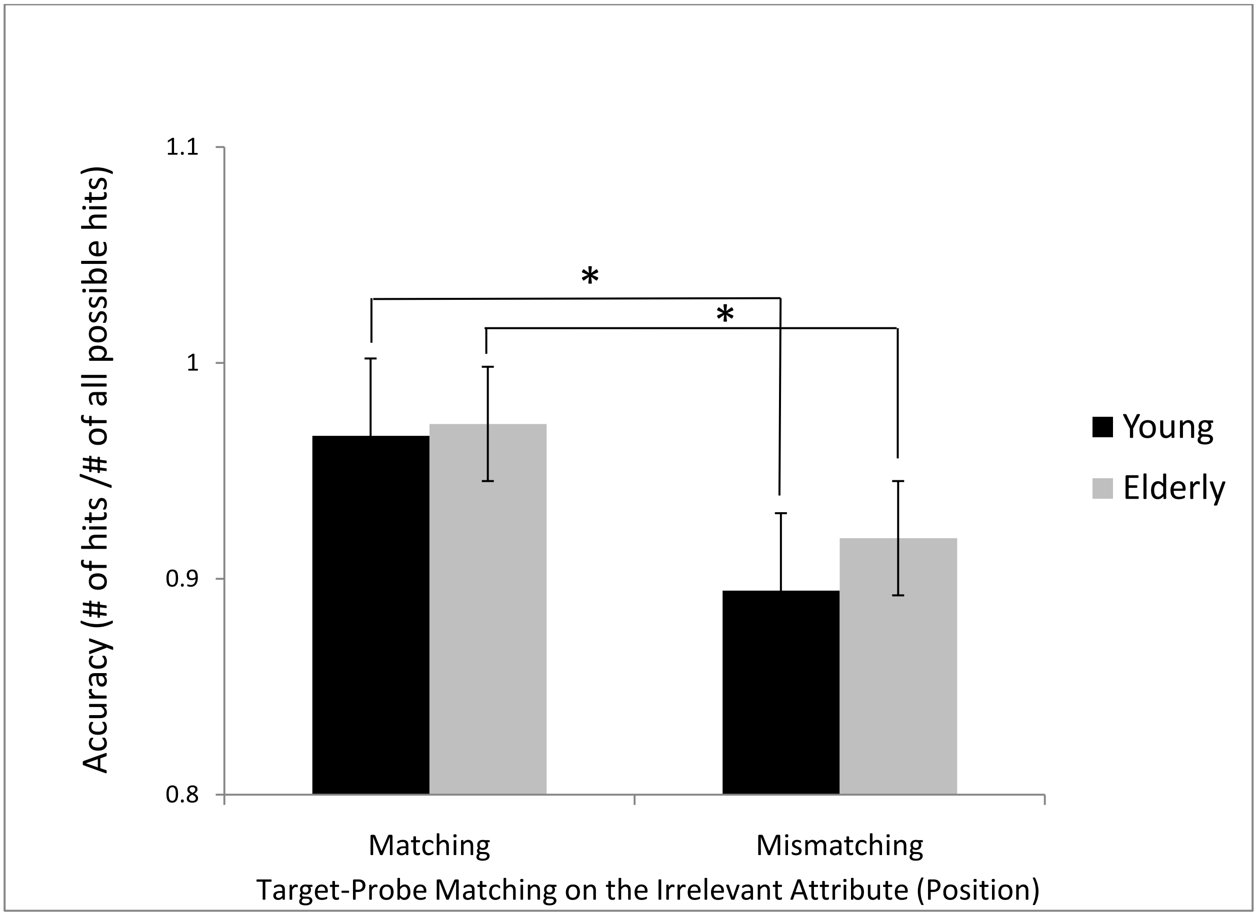
Elderly Controls

Paired *t*-tests revealed significantly higher accuracy scores in the matched vs. mismatched trials in both the remapping right ($t(16)=2.35$, $p<.05$) and remapping left ($t(16)=2.36$, $p<.001$) conditions (Figure 7).

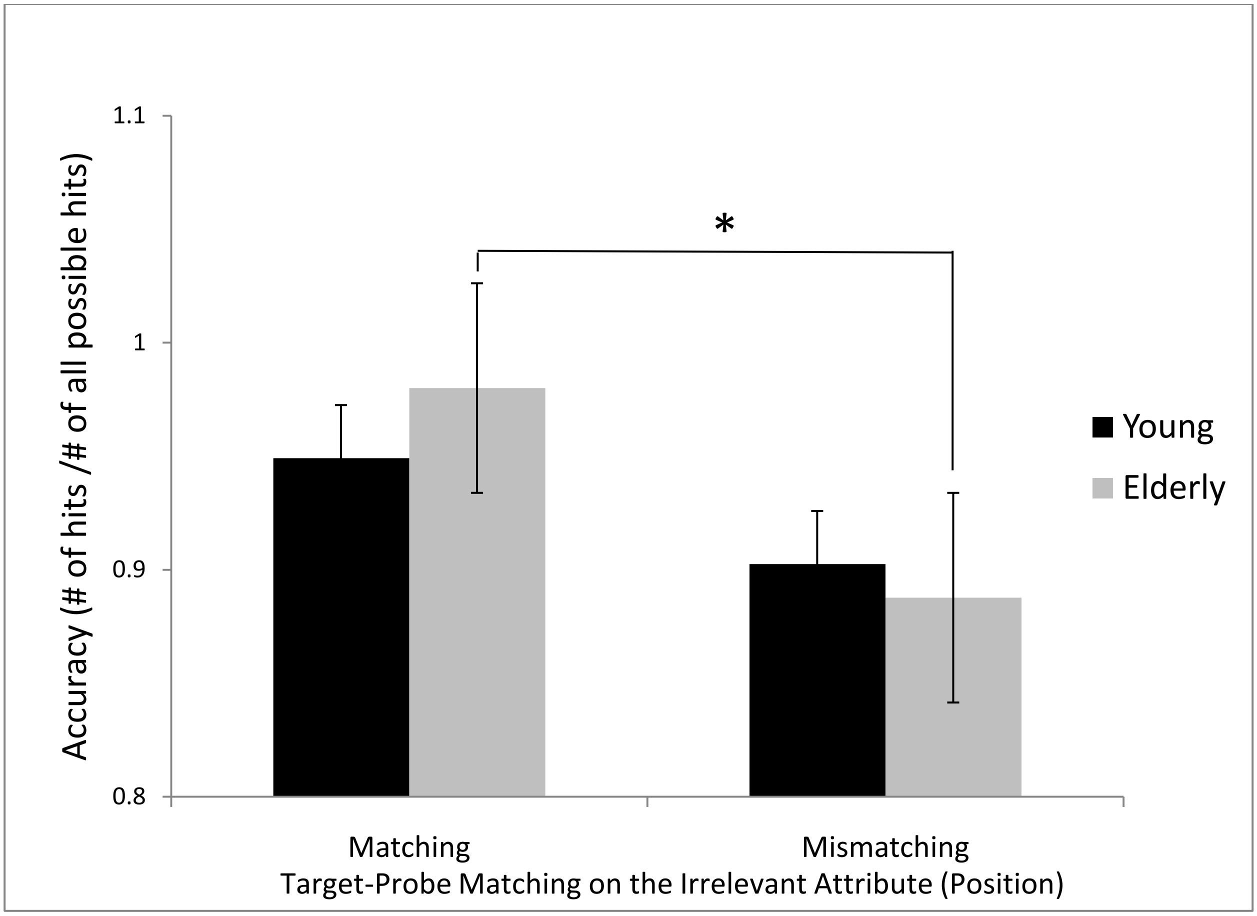
Figure 7.

Effect of target-probe matching on the irrelevant feature (i.e., position) on object memory performance in young and healthy participants in a) remapping right condition and b) remapping left condition. Same position, same identity = matching; different position, same identity = mismatching. Performance is measured as an accuracy score by dividing the number of hits for a specific scenario (e.g., when there was target-probe matching) by the total number of possible hits one could have made for that particular scenario.* represents a significant difference at *p* < .05.

a)



b)


1.1
1
0.9
0.8
Accuracy (# of hits /# of all possible hits)
*
■ Young
■ Elderly
Matching
Mismatching
Target-Probe Matching on the Irrelevant Attribute (Position)

Object-Location Binding Task

Memory for both object identity and object location was initially analyzed in the no remapping condition to determine whether there were any biases in memory performance relative to the position of the to-be-remembered target. Repeated measures ANOVA examined memory performance in each of the four quadrants and found no significant differences in the young group (*F*(2.11, 50.64)=1.62, *p*=.21) and in the elderly group (*F*(1.39, 23.56)=.48, *p*=.56).

A 2 (group; young vs. elderly) x 3 (remapping condition; remap right, remap left and no remapping) repeated measures mixed ANOVA showed a significant main effect of remapping (*F*(1.45, 59.51)=4.99, *p*<.05), with paired *t*-tests collapsed across groups revealing a greater cost associated with remapping right (*M*=.83, *SD*=.17) compared to the no remapping condition (*M*=.91, *SD*=.10; (*t*(42)=-2.84, *p*<.01) and a trend in the same direction when remapping right was compared to remapping left (*M*=.86, *SD*=.16; *t*(42)=1.73, *p*=.09). No main effect was found for group (*F*(1, 41)=1.43, *p*=.24) and the interaction between group and remapping was not significant (*F*(1.45, 59.51)=.09, *p*=.86). However, since the young group showed a decrement for remapping right compared to no remapping in the position memory task discussed above, and because we had hypothesized a priori that the position aspect of the object-location binding task might result in a decrement for remapping right, we decided to examine the effects of remapping within-group.

Within-Group Analyses

Young Controls

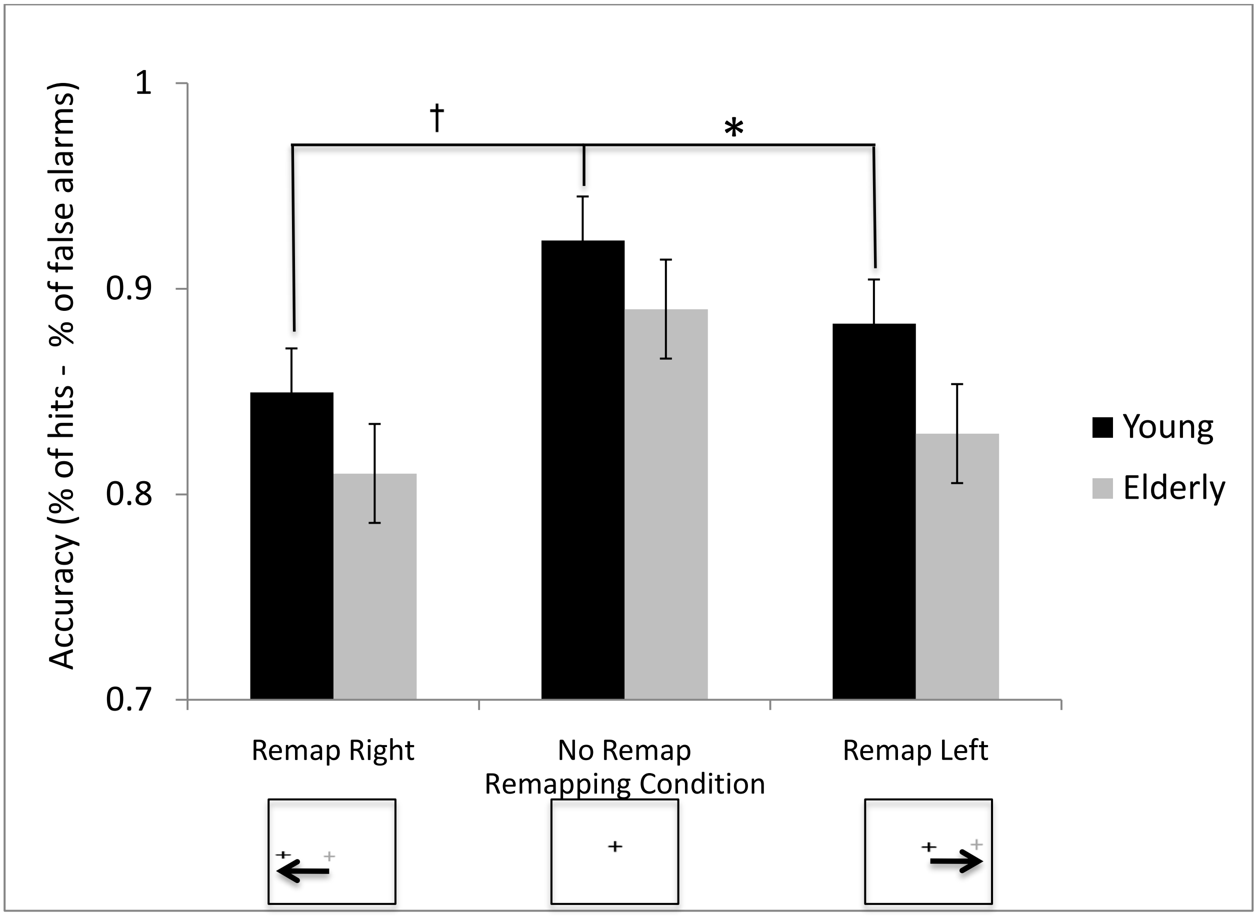
A repeated measures ANOVA with the three levels of saccadic remapping (no remapping, remap right, remap left) revealed a significant effect of remapping, (*F*(2, 48)=7.59, *p*<.01; Figure 8). Paired samples *t*-tests showed a significant decrement in performance for both remapping right and remapping left when each were compared to the no remapping condition (*t*(24)=-4.02, *p*<.01 and *t*(24)=-2.10, *p*<.05 respectively). A pairwise *t*-test comparing difference scores (i.e., the remapping direction of interest subtracted from the no remapping condition) revealed a trend for a greater cost to memory performance for remapping right vs. remapping left, (*t*(24)=1.73, *p*=.096).

Elderly Controls

The same analysis carried out in the elderly control group found no significant effect of remapping (*F*(1.24, 21.09)=1.28, *p*=.28; Figure 8).

Figure 8.

Mean accuracy (±SE) in young (black bars) and elderly (grey bars) participants as a function of remapping direction. * represents a significant difference between conditions at *p* < .05, and † represents a significant difference at *p* < .01.

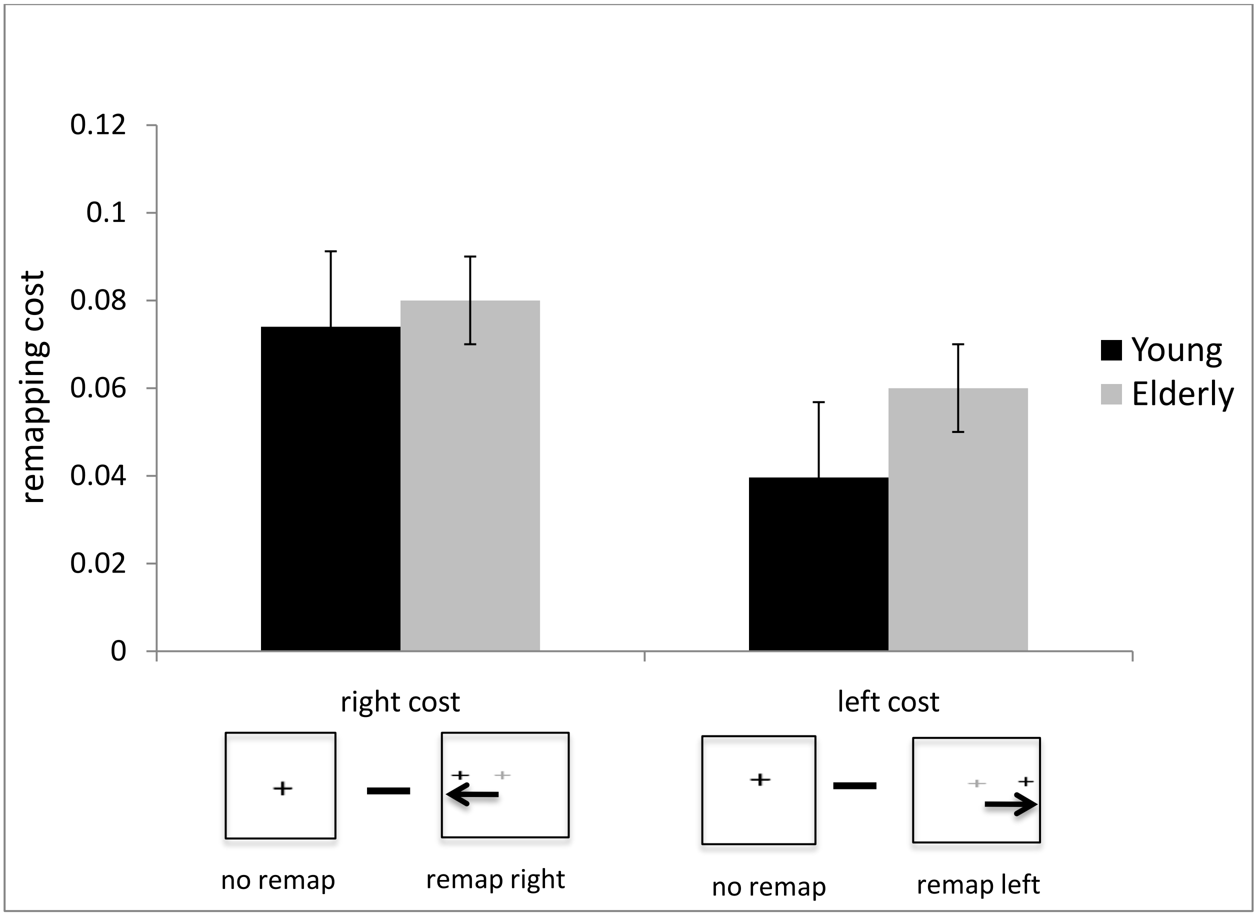


Between-Group Post-hoc Tests

We ran post-hoc independent samples *t*-tests between the young and elderly groups to examine whether there were age differences in object-location binding performance in any of the remapping conditions (though we were primarily interested in determining whether there were any age differences in memory for bound information independent of remapping (i.e., in the no remapping condition) since older adults have been known to perform more poorly than young adults when tested on memory for bound information; Chalfonte & Johnson, 1996). Bonferroni corrections accounting for the number of comparisons made set alpha at 0.05/5 = .01. These *t*-tests were not significant (remap left, *t*(41)=1.10, *p*=.30, remap right, *t*(41)=.76, *p*=.32, no remap, *t*(25.67)=1.03, *p*=.31). However, it is notable that Levene's test for equality of variances was significant between groups for object-location binding memory performance when no remapping was required (*p*<.05). In this case, the elderly group showed more variability in terms of mean standard deviation than the young group (.073 vs. .122 for young versus old respectively). To assess differences in performance between groups, independent samples *t*-tests were conducted using difference scores. Difference scores were derived by subtracting accuracy in the remapping condition of interest from accuracy in the no remapping condition (i.e., no remapping – remap right, and no remapping – remap left). The analysis showed no difference between young and elderly controls in the remap right (*t*(41)=-1.09, *p*=.91) and remap left conditions (*t*(41)=-.349, *p*=.73; Figure 9).

Figure 9.

Remapping costs represented as difference scores for object-location binding accuracy contrasting remapping right and left each with the no remapping condition. A difference score approaching zero indicates no significant cost to object-location binding performance. The schematic below the data illustrates the method used to calculate each cost.



Finally, we decided to test the hypothesis that performance in the object-location binding task will result in less of a cost to memory in the remapping right condition compared to the position memory task since participants might be able to benefit from bootstrapping the identity memory processes onto the position memory system. Paired *t*-tests revealed no significant difference in the young group (*t*(24)=.58, *p*=.57) and in the elderly group (*t*(16)=-.60, *p*=.56).

Discussion

The current experiment found a consistent effect of saccadic remapping only in tasks that involved a positional memory component. Specifically, the influence of saccadic remapping on position memory and object-location binding in young adults revealed that remapping the target array towards right space incurs a cost to memory performance (Figures 3 and 8). These effects were largely absent in the healthy elderly group although in general, the elderly did not perform any of the tasks involving a position memory component as well as the younger participants and also demonstrated spatial asymmetries in the target detection task suggesting that the lack of an effect of saccadic remapping on SWM may be due to a general decrement in performance in this group (note: in addition, the elderly tended to be more variable and demonstrated smaller effect sizes than the younger controls). Several aspects of the results warrant further discussion.

Oddball Detection

Target detection was better in both groups for near versus far targets. However, overall target detection across the display was quite high for both groups (i.e., greater than 92% accuracy in all conditions; Table 1). Whereas the young group showed no effect of visual quadrant on target detection, the elderly were better at detecting targets on the left vs. right side of the display**.** This asymmetry could be accounted for by the right-hemisphere's dominance for spatial attentional processes. Across a variety of studies and methodologies, the right hemisphere has been shown to direct attention to both the left and right visual fields, whereas the left hemisphere modulates attention only in right space (Corbetta et al., 1993; Mesulam, 1999; Gitelman et al., 1999; Mesulam, 1981; Kim et al., 1999). Thus, right hemisphere specialization for attention may explain, at least in part, the left hemifield advantage in target detection seen in the elderly. Although not significant, the elderly participants had lower oddball detection accuracy in all conditions when compared with the younger participants (Table 1). It may be the case then that the younger participants were performing at ceiling on this component of the task thereby masking any asymmetries in performance. In contrast, the elderly participants revealed an asymmetry in the context of slightly worse overall performance (Table 1).

Although there was no significant difference in target detection accuracy between upper and lower space in the elderly participants, it is noteworthy that a large effect size was found for the contrast between left and right quadrants in upper space (.89 vs. .52 for the contrasts between left and right in upper and lower space respectively). In other words, the left-right asymmetry evident in elderly participants was strongest in upper space. This finding may be best understood in the context of Previc's (1990, 1998) neuropsychological model of three-dimensional space. This model posits that different brain regions are specialized for processing information in specific regions of space, or more importantly, these regions show distinct functional specialisation. The ventral visual stream (from primary visual cortex to inferotemporal cortex) is known to support conscious visual perception (Milner & Goodale, 2006) and in Previc's model is thought to demonstrate a preference for processing information in extrapersonal (far) space such that processes such as visual search and visual memory have been shown to be superior in upper visual space – an analogue of far, extrapersonal space (e.g., Previc & Intraub, 1997). In contrast, the dorsal visual stream (from primary visual cortex to posterior parietal cortex; Milner & Goodale, 2006) is specialized for the control of visually guided actions and has been shown to demonstrate a bias towards processing information in peripersonal (near) space (Danckert & Goodale, 2001, 2003). Remembering spatial locations in the current experiment bears some similarities to visual search tasks and may therefore employ some of the same neural substrates purported to be more efficiently executed in extrapersonal (far) space[1]. In light of this, the large effect size of the upper left vs. upper right contrast in the elderly group may reflect an influence of the evolved specialization of the ventral visual stream for enhanced visual processing in upper

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[1] In the current study, upper visual space serves as an imperfect analogue to extrapersonal space.

visual space. Once again, the lack of any such asymmetry in the younger group may simply reflect the fact that they were performing at ceiling to begin with. It is perhaps worth noting, however, that the young group shows the same direction of effects that were significant in the elderly in all instances (i.e., higher accuracy for left versus right space and higher accuracy for upper vs. lower space; Table 1).

Memory Tasks

In the young group we replicated the earlier results of Vasquez and Danckert (2008) such that there was a significant cost in position memory performance when remapping right space compared to the no remapping condition (Figure 3). Hemispheric differences in the ability to process spatial information may account, at least in part, for such findings. Several studies have demonstrated more efficient processing of metric information (i.e., specific, coordinate-based information about distance and direction) by the right hemisphere compared to the left (Hellige & Michimata, 1989; Kessels et al., 2002; Kosslyn et al., 1989). As mentioned above, the right hemisphere has also been shown to be dominant for spatial attention (Corbetta et al., 1993; Mesulam, 1981). These hemispheric asymmetries may explain the decrement in position memory for remapping right space, given that this condition presumably relies on the less spatially adept left hemisphere structures.

As expected, remapping had no influence on young participants' ability to remember object identities. Recall that in the change-detection study, by Pisella and colleagues (2004), for neglect patients working memory for an object's color and shape were spared whereas memory for object locations was impaired. It is likely then that the recall of object identities, independent of space, relies on the ventral visual stream whereas the position memory and SR tasks likely rely more so on the dorsal visual stream (Owen et al., 1996). Since the object-location binding task also involved a position memory component, we were not surprised to see a cost to memory performance when remapping right space was required in this task. That is, although object memory appears to suffer no consequences from saccadic remapping, when location is bound to identity the same costs found in location memory alone are observed (Figures 3 and 8). This can be seen in the fact that there was no difference in terms of cost to position memory from remapping right space in the position memory and object-location binding tasks. It seems then that rather than ‘bootstrapping’ onto the success (in terms of no SR cost) of object identity processes, position memory processes instead dominate in this task leading to the same costs observed when only position memory is tested.

We also examined the interaction between saccadic remapping processes and the three memory tasks (position memory, object memory, and object-location binding) in a group of elderly individuals to explore how these processes are affected by aging. No significant effect of remapping was found in any of the memory tasks for the elderly group (Figs. 3, 6 and 8). It may be the case that the lack of a significant effect of remapping was due to the large between-subject variability in the elderly group’s data compared with the younger group. This was certainly the case in the position memory task. In the object-location binding task, the elderly were significantly more variable ($p < .05$) than the young group in terms of mean standard deviations in the no remapping condition (.12 vs. .07 for the elderly and young groups respectively). No such differences in variability were found between groups in the object memory task. It appears then that there is a tendency for the elderly group to show more variability than the young group in the tasks involving a position memory component. Considering that age has a detrimental effect on position memory and object-location binding performance (Chalfonte & Johnson, 1996), the increased variability in the elderly in these tasks is not particularly surprising. To examine this further, we correlated age and accuracy in the no remapping condition for the elderly group in both the position memory and object-location binding tasks. The correlations between age and accuracy were not significant in either task, though a trend was found in the position memory task (*r* = -.415, *p* = .098; object-location binding task *r* = -.210, *p* = .402). Despite the lack of significance, it is interesting to note that both correlations were negative suggesting that as age increases performance on the two tasks decreases.

When examining differences between the young and the elderly groups in performance on each memory task when remapping was not required (i.e., in the no remapping condition), we did not find any significant differences. However, we did find a trend toward better position memory performance in the young group compared to the elderly group. This trend coincides with previous work in which elderly adults, compared to young adults, showed deficiency in remembering the locations of objects in space (Chalfonte & Johnson, 1996, but see Olson et al., 2004). Moreover, it has been found that elderly adults perform more poorly on memory tests for bound information compared to young adults, (Chalfonte & Johnson, 1996; Mitchell, Johnson, Raye, Mather & D'Esposito, 2000). Although the elderly performed more poorly on the object-location binding memory task than the young group, this difference was not statistically significant.

Alternatively, the lack of a remapping effect on memory performance in the elderly may be due to hemispheric changes in the brain as a result of aging (Cabeza, 2002). Behavioural studies have revealed that the cerebral hemispheres age in different ways with more obvious impairments for right-hemisphere dominant skills (Goldstein & Shelly, 1981; Cherry, Adamson, Duclos & Hellige, 2005). In other words, the right hemisphere is more sensitive to the detrimental effects of aging than the left hemisphere (Daselaar & Cabeza, 2005). Moreover, research suggests that lateral asymmetries in a variety of domains diminish with age (e.g., right hand dominance, Kalisch, Wilimzig, Kleibel, Tegenthoff & Dinse, 2006; episodic memory, Cabeza, Grady, et al., 1997; sensorimotor processing, Grady et al., 2000; inhibition, Nielson, Langenecker & Garavan, 2002). For example, in a positron emission tomography (PET) study investigating spatial working memory, Reuter-Lorenz and colleagues (2000) found that older adults showed a pattern of anterior bilateral frontal lobe activation whereas young adults demonstrated more lateralized activation in the right anterior frontal regions. Assuming that spatial working memory and saccadic remapping processes are controlled largely by right hemisphere structures, right-hemisphere aging and/or the decreased lateralization of these functions may explain the lack of a directional remapping effect on position memory in our elderly group (but see Meadmore, Dror & Bucks, 2009 for evidence of preserved spatial processing asymmetries with age).

In the current study we also examined whether performance in a particular memory task was boosted when additional, though irrelevant, information was matched between the target and the probe (e.g., in the position memory task, were participants better at remembering the position of targets when the target and probe also matched in terms of identity?). In the position memory task, the young group exhibited a benefit in position memory performance when the probe and target were also the same object, however this only occurred for remapping right space (Figure 5). It appears then that the benefit of bootstrapping the additional object-identity information onto the position information only emerged when participants actually needed the aid (i.e., in the remapping right condition where a cost to position memory was incurred). In the object memory task, memory was improved when the target and probe were also in the same position, but again only for remapping right space (Figure 7). The elderly group exhibited a benefit from target-probe matching on the irrelevant stimulus in both the position memory and identity memory tasks for both left and right remapping conditions. Because this group was slightly less accurate in memory performance than the young group (Table 3), they may have needed to make use of the additional information in both remapping conditions to improve performance.

Table 3.

Hits and false alarm data for all tasks and conditions.

Position Memory Task

	Young Participants		Elderly Participants	
	Hits	False Alarms	Hits	False Alarms
Remap Right	.88 (.08)	.09 (.06)	.86 (.14)	.09 (.07)
No Remapping	.94 (.06)	.06 (.06)	.90 (.09)	.09 (.09)
Remap Left	.92 (.08)	.08 (.06)	.86 (.10)	.08 (.10)

Object Memory Task

	Young Participants		Elderly Participants	
	Hits	False Alarms	Hits	False Alarms
Remap Right	.91 (.10)	.06 (.04)	.93 (.08)	.06 (.06)
No Remapping	.96 (.06)	.04 (.03)	.95 (.10)	.06 (.06)
Remap Left	.92 (.09)	.04 (.04)	.93 (.09)	.05 (.04)

Object-Location Binding Task

	Young Participants		Elderly Participants	
	Hits	False Alarms	Hits	False Alarms
Remap Right	.93 (.07)	.02 (.04)	.94 (.06)	.03 (.06)
No Remapping	.93 (.07)	.04 (.06)	.94 (.07)	.05 (.07)
Remap Left	.93 (.09)	.04 (.06)	.93 (.09)	.02 (.05)

In conclusion, the current study replicated an effect of remapping on position memory such that there was a cost to position memory performance when remapping right space (Vasquez & Danckert, 2008). No such costs were observed in an elderly group perhaps due to diminished lateralisation of function (Reuter-Lorenz et al., 2000). In other words, if the normal right hemisphere advantage for spatial processing leads to improved leftward vs. rightward remapping performance in the young adults, this asymmetry would be diminished in a group of elderly adults who fail to demonstrate that normal asymmetry in the first instance. Further studies of this kind could benefit from the inclusion of a neuropsychological assessment of hemisphere-dominant skills (e.g., spatial attention, finger tapping, visuoconstructional skills, etc.). Performance on such a battery could then be correlated with SWM and remapping performance to determine the extent to which each domain relates to functions known to be lateralised to the right hemisphere.

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