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Cortical thickness and gray matter volume supporting object-based and egocentric perspective transformations

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Introduction

Spatial visualization involves several spatial processes such as encoding, manipulation, and recognition of spatial information and is a crucial ability necessary to mentally transform (i.e., move, turn, rotate, etc.) spatial forms and objects (Salthouse et al., 1990). Spatial visualization can be tested using small scale spatial tasks such as paper folding, mental rotation, and assembling objects. All of these small-scale tests are traditionally administered as paper-and-pencil tests or computerized versions and involve mentally manipulating or transforming small shapes such as blocks or paper sheets (Hegarty et al., 2006). Egocentric perspective transformation refers to the perspective changes derived from the rotation of the person viewing a scene or array (Huttenlocher & Presson, 1979) and it is a crucial cognitive ability that enables someone to mentally represent spatial relationships between objects and themselves and imagine how an object or a scene would appear if they view it from a different vantage point (He et al., 2022). The goal of this project is to test the relationship between these small-scale spatial abilities and measures of regional brain volume, as well as to test whether these relationships differ by sex.

Previous studies suggest a dissociation between two types of spatial transformations, i.e., object-based transformations (the ability to imagine movements or rotations of an object, or a set of objects relative to each other, e.g., mental rotation) and egocentric transformations (the ability to imagine how the objects would appear from a different point of view, e.g., perspective taking) (Hegarty & Waller, 2004; Huttenlocher & Presson, 1973, 1979; Rieser, 1989; Wraga et al., 2000; Zacks et al., 1999). For example, one can stand in front of a rectangular object and face the length of it, and imagine the object rotated 90 degrees such that now the person faces the width of the object, or one can imagine themselves rotating 90 degrees around the object to view the width of the object. Egocentric perspective transformation abilities have been investigated across navigation tasks such as the immersive Viewpoint Transformation Task (iVTT), which involves changing viewpoints to walk to a target, and desktop tasks such as the Spatial Orientation Test (SOT), in which people are shown an array of objects and they have to imagine standing at one object, facing a second object, and then they should point to a third object (He et al., 2022). Using a confirmatory factor analysis (CFA), one study demonstrated that a two-factor model which assumes that perspective taking and mental rotation are distinct abilities provided a better fit for the data than one-factor model that assumes these abilities are the same (Hegarty & Waller, 2004). Behavioral studies show that the accuracy patterns and the response time for egocentric perspective transformation tasks and object-based transformation tasks are different (Presson, 1982; Wraga et al., 2000; Zacks & Tversky, 2002). Some studies suggest faster response time and better accuracy for egocentric perspective transformation tasks compared to object-based transformation tasks (Amorim & Stucchi, 1997; Creem et al., 2001; Wraga et al., 2000).

Neural correlates underlying egocentric and object-based transformations

Previous studies that investigated the relationship between small scale and large scale spatial abilities using object-based spatial tasks and large scale navigation tasks (Hegarty et al.,

2006), show that small scale and large scale spatial abilities are partially dissociated. Neuroimaging studies have also shown that different scales of spatial abilities rely on different neural mechanisms (Kosslyn & Thompson, 2003; Li et al., 2019). For example, Kosslyn and Thompson revealed a higher activation of the parietal lobes associated with small scale spatial abilities such as mental rotation. Other studies revealed that greater activation of the hippocampus is associated with large scale spatial abilities such as allocentric or map-based navigation (Iglói et al., 2010). In the present research we will focus mainly on studies related to small-scale spatial abilities.

According to the results of one fMRI study, bilateral superior parietal cortex is involved in mental rotation tasks (Keehner et al., 2006). Activation in the intraparietal sulcus linearly increases with increase in angular disparity in mental rotation tasks (Carpenter et al., 1999). Moreover, one study showed that there is a significant relationship between white matter organization in posterior parietal cortex and mental rotation ability. They found that high fractional anisotropy (a quantitative biomarker of white matter integrity) near the anterior part of the intraparietal sulcus was positively correlated with performance in individuals with high mental rotation abilities (Wolbers et al., 2006). Premotor and primary motor areas are also activated during mental rotation tasks (Cohen et al., 1996; Eisenegger et al., 2007; Kosslyn et al., 1998; Parsons et al., 1995). Due to the significant role of the motor cortex in the mental rotation of abstract figures (Richter et al., 2000; Vingerhoets et al., 2001; Wexler et al., 1998), there is a possibility that some subcortical components of motor cortex, such as basal ganglia, might also play a role in mental rotation. Some lesion studies have shown that patients with Parkinson's disease showed significant impairment in their mental rotation abilities (Boller et al., 1984; Lee et al., 1998). One study has shown that the activation of right caudate nucleus is associated with mental rotation performance (Alivisatos & Petrides, 1997). Moreover, patients with Huntington's disease (in which the primary neuropathology is caudate nucleus impairment) show impaired spatial working memory and visuospatial short-term memory (Lawrence et al., 2000). Another study found that lesions to the right basal ganglia (including caudate, putamen, and globus pallidus) led to significant impairments in mental rotation of visual images (Harris et al., 2002). Thus, some components of basal ganglia such as caudate nucleus and putamen might play a role in mental rotation tasks.

Shared neural processes and operations might play a role in both egocentric and object-based transformations. For example, both transformations can be solved by encoding the spatial locations of the objects, storing them as a mental image and doing image transformations (Zacks et al., 2003). However, neuroimaging studies show that distinct processing systems are also involved in egocentric perspective transformation and object-based transformations (Wraga et al., 2005). Object-based transformations rely on pre-motor as well as primary motor areas (i.e., motor representations associated with manipulation), whereas egocentric perspective transformations rely on supplementary motor areas (Wraga et al., 2005). The results of one functional magnetic resonance imaging (fMRI) study showed that increases in the activation of the right parietal cortex and decreases in the activation of left parietal cortex occurred during an object-based

transformation task in which participants were asked to imagine an array of objects rotating. In contrast, left temporal cortex was activated during a perspective transformation task in which they were asked to imagine themselves rotating around an array of objects (J. M. Zacks et al., 2003). Some studies showed left lateralization in brain activation for egocentric transformation tasks and right lateralization for object-based transformation tasks (Thakkar et al., 2009; J. Zacks et al., 1999). Lesion studies also showed that impairment in mental rotation abilities occurred following lesions to the right posterior cortex (including posterior parietal, posterior temporal, and occipital lobes) (Ratcliff, 1979).

In addition, there are processes related to transforming between egocentric viewpoints (involving first-person perspective where the observer sees objects from their own point of view) and allocentric viewpoints (involving aerial or third-person perspective where the observer sees objects from a viewpoint different from their own). One of the main roles of retrosplenial cortex is in shifting perspective across different spatial reference frames (Alexander et al., 2023). Retrosplenial cortex contains various cell types that are specialized in encoding the structure of the environment and routes as well as one's egocentric position and spatial orientation relative to environmental cues and boundaries. This comprehensive encoding of spatial information leads to a detailed mental representation of the environment which in turn facilitates the transformation between egocentric and allocentric reference frames. One study found that retrosplenial cortex activity is linked to route learning from a first person perspective (i.e., egocentric perspective) (Wolbers & Büchel, 2005). Another study showed that activation of retrosplenial cortex is linked to navigating from an egocentric viewpoint after learning the environment from an aerial-view map (i.e., allocentric viewpoint) (Zhang et al., 2012). Lesion studies also found that damage to the retrosplenial cortex and nearby posterior cingulate cortex can cause disruption in integrating spatial information across egocentric and allocentric reference frames (Hashimoto et al., 2010; Suzuki et al., 1998). Level 1 visuospatial perspective taking measures the ability to imagine what can or cannot be seen from a different location in an environment and level 2 visuospatial perspective taking measures the ability to imagine how a scene looks from a viewpoint that is different than the person's viewpoint. The results of previous studies show that both precuneus and posterior cingulate cortex are involved in level 1 visuospatial perspective taking and posterior cingulate cortex is involved in level 2 visuospatial perspective taking (Gunia et al., 2021). Thus, retrosplenial cortex and nearby posterior cingulate and precuneus regions are implicated in viewpoint transformations.

Cortical Thickness and Cognitive Ability

The human cerebral cortex is a folded layer of nerve cells and its thickness ranges from 1 to 4.5 mm in different cortical regions (M. B. Carpenter & Sutin, 1983). Cortical thickness can reflect various information about the structural characteristics of the neuropil, such as neuronal arrangement and synaptic density (Narr et al., 2007). Despite the correlation between cortical thickness and local measures of grey matter volume (Narr et al., 2005), cortical thickness measures are more strongly associated with cognitive and intellectual abilities (Narr et al., 2007). Several

studies have investigated the relationship between cortical thickness and general intelligence (Bajaj et al., 2018; Heyer et al., 2022; Menary et al., 2013; Schmitt et al., 2019; Schnack et al., 2015; Zhao et al., 2019). These longitudinal and cross-sectional studies suggest that cortical thickness is negatively associated with intelligence during early childhood (Schnack et al., 2015; Shaw et al., 2006), and negatively correlated with cognitive abilities such as executive function (Tamnes et al., 2010), working memory (Krogsrud et al., 2021), and associative memory (de Chastelaine et al., 2019) during adolescence and young adulthood. However, the relationship between cortical thickness and cognitive abilities shifts to a positive correlation in older adults (de Chastelaine et al., 2019; Karama et al., 2014; Salthouse et al., 2015). Previous studies found that in children and adolescence, thinner parietal cortex is associated with better visuo-spatial working memory performance (Darki & Klingberg, 2015), and thinner parietal and frontal cortex is associated with visuo-spatial working memory (Østby et al., 2011; Tamnes et al., 2010). Thus, since cortical thickness plays an important role in visuospatial working memory, performance on small-scale tasks involving visuospatial working memory—such as the Corsi block task, mental rotation, and paper folding—might also be related to cortical thickness in several brain regions, including the parietal cortex.

Training could also have short-term effects on cortical thickness. Memory training in middle-aged and healthy elderly participants was associated with cortical thickening of the right fusiform and lateral orbitofrontal cortex (Engvig et al., 2010). In spatial navigation contexts, one study showed that four months of spatial training increased the cortical thickness of the left precuneus and paracentral lobule in young adults only (Wenger et al., 2012). Both young and older adults showed improvements in navigation performance after training, however, older adults exhibited poorer performance compared to young adults. Together, the cortical thickness literature suggests that both thicker and thinner cortical thickness are associated with better cognitive abilities in younger adults, although with age these relationships tend to reflect thicker cortical thickness as a marker of ability.

Hippocampal Grey Matter Volume and Cognitive Ability

The hippocampus is a brain structure that plays a critical role in spatial information processing. The anterior hippocampus is involved in encoding or acquiring new visuospatial information whereas the posterior hippocampus is involved in retrieval (Hartley et al., 2003; Iaria et al., 2007; Lepage et al., 1998; Squire, 1992). The result of some functional MRI studies showed that anterior hippocampus is more involved in imagination tasks than memory tasks (Addis et al., 2007, 2009), as well as encoding head direction information and angular features (Maguire et al., 1998). Small-scale spatial tasks such as mental rotation also involve encoding abstract and novel objects and angular features as well as encoding or acquiring visuospatial information, suggesting that the anterior hippocampus could be involved in small-scale spatial tasks. Damage to the hippocampus causes spatial working memory deficits (Abrahams et al., 1997; Bohbot et al., 1998; Holdstock et al., 2000). One rodent study showed that bilateral hippocampal lesions disrupt spatial working memory (Duda & Węsierska, 2021), suggesting that the hippocampus could be important

for maintaining spatial information required in small-scale spatial tasks such as mental rotation, paper folding and Corsi block. One study found that damage to the dentate gyrus (DG) can disrupt the perceptual discrimination of novel objects (Mitchnick et al., 2022). In that study, an individual with bilateral dentate gyrus lesions had difficulty selecting a perceptually impossible object from among similar perceptually possible objects presented at different rotations, despite intact visuospatial attention, working memory, and mental rotation abilities. Another study assessed the relationship between memory performance and hippocampal subfield volumes in a young healthy population using Wechsler Memory Scale (WMS) (Travis et al., 2014). The results revealed a significant positive correlation between short-term visual-spatial memory and both a combined CA1/2/3 and dentate gyrus (DG) volumes. The apparent contrast in working memory between Mitchnick and Travis's studies could be due to several factors such as differences in populations (i.e., lesioned patients versus correlations in healthy individuals), sample sizes, and cognitive tasks. Moreover, this discrepancy underscores the complexity of brain-behavior relationships and the need for further research to deepen our understanding of the dentate gyrus (DG)'s role in cognition.

Human (Hartley & Harlow, 2012; Maguire et al., 2000; Nedelska et al., 2012; Schinazi et al., 2013; Sodoma et al., 2022) and animal studies (Jacobs & Spencer, 1994; Krebs et al., 1989; Rehkamper et al., 1988; Sherry et al., 1989) have shown that hippocampal volume is also correlated with large-scale spatial abilities, especially wayfinding and allocentric processing. However, the results of studies on the relationship between hippocampal volume and navigation abilities in healthy young adults are mixed. More recent, well-powered studies, have found no relationship with navigation performance in healthy young individuals (Clark et al., 2020; Weisberg et al., 2019), whereas another one did find a relationship (Tu et al., 2024). The mixed results for large-scale spatial abilities in healthy young adults could also be due to different neuroimaging techniques and statistical methods used in different studies.

Only one study has tested hippocampal subfield volume and spatial skills, in a large-scale navigation task; participants had to navigate through similar-looking virtual maze hallways (Tu et al., 2024). The results showed a significant positive correlation between hippocampal CA3 and dentate gyrus (DG) subfield volumes and navigation success due to these regions' roles in pattern separation (Suthana et al., 2021).

Although we are not focusing on navigation tasks in this paper, common processes between small-scale and navigation tasks suggest that the hippocampus might also be involved in small-scale spatial abilities. Due to anterior hippocampus's role in encoding new visuospatial information, we theorize that it is involved in small-scale spatial tasks such as mental rotation and paper folding. Moreover, since the ability to distinguish between identical objects is necessary for many small-scale spatial tasks – including mental rotation, which measures visuospatial memory – hippocampal subfields involved in pattern separation and visuospatial memory, such as the dentate gyrus (DG) and CA3, could also play a role in these tasks.

Sex Differences in Small-Scale Spatial Abilities

Many studies have demonstrated sex differences favoring men in small-scale spatial abilities, with mental rotation tasks consistently showing moderate-to-large sex differences in adults (Levine et al., 2016; Linn & Petersen, 1985; Voyer et al., 1995). The results of a meta-analysis showed that sex differences in mental rotation abilities increase with age: there is a small sex difference in mental rotation performance during childhood (males outperform females) and it increases substantially with age and reaches a moderate effect size during adulthood (Lauer et al., 2019). This study also found that task parameters can moderate sex differences in mental rotation abilities. For example, sex differences in mental rotation performance were larger when participants had to do the task under a time limit, when incorrect choices were mirror images of the main stimulus instead of being structurally different, or when using three-dimensional stimuli instead of two-dimensional objects. According to the results of another meta-analysis, the magnitude of gender differences in mental rotation tasks is linearly correlated with the total time available for completing those tasks (Voyer, 2011). Moreover, sex differences vary with the type of the task. For example, despite the similarities of mental rotation and paper folding task in many aspects (i.e., both tasks require visual encoding, object rotation, and making judgments on whether two objects are the same or different), sex differences are not observed in paper folding tasks (Harris et al., 2013).

One study investigated sex differences in mental rotation tasks using two paradigms: Vandenberg and Kuse (Vandenberg & Kuse, 1978) where participants choose 2 of 4 options representing rotations of a three-dimensional image, with incorrect options being either mirror versions or structurally different from the main image, and Shepard and Metzler (Shepard & Metzler, 1971), where participants determine whether two images are the same (i.e., one is a rotated version of the other), or different (i.e., one is the mirror version of the other) (Boone & Hegarty, 2017). The results showed that in both paradigms, males and females showed better performance (i.e., higher accuracy and faster reaction times) when the incorrect choices were structurally different than the main stimulus. Moreover, when angular disparities between the targets and the image were small, no sex differences were observed. However, with larger angular disparities, males outperformed females, even though both sexes showed impaired performance. This result suggests that males may be better at finding alternative strategies as the task becomes more challenging.

Compared with mental rotation abilities, sex differences in perspective taking abilities have not received as much focus. However, according to the results of some studies, males outperform females in some perspective taking tasks such as the Money Road Map test (Money et al., 1965) and the Object-Perspective-Taking/Spatial Orientation test (Fields & Shelton, 2006; Hegarty & Waller, 2004; Meneghetti et al., 2012; Zacks & Tversky, 2002). This sex difference is moderated by social factors, such as the inclusion of a human figure (Tarampi et al., 2016).

Due to the anterior hippocampus's role in encoding new spatial information, one study investigated the relationship between grey matter volume in the anterior hippocampus and sex differences in 3D mental rotation (Wei et al., 2016). They found that men's anterior hippocampus was larger than that of females, and the grey matter volume in the right anterior hippocampus was significantly correlated with mental rotation scores. After controlling for grey matter volume in the right anterior hippocampus, the male advantage in 3D mental rotation was no longer observed. The results of this study suggest that the structural differences in the anterior hippocampus of men and women are the neurobiological mechanisms underlying sex differences in mental rotation abilities.

Besides small-scale spatial tasks, a recent meta-analysis investigating sex differences in large-scale spatial navigation tasks showed a small-to-moderate male advantage in navigation abilities (Nazareth et al., 2019). According to this study, several factors such as task goals, time constraints, and age can moderate sex differences in navigation abilities.

The Present Study

The previous literature has demonstrated that shared and distinct neural processes and brain regions are involved in object-based and egocentric perspective transformations. However, there is a lack of comprehensive studies that simultaneously investigate different aspects of these brain structures and their relationship to object-based and egocentric perspective transformation abilities. Additionally, there is a gap in the literature on investigating neural structures supporting these transformations across multiple tasks. The first goal of this study is to determine, at the behavioral level, whether object-based transformation and egocentric perspective transformation abilities are distinct or similar abilities. Several studies highlight the significant role of cortical thickness and grey matter volume in various brain regions involved in cognitive functions such as fluid intelligence, spatial navigation, and working memory. However, the relationship between aspects of brain structures – including grey matter volume and cortical thickness – and performance in object-based and egocentric perspective transformation tasks has been rarely discussed. Sex differences observed in mental rotation and perspective-taking abilities may be linked to variations in brain structures supporting these functions. This study aims to investigate the relationship between these structural characteristics (i.e., grey matter volume and cortical thickness) of specific brain regions and performance in object-based and egocentric perspective transformation tasks among males and females.

The tasks used in the current study include three object-based transformation tasks (mental rotation (MRT), paper folding (PFT), and Corsi blocks (CBT)), and three egocentric-perspective transformation tasks (Road Map Test (RMT), spatial orientation test (SOT), viewpoint transformation task (iVTT))

Hypotheses

Confirmatory Factor Analysis (CFA)

- We hypothesize that object-based and egocentric perspective transformation abilities are distinct, thus, using CFA, we expect that a 2-factor model will fit the data better than the one-factor model.

Sex Differences in Behavior

- According to the results of previous studies on sex differences in object-based and perspective transformation tasks, we hypothesize that males will outperform females in the task that highly rely on object-based spatial abilities (i.e., the mental rotation task), and on tasks that require perspective transformations such as the road map task (it also involves egocentric mental rotation) as well as spatial orientation task.
- According to previous studies (Harris et al., 2013; Linn & Petersen, 1985; Voyer et al., 1995), sex differences are not observed in paper folding tasks. Thus, we do not expect to see sex differences in this task. **Cortical Thickness (CT)**

- Based on the results of previous functional MRI studies, we hypothesize that regions important for motor imagery, visuospatial information, and perspective taking processing play a role in object-based and egocentric perspective transformation tasks. We will examine cortical thickness of these regions. Our ROIs include regions involved in those functions: parietal areas important for personal spatial awareness and have previously been associated with mental rotation in functional imaging (superior parietal, inferior parietal, supramarginal gyrus, precuneus, superior temporal), retrosplenial areas associated with transformation between egocentric and allocentric perspectives (isthmus cingulate, precuneus, posterior cingulate), and motor areas (precentral). We hypothesize that spatial abilities will be related to the cortical thickness of these regions. More specifically, we expect that the parietal regions will be related to all small-scale tasks, but motor areas will also be related to object-based transformation tasks (mental rotation, Corsi blocks, and paper folding) and retrosplenial areas will only be related to egocentric transformation tasks (SOT, Road Map, and iVTT).

Subcortical Grey Matter Volume (GMV)

- Based on the previous functional imaging literature, we hypothesize that subcortical areas related to motor control will have gray matter volumes associated with mental rotation ability. Putamen and caudate grey matter volumes will be associated with MRT due to their role in hand-specific motor imagery and motor control.
- We also theorize that motor imagery, working memory, and motor control are involved in the Paper Folding and Corsi Blocks tests, thus we expect to see the

associations with grey matter volumes in putamen and caudate in these tasks as well.

- We predict that there will be correlation between anterior hippocampal grey matter volume and performance in both object-based and egocentric perspective transformation tasks due to the anterior hippocampus' significant role in encoding novel objects, visuospatial information, head direction information, and angular features. We will also explore grey matter volumes in hippocampal subfields. Our ROIs include hippocampal subfields involved in pattern separation (i.e., dentate gyrus and CA3). We predict that DG and CA3 volume will be associated with performance in mental rotation and paper folding because they involve discrimination between similar objects.

Methods

This study is part of a large study on individual differences in human navigation ability. Over 40 navigation and cognitive tasks were used in the main study to measure human variability in navigation performance and ability.

In the present study, we will use three object-based spatial tasks (mental rotation, paper folding, Corsi blocks) and three perspective transformation tasks (Road Map, spatial orientation test, viewpoint transformation task) to investigate the relationship between object-based and egocentric spatial abilities and the brain structures supporting them.

Participants

112 participants (age: 18 to 35) will be recruited from the UCI communities. An *a priori* power analysis (G*Power App) (Faul et al., 2007) with $\alpha = 0.05$, a small-to-moderate effect size for correlations of 0.3, and β (power) = 0.90 yielded a total sample size of 109.

The behavioral component will also include participants from UCSB. An additional 138 participants (age: 18 to 35) will be included for that analysis to provide more statistical power for the confirmatory factor analysis.

Display and Equipment

Desktop Tasks

VEs were also created for desktop use and were built and rendered in Unity using custom scripts. For these VEs, participants virtually move in the environment using the keyboard and mouse controls. Questionnaires and post-task surveys are presented in Qualtrics.

On the University of California, Irvine campus, desktop experiments are displayed on a 23-inch Acer G6 Series monitor with 1920 x 1080 resolution at a 60 Hz refresh rate. The Acer

Predator Orion 5000 610 rgb desktop computer is powered by a 3.60 GHz Intel Core i7-9700K central processing unit, an Nvidia GeForce RTX 2070 graphics card with 8GB of dedicated memory, and 16 GB of system memory. On the University of California, Santa Barbara campus, these desktop tasks are displayed on a 24-inch Dell Professional P2412HB LED monitor with 1920 x 1080 resolution at a 60 Hz refresh rate. The Dell OptiPlex 7070 desktop computer is powered by a 3.00 GHz Intel Core i7-9700 central processing unit, an AMD Radeon RX 550 graphics processing unit, and 16 GB of system memory.

Immersive VR Task

Experimental sessions utilizing viewpoint transformation task take place either at the Center for Ambulatory Virtual Environment Research in Navigation (CAVERN) on the University of California, Irvine campus or at the Research Center for Virtual Environments and Behavior (ReCWEB) on the University of California, Santa Barbara campus. A Virtual Environment (VE) was built to fit in both CAVERN and ReCWEB, yielding a maximum of 7 m 7 m size environments. At both sites, experiments were displayed using an HTC VIVE Pro Eye VR head-mounted display (HMD) with Dual OLED 3.5” diagonal display (1440 1600 pixels per eye or 2880 1600 pixels combined), a 90 Hz refresh rate, and a 110° field of view capable of delivering high-resolution audio through removable headphones. In addition to the HMD, the VR interface included two HTC VIVE wireless handheld controllers for interacting with the experiment and four HTC Base Station 2.0 infrared tracking sensors for large-scale open space tracking. The Virtual Environment (VE) for the viewpoint transformation task was built and rendered in Unity; the task was programmed in Unity using custom scripts and scripts modified from the Landmarks Unity package (Starrett et al., 2021). In this task, participants physically walk in the environment while wearing a HMD . The VE provide complexity and ecological validity, as well as vestibular and proprioceptive information, while maintaining experimental control over the navigational factors of interest.

Experimental Tasks

Perspective Taking Tasks

Perspective taking involves the mental transformation of one viewpoint to another viewpoint. Rather than mentally manipulating objects, mental manipulation is of one's own viewpoint. Often this transformation includes viewing a top-down map of an environment and then making spatial decisions based on a first-person view. A previous study indicated that perspective taking mediated the relationship between small-scale spatial abilities and navigation abilities (He et al., 2022) possibly by being a large-scale analogue.

Spatial Orientation Test (SOT) (Friedman et al., 2020; Hegarty & Waller, 2004) . In this test of perspective taking, participants view a layout of objects on a screen. They are asked to imagine standing at one object, facing a second object, then pointing to a third object. The imagined facing direction differs from their actual direction, measuring spatial perspective-taking ability. Three practice trials are given, and participants are allowed 5 minutes to complete 12 test

trials. The main outcome measure is the absolute angular error of each trial - ranging from 0° to 180° - averaged across trials, with a lower angular error indicating better perspective-taking ability.

Road Map Test (RMT) (Money et al., 1965). In this test of perspective taking, participants are shown a meandering travel path on a map of a town. Without turning the map, they indicate whether each turn is to the left or right. There are 32 turns in the route, and the participants have 20 seconds to respond. The main outcome measure is the total number of correct turns, resulting in a maximum possible score of 32. A higher score indicates better perspective-taking ability.

Viewpoint Transformation Task (VTT) (He et al., 2022). The VTT is a new test, designed to be an immersive VR version of the SOT, including spatial updating of one's position while trying to reach a target location. The ambulatory VE for this task is a virtual desert with a circular walled arena. Each trial includes a map presentation and a navigation phase. First, the participant is shown a map for 2 seconds, indicating the location and orientation of the participant at the start of the trial, and the location of their goal. Then, during the navigation phase, the participant is returned to the first-person view at the center of the arena. They must then turn and walk to where they think the goal is located, and click the trigger of the handheld controller when they think they have reached the target. Critically, the heading orientation of the participant on the map does not align with the actual facing direction of the participant. In order to successfully reach the goal, the participant must both transform the perspective from an overhead viewpoint to a first-person viewpoint and update their heading with respect to the orientation in the map. There are 24 trials in total. Three main trial attributes are Perspective Shift, Traveling Direction, and Traveling Distance. The Perspective Shift is the divergence of the imagined heading from the vertical direction, ranging from 90° to 180°, counterbalanced between right and left sides. Traveling Direction is the direction of travel to the target, after the perspective shift has taken place. This ranges from 0° to 180°, counterbalanced between right and left. Traveling Distance is the distance between the starting location and the target, ranging between 1.5 to 2.5 meters. The primary outcome measure is the position error which includes the distance error and the absolute angular error. The distance error is the absolute difference between correct distance and the actual distance traveled. The absolute angular error is the angular difference between the correct heading and the actual heading traveled.

Object-Based Spatial Abilities Tasks

Object-based or “small-scale” spatial ability tasks have been the traditional method of measuring spatial abilities. These show small objects and require spatial mental imagery or mental manipulation of spatial information to solve.

Mental Rotation Test (MRT) (Shepard & Metzler, 1971). This task tests spatial visualization and accurate mental rotation of objects. Two sets of three-dimensional cubed objects are displayed side-by-side on the screen, which are either exactly the same or are mirror images of

each other. The cubed objects are also rotated, so they are not in the same picture plane. Participants decide whether the figures are the same or different. There are 60 trials and this test is untimed. The main outcome measure is the total number of correct responses, resulting in a maximum possible score of 60. Another commonly-used measure is reaction time for correct trials, with faster responses indicating more ability. We will compute both measures and the measure of ability will be the average of the Z-scores of the two measures.

Paper Folding Test (PFT) (Ekstrom et al., 1976). This task requires the ability to mentally manipulate a piece of paper and imagine how the hole punch shows up spatially when the paper is unfolded. A piece of paper is shown folded various times, and one hole is punched through all folds of the folded paper. The participant must decide from 5 options which unfolded paper matches what the paper would look like after the hole-punch. There are 2 parts with 10 trials each, and a 3-minute time limit for each part. The main outcome measure is the total number of correct responses, resulting in a maximum possible score of 20. A higher score indicates better spatial ability.

Corsi Block Test (CBT) (Corsi, 1972). CBT measures the short-term visuospatial memory. In the original version of this task, the experimenter taps a sequence of blocks in front of the participant, who must then tap the blocks in the same order as the experimenter. There are a total of 9 blocks, and the number of blocks tapped by the experimenter varies in each trial. We are using the computerized version of this task.

Neuroimaging Data Collection

In a final session that concluded the study, 112 of the participants were first screened for MRI eligibility. Eligible participants were then scanned at UCI's Facility for Imaging and Brain Research (FIBRE), which houses a 3 Tesla Siemens Prisma scanner with a 32-channel head coil.

The scanning protocol included a whole-brain structural T1-weighted image using an MPRAGE sequence with the following parameters: repetition time (TR) = 2300 ms, echo time (TE) = 2.38 ms, inversion time (TI) = 902 ms, slices = 240, resolution = $0.8 \times 0.8 \times 0.8 \text{ mm}^3$, flip angle = 8° . A high-resolution T2-weighted image was acquired, which had partial-brain coverage, was orientated perpendicular to the long axis of the hippocampus for segmentation of the entorhinal cortex, and included the following parameters: TR = 8020 ms, TE = 50 ms, slices = 30, resolution = $0.4 \times 0.4 \times 2.0 \text{ mm}^3$, flip angle = 122° . At the end of the scanning session, whole-brain echo-planar-imaging (EPI) images were acquired as the participant completed a functional task described below. These images were set up perpendicular to the long axis of the hippocampus with the following parameters: TR = 2000 ms, TE = 25 ms, slices = 81, resolution = $2.0 \times 2.0 \times 2.0 \text{ mm}^3$, flip angle = 70° . A diffusion-weighted scan, an fMRI resting-state scan, and task-based fMRI scan were also acquired during this session, but will not be discussed further in this study.

To ensure data quality, we will exclude problematic scans from analysis, particularly those compromised by artifacts, excessive head motion, or other technical issues.

Analysis

Behavioral Analysis

We will conduct correlational analyses to investigate the relationship between object-based and egocentric perspective transformation abilities at the behavioral level. We will analyze the performance of participants on tests of object-based transformations and egocentric perspective transformations using Confirmatory Factor Analysis (CFA) in two phases. First, we will do the CFA without including the Corsi Block Test to maintain a larger sample size (approximately 250 participants), as including it would reduce the number of participants available for analysis. This initial CFA will help us assess the overall model fit and the relationships between the constructs. In the second phase, we will include the Corsi Block Test and perform the CFA with a smaller sample size (98 participants) to investigate how its inclusion affects the model fit and the overall structure. By comparing the results from both analyses, we aim to ensure a comprehensive evaluation of the model while addressing the limitations posed by sample size. . CFA allows us to impose a specific model on our data and assess how well that model fits, enabling us to test our hypothesis more directly. If object-based transformations and egocentric perspective transformation abilities are distinct, then a model that assumes tests of both abilities load onto a single factor should not fit the data as well as a two-factor model that treats them as separate factors. If object-based transformations and egocentric perspective transformation abilities are similar abilities, then a model that assumes these abilities load onto a single spatial factor should fit the data best. If the two-factor model wins, we will then look at the correlation between these factors to estimate the extent to which these abilities are related. Conversely, if a one-factor model wins, we will look at correlations with that single factor. We will also do independent samples t-tests to investigate the sex differences in object-based tasks as well as egocentric perspective transformation tasks.

Object-based transformation abilities will be measured by three tasks: Mental Rotation Test, Paper Folding Test, and Corsi Block Test, and egocentric perspective transformation abilities will be measured by three tasks: Spatial Orientation Test, Road Map Test, and Viewpoint Transformation Test. We will remove cases in which a participant was not able to complete the task properly, for example, if they are due to the participant's motion sickness. Before starting the analyses, we will identify multivariate outliers (e.g., participants who did not follow task instructions) and remove them. If the data is not normally distributed, we will use a log transform to reduce skewness of the variables. We will also look at the distribution of the participants' performance in each task separately to detect outliers more than 3 standard deviations from the mean; values that exceed 3 standard deviations from the mean will be set to 3 standard deviations from the mean (winsorized).

Neuroimaging Analysis

We will also analyze the relationship between different brain structures and object-based and egocentric perspective transformation abilities. Cortical thickness and grey matter volumes

will be measured by Advanced Normalization Tools version 2.3.3 (ANTs) (Avants et al., 2011) and FreeSurfer software (<http://surfer.nmr.mgh.harvard.edu>) version 6.0.

For the region-level ROI analysis, we will use FreeSurfer, which utilizes a surface-based approach. Cortical thickness will be calculated as the distance between white matter boundaries and pial surface. The mean cortical thickness values will be calculated for the cortical *a priori* ROIs defined by Desikan-Killiany atlas (Desikan et al., 2006): superior parietal, inferior parietal, supramarginal gyrus, precuneus, superior temporal, isthmus cingulate, precuneus, posterior cingulate. Correlational analyses will be conducted to assess the relationship between task performance and cortical thickness within each ROI. FreeSurfer will also be used to calculate the grey matter volumes in our subcortical *a priori* ROIs: the caudate, putamen, and hippocampal volume (total). Manual and Automatic Segmentation of the Hippocampal Subfields (ASHS) will be used to calculate the anterior/posterior hippocampal volume, and grey matter volume in DG and CA3 regions. Manual adjustments will be made using the ITK-SNAP software application (Yushkevich et al., 2006) to refine the boundaries of the ASHS output, following the hippocampal subfield protocols outlined by (Dalton et al., 2017) and (Berron et al., 2017). We will control for age, sex and total intracranial volume and do sex stratified analyses to investigate the relationship between cortical thickness and performance in males and females separately. A Benjamini-Hockberg correction for multiple comparisons across the ROIs will be applied for each task.

For the exploratory whole-brain analysis, the mean cortical thickness values will be calculated for all 34 cortical ROIs per hemisphere defined by Desikan-Killiany atlas (Desikan et al., 2006). For the exploratory whole brain network analysis, estimates of cortical thickness will be obtained within each parcel of the Schaefer 400-region 17-Networks using T1-weighted scans and ANTs cortical thickness pipeline (antsCorticalThickness). We will then calculate the average cortical thickness across all parcels within each sub-network (e.g., average cortical thickness in the temporal part of the DMN (Default Network)). Correlational analyses will be conducted to assess the relationship between the task performance and average cortical thickness within each network. Due to increased risk of type I errors resulting from conducting multiple tests, we will correct for multiple comparisons using the False Discovery Rate (FDR) approach and adjusted-p values. We will control for age, sex and total intracranial volume and do sex stratified analyses to investigate the relationship between cortical thickness and performance in males and females separately. We will do the same exploratory analyses for subcortical grey matter volumes as well.

Power Analysis

To ensure adequate statistical power for our confirmatory factor analysis (CFA) model, an *a priori* power analysis (G*Power App) (Faul et al., 2007) was done with $\alpha = 0.05$, a medium effect size of 0.15, and β (power) = 0.90, and it yielded a total sample size of 88 for two-factor model, and a total sample size of 73 for one-factor model. We used the same parameters for our neuroimaging analyses; therefore, the required total sample size for detecting a medium effect size is 73. Given that we have 112 participants scanned, this sample size is sufficient for our analyses of cortical thickness and grey matter volume.

To ensure adequate statistical power to detect sex differences in mental rotation and egocentric perspective transformation tasks, an a priori power analysis was done with $\alpha = 0.05$, a medium effect size of 0.5, and β (power) = 0.90, and it yielded a total sample size of 172 (i.e., 86 males and 86 females). Given that we have approximately 250 participants performing our behavioral tasks, this sample size is sufficient for our t-test analyses.

References

- Abrahams, S., Pickering, A., Polkey, C. E., & Morris, R. G. (1997). Spatial memory deficits in patients with unilateral damage to the right hippocampal formation. *Neuropsychologia*, 35(1), 11–24. [https://doi.org/10.1016/S0028-3932\(96\)00051-6](https://doi.org/10.1016/S0028-3932(96)00051-6)
- Addis, D. R., Pan, L., Vu, M. A., Laiser, N., & Schacter, D. L. (2009). Constructive episodic simulation of the future and the past: Distinct subsystems of a core brain network mediate imagining and remembering. *Neuropsychologia*, 47(11), 2222–2238. <https://doi.org/10.1016/j.neuropsychologia.2008.10.026>
- Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, 45(7), 1363–1377. <https://doi.org/10.1016/j.neuropsychologia.2006.10.016>
- Alexander, A. S., Place, R., Starrett, M. J., Chrastil, E. R., & Nitz, D. A. (2023). Rethinking retrosplenial cortex: Perspectives and predictions. *Neuron*, 111(2), 150–175. <https://doi.org/10.1016/j.neuron.2022.11.006>
- Alivisatos, B., & Petrides, M. (1997). Functional activation of the human brain during mental rotation. *Neuropsychologia*, 35(2), 111–118.
- Amorim, M. A., & Stucchi, N. (1997). Viewer- and object-centered mental explorations of an imagined environment are not equivalent. *Cognitive Brain Research*, 5(3), 229–239. [https://doi.org/10.1016/S0926-6410\(96\)00073-0](https://doi.org/10.1016/S0926-6410(96)00073-0)
- Avants, B. B., Tustison, N. J., Song, G., Cook, P. A., Klein, A., & Gee, J. C. (2011). A reproducible evaluation of ANTs similarity metric performance in brain image registration. *NeuroImage*, 54(3), 2033–2044. <https://doi.org/10.1016/j.neuroimage.2010.09.025>
- Bajaj, S., Raikes, A., Smith, R., Dailey, N. S., Alkozei, A., Vanuk, J. R., & Killgore, W. D. S. (2018). The Relationship Between General Intelligence and Cortical Structure in Healthy Individuals. *Neuroscience*, 388, 36–44. <https://doi.org/10.1016/j.neuroscience.2018.07.008>
- Berron, D., Vieweg, P., Hochkeppeler, A., Pluta, J. B., Ding, S. L., Maass, A., Luther, A., Xie, L., Das, S. R., Wolk, D. A., Wolbers, T., Yushkevich, P. A., Düzel, E., & Wisse, L. E. M. (2017). A protocol for manual segmentation of medial temporal lobe subregions in 7 Tesla

- MRI. *NeuroImage: Clinical*, 15(May), 466–482. <https://doi.org/10.1016/j.nicl.2017.05.022>
- Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, 36(11), 1217–1238. [https://doi.org/10.1016/S0028-3932\(97\)00161-9](https://doi.org/10.1016/S0028-3932(97)00161-9)
- Boller, F., Passafiume, D., Keef, N. C., Rogers, K., & Morrow, L. (1984). Visuospatial Impairment in Parkinson ' s Disease: Role of perceptual and motor factors. *Archives of Neurology*.
- Boone, A. P., & Hegarty, M. (2017). Sex Differences in Mental Rotation Tasks : Not Just in the Mental Rotation Process ! *Journal of Experimental Psychology: Learning, Memory, and Cognition*. <https://doi.org/10.1037/xlm0000370>
- Carpenter, M. B., & Sutin, J. (1983). *Human neuroanatomy* (8th ed.). Williams & Wilkins.
- Carpenter, P. A., Just, M. A., Keller, T. A., Eddy, W., & Thulborn, K. (1999). Graded functional activation in the visuospatial system with the amount of task demand. *Journal of Cognitive Neuroscience*, 11(1), 9–24. <https://doi.org/10.1162/089892999563210>
- Clark, I. A., Monk, A. M., Hotchin, V., Pizzamiglio, G., Liefgreen, A., Callaghan, M. F., & Maguire, E. A. (2020). Does hippocampal volume explain performance differences on hippocampal-dependant tasks? *NeuroImage*, 221(July), 117211. <https://doi.org/10.1016/j.neuroimage.2020.117211>
- Cohen, M. S., Kosslyn, S. M., Breiter, H. C., Digirolamo, G. J., Thompson, W. L., Anderson, A. K., Bookheimer, S. Y., Rosen, B. R., & Belliveau, J. W. (1996). Changes in cortical activity during mental rotation: A mapping study using functional MRI. *Brain*, 119(1), 89–100. <https://doi.org/10.1093/brain/119.1.89>
- Corsi, P. M. (1972). Human memory and the medial temporal region of the brain. *Dissertations Abstracts International*, 34(2), 819B.
- Creem, S. H., Wraga, M., & Proffitt, D. R. (2001). Imagining physically impossible self-rotations: Geometry is more important than gravity. *Cognition*, 81(1), 41–64. [https://doi.org/10.1016/S0010-0277\(01\)00118-4](https://doi.org/10.1016/S0010-0277(01)00118-4)
- Dalton, M. A., Zeidman, P., Barry, D. N., Williams, E., & Maguire, E. A. (2017). Segmenting subregions of the human hippocampus on structural magnetic resonance image scans: An illustrated tutorial. *Brain and Neuroscience Advances*, 1, 239821281770144. <https://doi.org/10.1177/2398212817701448>
- Darki, F., & Klingberg, T. (2015). The role of fronto-parietal and fronto-striatal networks in the development of working memory: A longitudinal study. *Cerebral Cortex*, 25(6), 1587–1595. <https://doi.org/10.1093/cercor/bht352>
- de Chastelaine, M., Donley, B. E., Kennedy, K. M., & Rugg, M. D. (2019). Age moderates the relationship between cortical thickness and cognitive performance. *Neuropsychologia*, 132(July), 107136. <https://doi.org/10.1016/j.neuropsychologia.2019.107136>
- Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., Buckner, R.

- L., Dale, A. M., Maguire, R. P., Hyman, B. T., Albert, M. S., & Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage*, 31(3), 968–980. <https://doi.org/10.1016/j.neuroimage.2006.01.021>
- Duda, W., & Węsierska, M. (2021). Spatial working memory in rats: Crucial role of the hippocampus in the allothetic place avoidance alternation task demanding stimuli segregation. *Behavioural Brain Research*, 412(June). <https://doi.org/10.1016/j.bbr.2021.113414>
- Eisenegger, C., Herwig, U., & Jäncke, L. (2007). The involvement of primary motor cortex in mental rotation revealed by transcranial magnetic stimulation. *European Journal of Neuroscience*, 25(4), 1240–1244. <https://doi.org/10.1111/j.1460-9568.2007.05354.x>
- Ekstrom, R. B., French, J. ., & Harmon, H. H. (1976). Manual for Kit of Reference Tests for Cognitive Factors. *Undefined*, 151–174.
- Engvig, A., Fjell, A. M., Westlye, L. T., Moberget, T., Sundseth, O., Larsen, V. A., & Walhovd, K. B. (2010). Effects of memory training on cortical thickness in the elderly. *NeuroImage*, 52(4), 1667–1676. <https://doi.org/10.1016/j.neuroimage.2010.05.041>
- Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39(2), 175–191. <https://doi.org/10.3758/BF03193146>
- Fields, A. W., & Shelton, A. L. (2006). Individual skill differences and large-scale environmental learning. *Journal of Experimental Psychology: Learning Memory and Cognition*, 32(3), 506–515. <https://doi.org/10.1037/0278-7393.32.3.506>
- Friedman, A., Kohler, B., Gunalp, P., Boone, A. P., & Hegarty, M. (2020). A computerized spatial orientation test. *Behavior Research Methods*, 52(2), 799–812. <https://doi.org/10.3758/s13428-019-01277-3>
- Gunia, A., Moraresku, S., & Vlček, K. (2021). Brain mechanisms of visuospatial perspective-taking in relation to object mental rotation and the theory of mind. *Behavioural Brain Research*, 407(November 2020). <https://doi.org/10.1016/j.bbr.2021.113247>
- Harris, I. M., Harris, J. A., & Caine, D. (2002). Mental-rotation deficits following damage to the right basal ganglia. *Neuropsychology*, 16(4), 524–537. <https://doi.org/10.1037/0894-4105.16.4.524>
- Harris, J., Hirsh-Pasek, K., & Newcombe, N. S. (2013). Understanding spatial transformations: Similarities and differences between mental rotation and mental folding. *Cognitive Processing*, 14(2), 105–115. <https://doi.org/10.1007/s10339-013-0544-6>
- Hartley, T., & Harlow, R. (2012). An association between human hippocampal volume and topographical memory in healthy young adults. *Frontiers in Human Neuroscience*, 6(DEC), 1–11. <https://doi.org/10.3389/fnhum.2012.00338>
- Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, 37(5), 877–888. [https://doi.org/10.1016/S0896-6273\(03\)00095-3](https://doi.org/10.1016/S0896-6273(03)00095-3)

- Hashimoto, R., Tanaka, Y., & Nakano, I. (2010). Heading disorientation: A new test and a possible underlying mechanism. *European Neurology*, 63(2), 87–93. <https://doi.org/10.1159/000276398>
- He, C., Chrastil, E. R., & Hegarty, M. (2022). A new psychometric task measuring spatial perspective taking in ambulatory virtual reality. *Frontiers in Virtual Reality*, 3(October), 1–12. <https://doi.org/10.3389/frvir.2022.971502>
- Hegarty, M., Montello, D. R., Richardson, A. E., Ishikawa, T., & Lovelace, K. (2006). Spatial abilities at different scales: Individual differences in aptitude-test performance and spatial-layout learning. *Intelligence*, 34(2), 151–176. <https://doi.org/10.1016/j.intell.2005.09.005>
- Hegarty, M., & Waller, D. (2004). A dissociation between mental rotation and perspective-taking spatial abilities. *Intelligence*, 32(2), 175–191. <https://doi.org/10.1016/j.intell.2003.12.001>
- Heyer, D. B., Wilbers, R., Galakhova, A. A., Hartsema, E., Braak, S., Hunt, S., Verhoog, M. B., Muijtjens, M. L., Mertens, E. J., Idema, S., Baayen, J. C., De Witt Hamer, P., Klein, M., McGraw, M., Lein, E. S., De Kock, C. P. J., Mansvelder, H. D., & Goriounova, N. A. (2022). Verbal and General IQ Associate with Supragranular Layer Thickness and Cell Properties of the Left Temporal Cortex. *Cerebral Cortex*, 32(11), 1–15. <https://doi.org/10.1093/cercor/bhab330>
- Holdstock, J. S., Mayes, A. R., Cezayirli, E., Isaac, C. L., Aggleton, J. P., & Roberts, N. (2000). A comparison of egocentric and allocentric spatial memory in a patient with selective hippocampal damage. *Neuropsychologia*, 38(4), 410–425. [https://doi.org/10.1016/S0028-3932\(99\)00099-8](https://doi.org/10.1016/S0028-3932(99)00099-8)
- Huttenlocher, J., & Presson, C. C. (1973). Mental Rotation and the Perspective Problem. *Cognitive Psychology*, 299, 277–299.
- Huttenlocher, J., & Presson, C. C. (1979). The coding and transformation of spatial information. *Cognitive Psychology*, 11(3), 375–394. [https://doi.org/10.1016/0010-0285\(79\)90017-3](https://doi.org/10.1016/0010-0285(79)90017-3)
- Iaria, G., Chen, J. K., Guariglia, C., Ptito, A., & Petrides, M. (2007). Retrosplenial and hippocampal brain regions in human navigation: Complementary functional contributions to the formation and use of cognitive maps. *European Journal of Neuroscience*, 25(3), 890–899. <https://doi.org/10.1111/j.1460-9568.2007.05371.x>
- Iglói, K., Doeller, C. F., Berthoz, A., Rondi-Reig, L., & Burgess, N. (2010). Lateralized human hippocampal activity predicts navigation based on sequence or place memory. *Proceedings of the National Academy of Sciences of the United States of America*, 107(32), 14466–14471. <https://doi.org/10.1073/pnas.1004243107>
- Jacobs, L. F., & Spencer, W. D. (1994). Natural space-use patterns and hippocampal size in kangaroo rats. *Brain, Behavior and Evolution*, 44(3), 125–132. <https://doi.org/10.1159/000113584>
- Karama, S., Bastin, M. E., Murray, C., Royle, N. A., Penke, L., Muñoz Maniega, S., Gow, A. J., Corley, J., Valdés Hernández, M., Lewis, J. D., Rousseau, M. E., Lepage, C., Fonov, V., Collins, D. L., Booth, T., Rioux, P., Sherif, T., Adalat, R., Starr, J. M., ... Deary, I. J. (2014). Childhood cognitive ability accounts for associations between cognitive ability and

- brain cortical thickness in old age. *Molecular Psychiatry*, 19(5), 555–559.
<https://doi.org/10.1038/mp.2013.64>
- Keehner, M., Guerin, S. A., Miller, M. B., Turk, D. J., & Hegarty, M. (2006). Modulation of neural activity by angle of rotation during imagined spatial transformations. *NeuroImage*, 33(1), 391–398. <https://doi.org/10.1016/j.neuroimage.2006.06.043>
- Kosslyn, S. M., DiGirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography. *Psychophysiology*, 35(2), 151–161. <https://doi.org/10.1017/S0048577298001516>
- Kosslyn, S. M., & Thompson, W. L. (2003). When Is Early Visual Cortex Activated during Visual Mental Imagery? *Psychological Bulletin*, 129(5), 723–746.
<https://doi.org/10.1037/0033-2909.129.5.723>
- Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H., & Vaccarino, A. L. (1989). Hippocampal specialization of food-storing birds. *Proceedings of the National Academy of Sciences of the United States of America*, 86(4), 1388–1392. <https://doi.org/10.1073/pnas.86.4.1388>
- Krogsrud, S. K., Mowinckel, A. M., Sederevicius, D., Vidal-Piñeiro, D., Amlien, I. K., Wang, Y., Sørensen, Ø., Walhovd, K. B., & Fjell, A. M. (2021). Relationships between apparent cortical thickness and working memory across the lifespan - Effects of genetics and socioeconomic status. *Developmental Cognitive Neuroscience*, 51(June).
<https://doi.org/10.1016/j.dcn.2021.100997>
- Lauer, J. E., Yhang, E., & Lourenco, S. F. (2019). The Development of Gender Differences in Spatial Reasoning: A Meta-Analytic Review. *Psychological Bulletin*, 145(6).
<https://doi.org/10.1037/bul0000191>
- Lawrence, A. D., Watkins, L. H. A., Sahakian, B. J., Hodges, J. R., & Robbins, T. W. (2000). Visual object and visuospatial cognition in Huntington's disease: Implications for information processing in corticostriatal circuits. *Brain*, 123(7), 1349–1364.
<https://doi.org/10.1093/brain/123.7.1349>
- Lee, A. C., Harris, J. P., & Calvert, J. E. (1998). Impairments of mental rotation in Parkinson's disease. *Neuropsychologia*, 36(1), 109–114. [https://doi.org/10.1016/S0028-3932\(97\)00017-1](https://doi.org/10.1016/S0028-3932(97)00017-1)
- Lepage, M., Habib, R., & Tulving, E. (1998). Hippocampal PET activations of memory encoding and retrieval: The HIPER model. *Hippocampus*, 8(4), 313–322.
[https://doi.org/10.1002/\(SICI\)1098-1063\(1998\)8:4<313::AID-HIPO1>3.0.CO;2-I](https://doi.org/10.1002/(SICI)1098-1063(1998)8:4<313::AID-HIPO1>3.0.CO;2-I)
- Levine, S. C., Foley, A., Lourenco, S., Ehrlich, S., & Ratliff, K. (2016). Sex differences in spatial cognition: Advancing the conversation. *Wiley Interdisciplinary Reviews: Cognitive Science*, 7(2), 127–155. <https://doi.org/10.1002/wcs.1380>
- Li, Y., Kong, F., Ji, M., Luo, Y., Lan, J., & You, X. (2019). Shared and distinct neural bases of large- And small-scale spatial ability: A coordinate-based activation likelihood estimation meta-analysis. *Frontiers in Neuroscience*, 13(JAN), 1–20.
<https://doi.org/10.3389/fnins.2018.01021>
- Linn, M. C., & Petersen, A. C. (1985). Emergence and Characterization of Sex Differences in

- Spatial Ability : A Meta-Analysis. *Child Development*, 56(6), 1479–1498.
- Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Frith, C. D., & O’Keefe, J. (1998). Knowing where and getting there: A human navigation network. *Science*, 280(5365), 921–924. <https://doi.org/10.1126/science.280.5365.921>
- Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S. J., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences of the United States of America*, 97(8), 4398–4403. <https://doi.org/10.1073/pnas.070039597>
- Menary, K., Collins, P. F., Porter, J. N., Muetzel, R., Olson, E. A., Kumar, V., Steinbach, M., Lim, K. O., & Luciana, M. (2013). Associations between cortical thickness and general intelligence in children, adolescents and young adults. *Intelligence*, 41(5), 597–606. <https://doi.org/10.1016/j.intell.2013.07.010>
- Meneghetti, C., Pazzaglia, F., & De Beni, R. (2012). Which spatial abilities and strategies predict males’ and females’ performance in the object perspective test? *Cognitive Processing*, 13(1 SUPPL), 267–270. <https://doi.org/10.1007/s10339-012-0500-x>
- Mitchnick, K. A., Ahmad, Z., Mitchnick, S. D., Ryan, J. D., Rosenbaum, R. S., & Freud, E. (2022). Damage to the human dentate gyrus impairs the perceptual discrimination of complex, novel objects. *Neuropsychologia*, 172(April), 108238. <https://doi.org/10.1016/j.neuropsychologia.2022.108238>
- Money, J., Alexander, D., & Walker, H. T. (1965). A standardized road-map test of direction sense. *Johns Hopkins Press*.
- Narr, K. L., Bilder, R. M., Toga, A. W., Woods, R. P., Rex, D. E., Szeszko, P. R., Robinson, D., Sevy, S., Gunduz-Bruce, H., Wang, Y. P., DeLuca, H., & Thompson, P. M. (2005). Mapping cortical thickness and gray matter concentration in first episode schizophrenia. *Cerebral Cortex*, 15(6), 708–719. <https://doi.org/10.1093/cercor/bhh172>
- Narr, K. L., Woods, R. P., Thompson, P. M., Szeszko, P., Robinson, D., Dimtcheva, T., Gurbani, M., Toga, A. W., & Bilder, R. M. (2007). Relationships between IQ and regional cortical gray matter thickness in healthy adults. *Cerebral Cortex*, 17(9), 2163–2171. <https://doi.org/10.1093/cercor/bhl125>
- Nazareth, A., Huang, X., Voyer, D., & Newcombe, N. (2019). A meta-analysis of sex differences in human navigation skills. In *Psychonomic Bulletin and Review* (Vol. 26, Issue 5, pp. 1503–1528). Springer New York LLC. <https://doi.org/10.3758/s13423-019-01633-6>
- Nedelska, Z., Andel, R., Laczó, J., Vlcek, K., Horinek, D., Lisy, J., Sheardova, K., Bureš, J., & Hort, J. (2012). Spatial navigation impairment is proportional to right hippocampal volume. *Proceedings of the National Academy of Sciences of the United States of America*, 109(7), 2590–2594. <https://doi.org/10.1073/pnas.1121588109>
- Østby, Y., Tamnes, C. K., Fjell, A. M., & Walhovd, K. B. (2011). Morphometry and connectivity of the fronto-parietal verbal working memory network in development. *Neuropsychologia*, 49(14), 3854–3862. <https://doi.org/10.1016/j.neuropsychologia.2011.10.001>

- Parsons, L. M., Fox, P. T., Downs, J. H., Glass, T., Hirsch, T. B., Martin, C. C., Jerabek, P. A., & Lancaster, J. L. (1995). *Use of implicit motor imagery for visual shape discrimination as revealed by PET*. 375(May), 4–8.
- Presson, C. C. (1982). Strategies in spatial reasoning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 8(3), 243–251. <https://doi.org/10.1037/0278-7393.8.3.243>
- Ratcliff, G. (1979). Spatial thought, mental rotation and the right cerebral hemisphere. *Neuropsychologia*, 17(1), 49–54. [https://doi.org/10.1016/0028-3932\(79\)90021-6](https://doi.org/10.1016/0028-3932(79)90021-6)
- Rehkamper, G., Haase, E., & Frahm, H. D. (1988). Allometric comparison of brain weight and brain structure volumes in different breeds of the domestic pigeon, *Columba livia* f.d. (fantails, homing pigeons, strassers). *Brain, Behavior and Evolution*, 31(3), 141–149. <https://doi.org/10.1159/000116581>
- Richter, W., Somorjai, R., Summers, R., Jarmasz, M., Menon, R. S., Gati, J. S., Georgopoulos, A. P., Tegeler, C., Ugurbil, K., & Kim, S. G. (2000). Motor area activity during mental rotation studied by time-resolved single-trial fMRI. *Journal of Cognitive Neuroscience*, 12(2), 310–320. <https://doi.org/10.1162/089892900562129>
- Rieser, J. J. (1989). Access to Knowledge of Spatial Structure at Novel Points of Observation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15(6), 1157–1165. <https://doi.org/10.1037/0278-7393.15.6.1157>
- Salthouse, T. A., Babcock, R. L., Mitchell, D. R. D., Palmon, R., & Skovronek, E. (1990). Sources of individual differences in spatial visualization ability. *Intelligence*, 14(2), 187–230. [https://doi.org/10.1016/0160-2896\(90\)90004-D](https://doi.org/10.1016/0160-2896(90)90004-D)
- Salthouse, T. A., Habeck, C., Razlighi, Q., Barulli, D., Gazes, Y., & Stern, Y. (2015). Breadth and age-dependency of relations between cortical thickness and cognition. *Neurobiology of Aging*, 36(11), 3020–3028. <https://doi.org/10.1016/j.neurobiolaging.2015.08.011>
- Schinazi, V. R., Nardi, D., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2013). Hippocampal size predicts rapid learning of a cognitive map in humans. *Hippocampus*, 23(6), 515–528. <https://doi.org/10.1002/hipo.22111>
- Schmitt, J. E., Raznahan, A., Clasen, L. S., Wallace, G. L., Pritikin, J. N., Lee, N. R., Giedd, J. N., & Neale, M. C. (2019). The Dynamic Associations between Cortical Thickness and General Intelligence are Genetically Mediated. *Cerebral Cortex*, 29(11), 4743–4752. <https://doi.org/10.1093/cercor/bhz007>
- Schnack, H. G., Van Haren, N. E. M., Brouwer, R. M., Evans, A., Durston, S., Boomsma, D. I., Kahn, R. S., & Hulshoff Pol, H. E. (2015). Changes in thickness and surface area of the human cortex and their relationship with intelligence. *Cerebral Cortex*, 25(6), 1608–1617. <https://doi.org/10.1093/cercor/bht357>
- Shaw, P., Greenstein, D., Lerch, J., Clasen, L., Lenroot, R., Gogtay, N., Evans, A., Rapoport, J., & Giedd, J. (2006). Intellectual ability and cortical development in children and adolescents. *Nature*, 440(7084), 676–679. <https://doi.org/10.1038/nature04513>
- Shepard, R. N., & Metzler, J. (1971). Mental Rotation of Three-Dimensional Objects Abstract .

- The time required to recognize that two perspective drawings portray. *Science (New York, N.Y.)*, 171(FEBRUARY), 701–703.
- Sherry, D. F., Vaccarino, A. L., Buckenham, K., & Herz, R. S. (1989). The hippocampal complex of food-storing birds. *Brain, Behavior and Evolution*, 34(5), 308–317. <https://doi.org/10.1159/000116516>
- Sodoma, M. J., Cole, R. C., Sloan, T. J., Hamilton, C. M., Kent, J. D., Magnotta, V. A., & Voss, M. W. (2022). *Hippocampal acidity and volume are differentially associated with spatial navigation in older adults*. <https://doi.org/10.1016/j.neuroimage.2021.118682>.Sodoma
- Squire, L. R. (1992). Memory and the Hippocampus: A Synthesis From Findings With Rats, Monkeys, and Humans. *Psychological Review*, 99(2), 195–231. <https://doi.org/10.1037/0033-295X.99.2.195>
- Starrett, M. J., McAvan, A. S., Huffman, D. J., Stokes, J. D., Kyle, C. T., Smuda, D. N., Kolarik, B. S., Laczko, J., & Ekstrom, A. D. (2021). Landmarks: A solution for spatial navigation and memory experiments in virtual reality. *Behavior Research Methods*, 53(3), 1046–1059. <https://doi.org/10.3758/s13428-020-01481-6>
- Suthana, N., Ekstrom, A. D., Yassa, M. A., & Stark, C. (2021). Pattern Separation in the Human Hippocampus: Response to Quiroga. *Trends in Cognitive Sciences*, 25(6), 423–424. <https://doi.org/10.1016/j.tics.2021.02.005>
- Suzuki, K., Yamadori, A., Hayakawa, Y., & Fujii, T. (1998). Pure topographical disorientation related to dysfunction of the viewpoint dependent visual system. *Cortex*, 34(4), 589–599. [https://doi.org/10.1016/S0010-9452\(08\)70516-1](https://doi.org/10.1016/S0010-9452(08)70516-1)
- Tamnes, C. K., Østby, Y., Walhovd, K. B., Westlye, L. T., Due-Tønnessen, P., & Fjell, A. M. (2010). Neuroanatomical correlates of executive functions in children and adolescents: A magnetic resonance imaging (MRI) study of cortical thickness. *Neuropsychologia*, 48(9), 2496–2508. <https://doi.org/10.1016/j.neuropsychologia.2010.04.024>
- Tarampi, M. R., Heydari, N., & Hegarty, M. (2016). A Tale of Two Types of Perspective Taking: Sex Differences in Spatial Ability. *Psychological Science*, 27(11), 1507–1516. <https://doi.org/10.1177/0956797616667459>
- Thakkar, K. N., Brugger, P., & Park, S. (2009). Exploring empathic space: Correlates of perspective transformation ability and biases in spatial attention. *PLoS ONE*, 4(6), 1–8. <https://doi.org/10.1371/journal.pone.0005864>
- Travis, S. G., Huang, Y., Fujiwara, E., Radomski, A., Olsen, F., Carter, R., Seres, P., & Malykhin, N. V. (2014). High field structural MRI reveals specific episodic memory correlates in the subfields of the hippocampus. *Neuropsychologia*, 53(1), 233–245. <https://doi.org/10.1016/j.neuropsychologia.2013.11.016>
- Tu, A. S., Krohn, N., Cooper, O. C., Puthusserypaddy, V., McIntyre, C., & Chrástil, E. R. (2024). *Do total hippocampus and hippocampal subfield volumes relate to navigation ability? A call towards methodological consistency*. 1(April).
- Vandenberg, S. G., & Kuse, A. R. (1978). Mental rotations, a group test of three-dimensional spatial visualization. *Perceptual and Motor Skills*, 47, 599–604.

- Vingerhoets, G., Santens, P., Van Laere, K., Lahorte, P., Dierckx, R. A., & De Reuck, J. (2001). Regional brain activity during different paradigms of mental rotation in healthy volunteers: A positron emission tomography study. *NeuroImage*, 13(2), 381–391. <https://doi.org/10.1006/nimg.2000.0690>
- Voyer, D. (2011). *Time limits and gender differences on paper-and-pencil tests of mental rotation : a meta-analysis*. 267–277. <https://doi.org/10.3758/s13423-010-0042-0>
- Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, 117(2), 250–270. <https://doi.org/10.1037/0033-2909.117.2.250>
- Wei, W., Chen, C., Dong, Q., & Zhou, X. (2016). Sex differences in gray matter volume of the right anterior hippocampus explain sex differences in three-dimensional mental rotation. *Frontiers in Human Neuroscience*, 10(NOV2016), 1–9. <https://doi.org/10.3389/fnhum.2016.00580>
- Weisberg, S. M., Newcombe, N. S., & Chatterjee, A. (2019). Everyday taxi drivers: Do better navigators have larger hippocampi? *Cortex*, 115, 280–293. <https://doi.org/10.1016/j.cortex.2018.12.024>
- Wenger, E., Schaefer, S., Noack, H., Kühn, S., Mårtensson, J., Heinze, H. J., Düzel, E., Bäckman, L., Lindenberger, U., & Lövdén, M. (2012). Cortical thickness changes following spatial navigation training in adulthood and aging. *NeuroImage*, 59(4), 3389–3397. <https://doi.org/10.1016/j.neuroimage.2011.11.015>
- Wexler, M., Kosslyn, S. M., & Berthoz, A. (1998). Motor processes in mental rotation. *Cognition*, 68(1), 77–94. [https://doi.org/10.1016/S0010-0277\(98\)00032-8](https://doi.org/10.1016/S0010-0277(98)00032-8)
- Wolbers, T., & Büchel, C. (2005). Dissociable retrosplenial and hippocampal contributions to successful formation of survey representations. *Journal of Neuroscience*, 25(13), 3333–3340. <https://doi.org/10.1523/JNEUROSCI.4705-04.2005>
- Wolbers, T., Schoell, E. D., & Büchel, C. (2006). The predictive value of white matter organization in posterior parietal cortex for spatial visualization ability. *NeuroImage*, 32(3), 1450–1455. <https://doi.org/10.1016/j.neuroimage.2006.05.011>
- Wraga, M., Creem, S. H., & Proffitt, D. R. (2000). Updating Displays after Imagined Object and Viewer Rotations. *Journal of Experimental Psychology: Learning Memory and Cognition*, 26(1), 151–168. <https://doi.org/10.1037/0278-7393.26.1.151>
- Wraga, M., Shephard, J. M., Church, J. A., Inati, S., & Kosslyn, S. M. (2005). Imagined rotations of self versus objects: An fMRI study. *Neuropsychologia*, 43(9), 1351–1361. <https://doi.org/10.1016/j.neuropsychologia.2004.11.028>
- Yushkevich, P. A., Piven, J., Hazlett, H. C., Smith, R. G., Ho, S., Gee, J. C., & Gerig, G. (2006). User-guided 3D active contour segmentation of anatomical structures: Significantly improved efficiency and reliability. *NeuroImage*, 31(3), 1116–1128. <https://doi.org/10.1016/j.neuroimage.2006.01.015>
- Zacks, J. M., & Tversky, B. (2002). Mental spatial transformations of bodies and objects. *Abstracts of the Psychonomic Society*, 5, 72.

- Zacks, J. M., Vettel, J. M., & Michelon, P. (2003). Imagined Viewer and Object Rotations Dissociated with Event-Related fMRI. *Journal of Cognitive Neuroscience*, 15(7), 1002–1018. <https://doi.org/10.1162/089892903770007399>
- Zacks, J., Rypma, B., Gabrieli, J. D. E., Tversky, B., & Glover, G. H. (1999). Imagined transformations of bodies: An fMRI investigation. *Neuropsychologia*, 37(9), 1029–1040. [https://doi.org/10.1016/S0028-3932\(99\)00012-3](https://doi.org/10.1016/S0028-3932(99)00012-3)
- Zhang, H., Copara, M., & Ekstrom, A. D. (2012). Differential Recruitment of Brain Networks following Route and Cartographic Map Learning of Spatial Environments. *PLoS ONE*, 7(9). <https://doi.org/10.1371/journal.pone.0044886>
- Zhao, Q., Zhang, L., Shen, C., Cheng, W., & Feng, J. (2019). *Association Between Intelligence and Cortical Thickness in Adolescents: Evidence from the ABCD Study*. August.