

**AN EXPLORATION OF SPATIAL MEMORY THROUGH EYE
MOVEMENTS AND NAVIGATION IN VIRTUAL REALITY**

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Abstract

Finding one's way in different environments is a common everyday experience. As experiences navigating an environment accumulate over time, spatial representations of visuoperceptual identities of landmarks and geometric relations between them are formed in the brain. Navigation in a familiar environment may be guided by a neural interaction between different types of spatial representations: visual percepts and long-term spatial knowledge of geometric relations, resembling schemas. This thesis explores whether navigation in a virtual-reality simulation of a familiar environment can be explained by analysis of eye movements during travel periods and the quality of spatial memories, which were acquired when individuals navigated the same environment in real life over months to years. Results show a link between spatial memory integrity and eye movements during navigation in virtual reality. In multilevel models of navigation performance, the interaction between spatial memory and eye movements did not adequately predict outcomes after practice effects were controlled. These findings suggest that analysis of eye movements during navigation in a familiar environment may provide insight into retrieval cues that activate schema-like spatial representations to guide optimal wayfinding decisions.

Keywords: Spatial Memory, Cognitive Map, Schema, Navigation, Virtual Reality, Eye tracking

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And thanks to space for inspiring me to question the appearance of things.

Declaration

I hereby declare that this thesis represents my original work. This thesis was part of a large collaborative project across three labs at the Centre for Vision Research at York University. The theoretical rationale has been developed as part of a review article. A novel research tool that enabled data collection was created in collaboration with several members of the research team.

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Introduction

Many of our everyday experiences involve navigating familiar environments to reach a destination. As we move through our environment towards a goal, we must retrieve knowledge from our memory stores, plan our actions and make decisions in response to incoming sensory stimuli. We often need to update our plans depending on the degree of consistency between our ‘mental representations’ and perceived sensory cues from the surroundings. Visual cues are crucial to human navigation (Ekstrom, 2015), however, the exact nature of these cues and their role in mediating memory retrieval remains unclear.

Research on spatial navigation spans a wide range of disciplines, including neurophysiology, cognitive neuroscience, linguistics, urban planning, computational neuroscience, and artificial intelligence (Waller & Nadel, 2013). Our scientific understanding of navigation comes from studies at different scales of analysis in diverse species such as rodents, macaques, and humans (Ekstrom et al., 2018; Epstein et al., 2017). This diversity has resulted in a lack of clarity with respect to key concepts and interpretations in the field, emphasizing the need for a common approach to understanding the cognitive processes underlying navigation. I approach this topic from the perspective of multiple memory systems in the human brain. I hold the view that cognitive processes underlying navigation should be studied by examining the relationship between the perception of visual cues in an environment and spatial representations at different levels of abstraction in the brain, akin to the concept of ‘schematization’¹ of memories, which is delineated in systems consolidation theories (Tonegawa et al., 2018).

Previous research on memories of environments learned long ago (i.e., remote spatial memories) primarily relied on patient-lesion methods, for example, in individuals who sustained neurological damage to structures within the medial temporal lobe (MTL), a region crucial for encoding and storing episodic memories (Penfield & Milner, 1958; Rosenbaum et al., 2000; Spiers & Maguire, 2007). These patient studies often relied on mental navigation tasks² involving highly familiar environments such as one’s place of residence or childhood

¹ *Schematization*: a term that refers to the time-dependent transformation of memories from context-rich forms to context-independent representations that retain only the essential elements of an episode (i.e., gist). These gist-like spatial representations are thought to be stored in the neocortex.

² *Mental Navigation Tasks*: refers to tasks that involve imagining the experience of navigation or retrieving information about abstract spatial relations such as relative distances and directions between landmarks, without engaging in locomotive aspects of navigation.

neighbourhood. Subsequent neuroimaging studies using these tasks highlighted the role of the hippocampus (HPC) within the MTL, and cortical regions, notably the retrosplenial cortex (RSC), parahippocampal place area (PPA), posterior parietal cortex (PPC), and prefrontal cortex (PFC) for successful retrieval of spatial memories in navigation (Ekstrom et al., 2018; Rosenbaum et al., 2004). Research in this field may have become stagnated because of a lack of flexible experimental paradigms that enable researchers to study diverse populations' naturalistic abilities to navigate in their familiar environments.

This thesis has several aims: 1) provide a review of literature pertinent to an interdisciplinary study of navigation, 2) identify a current gap in the literature, 3) introduce a novel methodology to address a theoretical gap, and 4) present the findings of a study that uses this methodology to narrow this gap. The first section of the literature review aims to mitigate existing challenges regarding different interpretations of concepts in the field by first introducing the adopted framework.

Chapter 1: Review of Literature

1.1 Frames of reference

Navigation refers to the goal-directed movement of the self through the environment (Montello, 2005). It consists of two components: locomotion and wayfinding (Montello, 2005; Wiener et al., 2009). Locomotion relates to efferent motor commands in response to immediate sensory information such as proprioceptive, vestibular, and visual signals that are processed by different perceptual modalities (Montello, 2005). This component entails an egocentric mechanism for navigation (Figure 1) because it is dependent on information concerning the spatial relations between at least two objects in relation to the observer's body (Ekstrom et al., 2014; Wang & Spelke, 2000). In comparison, wayfinding entails spatial decision-making for often distant locations in macro-scale environments, which are not processed from a single viewpoint (i.e., beyond the observer's vista space³) (Ekstrom et al., 2018; Wolbers & Hegarty, 2010). Wayfinding is associated with an allocentric frame of reference in which spatial relations amongst objects are represented with respect to each other, independent of the observer's position in the environment (Wiener et al., 2009). This classification is generally well-established, but there are important limitations (Ekstrom et al., 2014).

The adoption of a reference frame depends on several factors, including the scale of an environment, the navigation task at hand and individual characteristics (Wolbers & Hegarty, 2010). In general, reliance on allocentric representations increases as the scale of an environment increases (Ekstrom et al., 2018). Wayfinding in macro-scale environments exerts higher demands on mnemonic functions such as spatial memory retrieval, partly because the goal location is hidden from the observer's vista space (Epstein & Vass, 2014). Navigation towards a goal could also depend on a second mechanism known as path integration or dead reckoning, which involves calculating changes in magnitude and direction of travel from a start location (Etienne & Jeffery, 2004). Path integration is a survival mechanism that helped animals in finding their way back to their nest or home after exploration (Ekstrom et al., 2018). Path integration is implicated in both allocentric and egocentric modes of spatial processing and strategies (Ekstrom et al., 2014; Ekstrom et al., 2018; Moser et al., 2017).

³ *Vista space*: small-scale environment surrounding the observer which can be comprehended from a single viewpoint

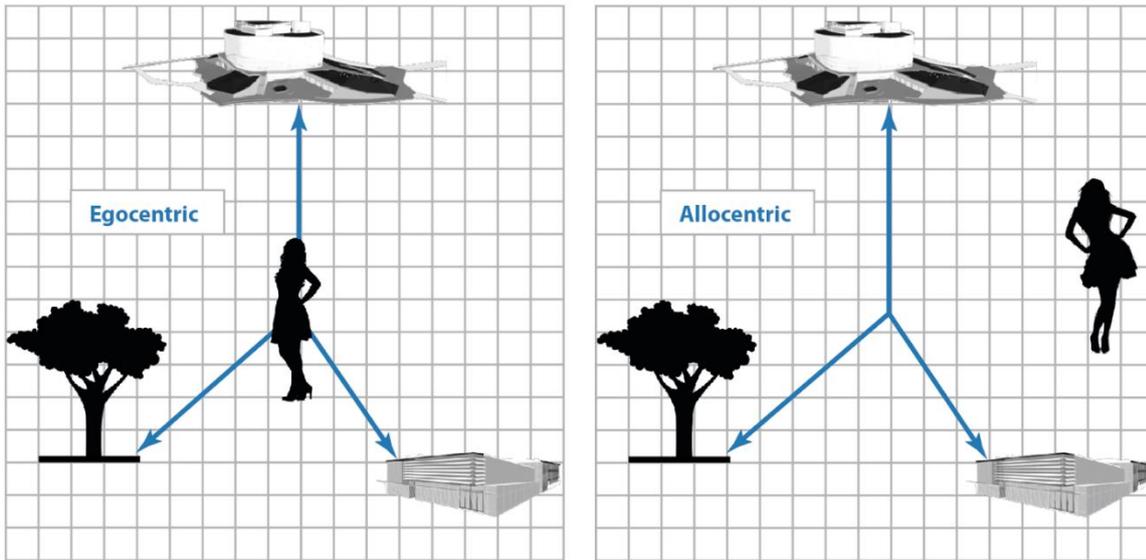


Figure 1. Allocentric and Egocentric Frames of Reference

Moreover, most navigation tasks studied in humans fall on an egocentric-allocentric spectrum; therefore, there are hardly any experimental tasks that purely depend on one kind of representation (Ekstrom et al., 2014). In most studies, mnemonic aspects of wayfinding are primarily associated with allocentric representations because these often require the hippocampus (Epstein et al., 2017; Maguire et al., 2006). However, it is now understood that the hippocampus is not required for all allocentric representations (Ekstrom et al., 2018; Rosenbaum et al., 2000). Egocentric processing is deemed more critical for primates than for rodents because primates spend more time processing objects in peri-personal spaces (e.g. for reaching and grasping food items) (Summerfield et al, 2020). The engagement of multiple interacting human brain networks during navigation indicate that the two modes of processing are highly overlapped in their neural underpinnings and behavioural expressions (Ekstrom et al., 2017).

1.2 Neural correlates of navigation

According to an influential model of navigation known as the ‘BBB’ model, most navigation requires a translation between egocentric and allocentric forms of representations (Byrne et al., 2007). It further argues that this translation can be achieved via a mathematical operation (i.e. a linear transformation), and a mechanism is likely to exist in the brain for this computation (Ekstrom et al., 2017). There is evidence for the involvement of the RSC as the neural locus of the translation between different frames of reference (Marchette et al., 2014;

Vann et al., 2009). RSC not only receives input from the PPC, a region important for egocentric processing of body movements, it also has reciprocal connections with MTL structures that encode allocentric spatial representations (Vann et al., 2009). Importantly, a navigator relies on the RSC to determine her heading direction and position in the broader context (Epstein & Vass, 2014). Allocentric spatial knowledge stored in MTL needs to be retrieved and aligned with a body-centred frame of reference to identify heading direction and guide immediate navigation decisions (Epstein & Vass, 2014). An alternative network-based model of navigation considers RSC and PPC as hubs that support allocentric and egocentric representations, respectively (Ekstrom et al., 2017). This does not, however, imply that the two systems are neuroanatomically distinct from one another.

Recent findings implicate the PPC in abstracting the structure of natural scenes over their content (Summerfield et al, 2020), a function that is also attributed to ventromedial prefrontal cortex (vmPFC), particularly concerning autobiographical memory (Ciaramelli, 2008; Ciaramelli et al., 2010; Ghosh et al., 2014). Neuropsychological studies in patients with PPC damage reveal deficits in the patients' abilities to describe imagined routes when navigating a familiar environment (Ciaramelli et al., 2010). Their experience is marked by a sense of disembodiment and poor alignment of spatial relations between their bodies and landmarks (Ciaramelli et al., 2010). Damage to PPC can also lead to constructional apraxia, which is characterized by an inability to assemble parts into a whole (Summerfield et al, 2020). These findings suggest that PPC is involved in representing abstract spatial relations, which are often associated with allocentric processing in an egocentric frame of reference, thus, further blurring the divide between these two forms of spatial processing. It has been suggested that representations of visuoperceptual identities and geometric relations can be supported by both MTL and PPC structures (Summerfield et al, 2020). In primates, PPC structures are part of the dorsal visual stream and may be particularly useful for generalizations and abstractions, whereas MTL structures are specialized for encoding visuoperceptual identities (Summerfield et al, 2020; Barense et al, 2012). Parallel to the overlap between networks that support egocentric and allocentric processing of space, dorsal and ventral visual streams have functional similarities, thus, the visual streams are not as independent as previously thought (Freud et al, 2016).

In spatial cognition literature, the term 'landmark' is loosely defined. In general terms, landmarks are entities in the environment that have orientational value, and, therefore,

modulate cognitive mechanisms underlying navigation (Epstein & Vass, 2014). Orientational value can be gained either by virtue of the entity's physical properties such as size and appearance, or its semantic characteristics, such as cultural, historical, or autobiographical significance (Auger et al., 2015; Chan et al., 2012). Alternatively, entities can gain 'landmark status' due to their presence at navigationally relevant locations (Epstein & Vass, 2014), for example, decision points, which are commonly at the intersections of roads. There are no standard guidelines for pre-selecting objects in an environment as 'landmarks' that are important in navigation, and further research is needed in this area.

Even though landmarks can come in the form of discrete objects (e.g., buildings, trees), they are encoded differently compared to objects in the human brain (Epstein & Vass, 2014). For example, the PPA, which is located at the boundary of parahippocampal/lingual gyri, is specialized in landmark processing (Epstein & Kanwisher, 1998; Epstein et al., 2017). Evidence for the involvement of PPA in landmark processing comes from neuroimaging studies in which human subjects viewed different everyday objects such as vehicles, tools, appliances, as well as environmental stimuli such as buildings, scenes, rooms and landscapes (Epstein & Vass, 2014). A stronger functional magnetic resonance imaging (fMRI) response is observed in PPA when subjects view the latter category of items, which have orientational value compared to common everyday objects (Epstein & Vass, 2014). It is peculiar that the human brain developed a specialized mechanism for processing landmarks, given that extensive neural machinery dedicated to object recognition exists in the lateral occipital cortex (Epstein & Vass, 2014). The specialization of PPA for landmark processing parallels the specialization of the fusiform face area (FFA) for processing faces (Ekstrom et al., 2018; Epstein et al., 2017). This observation highlights the importance of spatial cognition in humans, which possibly extends beyond the domain of space (Bellmund et al, 2019).

Consistent with these findings, patients with damage to the PPA exhibit difficulties in identifying landmarks and scenes, yet they seem able to recognize a location using visuoperceptual details (Ekstrom et al., 2018; Epstein & Vass, 2014). In contrast, patients with damage to RSC seem to have no difficulties with identifying landmarks. However, they cannot use these landmarks to orient themselves in the broader context (Aguirre & D'Esposito, 1999; Alsaadi et al., 2000; Takahashi et al., 1997). Neuropsychological studies show some dissociation in PPA and RSC for landmark and scene recognition, but whether these processes depend on conceptually distinct operations remains unclear. That is, the perception of a scene

and a landmark often overlap. For example, in addition to responding to buildings located at decision points (i.e., landmarks) or objects with navigational history for the observer, the PPA also encodes the geometry of a local scene (Epstein et al., 2017; Epstein & Vass, 2014). Multi-voxel pattern analyses found that PPA responds to the 3-dimensional (3D) arrangement of major surfaces in a scene, such as the layout of empty rooms, in addition to landscapes and urban scenes (Epstein et al., 2017; Epstein & Vass, 2014).

In neuroimaging studies, both the PPA and RSC show enhanced responses to scenes in familiar locations (Epstein & Vass, 2014). In neuropsychological studies of remote spatial memory, RSC is shown to track distance to goal in a familiar environment, and the PPA seems to code for the correct recognition of a familiar landmark (Patai et al., 2019; Rosenbaum et al., 2004). On the other hand, HPC has been shown to track proximity to goal in a newly learned environment and to be necessary for retrieval of visuoperceptual details of an environment that enable an episodic-like recollection of navigational experiences (Herdman et al., 2015; Howard et al., 2014; Patai et al., 2019). Furthermore, in the absence of functioning HPC, individuals with long-term knowledge of an environment are still capable of successful navigation using major street arteries and landmarks (Maguire et al., 2006; Rosenbaum et al., 2000; Spiers & Maguire, 2007). These findings suggest that PPA and RSC support the storage of essential components of long-term spatial memories and may play a role in connecting prior spatial knowledge to visual percepts (Epstein & Vass, 2014).

It is also suggested that RSC is involved in encoding locations without their identifying visuoperceptual features. In contrast, the PPA links visual snapshots of locations to the larger constellation of spatial relationships (Epstein & Vass, 2014). The representation of landmarks and scenes is a perceptual process which often but not always occurs through the visual modality (Schinazi et al., 2016). Neuroimaging studies in congenitally blind individuals show that PPA and RSC are activated for haptic or imagined exploration of scenes, on par with the activity of these regions during visual exploration of the same stimuli by sighted individuals (Kupers et al., 2010; Schinazi et al., 2016). Together these findings provide evidence for the presence of ‘amodal’ spatial representations, which do not necessarily depend on visual processing of the environment (Schinazi et al., 2016). Spatial representations likely consist of fragments of different types of spatial knowledge. These can come in the form of visuoperceptual details of landmarks, scene geometry, or amodal representations of spatial relationships in different frames of reference.

1.3 Systems Consolidation

The proposition that spatial representations can be amodal - abstract and superseding sensory content - may be supported by systems consolidation theories (Tonegawa et al., 2018) including the multiple trace theory (MTT) (Moscovitch et al., 2016; Nadel & Moscovitch, 1997) and the complementary learning systems (CLS) theory (Kumaran et al., 2016; McClelland et al., 1995). Memories continue to be processed and transformed after encoding via consolidation (Winocur et al., 2007), the process by which transient memories initially encoded within hippocampal-neocortical ensembles become stabilized over time (Tonegawa et al., 2018). During a new experience, a population of hippocampal neurons undergoes neurophysiological changes, producing an ‘engram’ or memory trace representing that experience, which is selectively reactivated during its retrieval (Tonegawa et al., 2018).

The CLS framework proposes that there are two learning systems in the brain (Kumaran et al., 2016; McClelland et al., 1995). A fast-learning system mediated by the HPC is suited to differentiate similar experiences and a slow-learning system mediated by the neocortex, which is involved in integrating information to create generalizations that can be flexibly applied to different situations. The hippocampal formation has anatomical and functional properties that support sparse spatial codes (Kumaran et al., 2016; Marr, 1971; Moser et al., 2017). Furthermore, sparse codes in HPC enable the storage of orthogonal representations of different environments and experiences, an essential feature for a system that supports both navigation and episodic memory (Preston & Eichenbaum, 2013). The neocortex system, however, exhibits less sparsity, a property that promotes generalizations (Kumaran et al., 2016).

Theories of consolidation generally agree on an indexing mechanism mediated by the interactions between the hippocampus and the neocortex (Tonegawa et al., 2018). The memory trace is thought to consist of an ensemble of hippocampal-neocortical neurons bound together (Moscovitch et al., 2016; Teyler & DiScenna, 1986). A sparse memory trace acts as an index which remains in the hippocampus at encoding and aids the retrieval of neocortical representations (Teyler & DiScenna, 1986). According to MTT, detailed hippocampal representations transform into schematized or gist-like forms that become less context-dependent during periods of rest or sleep, over time (Winocur & Moscovitch, 2011). Different theories debate the extent to which HPC is necessary for the retrieval of long-term memories that have been consolidated in the neocortex. Figure 2 depicts the hypothetical process of schematization for a landmark.

According to MTT, one form of representation is concerned with gist or schematic representations and another type of representation with visuo-perceptual details (Moscovitch et al., 2016). A schematic memory representation is formed through the transformation of a memory trace into a gist which captures the essential elements of an experience (Gilboa & Marlatte, 2017; Robin & Moscovitch, 2017). The gist of a memory is devoid of its contextual details, and the integration of overlapping gists may give rise to a schema. Studies of remote spatial memory suggest that the overall layout of a familiar environment learned long ago is analogous to a spatial gist, and it is not dependent on the hippocampus (Robin & Moscovitch, 2017). A spatial gist captures the essential features of an environment which are necessary for navigation within that environment. The retrieval of contextual details of encoded experiences continue to depend on the hippocampus for their retrieval according to MTT regardless of time passed (Rosenbaum et al., 2001; Winocur & Moscovitch, 2011). The role of a temporal gradient on consolidation differentiates MTT from CLS.

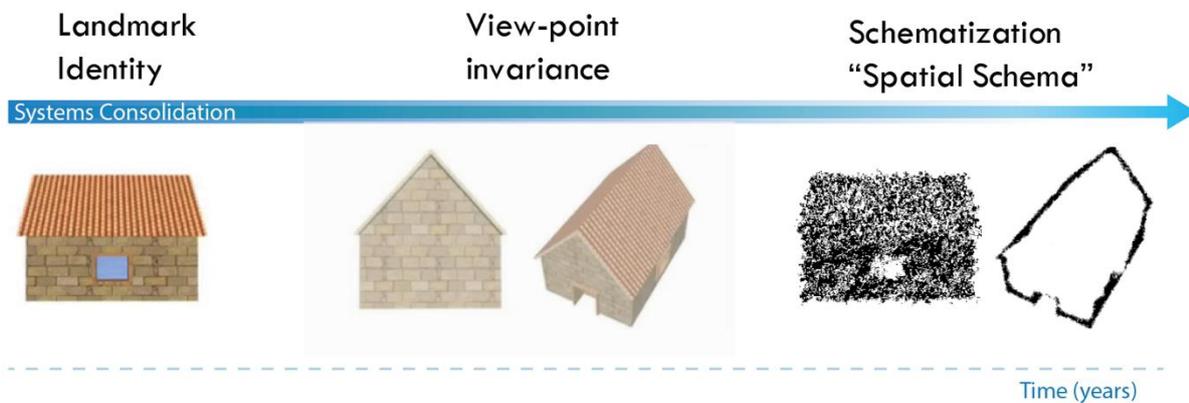


Figure 2. The process of schematization as it applies to spatial representations over time

Overall, sparsity (Kumaran et al., 2016) reflects the degree to which neuronal population codes reflect separation versus integration (Schlichting et al., 2015), detail versus gist (Robin & Moscovitch, 2017), and context-dependence versus schematization of stored knowledge (Kumaran et al., 2016; Winocur et al., 2007). These theories support the idea that the HPC and neocortex store different kinds of representations, and this concept can be extended to spatial memories (Winocur et al., 2010; Winocur et al., 2005; Winocur et al., 2007). It follows that the retrieval of long-term spatial representations for familiar environments are less prone to recall error if the consistency between sensory cues and spatial schemas are altered.

1.4 Neurophysiological basis of ‘cognitive maps’

To provide neurophysiological evidence for different types of spatial knowledge and explain how they inform our understanding of human spatial representations, it is crucial to turn to findings from navigation studies in rodents and macaques. This section focuses on relating the concept of a ‘cognitive map,’ born out of classic studies of navigation in rodents, to the broader concept of ‘spatial representations’ or prior knowledge in humans, which was originally rooted in the episodic memory literature.

The hippocampus is home to neurons that fire in response to specific locations in space, also known as ‘place cells’ (O’Keefe & Dostrovsky, 1971). The population activity of place cells in response to spatial learning of an environment gives rise to a neural representation specific to that particular environment, referred to as a ‘cognitive map’ (Moser et al., 2017)⁴. In contrast, the medial entorhinal cortex (MEC) is home to neurons that fire maximally in regular hexagonal patterns that cover the floor of an environment at varying scales (Hafting et al., 2005). These MEC neurons are referred to as ‘grid cells’ and provide input to hippocampal place cells. Given their regular firing patterns, grid cells are thought to provide metric input to allocentric cognitive maps instantiated by hippocampal place cells and play an active role in distance and direction calculations needed in path integration (Epstein et al., 2017). Hippocampal place cells have the capacity to store multiple unique cognitive maps of different environments or different states of the same environment. In contrast, grid cell inputs provide a yardstick for these allocentric representations (Epstein et al., 2017). Other interpretations suggest that grid cells provide the neurophysiological basis of “structure” while place cells encode the “content” of scenes (Summerfield et al, 2020).

Hippocampal place cells respond differently to changes in appearance versus geometric cues in the environment (Latuske et al., 2017). Geometry refers to the shape of extended 3D surfaces, such as the arrangement of walls or building facades, and is thought to be used for orientation (Cheng, 1986; Lee & Spelke, 2010; Marchette et al., 2017; Marchette et al., 2014). Appearance refers to 2D visual patterns, such as textures or surface features, which are used to identify goal locations and recognize landmarks (Lee & Spelke, 2010; Wystrach & Beugnon,

⁴ *Cognitive Map*: The term was first coined by Edward Tolman in 1948. He observed that rodents took unexpected shortcuts to find food rewards in maze arm experiments, a behavior that could not be explained by stimulus-response learning. He suggested that the rats acquired an integrated map-like representation or a cognitive map. John O’keefe and Lynn Nadal proposed a cognitive map theory of hippocampal function aimed to explain the formation of map-like representations that may shape cognition beyond the domain of space.

2009). The activity patterns of place cell ensembles change in response to modifications to familiar environments in a process known as ‘remapping’ (Kubie et al., 2019; Latuske et al., 2017). Experimental evidence from rodent studies indicates that remapping is more substantial when geometric features (e.g., shape or boundaries) rather than appearance features (e.g., colours or textures) are changed (Kubie et al., 2019; Leutgeb et al., 2005; Muller & Kubie, 1987).

Specialized processing of geometry and appearance cues is observed in many species, including humans (Becu et al., 2019; Epstein & Vass, 2014; Lee & Spelke, 2010; Spiers et al., 2015). Past studies suggest that geometric cues are particularly important for navigation (Becu et al., 2019; Spiers et al., 2015). For example, ants show rotational errors when they search for the location of a hidden food reward (Cheng, 1986). They are equally likely to search the correct corner of a rectangular environment and its geometrically equivalent corner (i.e., rotation of 180 degrees). Ants continue to search using geometric cues even when visual or olfactory cues are present and could help them find the reward with fewer errors. Similarly, human children reorient themselves in a room using geometric cues such as the relationship between a short and a long wall, rather than the colours or textures on the walls (Lee et al., 2006). These findings are consistent with the specialization of different brain regions such as the PPA and RSC for processing landmark and geometry cues, respectively (Bullens et al., 2010; Epstein et al., 2017), in addition to, amodal spatial representations signifying long-term knowledge stored in these regions (Schinazi et al., 2016).

An interesting question that arises is the extent to which amodal spatial representations reflect the generalizations of geometric properties of macro-scale environments (e.g., regularity in recurring structural forms such as colonnades) or the arrangement of surfaces that make-up discrete landmarks (e.g., the configuration of 2D surfaces making up its shape). Alternatively, amodal spatial representations are akin to semantic knowledge, concepts, categories or prototypes of space (Ralph et al., 2017). In addition, a psycholinguistic attribute associated with a landmark - ‘a place I call home’ - could modulate early perceptual processing of its complex visual features (Gilboa & Marlatte, 2017; McAndrews et al., 2016; Waller & Nadel, 2013). This top-down influence is observed in several studies that examine the effects of schemas on decision-making and perceptual processes (Gilboa & Marlatte, 2017). This observation parallels the influence of ‘expectations’ on early visual perception in a Bayesian framework for information processing in the brain (de Lange et al., 2018). Overall, the nature of long-term human spatial representations that may serve as ‘templates’ or schemas for

guiding navigation decisions for immediate and distant goals remains unclear. This is a subject of current interest and debate that will be touched on in the present thesis.

The concept of a cognitive map is similar to the idea of a schema or an expectation, albeit with important distinctions, at least in humans. A cognitive map is sometimes taken to be synonymous with a cartographic map of an environment encoded in the brain. Evidence for real-distance coding in the rodent hippocampus is stronger than that in humans (Ekstrom, 2015; Peacock & Ekstrom, 2019). Findings from human spatial cognition studies show that semantic knowledge and language cues exert a powerful influence on human spatial judgements (Noack et al., 2017; Waller & Nadel, 2013). These studies show that human spatial representations are prone to systematic biases and distortions (Poucet, 1993; Tversky et al., 1999). For example, distances from less familiar to more familiar places are often underestimated, compared to estimates of distances from more familiar to less familiar places (Tversky, 1992). Angles of intersections are remembered as being closer to 90 degrees (Waller & Nadel, 2013). Distances between two locations are overestimated if they are separated by a barrier or boundary, for example, in the case of country or state borders (Waller & Nadel, 2013). Spatial boundaries promote the regionalization of space (Noack et al., 2017). Landmarks belonging to a semantic category (vehicles, animals, buildings) result in implicit semantic regions that exert their influence on navigation decisions. Specifically, individuals prefer to take routes that cross fewer semantic regions even if they are the same length as routes that contain more regions.

A recent fMRI study showed that the presence of environmental barriers modulates the activity of grid-like cells in the human entorhinal cortex (He & Brown, 2019). These findings suggest that spatial memories are categorically and hierarchically organized, similar to the structure of semantic knowledge. A mathematical model of the hierarchical organization of spatial knowledge consists of two parameters of precision and bias. This model suggests that encoding for object locations occurs at a fine-grained level and at a categorical level (Waller & Nadel, 2013). The precision of memory at these levels differs, and recall bias can occur due to both category and boundary effects. These findings highlight that human spatial representations are often fragmented, meaning certain areas are more familiar than others, and these properties are highly dependent on the individual's personal experiences with an environment (i.e., prior knowledge). These findings also present a challenge for drawing a parallel between a cognitive map as understood from neurophysiological observations in rodents and mental representations of space in humans.

1.5 A theoretical gap: linking long-term spatial knowledge with visual percepts

Based on the findings presented, it can be established that 1) there are different kinds of spatial knowledge and 2) human spatial representations are distinct from rodent cognitive maps, and their characteristics are not well understood. Then, what aspect of human navigation may account for biases in human spatial judgements and guide us in a direction to better understand cognitive processes underlying navigation? Given that vision has a privileged role in egocentric navigation in humans compared to rodents (Ekstrom, 2015), it seems reasonable to question whether vision modulates the formation and retrieval of allocentric spatial representations in humans.

Rodents and primates are capable of using egocentric and allocentric modes of processing space; however, rodent HPC is larger and has increased functional significance compared to the neocortex in primates (Summerfield et al, 2020). Furthermore, rodents spend a greater amount of time moving through space using allocentric navigation, whereas, primates rely preferentially on their highly developed saccadic system to move and reach for items in their peri-personal and vista space using egocentric navigation (Summerfield et al, 2020). Despite the importance of vision for primate navigation, the link between visual percepts and long-term spatial knowledge for guiding goal-directed behaviour in humans remains largely unclear. Therefore, there is a gap in our understanding of the relationship between visual processing and spatial memory and their interactions with the adoption of different frames of references in guiding human navigation.

Recent neurophysiological studies provide insights into the relationship between task structure (i.e. geometry of goal locations) and visuoperceptual aspects of an environment (Baraduc et al., 2019). This dichotomy has also been referred to as mnemonic versus sensory representations in some primates studies (Gulli et al., 2020). In one study, macaques searched star-shaped arm mazes in search of food reward. After learning the spatial layout, animals were tested on their ability to find rewards in a novel environment that had the same geometry but altered visuoperceptual properties (i.e., different landmarks) (Baraduc et al., 2019). A group of hippocampal neurons termed ‘schema cells’ were observed to remain active in both environments, which shared task structure but not visuoperceptual properties (Baraduc et al., 2019).

Interestingly, the activity of these neurons was not driven by gaze density maps indicating that visual similarity between the environments did not derive the spatial selectivity of schema neurons (Baraduc et al., 2019). In a more recent study in primates, the question of whether separate hippocampal neuron populations code for space and sensory properties of stimuli was investigated (Gulli et al., 2020). This is an important question because some theories of consolidation hold that detailed aspects of memories, presumably, their sensory properties, continue to depend on the hippocampus regardless of time passed. This introduces a paradox about the representation of structure and content in the same brain region. The hippocampus houses place cells, which are highly spatially selective neurons and schema cells that represent similar task structure - goal and geometry. Findings suggest that the same neuronal population can code both mnemonic and sensory features of environments depending on the task at hand, as long as the geometry of the environment is preserved (Gulli et al., 2020).

Is geometric similarity also crucial for human navigation? A recent study in humans suggests that the use of geometry versus landmark cues for navigation can be predicted based on individuals' patterns of eye movements (Becu et al., 2019). For example, individuals who use geometric cues have a gaze bias towards the correct location and its geometrically opposite location when searching for a goal (Becu et al., 2019). These studies indicate that the encoding of geometry is an essential feature of spatial representations, and the retrieval of spatial knowledge for geometry facilitates navigation tasks. Whether preserving the geometry of a previously learned environment but not the visuo-perceptual properties impairs humans' ability to navigate in a highly familiar large-scale environment is not clear. This thesis seeks to tackle this theoretical question using a novel methodology that combines eye tracking with a simulation of a real-world environment in virtual reality.

Chapter Two: Proposal for a Novel Methodology

In order to study the extent to which spatial memory and visual exploration contribute to human navigation in familiar environments in the lab, a novel methodology is needed. Several criteria that must be considered in the creation of a new paradigm are 1) ecological validity, 2) immersion, 3) visual realism, 4) eye-tracking protocol and 5) landmark selection. Other factors such as 6) experimenter control and 7) the selection of an appropriate statistical method should also be considered.

2.1 Ecological Validity

Ecological validity refers to the ability to generalize experimental findings to real-world settings. In this context, ecological validity is improved by studying navigation in a virtual environment for which individuals encoded spatial memories in real life compared to training individuals to navigate a pre-selected environment. This criterion ensures that individuals are tested in a macro-scale familiar environment for which they have naturalistically acquired spatial knowledge through personal experience. Moreover, it is assumed that the larger scale of an outdoor environment places greater emphasis on retrieving allocentric representations. The availability of procedural 3D modelling tools (Smelik et al., 2009) provides a unique opportunity to address some of the limitations of previous studies through the creation of detailed large-scale 3D models of urban environments, allowing researchers to capture navigation behaviours in a simulation in the lab.

2.2 Immersion

The criterion of immersion is important because most research findings in human navigation are based on experimental set-ups that use small field-of-view (FOV) 2D displays with fixed head and body positions. In VR, subjects can experience the environment with an increased sense of immersion compared to traditional experimental set-ups as they offer larger FOVs and flexible head and body positions. The choice of the locomotion method in a virtual environment influences navigation performance (Paris et al., 2019). The decision for a locomotion method depends on factors such as the sense of presence, simulator sickness, room size and configuration, and the scale of the virtual environment (Paris et al., 2019). One study examined the influence of two types of discrete and continuous locomotion methods on navigation performance (Paris et al., 2019). An example of a discrete method is teleportation,

whereas continuous methods are more similar to using a joystick. Teleportation is usually based on ray-casting – a ray of about 20 m in length is cast forward towards the ground plane from the user’s hand controller. Subjects point towards the ground plane near the desired location to move to and pull the trigger to be transported to the (x, z) coordinates of their goal location. Teleportation is associated with the least amount of simulator sickness (Paris et al., 2019), a feature critical for developing experimental tools with future applications in clinical populations. Teleportation provides a reduced sense of presence compared to other locomotion methods in VR. However, the ability to move head and body movements, in addition to a wider FOV, is an improvement to traditional experimental set-ups in many navigation studies.

2.3 Visual realism

The level of realism in the virtual environment impacts navigation decisions when memory retrieval demands are increased - navigators must rely on visual cues rather than prior knowledge to make decisions. In one study, a virtual environment with varying levels of realism was used to route recall performance in young and older adults in different conditions of visual realism (Lokka et al., 2018). This study found that reduction in the overall amount of visual realism (e.g., colours and textures of buildings along a route) in a virtual environment and increased realism of landmarks at decision points led to improved route learning for both age groups (Lokka et al., 2018). Therefore, increased realism is not necessarily associated with improved navigation performance. A factor that modulates this relationship is visual attention. Even in highly familiar environments where the retrieval of reportedly gist-like or schematic spatial memories is sufficient, interference due to visual similarity may hinder wayfinding (Lokka et al., 2018).

2.4 Eye-tracking Protocol

There are similarities between neural mechanisms that support cognitive processes involving vision, memory and navigation (Ekstrom, 2015; Meister & Buffalo, 2016b; Nau et al., 2018). Eye movements captured using eye trackers measure a person’s visual attention but also memory for past experiences (Hannula et al., 2010; Meister & Buffalo, 2016b). Under normal conditions, visual input to the cortex consists of an alternation between rapid eye movements (saccades) and periods of fixation, typically 200-300 milliseconds in duration, during which gaze is stabilized on various parts of a scene (Hannula et al., 2010; Meister & Buffalo, 2016b).

Recognition memory depends on the number of fixations rather than the duration of time a picture is viewed, suggesting that fixations serve as an index of memory (Meister & Buffalo, 2016b). The number of fixations decrease while fixation durations increase when subjects view familiar stimuli, even in the absence of conscious awareness of recognition memory (Hannula et al., 2010). Whether fixation rate can also be used as a measure of long-term spatial memories of familiar environments is unclear, and a paradigm that combines VR with eye-tracking provides an opportunity to investigate this question.

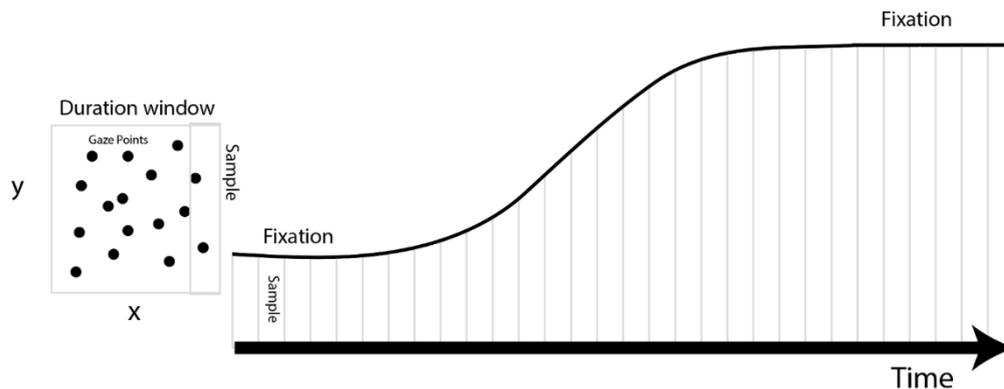


Figure 3. Fixation Identification using a dispersion-based algorithm

The identification of eye movement events, such as fixations, from raw eye tracker data, is achieved by translating gaze points to fixations using different algorithms (Salvucci & Goldberg, 2000). Depending on the frequency at which the eye tracking device is operating, many gaze points will be recorded every second. For example, Vive Pro Eye VR head-mounted displays (HMDs) operate based on the gaze frequency of 120 Hz, therefore, a gaze point will be recorded about every eight milliseconds. Different types of event detection algorithms, such as dispersion-based, velocity-based and area-based algorithms that classify gaze data into fixations, can produce different results (Nyström & Holmqvist, 2010; Salvucci & Goldberg, 2000). Fixations consist of sequences of gaze points that are grouped. Whereas gaze points only have spatial (x,y) locations, fixations have locations and durations. Therefore, the minimum duration of a fixation included in these computations can significantly influence fixation detection results (Nyström & Holmqvist, 2010). Dispersion-based algorithms identify fixations as groups of consecutive points within a particular dispersion (Salvucci & Goldberg, 2000). Dispersion is calculated as the average of the largest horizontal and vertical distances between any two samples within a duration window that has a length equal to the minimum fixation duration (Nyström & Holmqvist, 2010).

Dispersion-based algorithms have been used in commercial software such as Tobii technology and Cognitive3D. Other commercial software such as EyeLink uses a velocity-based algorithm combined with an acceleration criterion (Nyström & Holmqvist, 2010). Past research on the relationship between eye movements and memory has been almost exclusively based results from the EyeLink system, and most past studies analyzed fixations from gaze points on 2D visual displays. Eye-tracking in VR has an added challenge of tracking movements on moving stimuli, also known as smooth pursuit movements (Andersson et al., 2017). However, fixation event identification calculations are not different when an object is moving or stationary in 3D. The Cognitive3D platform can be used to obtain fixation data from raw gaze data collected from several VR HMDs. For the observer in VR to be able to move around in the environment and still fixate on the same point, fixation points are recorded as real points in 3D space rather than spatial locations in a 2D projection.

2.5 Landmark selection

As discussed previously, landmarks are loosely defined in spatial cognition literature to encompass any features in an environment that are useful for navigation. There is no guideline for selecting landmarks in the real-world environment since individuals have varied navigational experiences. The characterization of a method to identify landmarks is essential for future human navigation studies. Although robust findings indicate a specialization for landmark processing in the PPA, a set of visual features that consistently activate this region have not yet been proposed. Intuitively, however, most humans familiar with a city or neighbourhood learn a relatively common set of landmarks that they deem “central” for describing that environment and giving directions. This intuition has been a subject of extensive inquiry in urban design and architectural theory and has been expanded to understanding the organization of city blocks and neighbourhoods (Lee et al, 2017). A fresh perspective from urban planning can inform the neuroscientific studies of navigation in real-world settings.

Space syntax is a set of theories that aims to explain the relationship between social behaviour and spatial geometry (Hillier, 2007). Space syntax methods can be used to make predictions about landmarks that are salient for the group of individuals who are familiar with a particular environment, thus, predict which landmarks may appear in most individuals’ mental representations of an environment (Emo, 2018; Filomena et al., 2019; Lynch, 1960). These methods have been successful in predicting pedestrian navigation decisions (Emo et al.,

2012; Filomena et al., 2019). An urban theorist, Kevin Lynch in the *Image of the City*, proposed that landmarks, nodes, edges, paths, and districts are the basic urban elements that define the shared mental image of a city (Figure 4) (Filomena et al., 2019). A computational reformulation of Lynch’s approach has shown correspondence for all elements, including nodes but not landmarks (Filomena et al., 2019). One reason for the challenge in identifying landmarks is the influence of personal experiences with different locations. A node may be the closest element to a landmark, and it can be used as a proxy for landmark locations. Although individuals develop idiosyncratic spatial representations, a shared cognitive map can be hypothetically derived to define strategic foci expected to guide navigation for most residents or frequency travellers of a region (e.g. a university campus).

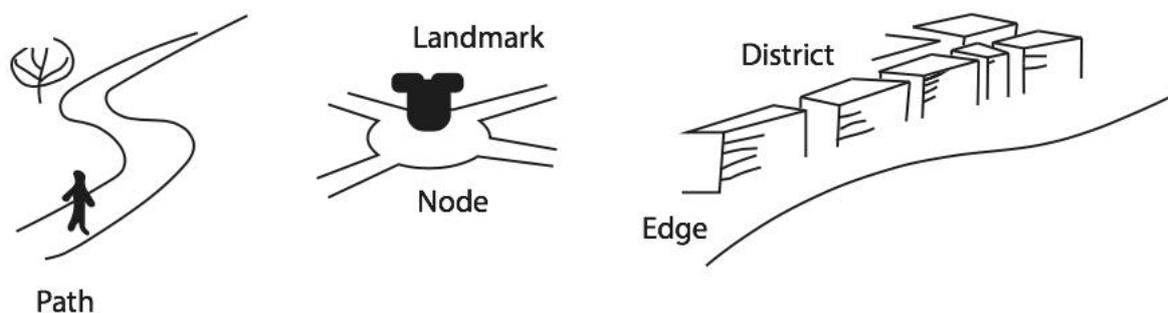


Figure 4. Kevin Lynch’s five elements of a city

To operationalize a node, a circulation network can be represented as a graph (Porta et al., 2006), where junctions are the ‘nodes,’ and path segments are the ‘links.’ The degree centrality measure of ‘betweenness’ can be calculated for each node to identify crucial decision points that are structurally positioned to be traversed most often (i.e., nodes with the highest betweenness centrality scores). A recent fMRI study found that activity in the hippocampus and prefrontal cortex correlates with changes in degree centrality measures as individuals navigate the streets of London (Javadi et al., 2017). This study provides some neurobiological support for the encoding of degree centrality measures in the brain, which can be used to identify locations of importance for navigation and spatial memory representations.

2.6 Experimental control

Factors such as age, sex, gender, strategies, anxiety level, economic wealth, developmental experiences, perspective-taking abilities result in high inter-individual variability in navigation performance (Coutrot et al., 2018; Wolbers & Hegarty, 2010). Perspective-taking is a measure of one's ability to acquire spatial knowledge from navigation experience (Hegarty & Waller, 2004; Kozhevnikov & Hegarty, 2001), therefore, improved performance may indicate an individual has a more detailed spatial representation of an area, given similar familiarity to another individual with lower perspective-taking abilities. In one study, better performance on a perspective-taking test was associated with the increased use of landmark cues compared to geometric cues in navigation (Becu et al., 2019), suggesting a correlation with egocentric representations that are scene-dependent. Sex differences are also observed in navigation behaviours, although findings are often mixed. A relatively robust finding is that females tend to preferentially use landmark cues and scene-based strategies, whereas the use of cardinal directions, metric distances and map-based strategies are more commonly reported in males (Wolbers & Hegarty, 2010).

When designing a study to assess navigation performance in a highly familiar environment, it is important to minimize constraints on participants' routine behaviour. For example, asking participants to navigate to a given location from a starting location using the routes they usually take adds fewer constraints than training individuals on specific routes to reach goals for an experiment. Even when specific routes are cued for retrieval, the training procedure introduces different biases in learning as individuals use different strategies to acquire spatial knowledge. Another factor is the influence of practice effects. Previous experience with VR environments and exposure to graphics quality of the simulation may influence results. A key feature of most tests of memory is that the subject is not 'primed' for the material that is to be retrieved from memory. Training subjects within the test environment will inevitably reduce or abolish reliance on long-term spatial knowledge and increase reliance on short-term working memory. Therefore, there is a trade-off in exposing subjects to the environment before retrieval tasks. Studying navigation in highly familiar environments is imbued with a lack of control for satisfying the requirements of basic experimental conditions. Since individuals take different routes to reach the same destination, the relationship between eye movements and navigation outcomes may be due to differences in stimuli within routes, rather than the relationship between visual exploration and navigation.

2.7 Selection of a Statistical Method

The selection of an appropriate statistical method for handling the rate of change in learning as subjects are exposed to the virtual environments may help reduce the influence of practice effects. Multilevel models (MLM) provide several advantages over repeated-measures analysis of variance (ANOVA) for analyzing hierarchical data (Singer et al., 2003) and in answering research questions related to learning and memory (Gordon, 2019). These are particularly helpful in understanding the contribution of variation due to time delays in memory experiments (Gordon, 2019).

Observations collected from an individual completing navigation tasks have a nested structure. Observations are nested within individuals and tasks. Having observations that belong to the same individuals in the dataset violates the assumption of independence needed in ANOVAs, and other ordinary least squares regression methods. The MLM approach helps in handling correlated residuals arising from observations belonging to the same individual. When practice effects are present, the performance on tasks is expected to change over time systematically. MLM allows the selection of a more flexible covariance structure (e.g. a first-order autoregressive covariance structure), which assumes that observations closer in time are more highly correlated. Therefore, the effects of practice across repeated navigation tasks can be accounted for in the model. Due to flexibility in the selection of covariance structures, MLM is also better able to handle bias due to missing data compared to traditional statistical methods such as repeated measures ANOVA.

The novel methodology proposed in this thesis aims to address discussed challenges associated with studying human navigation in highly familiar environments by considering factors such as ecological validity and immersion using a VR simulation, landmark selection procedure using space syntax methods, eye-tracking in 3D, and selection of an MLM statistical method for analyzing hierarchical observational datasets. The promise of this methodology for informing an interdisciplinary understanding of cognitive processes underlying human navigation is explored in the forthcoming study.

Chapter Three: The Current Experiment

Rationale

The ability to find our way in different environments is crucial to everyday life. A theoretical gap exists in our understanding of the link between long-term spatial knowledge and visual percepts for guiding navigation in highly familiar environments in humans. To narrow this gap, navigation success and eye movements of individuals navigating between different landmarks in a VR simulation of a large-scale environment are explored based on a proposed model of navigation depicted in Figure 5. Navigation performance is measured using travel time and path deviation - navigation outcomes that are correlated with hippocampal function based on neuroimaging findings (Spiers & Barry, 2015). Long-term spatial knowledge is assessed using standard paper-and-pencil mental navigation tasks such as sketch-mapping and placement of landmarks on a map (Howard et al., 2014; Schinazi et al., 2013). Fixation rate is used as a measure of memory-driven visual exploration (Hannula et al., 2010; Meister & Buffalo, 2016b). The immersive virtual reality environment has preserved geometry of the originally encoded environment, which participants navigated in real life for months to years, but it has altered appearance – reduced overall level of visual realism. The following hypotheses are tested:

Hypothesis 1: Given that geometry modulates the stability of cognitive maps in rodents (Mallory et al., 2018), it is expected that individuals familiar with the environment can still successfully navigate to various goal locations within that environment if geometric relations between landmarks are preserved, even if landmark appearances are impoverished in realistic detail.

Hypothesis 2: Since fixation rate serves as an index of memory (Meister & Buffalo, 2016b), it is hypothesized that fixation rates during navigation are correlated with performance on spatial memory tasks such as sketch-mapping, landmark recognition, and landmark placement. Specifically, better performance on spatial memory tasks is expected to correlate with a lower average fixation rate.

Hypothesis 3: Brain regions implicated in storing long term spatial memories, such as PPA and RSC, are also involved in scene-processing functions and have been suggested to link long-term spatial knowledge with visual percepts to guide navigation (Epstein & Vass, 2014).

It is hypothesized that the interaction between spatial memory and fixation rate predicts individual navigation outcomes in a highly familiar environment.

Hypothesis 4: It is expected that preference for allocentric (map-based) vs. egocentric (scene-based) navigation strategies (Brunec et al., 2018) interacts with spatial memory and fixation rate in predicting navigation outcomes. Specifically, a higher correlation between spatial memory and fixation rate predicts better navigation performance when a map-based rather than a scene-based strategy is preferred.

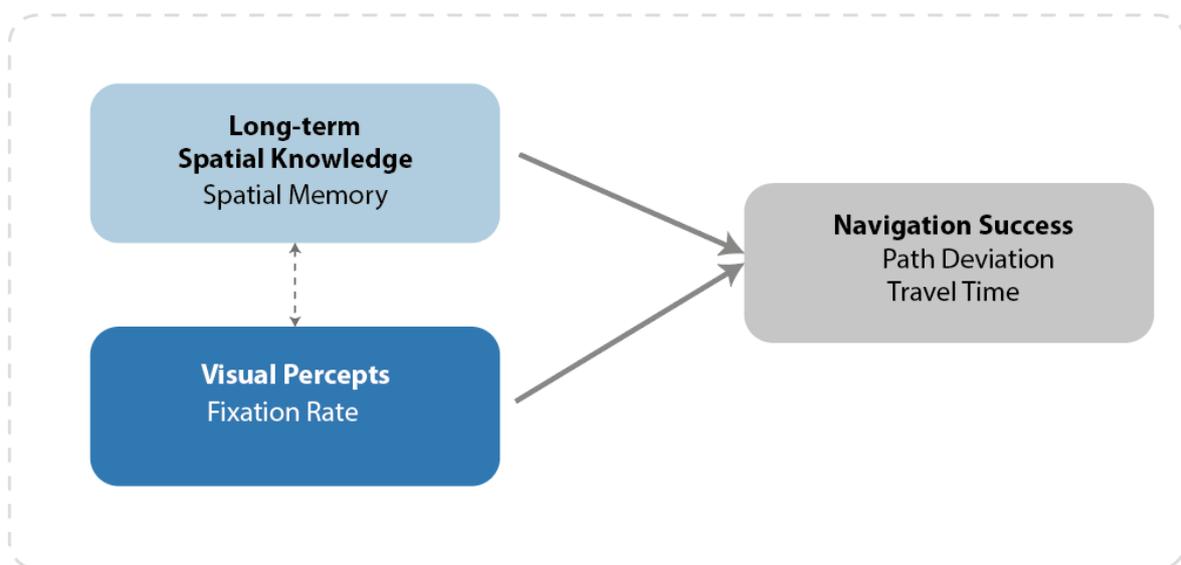


Figure 5. A theoretical model of navigation

Methods

Participants

Fifty young adults (28 males, 22 females, mean age = 25.67; SD = 6.11) with normal or corrected-to-normal vision were recruited from the York University community. All subjects reported at least six months of experience navigating within the York University Keele campus on a weekly basis in Toronto. Exclusion criteria included a history of stroke, epilepsy, or other active neurological disease. Three subjects were excluded due to motion sickness, discomfort, and inattention issues during the experiment, resulting in a sample size of 47. Participation was voluntary, and informed consent was obtained from all subjects. Subjects received financial compensation of \$15 for their participation in the experiment, which lasted 1.5 to 2 hours. All procedures were approved by the Office of Research Ethics at York University.

Primary Variables

Primary independent variables were fixation rate, spatial memory, and navigation strategy. Dependent variables were path deviation and travel time. Task order as a measure of practice effects was entered treated as a secondary independent variable. The total fixation rate was calculated as the number of fixations on 3D objects divided by the time taken to complete the task in seconds. Path deviation was calculated as the difference between path distance in meters and the Euclidean distance between origin and destination landmark main entrances (Figure 5). Travel time was the total time elapsed in seconds when the subject reported reaching the goal location.



Figure 7. VR Set-up

Eye-tracking Protocol

The Cognitive3D platform (<https://cognitive3d.com>) was used to detect fixations on model objects using a dispersion threshold technique by averaging directions from both eyes: gaze directions within 1° were identified as a common fixation, and if gaze fell outside this range for 10 milliseconds or more, the fixation was considered terminated. If the viewer's gaze was not directed toward an object in the model for 500 milliseconds or more, the fixation was also considered terminated. In Unity, a fixation point represents a point in the real-world rather than a direction obtained from the HMD using ray-casting. This means that the user can walk around a fixation point as long as steady eye contact is maintained. Ray-casting is used to determine where the user is looking at in a given moment. Several gaze points are recorded over multiple frames and converted to screen space to check whether gaze direction is within the threshold of fixation using a dispersion-based algorithm.

Navigation Task

Each subject completed a total of 12 navigation tasks consisting of different origin-destination landmark pairs in VR simulation of the study area. Ordering of route pairs was randomized across subjects. Four key landmarks were buildings identified using an analysis of street network centrality with a software package developed in a previous study (Filomena et al., 2019) and other criteria described in the appendix. Routes consisted of the same start and end locations in different combinations (e.g. Vari Hall to Bergeron, Lassonde to Vari Hall, Bennett to Bergeron). Subjects were instructed to navigate using the teleportation method as quickly as possible from a given start location to a goal location. They were instructed to end

the task by pressing a controller button when they arrived within 5 meters of the goal building. A task was deemed successful if the subject's position at the end of the task was within 50 meters of the goal building. All subjects completed one training trial to ensure that the task was understood.



Figure 8. Sketch Mapping Task

Spatial Memory Assessment

The subjects' prior knowledge of the environment was assessed using three tasks: sketch mapping, landmark recognition and landmark placement. A simple average of scores on these tasks was used to derive a single spatial memory index. The assessment strategy employed was based on the training method London taxi drivers use to learn the layout of London (Howard et al., 2014). This procedure was adapted and modified for the York University campus. In the first method, subjects were given a schematic template of the campus and asked to draw a sketch-map indicating as many buildings and roads as they could remember. This template only included the boundaries of the study region, one prominent landmark (Vari Hall), and an arrow pointing north (Figure 8 bottom right). Sketch maps were assessed using three criteria: number of elements (i.e. roads and buildings), placement of elements, and map orientation

(Figure 8 bottom panel). An overall sketch-map score was assigned as a percentage of the highest-ranking drawing. The second method employed a landmark recognition task in which subjects were shown 22 photographs of major buildings in the study region. In this task, they rated their familiarity with these locations on Likert scales ranging from 1 to 5 with the a maximum value of 110 (Figure 9). In the third task, a more detailed template of the study region was shown that included building and road information (Figure 10). Subjects were then asked to indicate using numbers where the locations of the landmarks previously rated on the landmark recognition task should be on this map. This task was scored based on the correctness and precision of responses.

a) Please indicate whether any of these places are familiar to you: (i.e. have you walked past them?)

#	Place Name	Familiarity Rating (1 = no familiarity, 5 = very familiar)
1	Vari Hall	1 — 2 — 3 — 4 — 5
2	Bergeron Engineering Building	1 — 2 — 3 — 4 — 5
3	Bennett Centre	1 — 2 — 3 — 4 — 5

1



2



3



Figure 9. Landmark Recognition Task

Spatial Abilities Questionnaires

The Santa Barbara Sense of Direction Scale (SBSOD) was used to assess individuals' spatial ability (Hegarty et al., 2002). This standardized self-report 15-item measure assesses the respondent's ability to update their location in space. The recommended scoring procedure for the scale was followed (Hegarty et al., 2002). An example item in SBSOD is: "I tend to think of my environment in terms of cardinal direction (N,S,E,W).

The Navigational Strategy Questionnaire (NSQ) was used to assess the tendency for map-based or scene-based navigation strategy. Each item corresponds to either a map-based, scene-based or another strategy. The mapping tendency was calculated as the difference between the number of map-based and scene-based responses (Brunec et al., 2018). A positive mapping tendency score indicates the use of a map-based strategy, and a negative score

indicates the use of a scene-based strategy. An example item in NSQ is: “Would you give directions to a friend in terms of landmarks (i.e. when you see the subway stop, turn left?) or in terms of map directions (i.e. walk north four blocks, then turn left?)?”

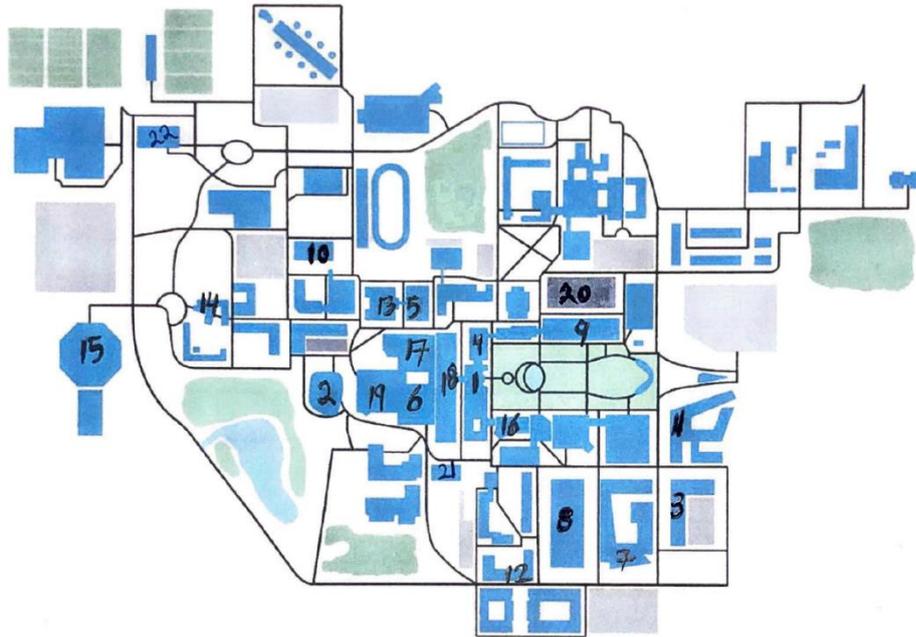


Figure 10. Landmark Placement Task

The Perspective-taking Test (PTT), in which participants are asked to determine the direction of a target object given different imagined viewpoints, was used to assess the ability to imagine how a scene looks from different viewpoints (Hegarty & Waller, 2004; Kozhevnikov & Hegarty, 2001). In this test, participants see a picture of an array of objects (e.g. cat, stop sign, house, tree) and a circle containing an error underneath. A question appears under the circle that asks about the direction between some of the objects given a particular standing location. For example, the subject is required to move the arrow within the circle to correct direction from cat to tree if he or she is standing at the house. A concrete example is shown in the Appendix. This test measures spatial orientation - the ability to learn large-scale spatial layout from navigational experiences (Wolbers & Hegarty, 2010). An openly available computerized version of this task (<https://github.com/TimDomino/ptsot>) was used. The average error in degrees across 12 time-limited trials was obtained for each individual. More details about PTT can be found in the appendix.

Statistical analysis

Hierarchical data structure

The structure of this observational dataset is hierarchical. There are two levels; navigation performance observations are nested within individuals (Figure 11). For each person, there are 12 observations. These observations are correlated with each other since they belong to one person, therefore, a statistical analysis method is needed that does not rely on the assumption of independence. In this dataset, practice effects need to be considered. Multilevel linear models have several advantages (Singer et al., 2003). A covariance structure is needed, which can account for systematic changes in the relationship between variables as a function of time. A first-order autoregressive covariance structure can accommodate the fact that observations closer in time are more highly correlated than those observations farther apart in time (Field et al., 2012; Singer et al., 2003). Therefore, practice effects can be controlled. These models are also more robust to missing data compared to ordinary least squares regression.

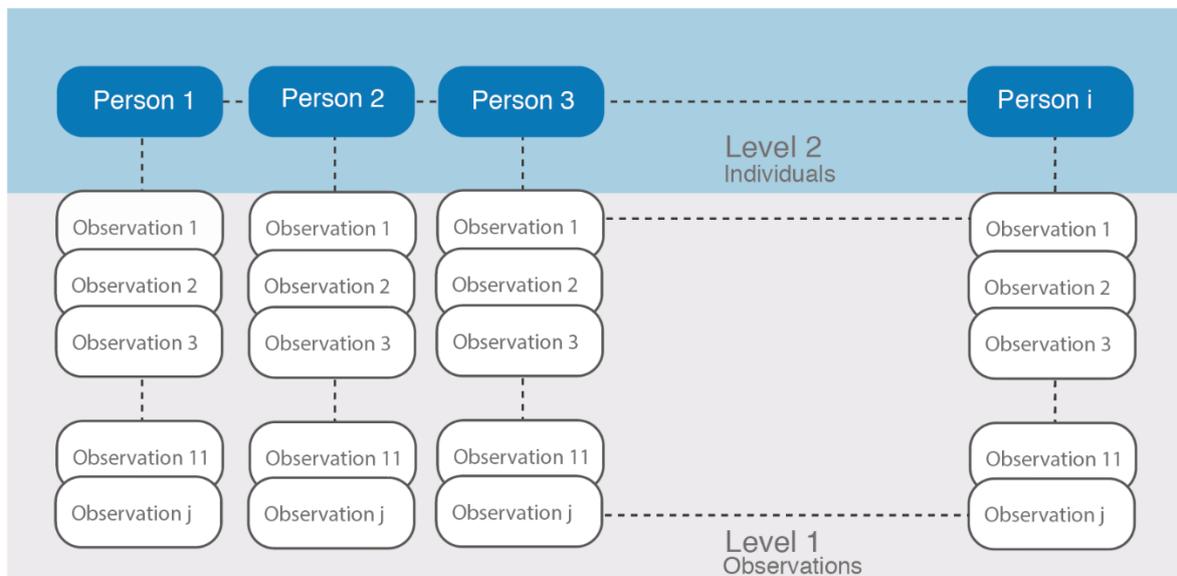


Figure 11. Two-level dataset structure

Fixed and Random Effects

Multilevel models are sometimes also referred to as mixed-effects models and have been proposed to provide powerful statistical tools for researchers investigating learning and memory (Gordon, 2019). MLMs are also used to distinguish between fixed and random effects. A fixed effect refers to an effect where all possible conditions that a researcher is interested in are present in the experiment, therefore, can only be generalized to situations in the study. A random effect relates to an effect in an experiment that contains only a random sample of possible conditions, therefore, it can be generalized beyond the conditions in the study (Field et al., 2012). It is important to distinguish between fixed and random effects versus time-fixed and time-varying variables. Fixed variables do not change over time, for example, individual

characteristics such as sex fall into this category. Time-varying variables vary over time, for example, repeated measures of performance on a task. Unlike other ordinary regression derivatives, parameters of a mixed-effects or MLM are not always fixed. In the case of a random parameter, we do not assume that the model fits the relationship between variables across the entire sample, in other words, the slopes and intercepts of the parameters vary across different levels. For example, slopes and intercepts can differ between observations in the same individual (level 1), but they also differ across different individuals (level 2). A random parameter estimates the intercept of the overall model in addition to the variability of intercepts around the overall model. Therefore, each individual in the dataset can have a “personal” intercept and slope (Field et al., 2012).

Model building and assessing model fit

The overall fit of a multilevel model is usually assessed using a chi-square likelihood ratio test. The smaller the value of the log-likelihood, the better the fit (Field et al., 2012; Singer et al., 2003). There are two adjusted forms of log-likelihood values, which are usually used to compare the fit of different models. Akaike’s information criterion (AIC) provides a goodness-of-fit measure that takes into account the number of parameters estimated. Bayesian Information Criterion (BIC) is more conservative than AIC in terms of penalizing for the number of additional parameters estimated. It is recommended to be used when the sample size is large, and the number of parameters is small. It is also recommended that for building a multilevel model, fixed coefficients are added first, followed by random coefficients and other covariates. The improvement in fit can then be assessed by performing a log-likelihood ratio test. The model selection procedure is less prone to error when cross-validation is used. However, cross-validation is needed when the analysis aims to find the ‘best’ model for predicting a particular outcome. The possible combinations of different predictors are used to create several models, and the combination with the highest fit is selected as the best predictive model. In the case of a hypothesis-driven analysis, particularly in the context of the current observational study, the goal is not to find the best statistical model. Rather, the interest lies in understanding the relationship between variables of interest, without the need to find the best combination of variables that predict an outcome.

The first step in the process of assessing the need for an MLM is to build a simple model with fixed effects only and determine the interclass correlation coefficient (ICC) (Singer et al., 2003). The ICC is a measure of the dependency between observations that are nested within

other variables, which, in this case, are individuals (Field et al., 2012). In this two-level dataset structure, ICC represents the proportion of the total variability in the outcome that is attributed to within-individual variability. Therefore, a smaller ICC indicates that much of the variability is not explained by variation in the performance of a task in the same individual, rather, it is explained by differences between individuals. A small ICC indicates that individual characteristics have less influence on observations compared to the influence of independent variables, therefore, variability is small within level 1, but large within level 2. In this study, A baseline model predicting path deviation (outcome) from only the intercepts, which are allowed to vary across people (Random Intercept Model) was built as follows (i = observations (level 1), j = person (level 2)):

$$\begin{aligned} \mathbf{Path}_{Deviation_{ij}} &= \beta_{0j} + \beta_{1j}(\mathbf{ID}) + \varepsilon_{ij} \\ \beta_{0j} &= \beta_0 + \mu_{0j} \\ \beta_{1j} &= \beta_1 + \mu_{1j} \end{aligned}$$

The ICC for this model was calculated to be 0.082 using the following equation:

$$ICC = \frac{\sigma_{\beta}}{\sigma_{\beta} + \sigma_{\varepsilon}}$$

This value indicates that approximately 91.8% of the variability in the outcome can be explained by variability across individuals and independent variables that will be later added. Only 8.2% of the variability is attributed to within-subject variability. Next, the effect of practice was added as a predictor:

$$\mathbf{Path}_{Deviation_{ij}} = \beta_{0j} + \beta_{1j}(\mathbf{ID}) + \beta_2(\mathbf{Practice}) + \varepsilon_{ij}$$

The log-likelihood ratio test was used to compare the random intercept model with the model that includes the effect of practice on outcome was significant, $\chi^2(1) = 5.82, p = .016$. This shows a significant improvement in fit when practice effects are accounted in the model. Next, this model was updated to allow the slopes in addition to the intercepts to differ across individuals with a random effects term for practice:

$$\mathbf{Path}_{Deviation_{ij}} = \beta_{0j} + \beta_{1j}(\mathbf{ID}) + \beta_{2j}(\mathbf{Practice}) + \varepsilon_{ij}$$

Following this initial step, hypothesis-driven independent variables were added using fixed effects terms. These included fixation rate, memory, strategy and a 3-way interaction term for these variables with the final model taking the following form:

$$\mathbf{Path}_{Deviation_{ij}} = \beta_{0j} + \beta_1\mathbf{Fixation} + \beta_2\mathbf{Memory} + \beta_3\mathbf{Strategy} + \beta_4(\mathbf{Fixation} \times \mathbf{Memory} \times \mathbf{Strategy}) + \beta_{5j}(\mathbf{Practice}) + \varepsilon_{ij}$$

A similar procedure was followed for travel time as the outcome variable and resulted in the following final model:

$$\mathbf{Travel}_{Time_{ij}} = \beta_{0j} + \beta_1\mathbf{Fixation} + \beta_2\mathbf{Memory} + \beta_3\mathbf{Strategy} + \beta_4(\mathbf{Fixation} \times \mathbf{Memory} \times \mathbf{Strategy}) + \beta_{5j}(\mathbf{Practice}) + \varepsilon_{ij}$$

Statistical software

All analyses were conducted in RStudio, Version 1.1.463. The nlme (Pinheiro, Bates, DebRoy, Sarkar & R Development Core Team, 2010) package was used for multilevel modelling in R. A long format dataset was compiled such that each row corresponded to one observation and an ID column was used to specify the individual to whom the observation belonged. Maximum likelihood estimation was used; variables were grand-mean centred. Grand mean entering was used as a way to reduce the effects of multicollinearity between predictor variables. This is helpful when predictors do not have meaningful zero points, such as the spatial memory index, which has arbitrary units (a.u). The interclass correlation coefficient was calculated to understand the proportion of variance due to inter-individual variability. Model selection was carried out using several statistics including the log-likelihood ratio tests. Graphs and figures were created using the ggplot2 package. A complete list of packages and scripts that are used are provided in the Appendix section to encourage the reproducibility of the current findings. Descriptive statistics are reported using means and standard deviations. Pearson correlations are computed to examine associations between measures of spatial memory, eye movements, and navigation. An alpha level of 0.05 is used for significance testing. Target sample size was based a power analysis prior to the study.

Results

Variable summaries are presented in Table 1. An approximately equal proportion of scene and map-based strategies was reported. About 64% of individuals had experience with a VR environment prior to the study. On average, participants recognized 72% of landmarks presented using both names and photographs, and correctly placed 60% of presented landmarks on a map of the study region, though performance was highly variable between individuals.

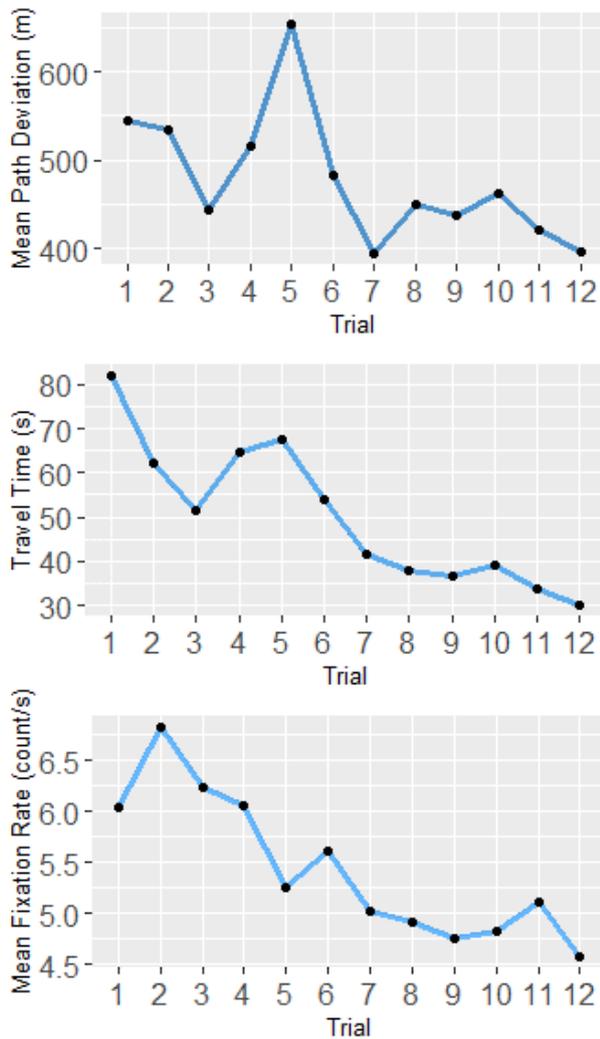


Figure 13. Practice effects

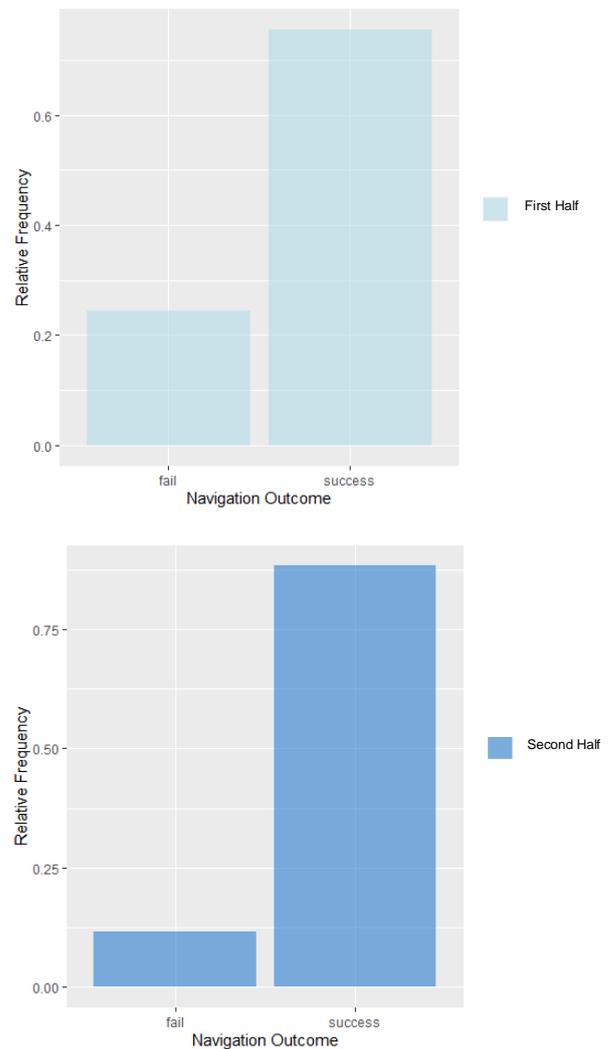


Figure 12. Navigation Success

Sketch maps produced by subjects were varied in terms of the amount of detail and accuracy (Figure 8). There was a decreasing trend for fixation rate, travel time, and path deviation across navigation tasks indicating that practice effects are present (Figure 12). The proportion of successful trials in the first half of the navigation tasks was significantly lower

than the proportion of trials in the second half of the tasks; $\chi^2(1) = 192.31, p < .0001$ (Figure 13).

Hypothesis 1: Overall navigation success in VR simulation

A total of 467 navigation tasks were completed by subjects with a success rate of 82.1 % using a success criterion of arriving within 50 meters to a target location (Figure 12). The average distance to goal location across all navigation tasks was 31.26 m (SD = 104.28), and the average travel time was 39.83 s (SD=17.05). These findings suggest that subjects were mostly successful in navigating to different target locations in the VR simulation of their familiar environment.

Hypothesis 2: Association between spatial memory and fixation rate

There is a relationship between spatial memory measured using paper-and-pencil tasks and fixation rate measured during VR navigation. A scatterplot of this relationship is presented in Figure 14. Pearson correlation between spatial memory and fixation rate was significant with moderate strength in the negative direction, $r(37) = -.33, p = .043$. The bivariate relationships between these variables are presented in Table 2.

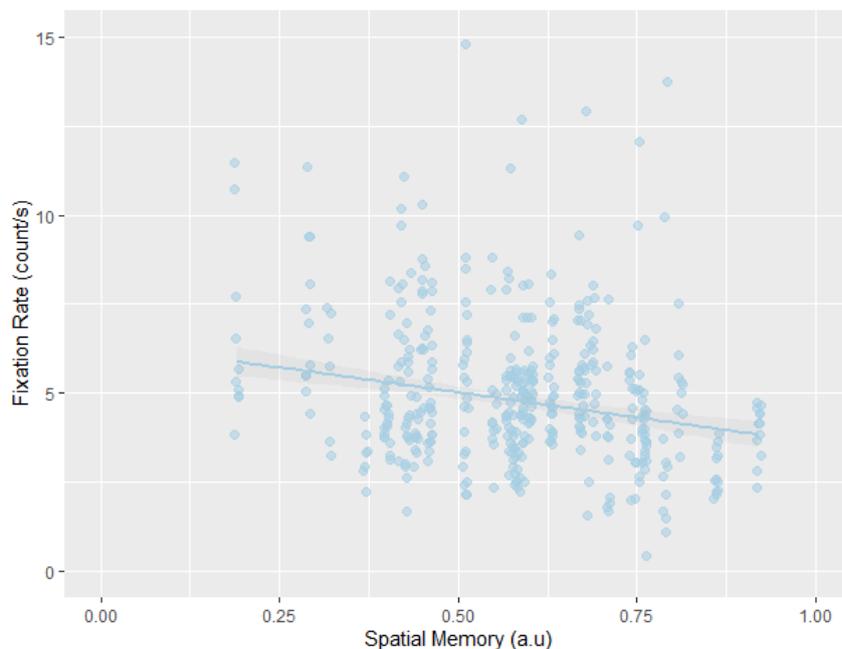


Figure 14. Scatterplot of fixation rate and spatial memory

Table 1. Variable Summary

Variable	n/Mean	%/SD
Age	25.67	6.04
Education (years)	15.46	3.57
Familiarity (years)	3.85	3.74
Sex		
Male	23	58.97
Female	16	41.03
Strategy (NSQ)		
Scene	19	48.72
Map	20	51.28
VR Experience		
Yes	25	64.10
No	14	35.90
Landmark Recognition		
Raw (Scored %)	79.71 (0.72)	16.32 (0.15)
Landmark Pairs (/10)		
Pair A: Vari-Lassonde	8.85	1.78
Pair B: Bergeron-Lassonde	7.74	2.18
Pair C: Vari-Bergeron	8.02	2.12
Pair D: Bergeron-Bennett	6.26	2.33
Pair E: Bennett-Lassonde	6.99	2.18
Pair F: Bennett-Vari	7.36	2.01
Sketch Mapping		
Raw (Scored)	13.82 (0.39)	8.19 (0.23)
Landmark Placement		
Raw (Scored)	13.23 (0.60)	5.18 (0.24)
Spatial Memory Index	0.57	0.16

Notes. Spatial Memory Index is a simple average of scores on three memory tasks. NSQ = Navigational Strategies Questionnaire; a score above 0 is categorized as map-based, a score below 0 is categorized scene-based (Brunec et al., 2018).

Table 2. A correlation matrix with confidence intervals

Variable	M (SD)	1	2	3	4	5	6
1. Spatial Memory	0.57 (0.16)						
2. SBSOD (1:7)	4.43 (1.07)	.28** [.19, .36]					
3. PTT (°)	37.18 (30.65)	-.36** [-.44, -.28]	-.21** [-.29, -.12]				
4. NSQ	-0.45 (5.39)	.45** [.37, .52]	.80** [.77, .83]	-.43** [-.50, -.35]			
5. Fixation Rate (c/s)	5.01 (1.24)	-.33** [-.40, -.24]	.14** [.05, .23]	-.16** [-.25, -.07]	.14** [.05, .23]		
6. Path Deviation (m)	458.56 (151.56)	-.41** [-.48, -.33]	-.17** [-.26, -.08]	.52** [.45, .58]	-.44** [-.51, -.36]	.05 [-.04, .14]	
7. Travel Time (s)	39.83 (17.05)	-.25** [-.34, -.17]	-.37** [-.45, -.29]	.44** [.37, .51]	-.52** [-.58, -.45]	-.35** [-.42, -.26]	.66** [.61, .71]

Note. *M* and *SD* are used to represent mean and standard deviation, respectively. Values in square brackets indicate the 95% confidence interval for each correlation. * indicates $p < .05$. ** indicates $p < .01$. SBSOD = Santa Barbara Sense of Direction Scale, PTT = Perspective-taking Test, NSQ = Navigation Strategies Questionnaire (positive values indicate higher tendency for map-based navigation)

Hypothesis 3 & 4: Interactions between fixation rate, memory, and strategy

Path Deviation MLM

The bivariate relationships between fixation rate and path deviation grouped by navigation strategy is presented in Figure 15, and the bivariate relationship between spatial memory and path deviation is shown in a scatterplot in Figure 16. Pearson correlations and confidence intervals are presented in Table 2. Multilevel model analysis showed that the main effects of fixation rate ($\beta = -1.523$, $t(388) = -0.1878$, $p = 0.851$, 95% CI = [-17.29, 14.24]), spatial memory ($\beta = 103.319$, $t(35) = 0.677$, $p = 0.503$, 95% CI = [-203.30, 409.94]), and scene strategy ($\beta = 25.821$, $t(35) = 0.724$, $p = 0.473$, 95% CI = [-45.74, 97.39]) on path deviation were not significant.

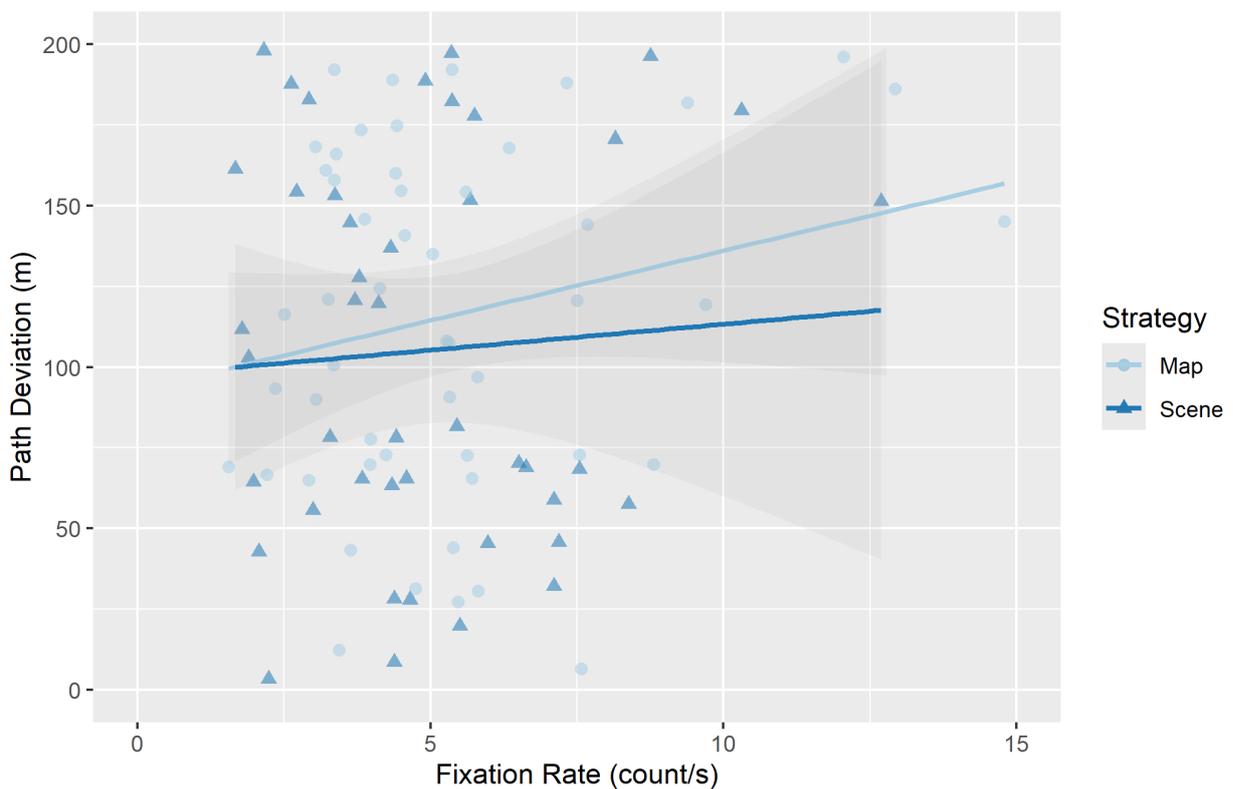


Figure 15. Scatterplot of fixation rate and path deviation

The 3-way interaction for these variables was also not significant ($\beta = 3.559$, $t(388) = .044$, $p = 0.964$, 95% CI = [-152.47, 159.58]). However, the interaction between spatial memory and egocentric strategy was marginal ($\beta = -448.786$, $t(35) = -1.99$, $p = 0.0537$, 95% CI = [-900.27, 2.70]). This shows that individuals with higher spatial memory who rely more on egocentric strategy have smaller overall deviation in their navigation trajectories from an

optimal distance. The relationship between these variables and path deviation showed significant variance in intercepts across individuals ($\beta = 4.12.638$, $t(388) = 11.987$, $p < .0001$, 95% CI = [345.67, 479.60]), showing that individuals' baseline performances differ from one another. The main effect of practice on path deviation was not significant ($\beta = -4.471$, $t(388) = -0.966$, $p = 0.335$, 95% CI = [-13.47, 4.53]) showing that, after taking into account practice effects, the relationships between independent variables and path deviation, nor their interactions, is significant. The predicted values from the model and a linear regression trend is shown in Figure 17.

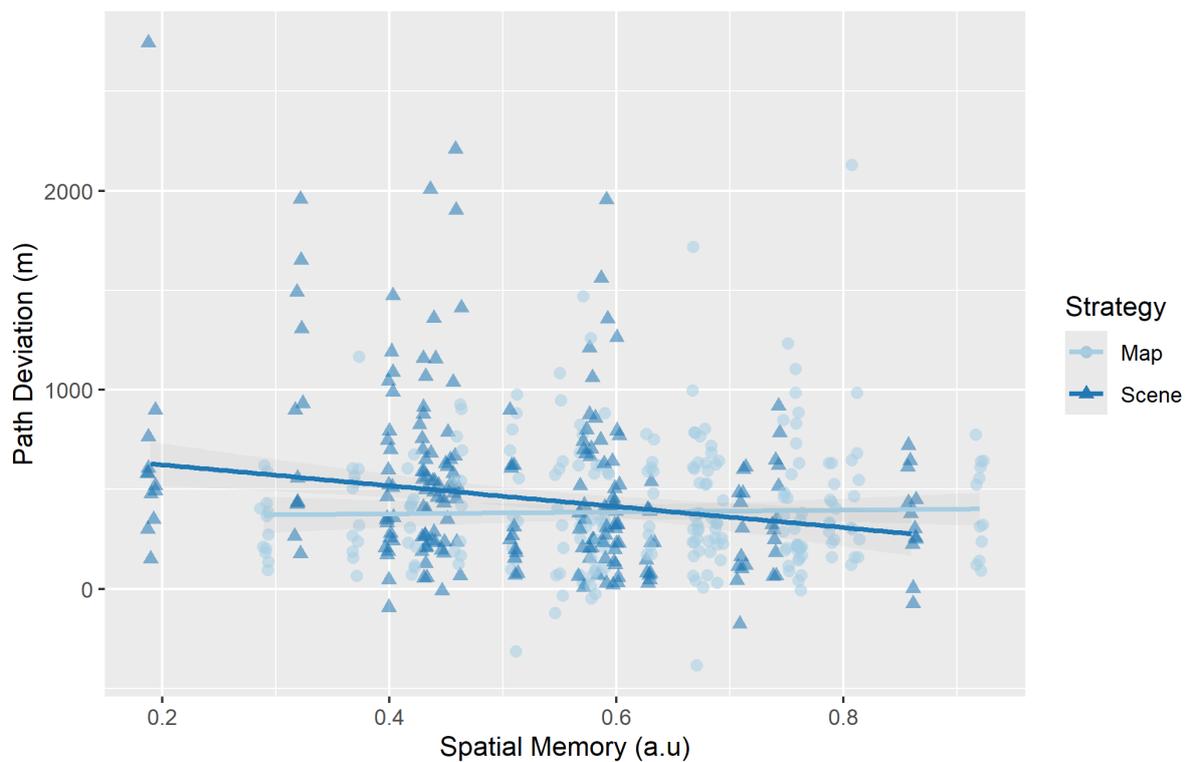


Figure 16. Scatterplot of spatial memory and path deviation

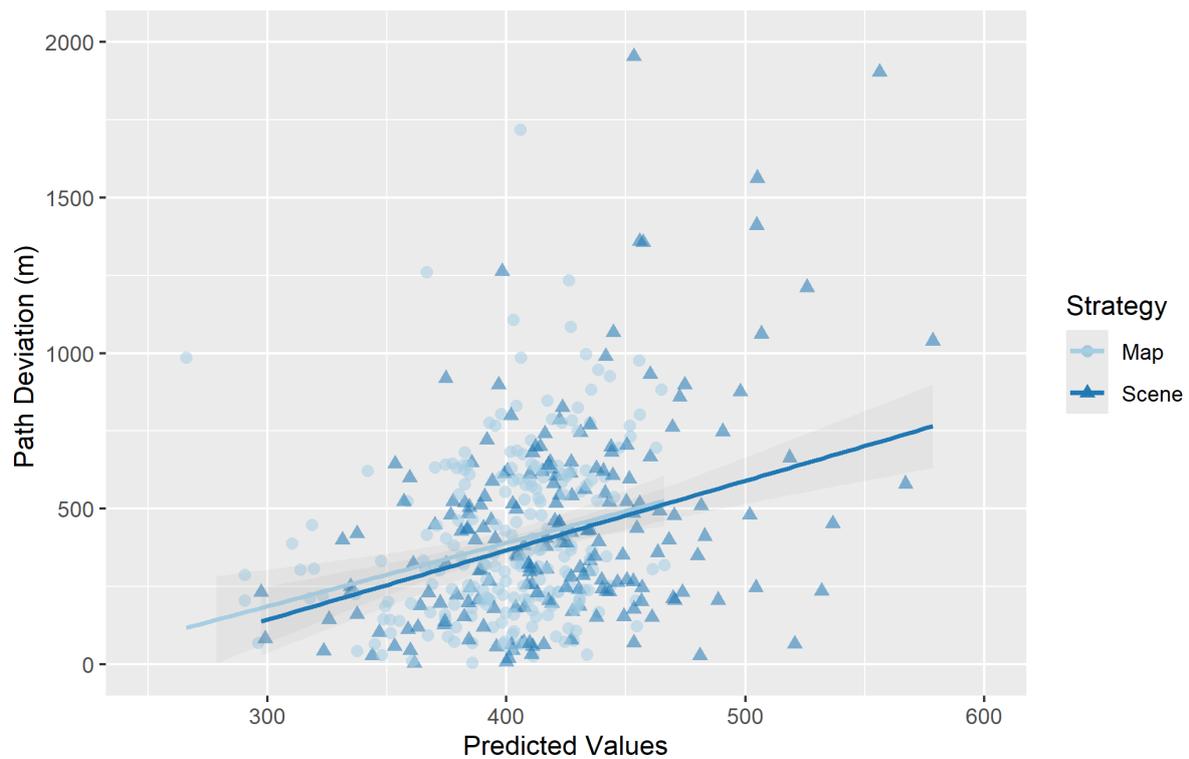


Figure 17. Scatterplot of model predicted values for path deviation

Travel Time MLM

The bivariate relationships between fixation rate and travel time grouped by navigation strategy are presented in Figure 18. Similarly, the bivariate relationship between spatial memory and travel time is shown in a scatterplot in Figure 19. Pearson correlations and confidence intervals are presented in Table 2. Multilevel model analysis showed that the main effects of fixation rate ($\beta = -2.753$, $t(388) = -4.163$, $p < 0.0001$, 95% CI = [-4.40, -1.46]) and egocentric strategy ($\beta = 7.495$, $t(35) = 2.196$, $p = 0.034$, 95% CI = [0.64, 14.35]) on travel time were significant. These results show that individuals with higher fixation rates navigate to goal locations faster. Also, individuals who use a scene strategy tend to be slower in reaching their goal destinations.

The main effect of spatial memory was not significant ($\beta = 16.81$, $t(35) = 1.167$, $p = 0.251$, 95% CI = [-12.11, 45.73]). The 3-way interaction for these variables was also not significant ($\beta = 7.065$, $t(388) = 1.059$, $p = 0.289$, 95% CI = [-5.90, 20.03]). However, the interaction between spatial memory and egocentric strategy was significant ($\beta = -55.368$, $t(35) = -2.612$, $p = 0.013$, 95% CI = [-97.94, -12.79]). This shows that individuals with higher spatial memory who rely less on egocentric strategy complete navigation tasks faster. The relationship

between these variables and travel time showed significant variance in intercepts across individuals ($\beta = 51.39$, $t(388) = 15.78$, $p < .0001$, 95% CI = [45.05, 57.72]), showing that individuals' baseline performances differ from one another. The main effect of practice on travel time was significant ($\beta = 51.39$, $t(388) = 25.78$, $p < 0.0001$, 95% CI = [-3.53, -2.14]), showing that travel time is significantly decreased over repeated task performance. These findings are controlled for practice effects. The predicted values from the model and a linear regression trend is shown in Figure 20.

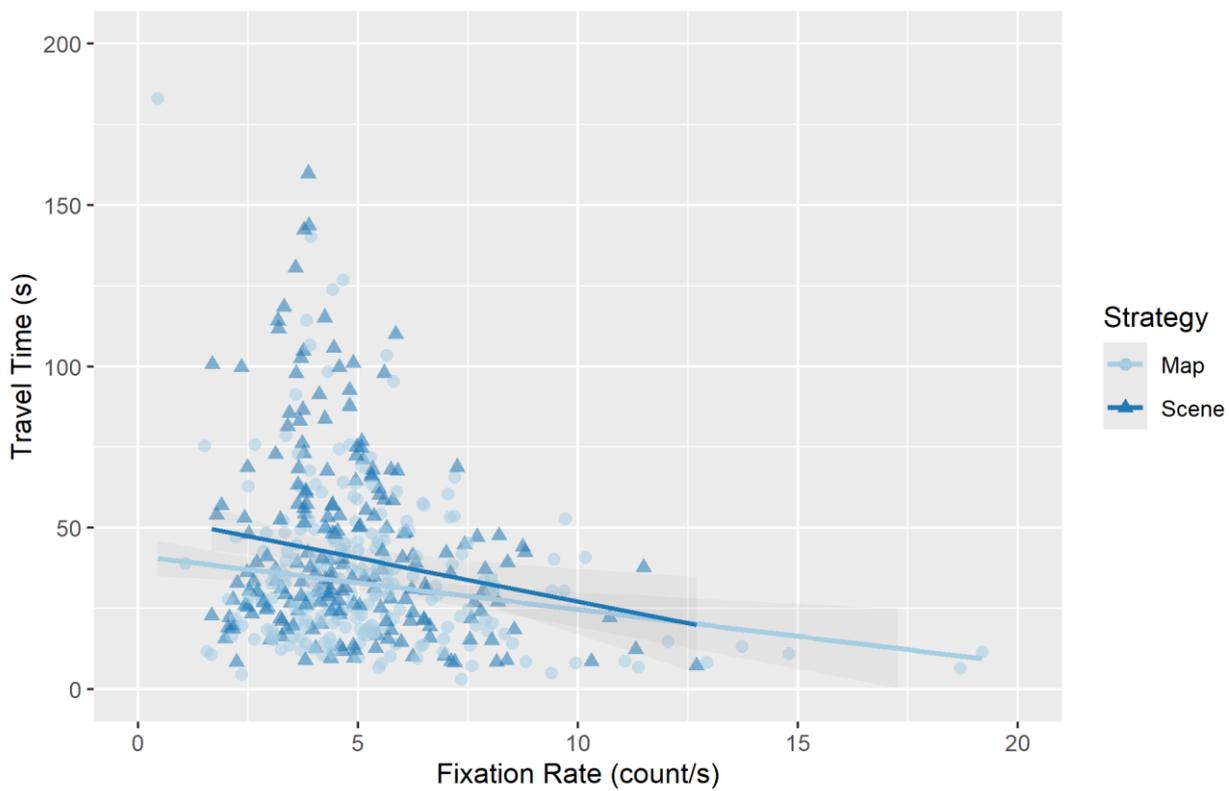


Figure 18. Scatterplot of fixation rate and travel time

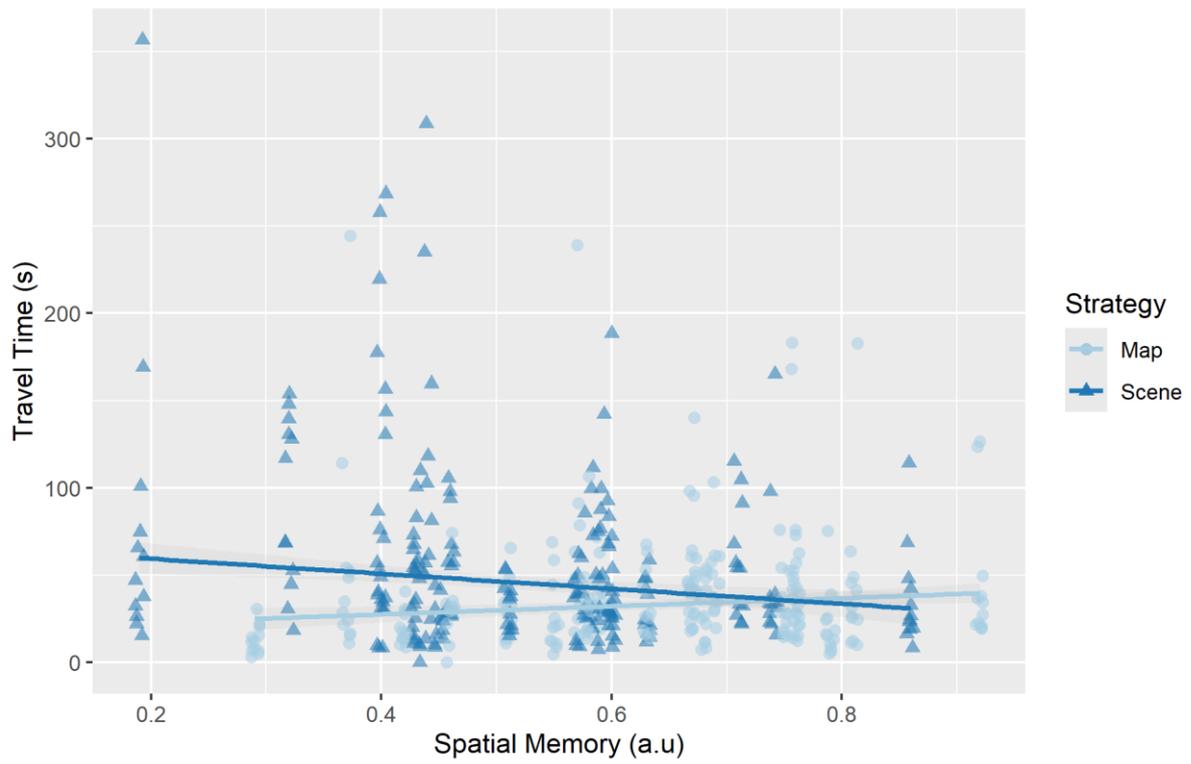


Figure 19. Scatterplot of spatial memory and travel time

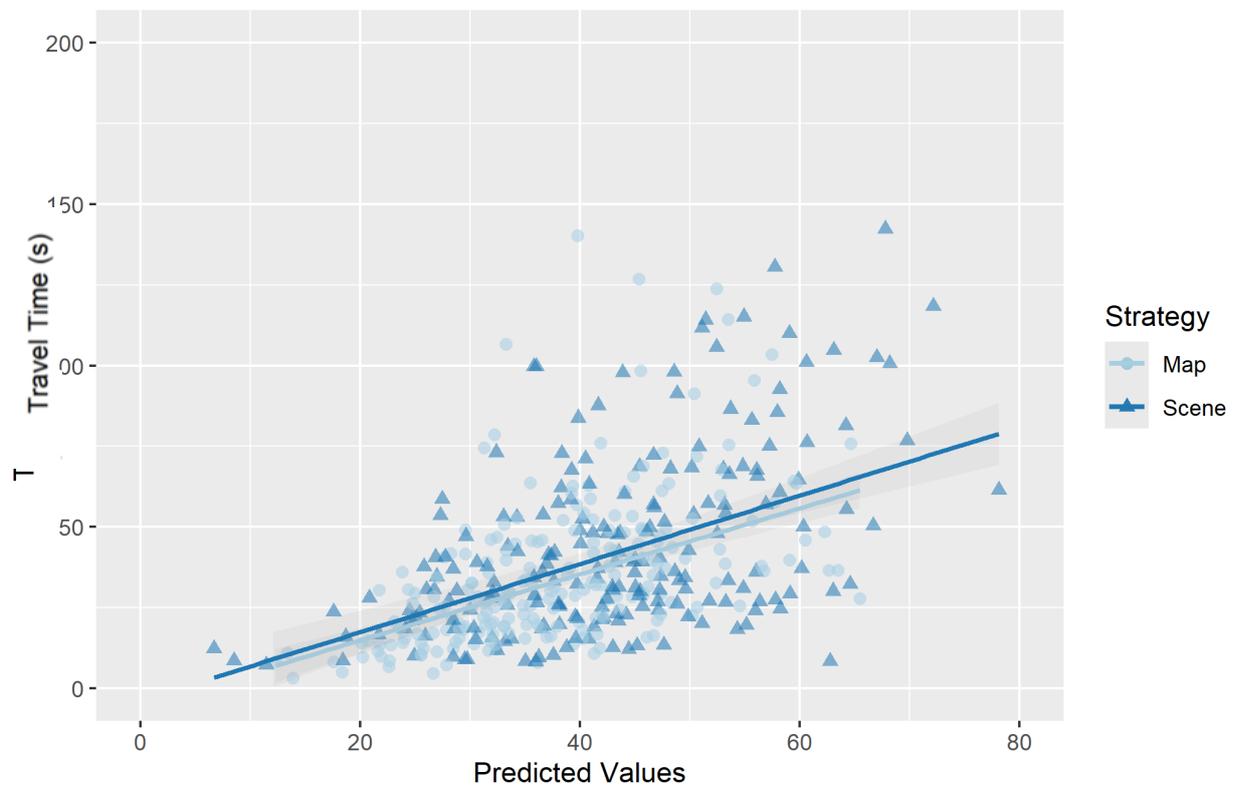


Figure 20. Scatterplot of model predicted values for travel time

Discussion

This study examined navigation performance and eye movements in a novel VR simulation of a macro-scale environment for which individuals acquired spatial representations via personal experience in real-world navigation. Specifically, individuals' ability to successfully navigate a virtual environment with preserved geometric relations and reduced appearance level was observed. The relationship between performance on static mental navigation tasks, fixation rate during travel to goal locations, allocentric-egocentric strategy preference, and overall navigation performance (i.e., travel time and path deviation) was explored. More than 80% of navigation tasks that required individuals to travel to various goal locations from randomly selected start locations were successfully completed – navigators reached within 50 meters of goal landmarks. This finding demonstrates that preserved geometry between landmark locations rather than high levels of visual detail is sufficient for successful navigation in a familiar environment.

Main results

A relationship was found between eye movements during navigation and long-term spatial knowledge for the familiar environment that was navigated. On average, individuals made approximately five fixations per second during travel periods, and better spatial memory on standard measures was significantly correlated with reduced fixation rates during navigation. This finding suggests that individuals who have acquired a more integrated spatial representation of an environment make fewer fixations per second on visual stimuli that they encounter along routes to goal. Therefore, fixation rate in a virtual environment may provide an index for spatial memory of that environment, acquired via real-world navigation. This finding supports the hypothesis of a link between long-term spatial knowledge and visual percepts for navigation.

Some evidence of construct validity was found for a composite measure of spatial memory obtained by combining performance on the standard spatial memory measures (sketch mapping, landmark recognition, and landmark placement). A significant positive correlation was found between this spatial memory index and SBSOD – a standardized measure of cognitive functions involved in navigation, including the ability to keep track of heading

direction and judging directions between landmarks using allocentric coordinates (Wolbers & Hegarty, 2010). In addition, a significant negative relationship was found between the spatial memory index and errors on a perspective-taking task (i.e. PTT). Perspective-taking is related to the ability to learn spatial layouts from direct navigation experience. This task requires participants to estimate directions to landmarks given different imagined viewpoint locations (Kozhevnikov & Hegarty, 2001). These relationships provide evidence of convergent validity for this spatial memory index because the measure is related to the hypothesized construct – the ability to acquire and use allocentric spatial representations.

A related finding is a positive correlation between the spatial memory index and a higher tendency for using a map-based (i.e. allocentric) navigation strategy compared to a scene-based (i.e. egocentric) strategy. This tendency was measured using a navigational strategies questionnaire (i.e. NSQ) in which map-based strategy items correlate with inter-voxel similarity patterns in the human hippocampus (Brunec et al., 2018). This finding provides some evidence of divergent validity for the spatial memory index introduced and suggests that performance is preferentially related to allocentric representations that are supported by MTL structures, including the hippocampus. Overall the findings suggest that the proposed composite measure of spatial memory has some construct validity.

A significant improvement in navigation success was observed as individuals completed more navigation tasks in the virtual environment. Specifically, the success rate in the first half of navigation tasks was at 67%, which was improved to 86% in the second half of the navigation tasks. This finding shows that visual cues influence navigation, even if their presence is not crucial to navigation (Maguire et al., 2006). Therefore, increased exposure to the familiar virtual environment impacts wayfinding, possibly independent of pre-experimental spatial memory.

Some differences in main effects and two-way interactions between path deviation and travel time models were found. In the model of path deviation, neither the main effects of fixation rate, spatial memory, and strategy nor their interaction was significant, however, the two-way interaction between spatial memory and strategy was marginal. In individuals who adopt a scene-based strategy, higher spatial memory predicts better navigation performance as indicated by travelling routes that deviate less in the distance from an optimal (i.e. Euclidean) path. However, for individuals who use a map-based strategy, higher spatial memory is not

associated with reduced path deviation. A similar interaction pattern was found to be significant in relation to predicting travel time. In individuals who adopt a scene-based strategy, higher spatial memory is predictive of faster travel time. In contrast, the relationship between spatial memory and travel time is not significant for individuals who primarily use a map-based strategy. Since the spatial memory index primarily relates to the quality of allocentric representations, this finding suggests that individuals who can adopt different strategies given the specific demands of the task at hand may develop better spatial learning and navigation capabilities (Wolbers & Hegarty, 2010). This is indicated by a positive trend of navigation performance in those who primarily use scene-based or landmark cues for navigation. An egocentric strategy may have been more useful in finding goal locations in a virtual environment (Doeller & Burgess, 2008), and those who adopted this strategy benefited more from increased exposure to specific visual cues in the simulation.

A second difference between navigation outcomes was found in the effect of practice. Learning was a significant predictor of travel time but not path deviation. Similarly, the main effect of fixation rate was only a significant predictor of travel time. Given a decreasing trend of fixation rate as a function of task order, these findings suggest that the relationship between fixation rate and travel time may be heavily influenced by the portion of variability shared between these two variables, rather than capturing a process-pure measure. The adoption of a scene-based strategy was predictive of lower travel time, possibly reflecting additional time taken for visual exploration of scenes prior to making decisions. However, the significant interaction between spatial memory and scene-based strategy is predictive of reduced travel time, indicating that allocentric representations and egocentric factors jointly influence navigation outcomes.

Relation to Prior Work

Previous findings on spatial navigation in familiar environments are based on performance in mental navigation tasks using paper-and-pencil or virtual navigation with photographs obtained from applications such as google street view (Patai et al., 2019; Rosenbaum et al., 2004; Spiers & Maguire, 2007). Few studies have used simulations of real-world environments. One exception is a landmark neuroimaging study that examined navigation in a virtual simulation of central London in taxi drivers with decades of experience in the area and patient TT, who sustained a bilateral hippocampal lesion (Maguire et al., 2006).

More recent studies have begun to use virtual 3D environments projected on 2D displays, or VR paradigms for novel environments that participants did not have prior real-world navigation experience (Becu et al., 2019; Chrastil & Warren, 2015; Kim & Maguire, 2018; Lokka et al., 2018). Very few navigation studies provide behavioural data combined with eye-tracking (Becu et al., 2019; Spiers & Maguire, 2008), particularly in VR. The current study is novel in analyzing navigation behaviour and gaze data obtained from individuals who navigated a 3D reconstruction of a real-world environment that they had personally experienced from months to years prior to testing. As expected, individuals were able to find target landmarks in various regions of the environment from multiple start locations, even though the environment had reduced levels of visual realism.

The finding that preserved geometry but not appearance is sufficient for navigation is consistent with experimental evidence in early human development and other species (Lee et al., 2006; Lee & Spelke, 2010). Moreover, individuals with damage to the hippocampus were still able to judge distances and directions between major landmarks in a highly familiar environment, draw accurate sketch maps and successfully navigate to different goal locations within that environment, even though they appear to no longer retain visual details contained within it (Herdman et al., 2015; Maguire et al., 2006; Rosenbaum et al., 2000; Spiers & Maguire, 2007). Since the hippocampus is needed for the retrieval of detailed aspects of autobiographical and spatial memories which enable rich re-experiencing of past events (Herdman et al., 2015), these patients likely relied on a different kind of spatial representation reflecting geometric features of encoded environments.

The relative independence of two types of spatial representation is also demonstrated by different types of recall errors for spatial location (Marchette et al., 2017). In one study, individuals learned the locations of objects positioned within four visually distinct but geometrically similar buildings (Marchette et al., 2017). The buildings were arranged in a larger environment with a spatial layout that was independent of the layout of objects within buildings. It was observed that individuals frequently used a common local representation that specified the location of the object and applied that template or “schema” when searching an incorrect building (Marchette et al., 2017). This type of geometric error was consistently observed even when the appearance of buildings (e.g., textures) was altered and only reversed when geometry was altered. This study provided evidence for independence between spatial representations at global and local levels, and further highlighted the role of geometry in

navigation. Given past findings, it is not surprising that individuals in this study did not have significant difficulties navigating an environment with impoverished visuo-perceptual details, since geometric relationships were unchanged.

An interesting finding was the association between a measure of long-term spatial knowledge and a measure of eye movements in virtual navigation. This is a novel finding, as previous studies have not examined this relationship in virtual reality. Past studies have examined the relationship between eye movements and memory using images projected onto 2D displays with small FOV. Different types of eye movements can be analyzed based on raw gaze data obtained from eye-trackers. Amongst these measures, fixations have been referred to as a “currency of memory” (Meister & Buffalo, 2016a). The use of fixations as an index of memory depends on the specific mechanisms involved in encoding and retrieval. For example, during encoding, a higher number of fixations is associated with improved picture recognition (Kafkas & Montaldi, 2011).

In contrast, when freely viewing visual scenes, a higher number of fixations is associated with scene novelty rather than familiarity. This finding is observed in 2D images (Meister & Buffalo, 2016a; Ryan et al., 2000) and virtual 3D environments (Kit et al., 2014). In the current study, a negative association between fixation rate and spatial memory was found, in agreement with findings related to memory mechanisms associated with encoding. This is a surprising finding because individuals were not previously exposed to the specific visual cues in the virtual environment, whereas in previous studies, memory-mediated eye movements were analyzed after individuals encoded the presented stimuli as part of the experiment. While the 3D reconstruction of the real-world environment was novel to subjects in this study, the average fixation rate was correlated with an objective measure of spatial memory related to allocentric representations of an external environment (i.e., external to the virtual environment). Therefore, the decreasing trend in fixation rate with practice may indicate reduced novelty to the stimuli, rather than indexing a mental representation.

The finding that the interaction between eye movements, memory, and strategy did not significantly predict navigation outcomes is inconsistent with a theory-driven hypothesis – that the link between long-term spatial knowledge and visual percepts guides goal-directed navigation. One possibility is that this hypothesis relates to the interactions of brain regions at the systems level based on theories of consolidation, however, it may not be directly observable at the level of human behaviour. An alternative is that an observational approach to studying a

multi-component behaviour such as navigation is not equipped with fine-grained analytic power needed to detect an interaction. Significant inter-individual differences in navigation may also mask the detection of effects, despite selecting a statistical method that can disentangle these contributions. The finding that the choice of strategy influences the degree to which prior knowledge predicts navigation performance highlights the significance of inter-individual differences.

Limitations

This study has several limitations. While the aim was to observe unrestrained navigation in individuals familiar with an environment, one restriction on movement had to be placed because the interiors of buildings were not available in the virtual simulation. A restriction was placed so that individuals navigated between landmarks without travelling through buildings. This restriction likely results in individuals taking routes that they would not normally take in real life, as many individuals familiar with the study area seem to travel through some buildings, particularly in colder months. A second limitation relates to the sense of immersiveness in virtual reality. Although individuals were provided with a relatively wide field-of-view to explore the environment and were able to freely move their heads and bodies, they were not able to navigate by walking. Instead, they had to rely on teleportation, which is the least immersive movement method in VR. A third limitation is about changes in the level of detail in the 3D models of landmarks. For example, many different types of details that may be particularly important for navigation purposes were not modelled, including several building facades, campus signage, outdoor furniture, campus art, and trees. This limitation rules out the possibility of understanding the different types of non-geometric cues that guide navigation decisions. Lastly, tasks used to assess spatial memory for the study area were experimental and not previously validated. Although similar tasks such as sketch mapping have been extensively used to assess spatial knowledge of a familiar environment, these have usually included larger urban areas with landmarks that have cultural and global significance, such as the CN Tower in Toronto. Landmarks in a campus setting may not benefit from this memory boost.

Moreover, familiarity with specific landmarks in this type of environment could be a function of specific academic activities performed by different individuals rather than a shared integrated representation. Interestingly, whether different individuals share a mental representation of the environment is related to a shared sense of community. For this reason, community engagement and shared values in an institution relate to whether individuals

working or studying in that environment have similar and integrated spatial representations in their memory stores (Lynch, 1960).

Future Work

Future research is needed in this area to investigate the theoretical gap in our understanding of the link between mnemonic and perceptual functions in spatial cognition using experimental study designs that employ different measures of eye movements. For example, examining the pattern of visual attention during navigation decision periods by analyzing saccades can provide a more fine-grained tool for understanding the relationship between visual perception and spatial memory in the context of navigation (Bicanski & Burgess, 2019). A future direction is to compare differences in visual exploration between healthy young adults, older adults, and clinical populations. For example, in older adults with dementia, explicit retrieval of memories through direct reporting may hinder access to care and social engagement (Hannula et al., 2010), and spatial deficits are proposed early diagnostic markers of memory decline in at-risk populations (Coughlan et al., 2018). Extending the use of eye movements as an index of memory for space can help researchers better understand the impact of various spatial designs in indoor and outdoor environments on wayfinding abilities. Further work is also needed to understand the role of different brain regions in encoding landmark and geometric cues in similar environments. It remains unclear how we construct internal schemas that guide navigation decisions in the face of unexpected changes in our environments.

General Conclusion

This thesis aimed to present a new interdisciplinary approach to the study of spatial navigation in familiar environments in humans. It reviewed findings from neurophysiology and cognitive neuroscience to present a theoretical framework that is grounded in memory systems consolidation and highlighted the concept of schematization in relation to space. It proposed that a current gap exists in understanding the relationship between long-term spatial knowledge and visual percepts in humans by drawing attention to distinctions between highly biased human spatial judgements and rodent cognitive maps. A novel methodology that combines eye tracking in virtual reality was applied to explore several hypotheses generated from the proposed theoretical rationale. Findings suggest that eye movements relate to long-term spatial representations and that the choice of a map-based or a scene-based navigation strategy moderates this relationship. Future research is needed to replicate and validate obtained findings and understand the types of spatial cues that help us better navigate and, consequently, feel more connected to others and the environments in which we live.

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Appendix A: Virtual Reality Paradigm

Sample Navigation Trial (Subject View)

1. Begin Trial (Given Starting Location)



2. Travel Period (Navigate to Goal)

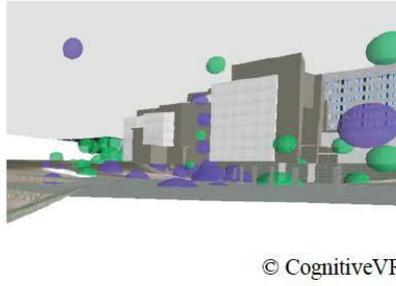
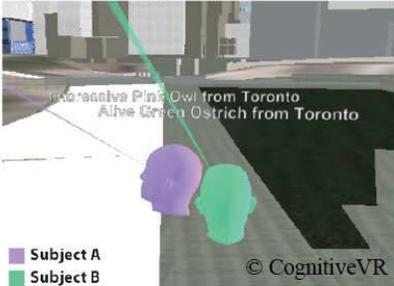


3. End Trial (Reached Goal)

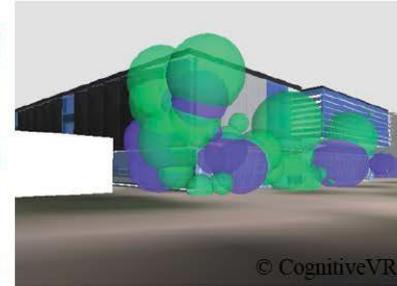


Experimenter View Fixation Recording

Origin Landmark: Bergeron



Destination Landmark: Lassonde



Aggregate Fixations on origin-destination landmarks for sample trial

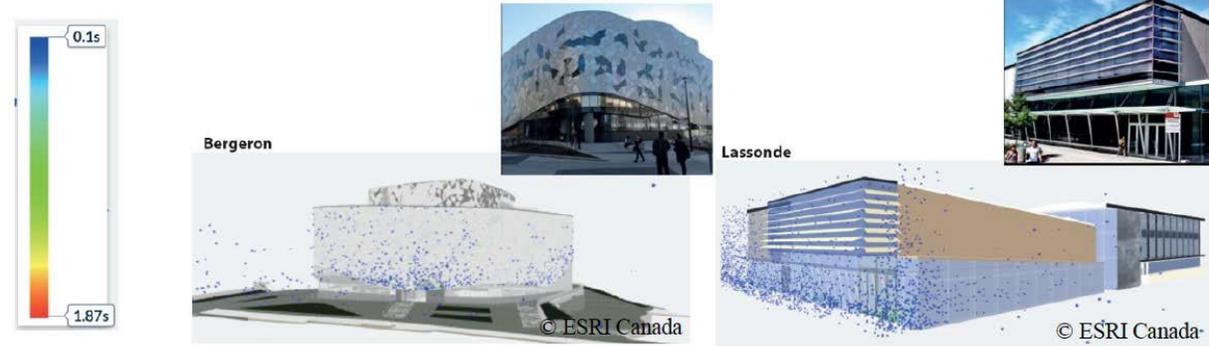


Figure A. Top panel showing a sample trial in VR as seen from the subjects' point of view. Middle panel showing the distribution of fixations in the same navigation scene by two individuals denoted using different colors. Bottom panel showing average fixation across all subjects and navigation tasks for different landmarks in the virtual environment. The color bar indicates the length of fixations with red indicating longer durations.

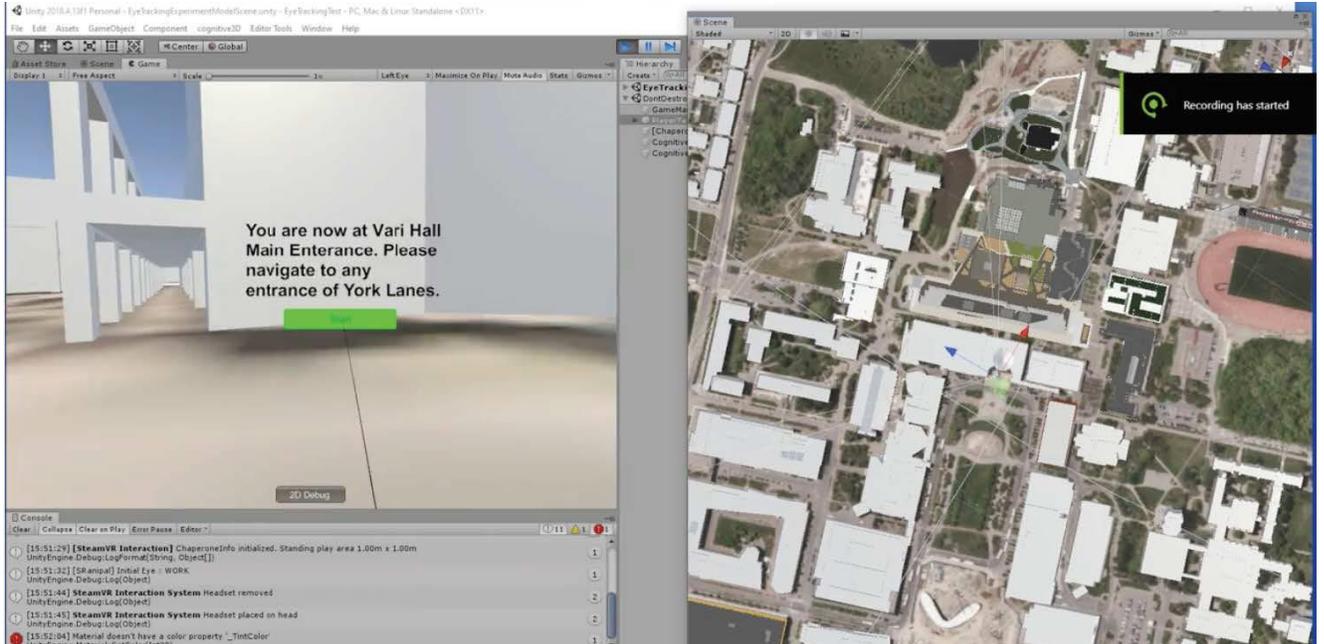


Figure B. Navigation Task Example. Left side is showing an example prompt inviting the subject to navigate to a specified goal location. The right side is showing the real-time position of the subject on the map as they navigate to the goal location (only seen by the experimenter and recorded for future analysis).

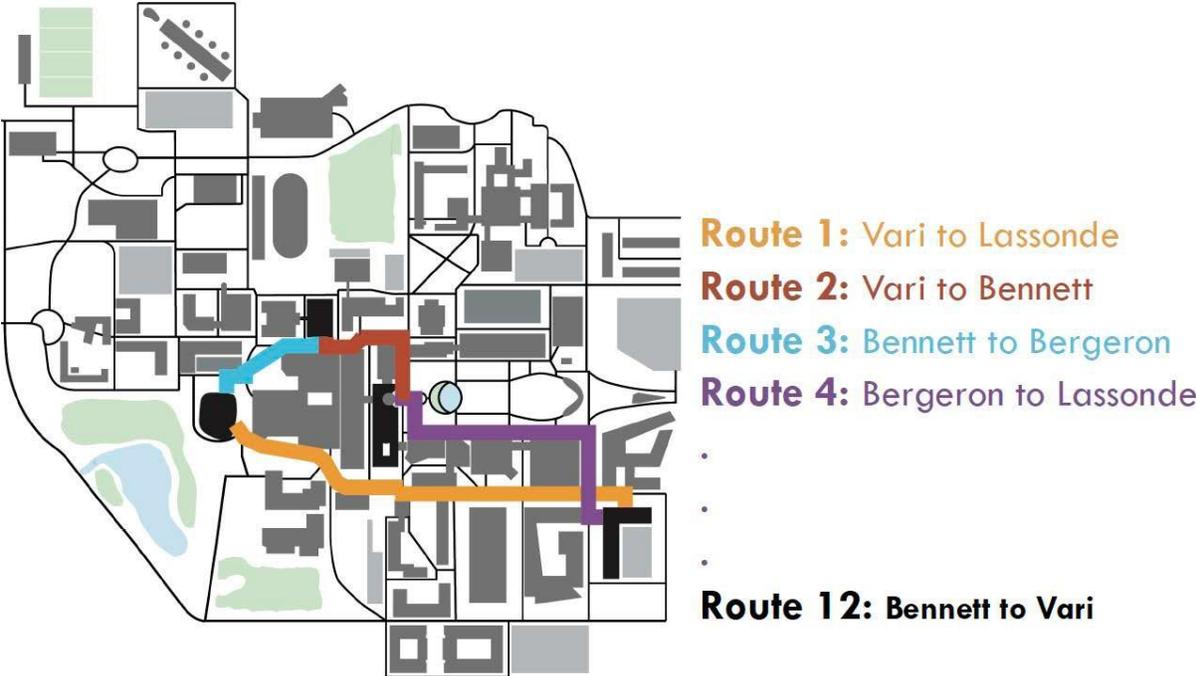


Figure C. Twelve navigation tasks consisting of different combinations of 4 landmark pairs

Appendix B: Spatial Memory Tasks

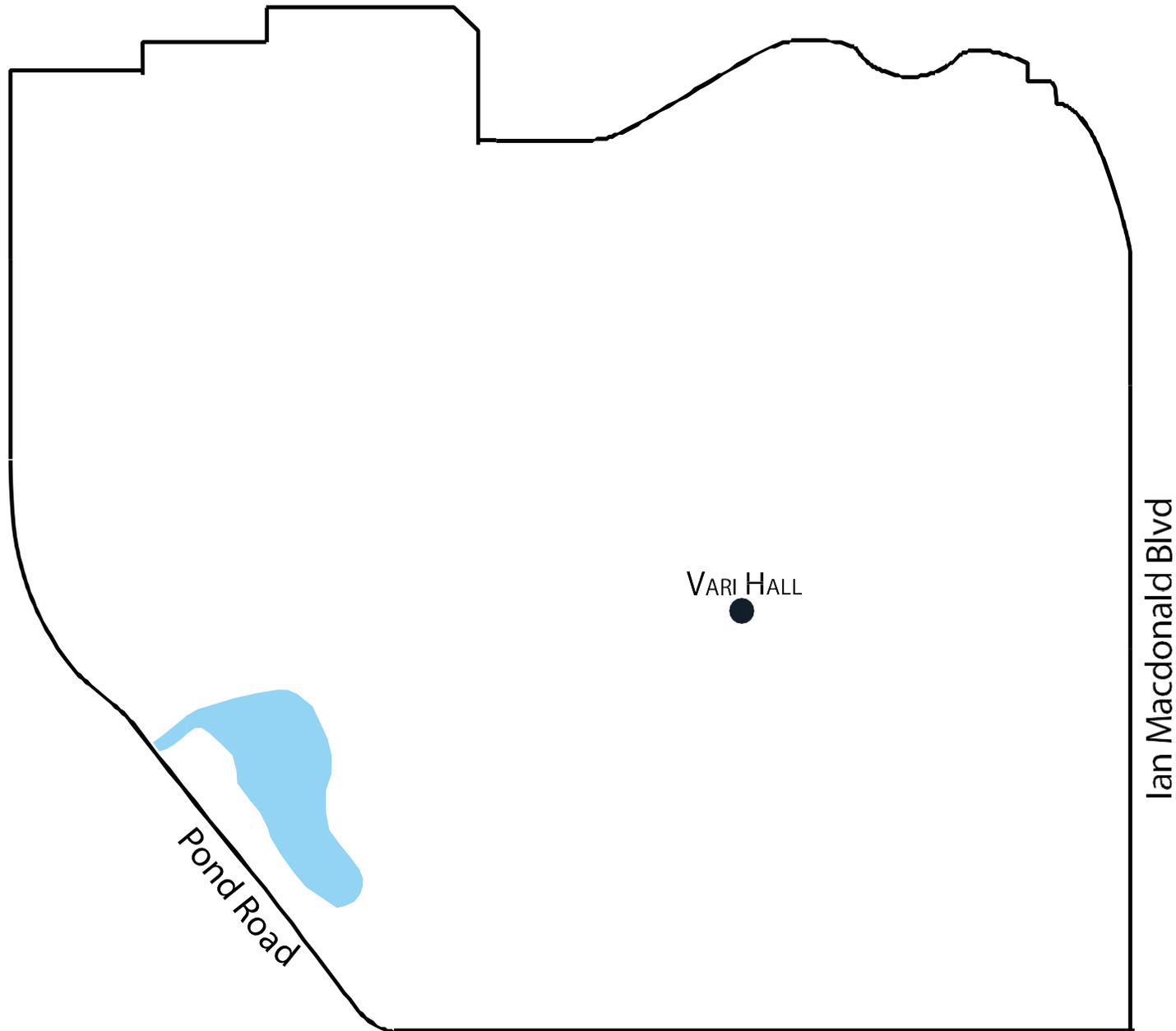
ID: _____

Date: _____

Time: _____

Task # 1

Please draw a sketch-map of the York University campus as you remember it using the boundaries provided. Include as many paths and buildings as you can. The location of Vari Hall has been marked for you.



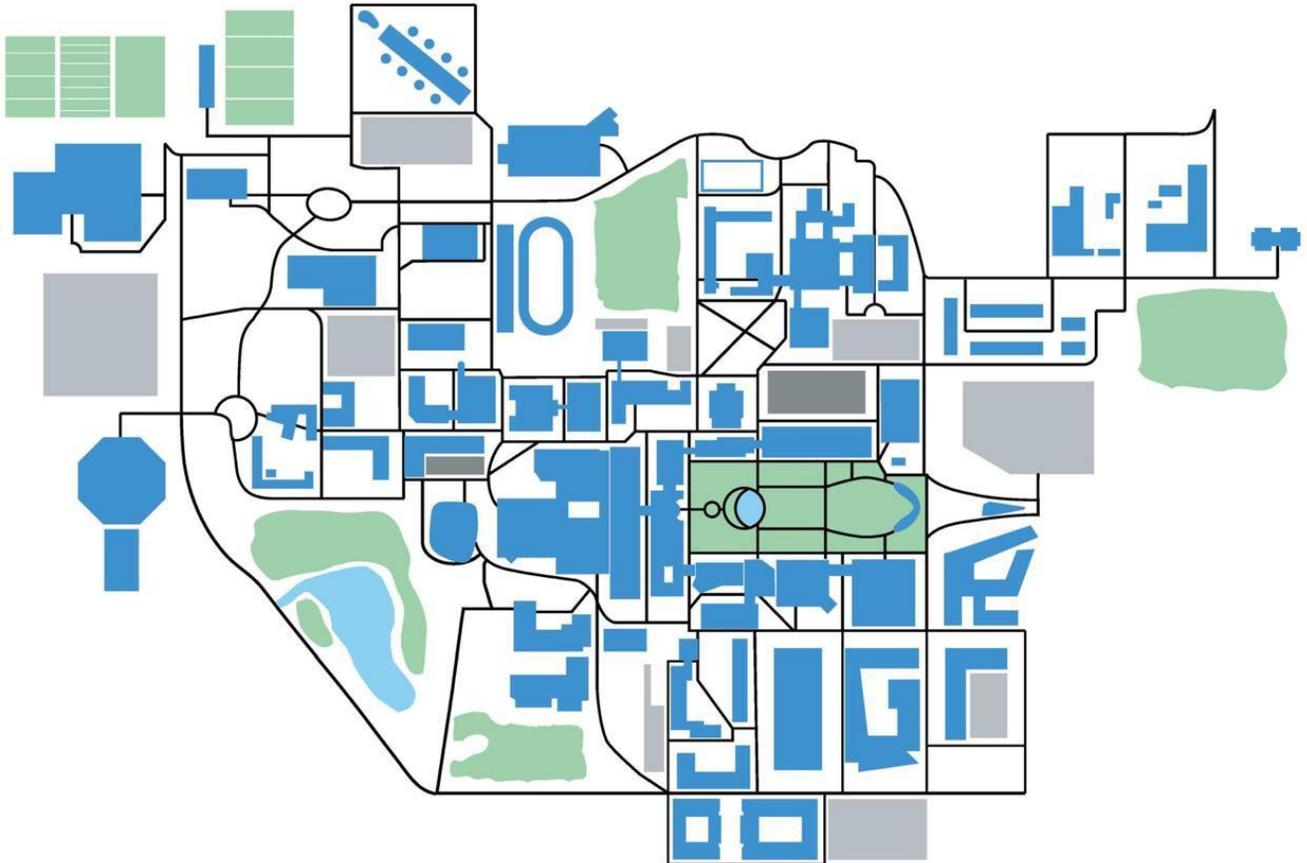
Part A: Landmark Familiarity

a) Please indicate whether any of these places are familiar to you: (i.e. have you walked past them?)

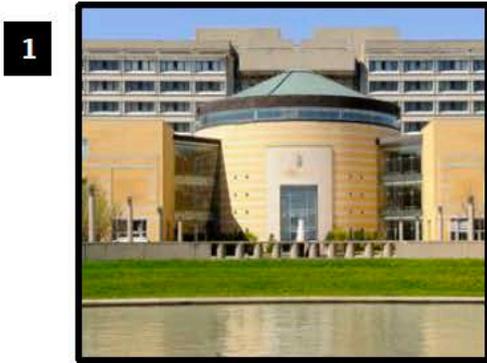
#	Place Name	Familiarity Rating (1 = no familiarity, 5 = very familiar)				
1	Vari Hall	1	2	3	4	5
2	Bergeron Engineering Building	1	2	3	4	5
3	Bennett Centre	1	2	3	4	5
4	Behavioural Science Building	1	2	3	4	5
5	Lassonde Building	1	2	3	4	5
6	Central Square	1	2	3	4	5
7	Seneca@York Building	1	2	3	4	5
8	Technology Enhanced Building	1	2	3	4	5
9	York Lanes	1	2	3	4	5
10	Life Sciences Building	1	2	3	4	5
11	Seymour Schulich Building	1	2	3	4	5
12	The Pond Road Residence	1	2	3	4	5
13	Steacie Science Building	1	2	3	4	5
14	Calumet College	1	2	3	4	5
15	Tennis Canada Aviva Centre	1	2	3	4	5
16	Accolade West	1	2	3	4	5
17	Curtis Lecture Hall	1	2	3	4	5
18	Ross Building	1	2	3	4	5
19	Scott Library	1	2	3	4	5
20	York Lanes Parking Garage	1	2	3	4	5
21	Second Student Centre	1	2	3	4	5
22	Sherman Health Science Research Centre	1	2	3	4	5

Part B: Landmark Placement

- a) Indicate using the numbers where your familiar places are on the map. Try to mark as many locations as you can remember.



Landmark Recognition



10



11



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22



Perspective-taking Test

Perspective Taking Test - Participant 42

Remaining Time: 285



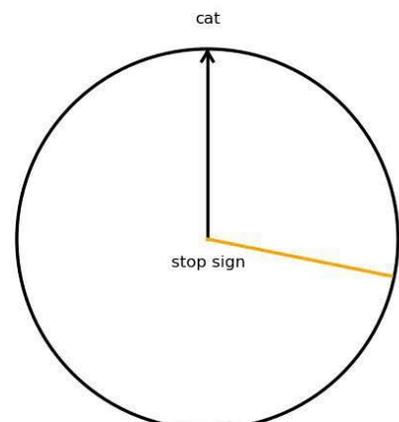
Instructions

This is a test of your ability to imagine different perspectives or orientations in space. On each of the following screens you will see a picture of an array of objects and an "arrow circle" with a question about the direction between some of the objects. For the question on each screen, you should imagine that you are standing at one object in the array (which will be named in the center of the circle) and facing another object, named at the top of the circle. Your task is to draw an arrow from the center object showing the direction to a third object from this facing orientation.

Look at the sample item in the other window. In this item you are asked to imagine that you are standing at the flower, which is named in the center of the circle, and facing the tree, which is named at the top of the circle. Your task is to draw an arrow pointing to the cat. In the sample item this arrow has been drawn for you. In the test items, your task is to draw this arrow. Can you see that if you were at the flower facing the tree, the cat would be in this direction? Please ask the experimenter now if you have any questions about what you are required to do.

There are 12 items in this test, one on each screen. For each item, the array of objects is shown at the top of the window and the arrow circle is shown at the bottom. Please do not pick up or turn the monitor, and do not make any marks on the maps. Try to mark the correct directions but do not spend too much time on any one question.

You will have 5 minutes for this test. Use SPACE in the other window to confirm your selections.



3. Imagine you are standing at the stop sign and facing the cat. Point to the house.

Source: <https://github.com/TimDomino/ptsot>

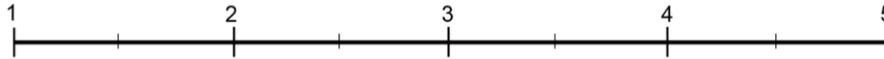
Appendix C: Questionnaires

15. How many days per week on average do you spend time on campus? _____.

16. Do you drive to campus? Yes No

If yes, where do you park? _____.

17. How would you rate your confidence in navigating between campus buildings and remembering their locations on campus from a scale of 1 (no confidence) to 5 (very confident)?



18. Please provide 3 routes that you travel on most often on campus by specifying their start and end locations, and your frequency of travel (average # per week, including travel in both directions):

Route 1: Start _____ End _____ Frequency of Travel: _____.

Route 2: Start _____ End _____ Frequency of Travel: _____.

Route 3: Start _____ End _____ Frequency of Travel: _____.

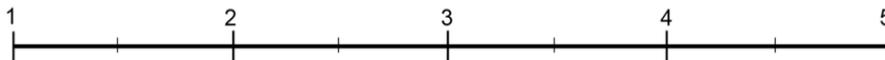
Part D: Technology Skills

19. Do you play video or computer games on a regular basis? Yes No

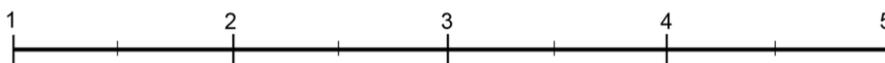
If yes, how many hours a week? _____.

For how many years have you played games regularly? _____.

20. How would you rate your experience with video or computer games from a scale of 1 (no experience at all) to 5 (a lot of experience)?



21. How would you rate your skills with video or computer games from a scale of 1 (no skills at all) to 5 (very good skills)?



22. Do you experience motion sickness? Yes No Specify: _____.

23. Do you have experience with VR? Yes, specify (how many times?): _____ No

Navigational Strategies Questionnaire

This questionnaire contains questions about your experience navigating, the strategies you use, and what helps you to navigate. Circle the answer for each question that best describes how you navigate or describe your answer in the space beside "Other" if neither applies.

1. When planning a route, do you picture a map of your route or do you picture scenes of what you will see along the way?

Map Scenes Other: _____.

2. Do you consider yourself a good navigator?

Yes No

3. Do you find it easy to read and use maps?

Yes Somewhat No

4. How often do you get disoriented while finding your way around?

Very often Somewhat often Very rarely

5. When thinking about a familiar street, how well can you picture the buildings along it?

Very clearly Somewhat clearly Hardly at all

6. Would you give directions to a friend in terms of landmarks (i.e., when you see the subway stop, turn left?) or in terms of map directions (i.e., walk north four blocks, then turn left?)?

Landmarks Map Directions Other: _____

7. Do you picture traveling a route on street level or from a bird's eye view?

Street-level Bird's Eye View Other: _____

8. When navigating in an area you know well, do you usually just know where to go or do you need to look around at the surroundings to decide (e.g., coming out of a subway station)?

Know it Some of each Need to look around

9. When traveling along a new route, do you usually remember what buildings you've passed?

Yes Somewhat Rarely

ID: _____

Date: _____

10. Would you prefer to navigate using a list of directions or a map?

Directions Map No preference

11. Do you use landmarks (i.e., familiar buildings) to orient yourself when navigating?

Often Sometimes Rarely

12. Do you find you're flexible navigating along routes (i.e., you can take new shortcuts easily), or do you prefer to follow the same path every time?

Flexible Somewhat flexible Prefer the same route

13. How easily could you draw a map of an area of the city that you know well?

Very easily Somewhat easily Not easily

14. Do you think that you navigate by following a mental map, or working on scene at a time?

Maps Scene at a time Other

Source: Brunec, I. K., Bellana, B., Ozubko, J. D., Man, V., Robin, J., Liu, Z. X., ... & Moscovitch, M. (2018). Multiple scales of representation along the hippocampal anteroposterior axis in humans. *Current Biology*, 28(13), 2129-2135.

Santa Barbara Sense of Direction Scale

This questionnaire consists of several statements about your spatial and navigational abilities, preferences, and experiences. After each statement, you should circle a number to indicate your level of agreement with the statement.

Circle "1" if you strongly agree that the statement applies to you, "7" if you strongly disagree, or some number in between if your agreement is intermediate. Circle "4" if you neither agree nor disagree.

1. I am very good at giving directions

strongly agree 1 2 3 4 5 6 7 strongly disagree

2. I have a poor memory for where I left things.

strongly agree 1 2 3 4 5 6 7 strongly disagree

3. I am very good at judging distances.

strongly agree 1 2 3 4 5 6 7 strongly disagree

4. My "sense of direction" is very good.

strongly agree 1 2 3 4 5 6 7 strongly disagree

5. I tend to think of my environment in terms of cardinal direction (N, S, E, W).

strongly agree 1 2 3 4 5 6 7 strongly disagree

6. I very easily get lost in a new city.

strongly agree 1 2 3 4 5 6 7 strongly disagree

7. I enjoy reading maps.

strongly agree 1 2 3 4 5 6 7 strongly disagree

8. I have trouble understanding directions.

strongly agree 1 2 3 4 5 6 7 strongly disagree

9. I am very good at reading maps.

strongly agree 1 2 3 4 5 6 7 strongly disagree

10. I don't remember routes very well while riding as a passenger in a car.

strongly agree 1 2 3 4 5 6 7 strongly disagree

11. I don't enjoy giving directions.

strongly agree 1 2 3 4 5 6 7 strongly disagree

12. It's not important to me to know where I am.

strongly agree 1 2 3 4 5 6 7 strongly disagree

13. I usually let someone else do the navigational planning for long trips.

strongly agree 1 2 3 4 5 6 7 strongly disagree

14. I can usually remember a new route after I have traveled it only once.

strongly agree 1 2 3 4 5 6 7 strongly disagree

15. I don't have a very good "mental map" of my environment.

strongly agree 1 2 3 4 5 6 7 strongly disagree

Source: Hegarty, M., Richardson, A. E., Montello, D. R., Lovelace, K., & Subbiah, I. (2002). Development of a self-report measure of environmental spatial ability. *Intelligence*, 30(5), 425-447.

Appendix D: Landmark Selection

Exploration of Study Area - Site Analysis



Figure A. Visibility graph analysis from DepthMap (<https://www.ucl.ac.uk/bartlett/architecture/research/space-syntax/depthmapx>) **Figure B.** Landmark Selection Criteria

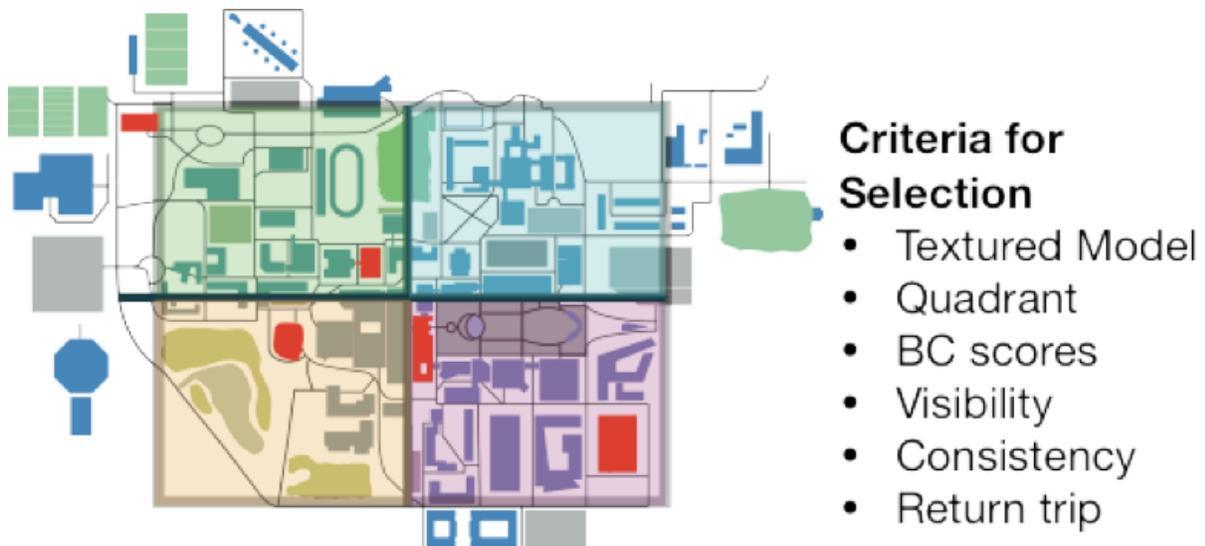


Figure B. Landmark Selection Criteria

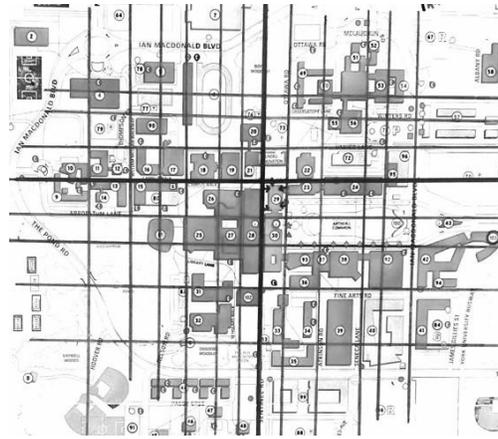
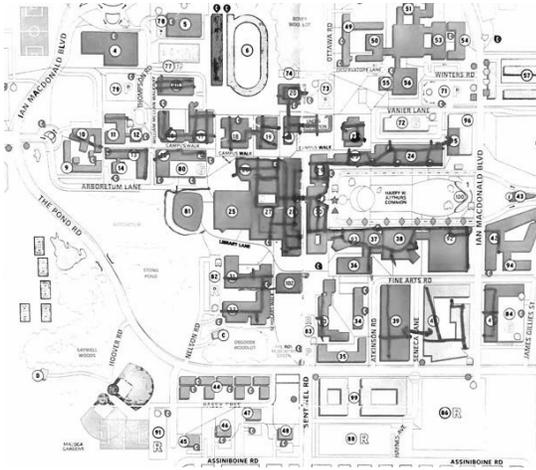


Figure C. Interior circulation network is shown on the left, followed by the exterior circulation grid

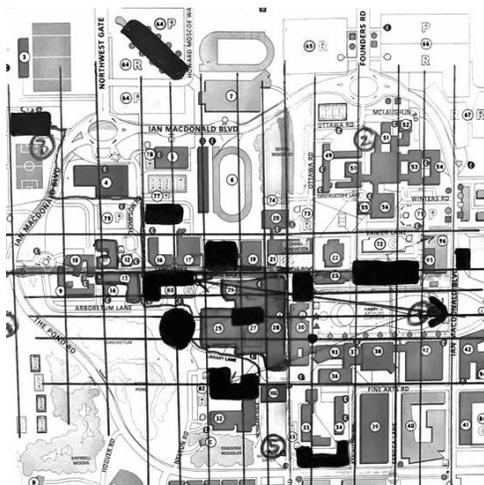


Figure D. Landmarks of Interest

Space Syntax Analyses

Table A. List of Campus Points of Interest and 3D Landmark detail level

<i>Number</i>	<i>Name</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Type</i>	<i>Function</i>	<i>High Detail</i>	<i>Low Detail</i>
1	190 Albany Road	43.77916	-79.49957	Building	Admin		
2	Accolade East	43.77337	-79.49902	Building	Academic		Yes
3	Accolade West	43.77247	-79.50169	Building	Academic		
4	Atkinson	43.77063	-79.50179	Building	Academic		
5	Behavioural Science	43.77524	-79.50395	Building	Academic		
6	Bennett Centre for Student Services, Admissions	43.77233	-79.498689	Building	Admin	Yes	
7	Bergeron Centre for Engineering Excellence	43.77268	-79.50459	Building	Academic	Yes	
8	Calumet College	43.77284	-79.50916	Building	Academic		
9	Central Square	43.77268	-79.50459	Area	Social	Yes	
10	Central Utilities Building	43.77774	-79.49847	Building	Admin		
11	Centre for Film & Theatre	43.77247	-79.50169	Building	Academic		Yes
12	Chemistry	43.7739	-79.50757	Building	Academic		
13	Curtis Lecture Halls	43.77268	-79.50459	Building	Academic	Yes	
14	Executive Learning Centre	43.77337	-79.49902	Building	Academic		
15	Farquharson Life Sciences	43.77524	-79.50395	Building	Academic	Yes	
16	Founders College	43.77615	-79.50238	Building	Academic		
17	Health, Nursing & Environmental Studies	43.77088	-79.50413	Building	Academic		
18	Ignat Kaneff Building, Osgoode Hall Law School	43.77088	-79.50413	Building	Academic		
19	Joan & Martin Goldfarb Centre for Fine Arts	43.77247	-79.50169	Building	Academic		
20	Kaneff Tower	43.77546	-79.50042	Building	Admin		
21	Kinsmen	43.77843	-79.49541	Building	Admin		
22	Lassonde Building	43.773964	-79.50525	Building	Academic	Yes	

<i>Number</i>	<i>Name</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Type</i>	<i>Function</i>	<i>High Detail</i>	<i>Low Detail</i>
23	Life Sciences Building	43.7739	-79.50757	Building	Academic	Yes	
24	Lorna R. Marsden Honour Court & Welcome Centre	43.77337	-79.49902	Building	Admin		
25	Lumbers	43.77524	-79.50395	Building	Admin		
26	McLaughlin College	43.77615	-79.50238	Building	Academic		
27	Norman Bethune College	43.77284	-79.50916	Building	Academic		
28	Observatory, Petrie	43.7739	-79.50757	Building	Academic		
29	Petrie Science & Engineering	43.7739	-79.50757	Building	Academic		
30	Physical Resources Building	43.77795	-79.49745	Building	Academic		
31	Rob and Cheryl McEwen Graduate Study & Research Building	43.774181	-79.497235	Building	Academic		
32	Ross Building	43.77268	-79.50459	Building	Academic	Yes	
33	Scott Library	43.77268	-79.50459	Building	Academic	Yes	
34	Scott Religious Centre, CSQ	43.77268	-79.50459	Building	Academic	Yes	
35	Seymour Schulich Building	43.77337	-79.49902	Building	Academic		Yes
36	Sherman Health Science Research Centre	43.7751	-79.51186	Building	Academic	Yes	
37	Steacie Science & Engineering Library	43.77382	-79.50569	Building	Academic		
38	Stedman Lecture Halls	43.77524	-79.50395	Building	Academic		
39	Stong College	43.77284	-79.50916	Building	Academic		
40	Student Centre	43.77524	-79.50395	Building	Commercial		
41	Tait McKenzie Centre	43.77441	-79.50959	Building	Athletic		
42	Vanier College	43.77615	-79.50238	Building	Academic		
43	Vari Hall	43.77268	-79.50459	Building	Academic		Yes
44	Victor Phillip Dahdaleh Building (Formerly TEL)	43.771406	-79.500781	Building	Academic		
45	West Office Building	43.77554	-79.50815	Building	Admin		

<i>Number</i>	<i>Name</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Type</i>	<i>Function</i>	<i>High Detail</i>	<i>Low Detail</i>
46	William Small Centre	43.7729	-79.50713	Building	Admin		
47	Winters College	43.77615	-79.50238	Building	Academic		
48	York Lanes	43.77456	-79.50161	Building	Commercial	Yes	
49	320 Assiniboine Road	43.76857	-79.5025	Building	Residential		
50	340 Assiniboine Road	43.76857	-79.5025	Building	Residential		
51	360 Assiniboine Road	43.76857	-79.5025	Building	Residential		
52	380 Assiniboine Road	43.76857	-79.5025	Building	Residential		
53	Atkinson Residence	43.77063	-79.50179	Building	Residential		
54	Bethune Residence	43.77284	-79.50916	Building	Residential		
55	Calumet Residence	43.77284	-79.50916	Building	Residential		
56	Founders Residence	43.77615	-79.50238	Building	Residential		
57	Passy Gardens, 2-18 Passy Cres.	43.7691	-79.505	Building	Residential		
58	The Pond Road Residence	43.77063	-79.50179	Building	Residential		
59	Stong Residence	43.77284	-79.50916	Building	Residential		
60	Tatham Hall	43.77615	-79.50238	Building	Residential		
61	Vanier Residence	43.77615	-79.50238	Building	Residential		
62	Winters Residence	43.77615	-79.50238	Building	Residential		
63	Arboretum Lane Parking Garage	43.77254	-79.50697	Building	Parking		
64	Student Services Parking Garage	43.77202	-79.49794	Building	Parking		
65	York Lanes Parking Garage	43.77456	-79.50161	Building	Parking		
66	Art Gallery of York University	43.77337	-79.49902	Building	Artistic		
67	Burton Auditorium	43.77247	-79.50169	Building	Artistic		
68	Gales Gallery	43.77337	-79.49902	Building	Artistic		
69	Joseph G. Green Studio Theatre	43.77337	-79.49902	Building	Artistic		
70	McLean Performance Studio	43.77337	-79.49902	Building	Artistic		
71	Price Family Cinema	43.77337	-79.49902	Building	Artistic		
72	Sandra Faire & Ivan Fecan Theatre	43.77337	-79.49902	Building	Artistic		

<i>Number</i>	<i>Name</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Type</i>	<i>Function</i>	<i>High Detail</i>	<i>Low Detail</i>
73	Tribute Communities Recital Hall	43.77337	-79.49902	Building	Artistic		
74	Tait McKenzie Centre	43.77441	-79.50959	Building	Athletic		
75	York Stadium	43.77625	-79.5126	Building	Athletic		
76	York Lions Stadium	43.77551	-79.50666	Building	Athletic		
77	Skennen'kó:wa Gamig	43.77088	-79.50413	Building	Historic		
78	Hoover House	43.76835	-79.50922	Building	Historic		
79	Stong Barn	43.78009	-79.4974	Building	Historic		
80	Stong House	43.78009	-79.4974	Building	Historic		
81	Archives of Ontario	43.77546	-79.50042	Building	Admin		
82	Canlan Ice Sports	43.77452	-79.51399	Building	Athletic		
83	Computer Methods Building	43.77843	-79.49541	Building	Academic		
84	Harry Sherman Crowe Housing Co-op	43.77628	-79.49812	Building	Residential		
85	Seneca @ York, Stephen E. Quinlan Building	43.77145	-79.49969	Building	Academic		
86	Tennis Canada - Aviva Centre	43.77524	-79.50395	Building	Athletic		
87	Track & Field Centre	43.77551	-79.50666	Building	Athletic		
88	The Quad Student Housing	43.76999	-79.50054	Building	Residential		
89	York University TTC Subway Station	43.77399	-79.50004	Building	Transportation		
90	Pioneer Village TTC Subway Station	43.77696	-79.50946	Building	Transportation		
91	Second Student Centre	43.77088	-79.50413	Building	Admin	Yes	
92	Stong Pond Pavillion	43.771549	-79.506774	Area	Social		
<i>Total</i>						13	4

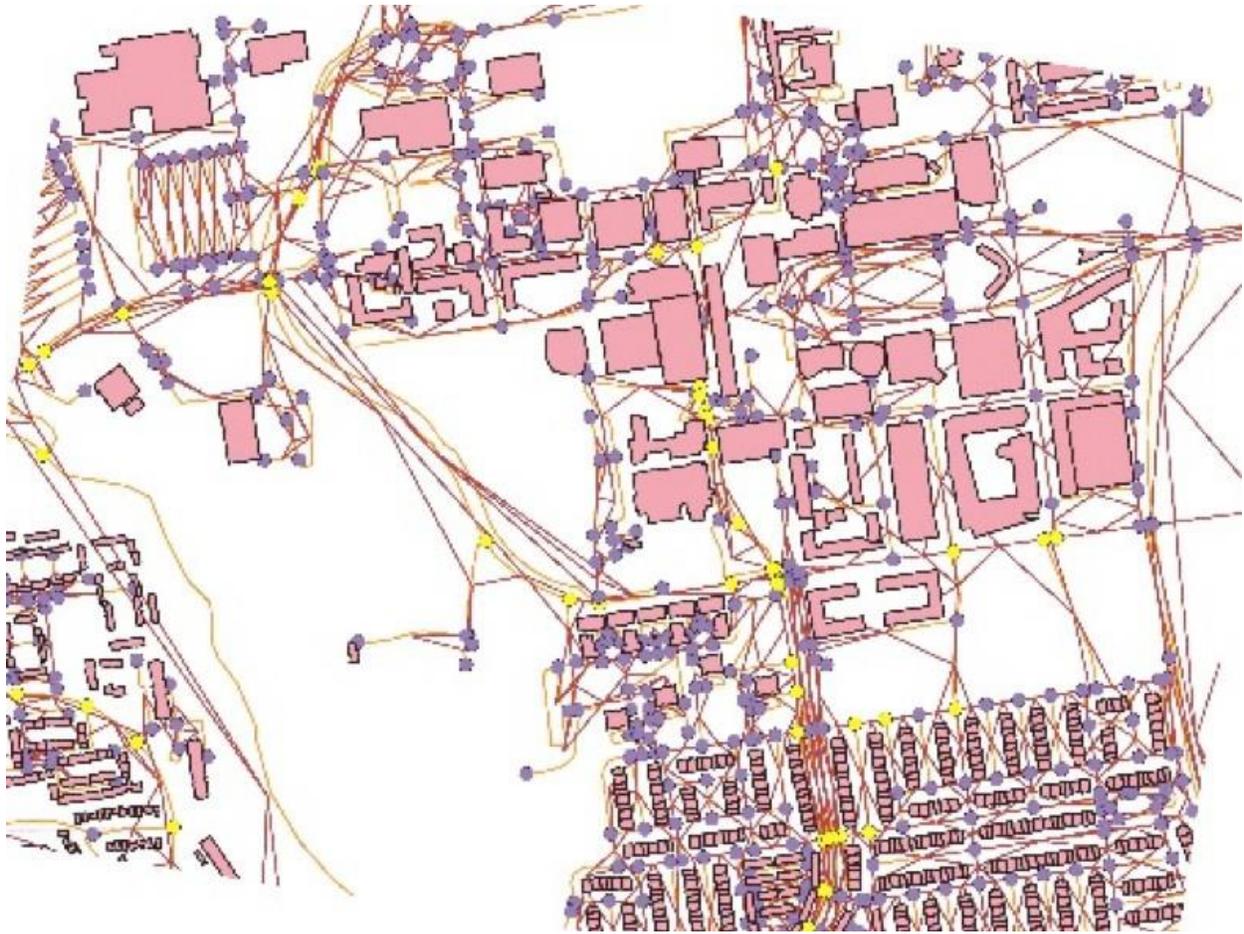


Figure E. Network analysis for York University Keele Campus from “Computational Image of the City” (<https://github.com/g-filomena/Computational-Image-of-the-City>) (Filomena et al, 2018).

Table 2. Betweenness centrality (BC) scores for the first 20 nodes

x	y	nodeID	height	BC	Sc
304944.9138	4847361.476	1	2	12245	0.725141287
303436.5234	4846672.889	2	2	11026	0.661681518
304484.2045	4847471.711	4	2	1269	0.621162354
304530.5331	4848334.777	5	2	10919	0.706007574
305023.2237	4847247.528	6	2	6195	0.736799506
304567.2603	4848418.886	7	2	4754	0.733251027
304628.2293	4847123.499	9	2	6596	0.706413238

304082.6168	4848146.348	10	2	23205	0.683206307
304463.1027	4847314.612	11	2	37346	0.661504656
304344.1521	4847414.816	12	2	18814	0.616867782
303831.8063	4846340.168	13	2	0	0.631295299
303486.4619	4847284.582	14	2	0	0.51024249
304114.5491	4846392.425	15	2	0	0.644113968
303513.0365	4847937.796	16	2	22699	0.695520796
303640.2886	4846303.681	17	2	6900	0.678971165
305446.8092	4847205.261	18	2	4064	0.77536828
304971.202	4846692.405	19	2	100	0.719383788
304602.6786	4846740.643	20	2	1432	0.653839368

Table 3. Landmark Selection based on betweenness centrality scores (BC)

Buildings with Textures	Node ID (close by)	BC
Bergeron	1219	5201
Bennett Centre	1570	5201
Scott Library	1524	11327
York Lanes	1031	28636
Second student centre	1050	42722
Life Science Building	850	50462
Ross Building	436	59098
Curtis Lecture Hall	400	62735
Lassonde School	400	62735
Farquason life science	1250	68272
Central Square	671	145017
Sherman	135	151294

Appendix E: Supplementary Graphs

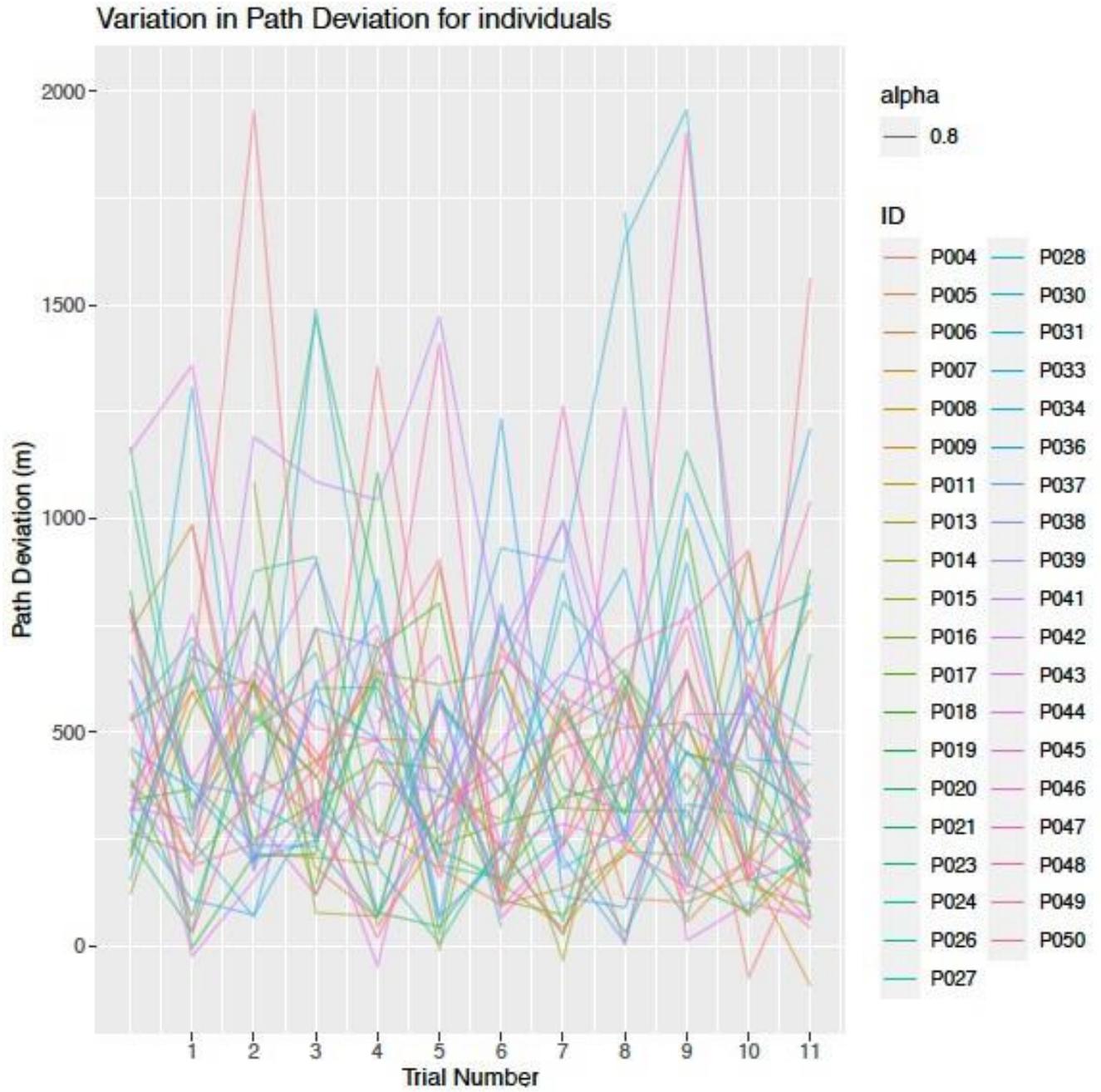


Figure A. Graph showing path deviation for each individual (denoted by a unique color) for each trial

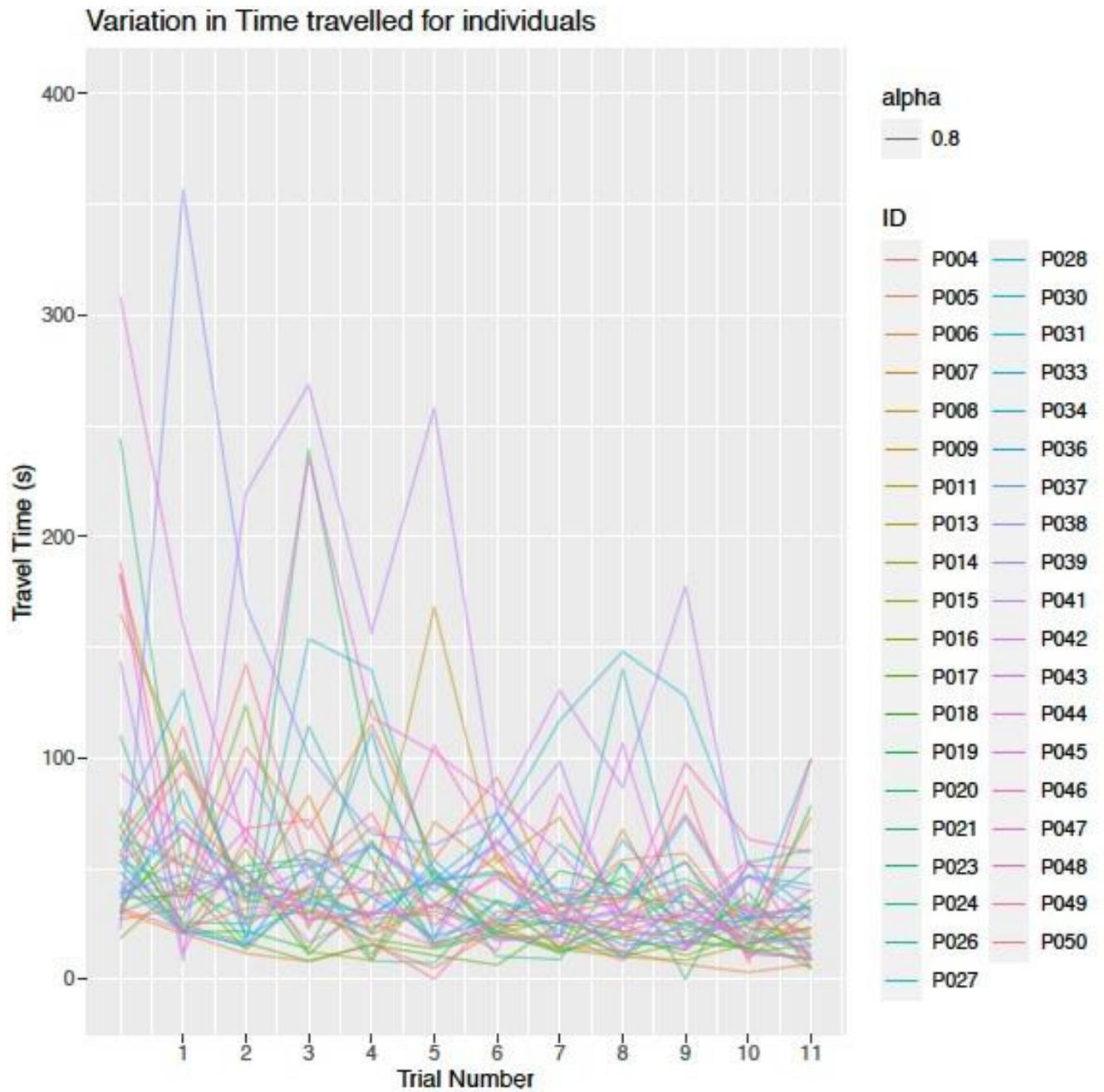


Figure B. Graph showing travel time for each individual (denoted by a unique color) for each trial

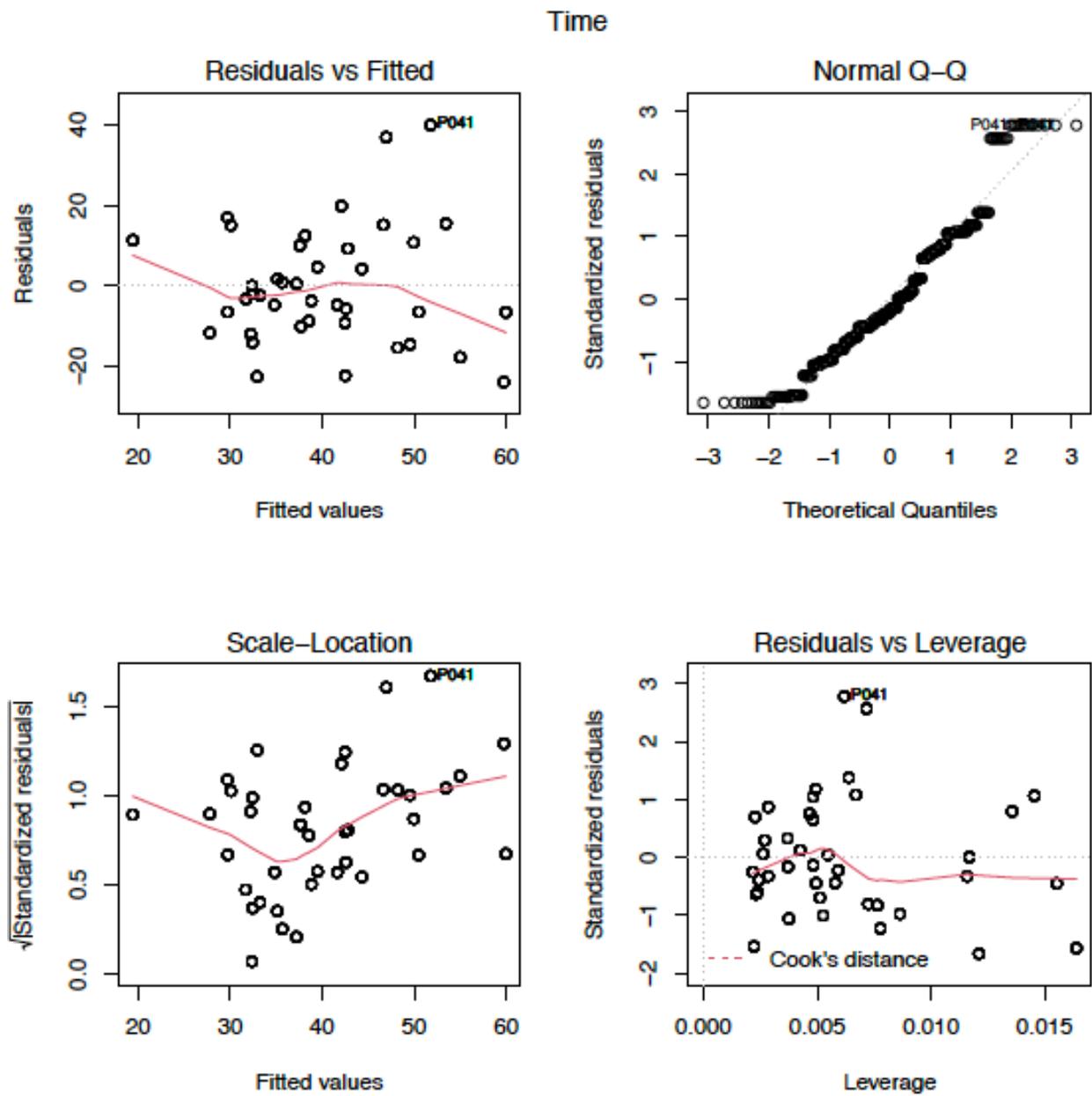


Figure C. Regression diagnostics plots for travel time as the outcome of interest

PathDeviation

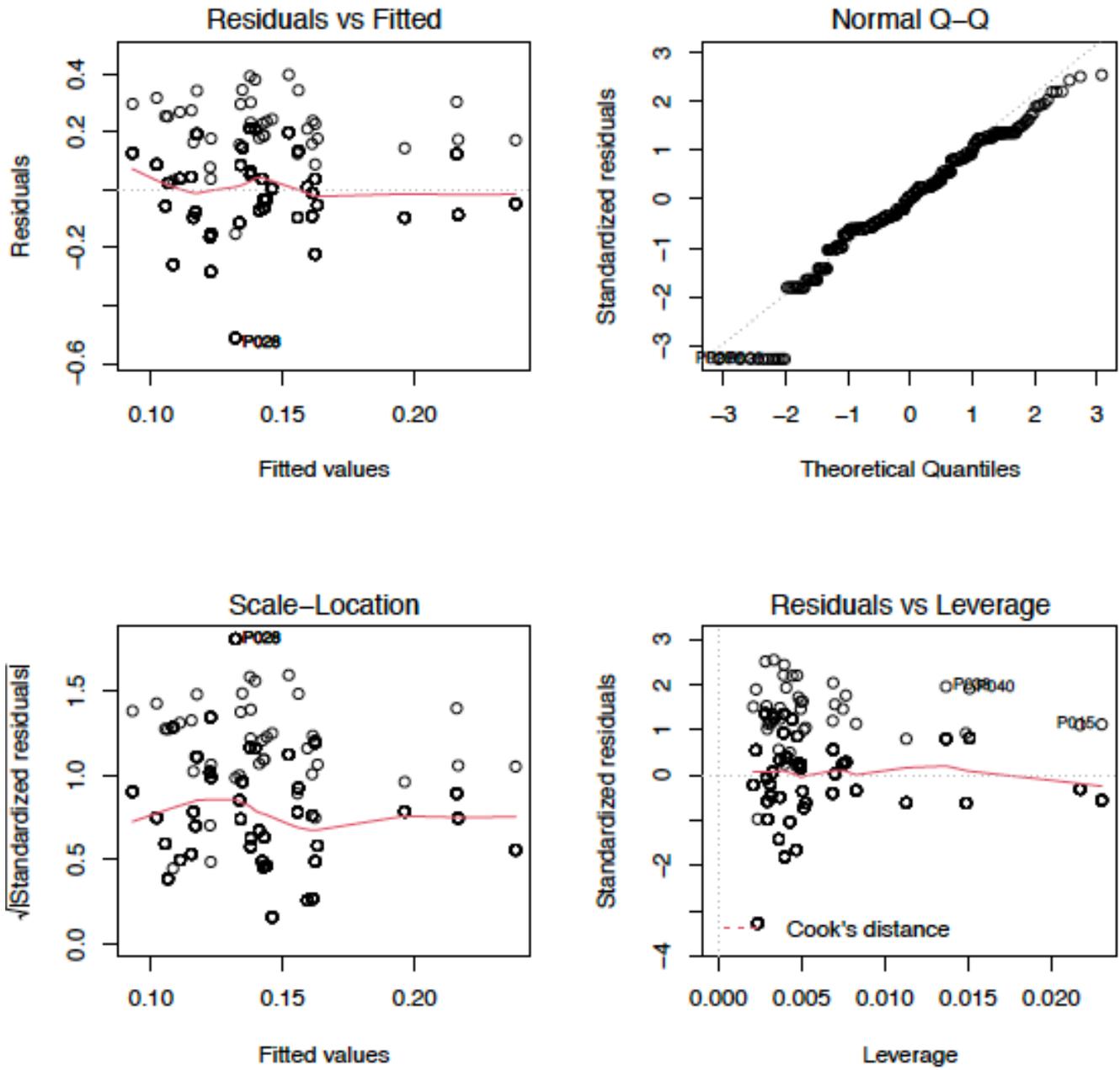


Figure D. Regression diagnostics plots for path deviation as the outcome of interest

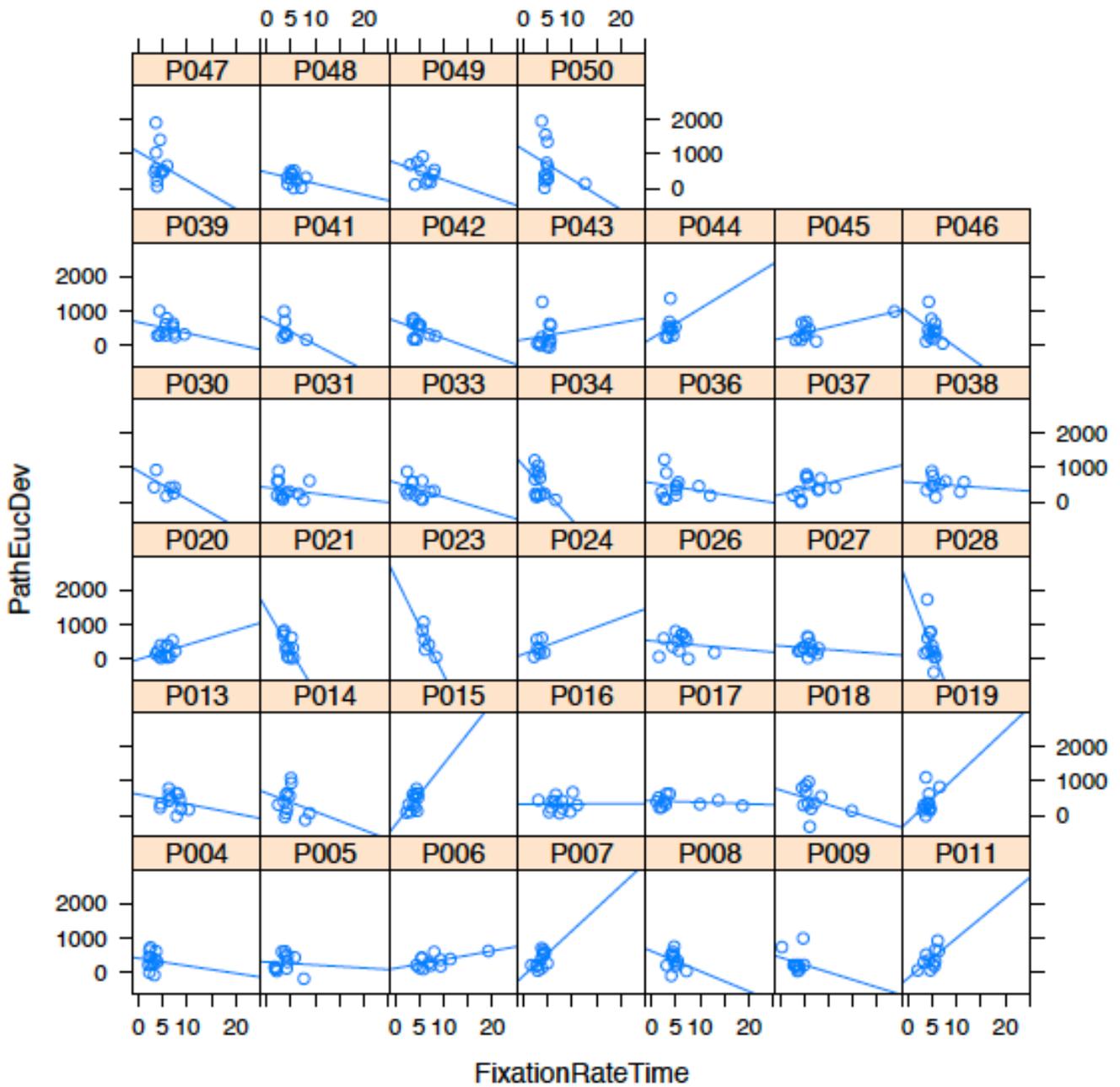


Figure E. Lattice plot showing the correlations between fixation rate and path deviation for each individual. Each circle represents data from a trial.

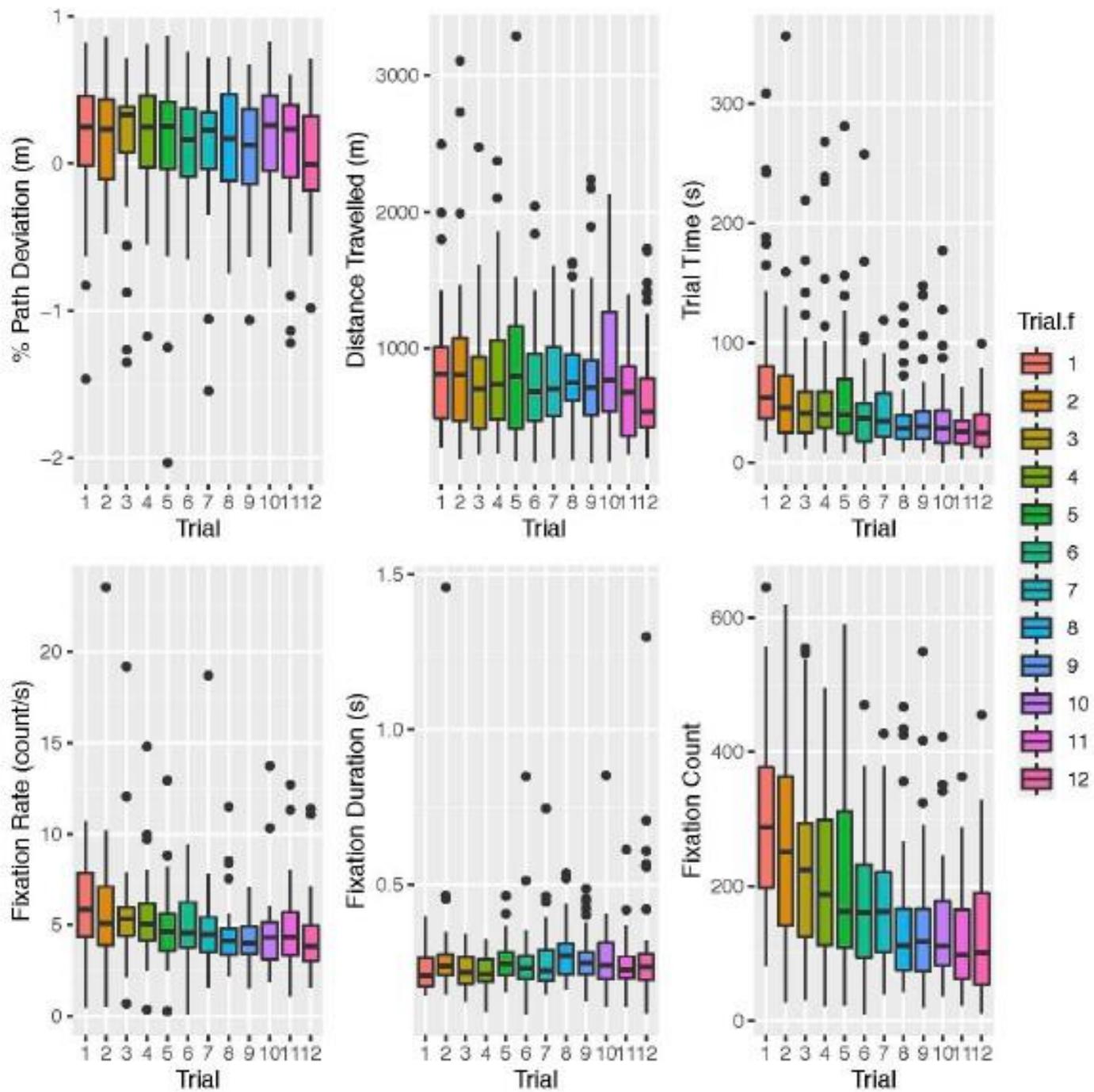


Figure F. Graphs showing practice effects across trials for several variables (path deviation, fixation rate, distance traveled, fixation duration, fixation count, and travel time)

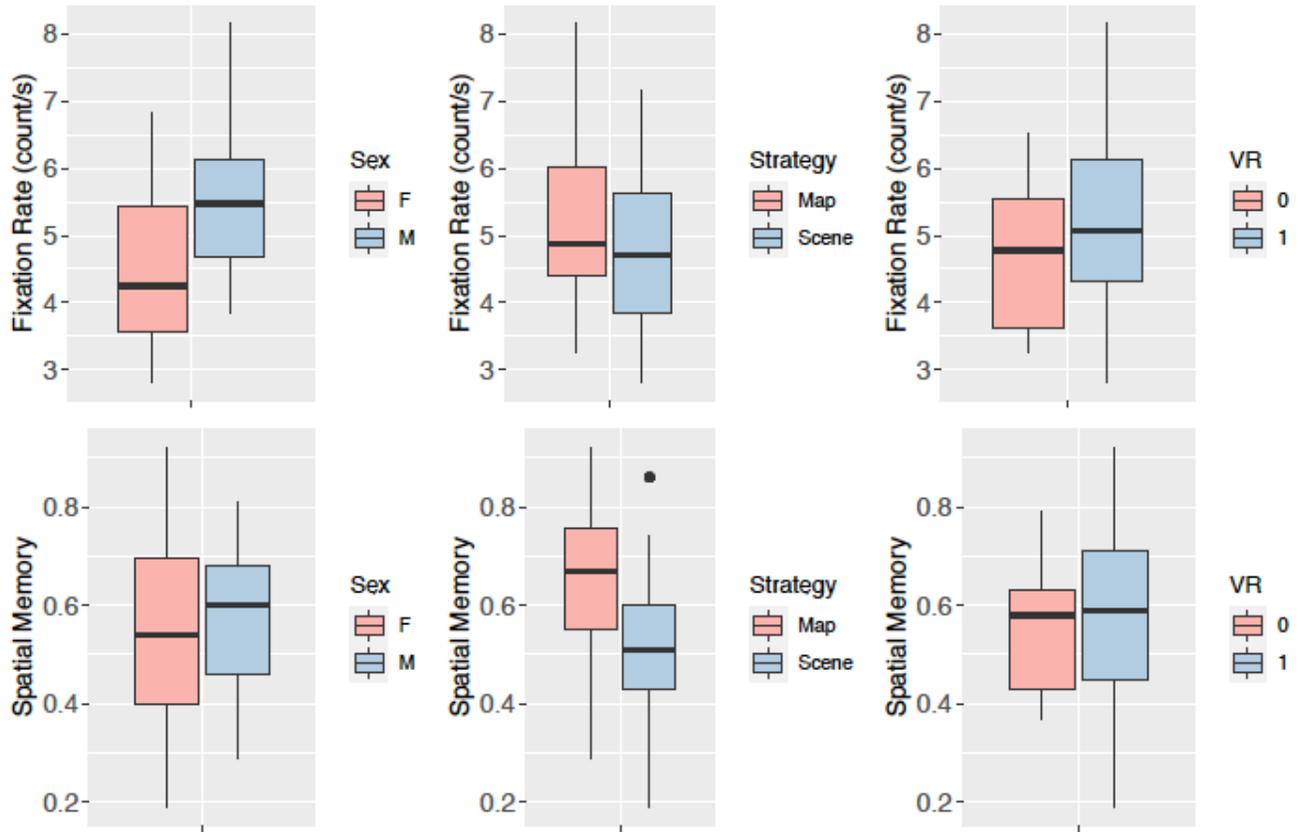


Figure G. Boxplots showing group differences in spatial memory and fixation rate across sex, strategy and VR experience. The horizontal line represents the mean and box height is determined by the interquartile range.

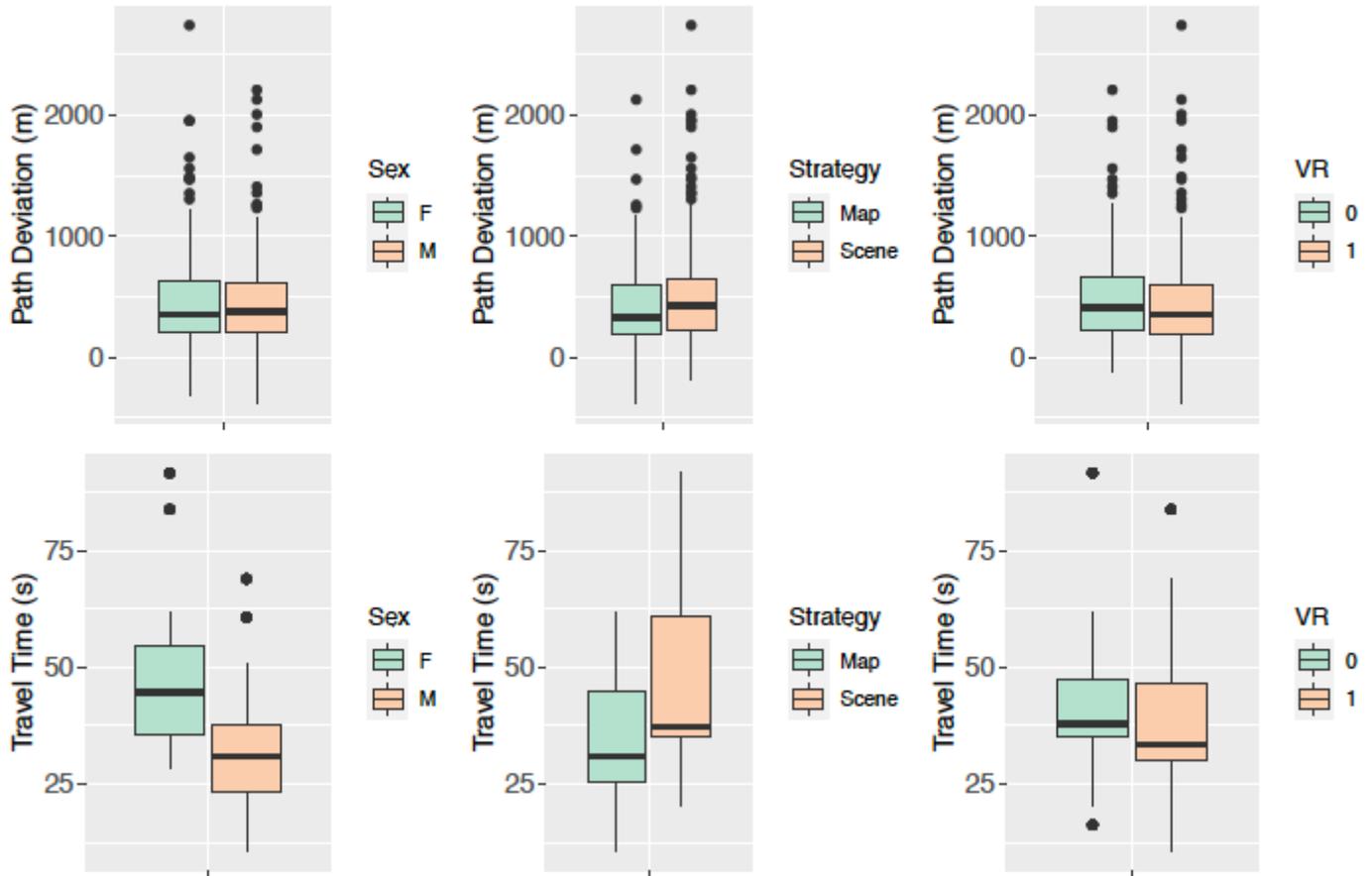


Figure H. Boxplots showing group differences in path deviation and travel time across sex, strategy and VR experience. The horizontal line represents the mean and box height is determined by the interquartile range.

Appendix F: R script for statistical analyses

```

####DF Thesis 2020
####Import dataset and load libraries ----
#Install dependencies
library(psych) #for basic functions
library(ggplot2) #for plotting
library(data.table) #for fast data management
library(nlme) #for mixed effects models
library(plyr) #for data management
library(EnvStats) # for outliers
library(grDevices) # for pdf output
library(car) # for recoding variables
library(sjPlot) # for table functions
library(sjmisc) # for sample
library(lme4) # for R^2 - MLM
library(MuMIn) # for R^2 - MLM
library(stargazer) #output tables
library(tableone) # for summary tables
library(summarytools) #for summary tables
library(apa) # for apa style
library(gridExtra) # for figure layout
library(dplyr) # for bar graphs
library(RColorBrewer) # for color theme
library(sjPlot) #residual plots
library(lattice) #for plots

#control settings
ctrl <- lmeControl(opt='optim'); #MLMoptimizer
options(scipen = 999) #change digit notation

#Import dataset
longdat <- read.csv("longdat.csv")

#removing pilot,intoxicated and confused participants
ldat <- longdat[!longdat$ID == "P003" & !longdat$ID == "P035" &
!longdat$ID == "P040", ]

####Identify Potential Outliers ----
#outcome 1: path deviation
x <- ldat$PathEucDev
x[which(x %in% boxplot.stats(x)$out)]
rosnerTest(x, k = 20, warn = F)
ldat <- ldat[!ldat$PathEucDev == 5112.94 & !ldat$PathEucDev == 3917.15 &
!ldat$PathEucDev == 3187.29 & !ldat$PathEucDev ==
2922.88,]
#outcome 2: travel time
x <- ldat$TimeTravelled

```

```

x[which(x %in% boxplot.stats(x)$out)]
rosnerTest(x, k = 20, warn = F)

####Recode variables --

#Recode trials to start at 0 for MLM
ldat$Trial <- ldat$Trial-1
#Recode route type as factor
ldat$RouteCode <- as.factor(ldat$RouteCode)
#Recode strategy as factor variable
ldat$Strategy <- car::recode(ldat$MapStrategy, "0:20 = 'Map'; else =
'Scene'")
ldat$Strategy <- as.factor(ldat$Strategy)
#Recode past VR experience as factor
ldat$VR <- as.factor(ldat$VR)
ldat$VR <- car::recode(ldat$VR, "0= 0; else= 1")

####Compute variables ----
#calculate mean of variables based on 12 trials for each subject in long
format
##fixation rate
FR <- aggregate (FixationRateTime ~ ID, ldat, mean)
names(FR)[2] <- "MeanFixation"
ldat <- merge(ldat,FR, by="ID")
##fixation length
FRD <- aggregate (FixationDuration ~ ID, ldat, mean)
names(FRD)[2] <- "MeanFDuration"
ldat <- merge(ldat, FRD, by="ID")
##path deviation
FRD2 <- aggregate (PathEucDev ~ ID, ldat, mean)
names(FRD2)[2] <- "MeanPathDeviation"
ldat <- merge(ldat, FRD2, by="ID")
##travel time
FRD3 <- aggregate (PathEucDev ~ ID, ldat, mean)
names(FRD3)[2] <- "MeanTime"
ldat <- merge(ldat, FRD3, by="ID")
##goal distance
FRD4 <- aggregate (DistancetoGoal ~ ID, ldat, mean)
names(FRD4)[2] <- "MeanGoalDistance"
ldat <- merge(ldat, FRD4, by="ID")

##spatial memory
FRD8 <- aggregate (ldat$SMIndex ~ ID, ldat, mean)
names(FRD8)[2] <- "MeanSM"
ldat <- merge(ldat, FRD8, by="ID")

#calculate mean of variables based on trial number in wide format
dataset

```

```
FRD5 <- aggregate (FixationRateTime ~ Trial, ldat, mean)
names(FRD5)[2] <- "MmeanFixation"
tdat <- FRD5 #add to a new dataset
FRD6 <- aggregate (PathEucDev ~ Trial, ldat, mean)
names(FRD6)[2] <- "MmeanPath"
tdat <- merge(tdat, FRD6, by="Trial")
FRD7 <- aggregate (TimeTravelled ~ Trial, ldat, mean)
names(FRD7)[2] <- "MmeanTime"
tdat <- merge(tdat, FRD7, by="Trial")
```

```

####Grand-mean center variables ----
#Center fixation rate variable
ldat$FixationRateTime.c <- ldat$FixationRateTime -
mean(ldat$FixationRateTime, na.rm = TRUE)
cor.test(ldat$FixationRateTime.c,ldat$FixationRateTime) #check that
centering was done correctly
#Center Spatial Memory Index
ldat$SMIndex.c <- ldat$SMIndex - mean(ldat$SMIndex, na.rm = TRUE)
#Center SBSOD
ldat$SBSOD.c <- ldat$SBSOD - mean(ldat$SBSOD, na.rm = TRUE)
#Center Age
ldat$Age.c <- ldat$Age - mean(ldat$Age, na.rm = TRUE)
#Center Fixation duration
ldat$FixationDuration.c <- ldat$FixationDuration -
mean(ldat$FixationDuration, na.rm = TRUE)

#####MLM1 Path Deviation Models A0,A1,A2-----
#random Intercept model
RandomIntercept <- lme(fixed = PathEucDev ~ 1,
                        random= ~ 1|ID,
                        data=ldat,
                        na.action = na.exclude, method = 'ML', control = 'ctrl')
summary(RandomIntercept)
#fixed intercept
VarCorr(RandomIntercept)
RandomEffectsUCM <- as.numeric(VarCorr(RandomIntercept)[,1])
RandomEffectsUCM
ICC1 <- RandomEffectsUCM[1]/(RandomEffectsUCM[1]+RandomEffectsUCM[2])
ICC1

#add task as fixed effect
timeRI <- update (RandomIntercept, .~. + Trial)

#add task as a fixed effect and make a random effect of task over people
timeRS <- update (timeRI, random = ~ Trial|ID,
control=lmeControl(opt="optim"))

#MLM1: compare random and fixed slope
anova(RandomIntercept,timeRI,timeRS) # no significant improvement in fit
when task is also added as random effect,
#that is the rate of change of the effect of task on path deviation may
not vary across individuals

```

```

#####MLM1 Path Deviation FinalModel-----
#MLM1: add fixed effect predictors
mod1Final <- lme(fixed = PathEucDev ~ 1 + Trial + FixationRateTime.c +
SMIndex.c + Strategy
                + FixationRateTime.c*SMIndex.c*Strategy,
                random= ~ 1 + Trial|ID,
                data=ldat,
                na.action = na.exclude, method = 'ML',
control=lmeControl(opt="optim"))
summary(mod1Final)
intervals(mod1Final, which =
"fixed")
ldat$fittedmlm1 <- fitted.values(mod1Final)

#####MLM2 Travel Time Models B0,B1,B2-----
RandomIntercept2 <- lme(fixed = TimeTravelled ~
1, random= ~ 1|ID,
                        data=ldat,
                        na.action = na.exclude, method = 'ML', control =
'ctrl') summary(RandomIntercept2)
#ICC Unconditional means model
VarCorr(RandomIntercept2)
RandomEffectsUCM2 <- as.numeric(VarCorr(RandomIntercept2)[,1])
RandomEffectsUCM2
ICC_UCM2 <-
RandomEffectsUCM2[1]/(RandomEffectsUCM2[1]+RandomEffectsUCM2[2])
ICC_UCM2

#MLM2 task as fixed effect
timeRI2 <- lme(fixed = TimeTravelled ~ 1 + Trial,
              random = ~ 1 |ID,
              data=ldat,
              na.action = na.exclude, method = 'ML', control='ctrl')
summary(timeRI2)
intervals(timeRI2)

#MLM2 task as fixed adn random effect
timeRS2 <- lme(fixed = TimeTravelled ~ 1 + Trial,
              random = ~1 + Trial |ID,
              data=ldat,
              na.action = na.exclude, method = 'ML',
control=lmeControl(opt="optim"))
summary(timeRS2)
#intervals(timeRS2)
anova(timeRI2,timeRS2)
#####MLM2 Travel Time Conditional Growth Models-----
mod2Final <- lme(fixed = TimeTravelled ~ 1 + Trial + FixationRateTime.c
+ SMIndex.c + Strategy

```

```

+ FixationRateTime.c*SMIndex.c*Strategy,
random= ~ 1 + Trial|ID,
data=ldat,
na.action = na.exclude, method = 'ML',
control=lmeControl(opt="optim"))
summary(mod2Final)
intervals(mod2Final, which =
"fixed")

ldat$fittedmlm2 <- fitted.values(mod2Final)

#####MLM1 Path Deviation Summary of All Models-----
#1summary of all models
summary(RandomIntercept)
summary(timeRI)
summary(timeRS)
summary(mod1Final)

#1variance stats in all models
VarCorr(RandomIntercept)
VarCorr(timeRI)
VarCorr(timeRS)
VarCorr(mod1Final)

#1summary of variance deviance between models
anova(RandomIntercept,timeRI,timeRS)

#MLM1 marginal and conditional R^2
round(r.squaredGLMM(RandomIntercept, round), digits = 3)
round(r.squaredGLMM(timeRI), digits = 3)
round(r.squaredGLMM(timeRS), digits = 3)
round(r.squaredGLMM(mod1Final), digits = 3)

#####MLM2 Travel Time Summary of All Models-----
#2summary of all models
summary(RandomIntercept2)
summary(timeRI2)
summary(timeRS2)
summary(mod2Final)

#1variance stats in all models
VarCorr(RandomIntercept2)
VarCorr(timeRI2)
VarCorr(timeRS2)
VarCorr(mod2Final)

```

```

#1summary of variance deviance between models
anova(RandomIntercept2,timeRI2,timeRS2)

#MLM1 marginal and conditional R^2
round(r.squaredGLMM(RandomIntercept2, round), digits = 3)
round(r.squaredGLMM(timeRI2), digits = 3)
round(r.squaredGLMM(timeRS2), digits = 3)
round(r.squaredGLMM(mod2Final), digits = 3)

#####Output MLM1 Path Deviation Result Tables-----
stargazer(RandomIntercept, type = "text",digits=3,
out="output/regression/Path/RandomIntercept.txt")
stargazer(timeRI, type = "text",digits=3,
out="output/regression/Path/timeRI.txt")
stargazer(timeRS, type = "text",digits=3,
out="output/regression/Path/timeRS.txt")
stargazer(mod1Final, type = "text",digits=3,
out="output/regression/Path/mod1Final.txt")
tab_model(RandomIntercept,timeRI,timeRS,mod1Final, file
= "output/regression/Path/outcome1PathDev.doc")

#####Output MLM2 Travel Time Result Tables-----
- stargazer(RandomIntercept2, type = "text",digits=3,
out="output/regression/Time/RandomIntercept2.txt")
stargazer(timeRI2, type = "text",digits=3,
out="output/regression/Time/timeRI2.txt")
stargazer(timeRS2, type = "text",digits=3,
out="output/regression/Time/timeRS2.txt")
stargazer(mod2Final, type = "text",digits=3,
out="output/regression/Time/mod2Final.txt")
tab_model(RandomIntercept2,timeRI2,timeRS2,mod2Final, file
= "output/regression/Time/outcome2Time.doc")

#####Reshape data and Sample Descriptive Statistics
Tables-----
wdat <- reshape(data=ldat,idvar="ID",
timevar = "Trial",
direction="wide")
subldat <- subset(ldat, select = c("SBSOD",

"RecognitionRaw","PlacementRaw","SketchMapRaw", "MapStrategy",
"PTT"
,
"DistanceTravelled","TimeTravelled","c.error","TrialSpeed",

"DevDis","FixationRateTime","FixationRateDistance",
"AvgPointingError",

"SMIndex","PathEucDev","Avg.DistancetoGoal","MeanFixation","MeanTime"))

```

```

subwdat <- reshape(data=subldat,idvar="ID",
                  timevar = "Trial",
                  direction="wide")

library(apaTables)
apa.cor.table(subldat, filename="Output/Correlation/CorTable1.doc")
apa.cor.table(subldat)

tab1sw <- print(CreateTableOne(data = subldat))
#write.table(tab1sw, file = "output/Summary/Wide/tab1w.txt", sep = ",",
quote = FALSE, row.names = T)
#tabs2w <- descr(subwdat)
#write.table(tab2,file="output/Summary/Wide/tabs2w.csv",sep="," ,
col.names= T)

#####Boxplot by group Figure in Results Section-----
-

My_Theme2 = theme(
  axis.title.x = element_blank(),
  axis.text.x = element_blank(),
  axis.title.y = element_text(size = 10),
  axis.text.y = element_text(size = 10))

b1s <- ggplot(ldat, aes(x="Group", y=PathEucDev, fill=Sex))
+ geom_boxplot()
b1s <- b1s + labs(y="Path Deviation (m)") + scale_fill_brewer(palette =
"Pastel2") + My_Theme2

b4s <- ggplot(ldat, aes(x="Group", y=AvgTimeTravelled, fill=Sex))
+ geom_boxplot()
b4s <- b4s + labs(y="Travel Time (s)") + scale_fill_brewer(palette =
"Pastel2") + My_Theme2

b2s <- ggplot(ldat, aes(x="Group", y=MeanFixation, fill=Sex)) +
geom_boxplot()
b2s <- b2s + labs(y="Fixation Rate (count/s)") +
scale_fill_brewer(palette = "Pastel1") + My_Theme2

b3s <- ggplot(ldat, aes(x="Group", y=SpatialMemory, fill=Sex)) +
geom_boxplot()
b3s <- b3s + labs(y="Spatial Memory") + scale_fill_brewer(palette =
"Pastel1") + My_Theme2

b1 <- ggplot(ldat, aes(x="Group", y=PathEucDev, fill=Strategy)) +
geom_boxplot()
b1 <- b1 + labs(y="Path Deviation (m)") + scale_fill_brewer(palette =
"Pastel2") + My_Theme2

```

```

b2 <- ggplot(ldat, aes(x="Group", y=AvgTimeTravelled, fill=Strategy)) +
geom_boxplot()
b2 <- b2 + labs(y="Travel Time (s)") + scale_fill_brewer(palette =
"Pastel2") + My_Theme2

b3 <- ggplot(ldat, aes(x="Group", y=MeanFixation, fill=Strategy)) +
geom_boxplot()
b3 <- b3 + labs(y="Fixation Rate (count/s)") + scale_fill_brewer(palette
= "Pastell") + My_Theme2

b4 <- ggplot(ldat, aes(x="Group", y=SpatialMemory, fill=Strategy)) +
geom_boxplot()
b4 <- b4 + labs(y="Spatial Memory") + scale_fill_brewer(palette =
"Pastell") + My_Theme2

v1 <- ggplot(ldat, aes(x="Group", y=PathEucDev, fill=VR))
+ geom_boxplot()
v1 <- v1 + labs(y="Path Deviation (m)") + scale_fill_brewer(palette =
"Pastel2") + My_Theme2

v2 <- ggplot(ldat, aes(x="Group", y=AvgTimeTravelled, fill=VR))
+ geom_boxplot()
v2 <- v2 + labs(y="Travel Time (s)") + scale_fill_brewer(palette =
"Pastel2") + My_Theme2

v3 <- ggplot(ldat, aes(x="Group", y=MeanFixation, fill=VR))
+ geom_boxplot()
v3 <- v3 + labs(y="Fixation Rate (count/s)") + scale_fill_brewer(palette
= "Pastell") + My_Theme2

v4 <- ggplot(ldat, aes(x="Group", y=SpatialMemory, fill=VR)) +
geom_boxplot()
v4 <- v4 + labs(y="Spatial Memory") + scale_fill_brewer(palette =
"Pastell") + My_Theme2

#output
grid.arrange(b1s,b1,v1,b4s,b2,v2,b2s,b3,v3,b3s,b4,v4, ncol=2)
#pdf("output/VariablePlots/Boxplots.pdf")
#grid.arrange(b1s,b1,v1,b4s,b2,v2,b2s,b3,v3,b3s,b4,v4, ncol=2)
#dev.off()

#####Trial Line graph Figure in Results Section-----
My_Theme3 = theme(
  axis.title.x = element_text(size = 10),
  axis.text.x = element_text(size = 12),
  axis.title.y = element_text(size = 10),
  axis.text.y = element_text(size = 12))

```

```

q <- ggplot(data=tdat, aes(x=Trial, y=MmeanFixation)) +
  geom_line(linetype="solid", color="steelblue1", size=1.2)+
  geom_point() + My_Theme3 + labs(y = "Mean Fixation Rate (count/s)")
q <- q + scale_x_discrete(name="Trial",

limits=c("1","2","3","4","5","6","7","8","9","10","11","12"))
q2 <- ggplot(data=tdat, aes(x=Trial, y=MmeanPath)) +
  geom_line(linetype="solid", color="steelblue3", size=1.2)+
  geom_point() + My_Theme3 + labs(y = "Mean Path Deviation (m)")
q2 <- q2 + scale_x_discrete(name="Trial",

limits=c("1","2","3","4","5","6","7","8","9","10","11","12"))
q3 <- ggplot(data=tdat, aes(x=Trial, y=MmeanTime)) +
  geom_line(linetype="solid", color="steelblue2", size=1.2)+
  geom_point() + My_Theme3 + labs(y = "Travel Time (s)")
q3 <- q3 + scale_x_discrete(name="Trial",

limits=c("1","2","3","4","5","6","7","8","9","10","11","12"))
#output
grid.arrange(q2,q3,q,ncol = 1)
#pdf("output/VariablePlots/Line.pdf")
#grid.arrange(q2,q3,q,ncol = 1)
#dev.off()

#####Bar graphs in Results Section-----
- My_Theme = theme(
  axis.title.x = element_text(size = 16),
  axis.text.x = element_text(size = 12),
  axis.title.y = element_text(size = 16),
  axis.text.y = element_text(size = 14))

#fixation time
ldat_summary <- ldat %>% # the names of the new data frame and the data
frame to be summarised
  group_by(RouteCode) %>% # the grouping variable
  summarise(mean_PL = mean(FixationRateTime, na.rm=TRUE), #
calculates the mean of each group
            sd_PL = sd(FixationRateTime, na.rm=TRUE), # calculates
the standard deviation of each group
            n_PL = n(), # calculates the sample size per group
            SE_PL = sd(FixationRateTime, na.rm=TRUE)/sqrt(n()))
#
calculates the standard error of each group

p <- ggplot(ldat_summary, aes(RouteCode, mean_PL, fill = RouteCode)) +
  geom_col() +
  geom_errorbar(aes(ymin = mean_PL - SE_PL, ymax = mean_PL + SE_PL,
width = 0.1))

```

```

p <- p + scale_fill_brewer(palette = "Pastell1")+
  labs(y="Fixation Rate (count/s)", x = "Route Type") +
  My_Theme

#path deviation
ldat_summary <- ldat %>% # the names of the new data frame and the data
frame to be summarised
  group_by(RouteCode) %>% # the grouping variable
  summarise(mean_PL = mean(PathEucDev, na.rm=TRUE), # calculates
the
mean of each group
            sd_PL = sd(PathEucDev, na.rm=TRUE), # calculates the
standard deviation of each group
            n_PL = n(), # calculates the sample size per group
            SE_PL = sd(PathEucDev, na.rm=TRUE)/sqrt(n())) # calculates
the standard error of each group

p2 <- ggplot(ldat_summary, aes(RouteCode, mean_PL, fill = RouteCode)) +
  geom_col() +
  geom_errorbar(aes(ymin = mean_PL - SE_PL, ymax = mean_PL + SE_PL,
width = 0.1))
p2 <- p2 + scale_fill_brewer(palette = "Pastell1")+
  labs(y="Path Deviation (m)", x = "Route Type") +
  My_Theme

#time travelled
ldat_summary <- ldat %>% # the names of the new data frame and the data
frame to be summarised
  group_by(RouteCode) %>% # the grouping variable
  summarise(mean_PL = mean(TimeTravelled, na.rm=TRUE), # calculates
the
mean of each group
            sd_PL = sd(TimeTravelled, na.rm=TRUE), # calculates
the standard deviation of each group
            n_PL = n(), # calculates the sample size per
group
            SE_PL = sd(TimeTravelled,
na.rm=TRUE)/sqrt(n())) #
calculates the standard error of eachgroup

p3 <- ggplot(ldat_summary, aes(RouteCode, mean_PL, fill = RouteCode)) +
  geom_col() +
  geom_errorbar(aes(ymin = mean_PL - SE_PL, ymax = mean_PL +
SE_PL, width = 0.1))
p3 <- p3 + scale_fill_brewer(palette =
"Pastell1")+ labs(y="Time (s)", x = "Route
Type") +My_Theme

#time travelled
ldat_summary <- ldat %>% # the names of the new data frame and the data

```

```

frame to be summarised
  group_by(RouteCode) %>%      # the grouping variable
  summarise(mean_PL = mean(RouteFamiliarity, na.rm=TRUE),      #
calculates the mean of each group
          sd_PL = sd(RouteFamiliarity, na.rm=TRUE), # calculates the
standard deviation of each group
          n_PL = n(), # calculates the sample size per group
          SE_PL = sd(RouteFamiliarity, na.rm=TRUE)/sqrt(n()))
#
calculates the standard error of each group

p4 <- ggplot(ldat_summary, aes(RouteCode, mean_PL, fill = RouteCode)) +
  geom_col() +
  geom_errorbar(aes(ymin = mean_PL - SE_PL, ymax = mean_PL + SE_PL,
width = 0.1))
p4 <- p4 + scale_fill_brewer(palette = "Pastell")+
  labs(y="Pair Recognition Score", x = "Route Type") + My_Theme

#output
grid.arrange(p,p2,p3,p4,ncol = 2)
#pdf("output/VariablePlots/Bargraphs.pdf")
#grid.arrange(p,p2,p3,p4,ncol = 2)
#dev.off()

#####Graph of individual performance in Results
Section-----
#pdf("output/VariablePlots/lineIDgraphs.pdf")
#plotting path deviation for individuals over trial
ggplot(data = ldat, aes(x = Trial, y = PathEucDev, group = ID, color=ID,
alpha=0.8)) +
  ggtitle("Variation in Path Deviation for individuals") +
  geom_line() +
  xlab("Trial Number") +
  ylab("Path Deviation (m)") + ylim(-100,2000) +
  scale_x_continuous(breaks=seq(1,12,by=1))

#plotting time travelled for individuals over trial
ggplot(data = ldat, aes(x = Trial, y = TimeTravelled, group = ID,
color=ID, alpha=0.8)) +
  ggtitle("Variation in Time travelled for individuals") +
  geom_line() +
  xlab("Trial Number") +
  ylab("Travel Time (s)") + ylim(-5,400) +
  scale_x_continuous(breaks=seq(1,12,by=1))

#plotting fixation rate for individuals over trial
ggplot(data = ldat, aes(x = Trial, y = TimeTravelled, group = ID,
color=ID, alpha=0.8)) +
  ggtitle("Variation in Fixation rate for individuals") +

```

```

geom_line() +
  xlab("Trial Number") +
  ylab("Fixation Rate (count/s)") + ylim(-5,400) +
  scale_x_continuous(breaks=seq(1,12,by=1))
#dev.off()

#####Regression Model Assumptions-----
#outcome1: path deviation
#pdf("output/Regression/Path/PathDx.pdf")
plot(modRC)
hist(modRC$residuals)
qqnorm(modRC)
plot_model(modRC, type='diag')
#dev.off()

#outcome2: travel time
#pdf("output/Regression/Time/TimeDx.pdf")
plot(modRC2)
qqnorm(modRC2)
hist(modRC2$residuals)
plot_model(modRC2, type='diag')
#dev.off()

#####Outcome1: Path Deviation MLM Model Graphs-----
#pdf("output/Regression/Path/Latticeplots.pdf")
xyplot(PathEucDev ~ FixationRateTime | ID, data=ldat, type = c("p","r"))
xyplot(PathEucDev ~ FixationRateTime | RouteCode, data=ldat, type =
c("p","r"))
xyplot(PathEucDev ~ SMIndex | RouteCode, data=ldat, type = c("p","r"))
#dev.off()

# The following graphs were created using the scripts made available
here:
# https://quantdev.ssri.psu.edu/tutorials/growth-modeling-basics

#plotting PREDICTED intraindividual change
ldat$pred_um <- predict(um_fit)
ldat$resid_um <- residuals(um_fit)

c1 <- coeffs(um_fit)

pg1 <- ggplot(data = ldat, aes(x = Trial, y = pred_um, group = IDN)) +
  ggtitle("Outcome 1. Unconditional Means Model 1") +
  geom_line(size=0.5) +
  theme(axis.text=element_text(size=12),
        axis.title=element_text(size=12)) +
  xlab("Trial") +
  ylab("PREDICTED Path Deviation") + ylim(0,1000) +

```

```

scale_x_continuous(breaks=seq(1,12,by=1))

#plotting RESIDUAL intraindividual change-----
ggplot(data = ldat, aes(x = Trial, y = resid_um, group = ID)) +
  ggtitle("Outcome 1. Unconditional Means Model") +
  # geom_point() +
  theme(axis.text=element_text(size=12),
        axis.title=element_text(size=12)) +
  geom_line() +
  xlab("Trial") +
  ylab("RESIDUAL Path Deviation")
  scale_x_continuous(breaks=seq(1,12,by=1))

#overlay PROTOTYPE (average individual)-----
#create the function for the prototype
fun_um <- function(x) {
  c1 + 0*x
}
#add the prototype as an additional layer
pg2 <- ggplot(data = ldat, aes(x = Trial, y = pred_um, group = ID)) +
  ggtitle("Outcome 1. Unconditional Means Model") +
  # geom_point() +
  theme(axis.text=element_text(size=12),
        axis.title=element_text(size=12)) +
  geom_line() +
  xlab("Trial") +
  ylab("PREDICTED Path Deviation") + ylim(100,1000) +
  scale_x_continuous(breaks=seq(1,12,by=1)) +
  stat_function(fun=fun_um, color="red", size = 1)

#Linear Growth Model - Fixed slope-----
summary(fl_ri_fit)
c2 <- coeffs(fl_ri_fit)[c(0,1)]
c2b <- coeffs(fl_ri_fit)[c(2,0)]
#Place individual predictions and residuals into the dataframe
ldat$pred_fl_ri <- predict(fl_ri_fit)
ldat$resid_fl_ri <- residuals(fl_ri_fit)
#Create a function for the prototype
fun_fl_ri <- function(x) {c2 + c2b*x}

```

```

#plotting PREDICTED intraindividual change
pg3 <- ggplot(data = ldat, aes(x = Trial, y = pred_fl_ri, group = ID)) +
  ggtitle("Linear Growth Fixed Slope") +
  theme(axis.text=element_text(size=12),
        axis.title=element_text(size=12)) +
  # geom_point() +
  geom_line() +
  xlab("Trial") +
  ylab("PREDICTED Path Deviation") + ylim(-100,1000) +
  scale_x_continuous(breaks=seq(1,12,by=1)) +
  stat_function(fun=fun_fl_ri, color="red", size = 1)

#plotting RESIDUAL intraindividual change
pg4 <- ggplot(data = ldat, aes(x = Trial, y = resid_fl_ri, group = ID))
+
  ggtitle("Linear Growth Residual Fixed Slope") +
  theme(axis.text=element_text(size=12),
        axis.title=element_text(size=12)) +
  # geom_point() +
  geom_line() +
  xlab("Trial") +
  ylab("RESIDUAL Path Deviation") + #ylim(0,100) + Note the removal of
limits on y-axis
  scale_x_continuous(breaks=seq(1,12,by=1))

#Place individual predictions and residuals into the dataframe
ldat$pred_fl_rl <- predict(fl_rl_fit)
ldat$resid_fl_rl <- residuals(fl_rl_fit)
c3 <- coeffs(fl_rl_fit)[c(0,1)]
c3b <- coeffs(fl_rl_fit)[c(2,0)]
#Create a function for the prototype
fun_fl_rl <- function(x) {
  c3 + c3b*x
}

#plotting PREDICTED intraindividual change
pg5 <- ggplot(data = ldat, aes(x = Trial, y = pred_fl_rl, group = ID)) +
  ggtitle("Linear Growth Random Slope") +
  theme(axis.text=element_text(size=12),
        axis.title=element_text(size=12)) +
  # geom_point() +
  geom_line() +
  xlab("Trial") +
  ylab("PREDICTED Distance Deviation") + ylim(-500,1000) +
  scale_x_continuous(breaks=seq(1,12,by=1)) +
  stat_function(fun=fun_fl_rl, color="red", size = 1)

```

```

#plotting RESIDUAL intraindividual change
ggplot(data = ldat, aes(x = Trial, y = resid_fl_rl, group = ID)) +
ggtitle("Outcome 1. Random Slope") +
theme(axis.text=element_text(size=12), axis.title=element_text(size=12))
+
  # geom_point() +
  geom_line() +
  xlab("Trial") +
  ylab("RESIDUAL Distance Deviation") + #ylim(0,100) + Note the removal
of limits on y-axis
  scale_x_continuous(breaks=seq(1,12,by=1))

grid.arrange(pg2,pg3,pg4,pg5, ncol=2)
pdf("output/Regression/Path/MLMplots.pdf")
grid.arrange(pg2,pg3,pg4,pg5, ncol=2)
dev.off()

#####Outcome2: Travel Time MLM Model Graphs-----
#pdf("output/Regression/Time/Latticeplots.pdf")
xyplot(TimeTravelled ~ FixationRateTime| ID, data=ldat, type =
c("p","r"))
xyplot(TimeTravelled ~ FixationRateTime| RouteCode, data=ldat, type =
c("p","r"))
xyplot(TimeTravelled ~ SMIndex| RouteCode, data=ldat, type = c("p","r"))
#dev.off()

#plotting PREDICTED intraindividual change
ldat$pred_um2 <- predict(um_fit2)
ldat$resid_um2 <- residuals(um_fit2)
c12 <- coeffs(um_fit2)

pg12 <- ggplot(data = ldat, aes(x = Trial, y = pred_um2, group = IDN)) +
  ggtitle("Outcome 2. Unconditional Means Model") +
  geom_line(size=0.5) +
  theme(axis.text=element_text(size=10),
        axis.title=element_text(size=10)) +
  xlab("Trial") +
  ylab("PREDICTED Time") + ylim(0,250) +
  scale_x_continuous(breaks=seq(1,12,by=1))

#plotting RESIDUAL intraindividual change-----
ggplot(data = ldat, aes(x = Trial, y = resid_um2, group = ID)) +
  ggtitle("Outcome 2. Unconditional Means Model") +
  # geom_point() +
  theme(axis.text=element_text(size=10),
        axis.title=element_text(size=10)) +
  geom_line() +
  xlab("Trial") +
  ylab("RESIDUAL Time")

```

```

scale_x_continuous(breaks=seq(1,12,by=1))

#overlay PROTOTYPE (average individual)-----
#create the function for the prototype
fun_um2 <- function(x) {
  c12 + 0*x
}
#add the prototype as an additional layer
pg22 <- ggplot(data = ldat, aes(x = Trial, y = pred_um2, group = ID)) +
  ggtitle("Outcome 2. Unconditional Means Model") +
  # geom_point() +
  theme(axis.text=element_text(size=10),
        axis.title=element_text(size=10)) +
  geom_line() +
  xlab("Trial") +
  ylab("PREDICTED Time") + ylim(0,100) +
  scale_x_continuous(breaks=seq(1,12,by=1)) +
  stat_function(fun=fun_um2, color="red", size = 2)

#Linear Growth Model - Fixed slope-----
summary(fl_ri_fit2)
c22 <- coeffs(fl_ri_fit2)[c(0,1)]
c2b2 <- coeffs(fl_ri_fit2)[c(2,0)]
#Place individual predictions and residuals into the dataframe
ldat$pred_fl_ri2 <- predict(fl_ri_fit2)
ldat$resid_fl_ri2 <- residuals(fl_ri_fit2)
#Create a function for the prototype
fun_fl_ri2 <- function(x) {
  c22 + c2b2*x
}

#plotting PREDICTED intraindividual change
pg32 <- ggplot(data = ldat, aes(x = Trial, y = pred_fl_ri2, group = ID))
+
  ggtitle("Linear Growth Fixed Slope") +
  theme(axis.text=element_text(size=10),
        axis.title=element_text(size=10)) +
  # geom_point() +
  geom_line() +
  xlab("Trial") +
  ylab("PREDICTED Time") + ylim(-100,250) +
  scale_x_continuous(breaks=seq(1,12,by=1)) +
  stat_function(fun=fun_fl_ri2, color="red", size = 2)

#plotting RESIDUAL intraindividual change
pg42 <- ggplot(data = ldat, aes(x = Trial, y = resid_fl_ri2, group =
ID)) +
  ggtitle("Linear Growth Residual Fixed Slope") +
  theme(axis.text=element_text(size=10),

```

```

      axis.title=element_text(size=10)) +
# geom_point() +
geom_line() +
xlab("Trial") +
ylab("RESIDUAL Time") +
scale_x_continuous(breaks=seq(1,12,by=1))

#Place individual predictions and residuals into the dataframe
ldat$pred_fl_rl2 <- predict(fl_rl_fit2)
ldat$resid_fl_rl2 <- residuals(fl_rl_fit2)
c32 <- coeffs(fl_rl_fit2)[c(0,1)]
c3b2 <- coeffs(fl_rl_fit2)[c(2,0)]
#Create a function for the prototype
fun_fl_rl2 <- function(x) {
  c32 + c3b2*x
}

#plotting PREDICTED intraindividual change
pg52 <- ggplot(data = ldat, aes(x = Trial, y = pred_fl_rl2, group = ID))
+
  ggtitle("Linear Growth Random Slope") +
  theme(axis.text=element_text(size=10),
        axis.title=element_text(size=10)) +
  # geom_point() +
  geom_line() +
  xlab("Trial") +
  ylab("PREDICTED Time") + ylim(0,250) +
  scale_x_continuous(breaks=seq(1,12,by=1)) +
  stat_function(fun=fun_fl_rl2, color="red", size =1)

#plotting RESIDUAL intraindividual change
ggplot(data = ldat, aes(x = Trial, y = resid_fl_rl2, group = ID)) +
  ggtitle("Outcome 2. Random Slope") +
  theme(axis.text=element_text(size=10),
        axis.title=element_text(size=10)) +
  # geom_point() +
  geom_line() +
  xlab("Trial") +
  ylab("RESIDUAL Path") + #ylim(0,100) + Note the removal of limits on
y-axis
  scale_x_continuous(breaks=seq(1,12,by=1))

grid.arrange(pg22,pg32,pg42,pg52, ncol=2)
#pdf("output/Regression/Time/MLMplots.pdf")
#grid.arrange(pg22,pg32,pg42,pg52, ncol=2)
#dev.off()

```

```
#####
library(MASS)
#Create a custom color scale
library(RColorBrewer)
myColors <- brewer.pal(4,"Paired")
names(myColors) <- levels(ldat$Strategy)
colScale <- scale_colour_manual(name = "Strategy",values = myColors)

#####

scatter <- ggplot(ldat, aes(FixationRateTime,PathEucDev, colour =
Strategy, alpha = 0.1))
scatter <- scatter + geom_point(aes(shape = Strategy), position =
"jitter", size = 2) +
  geom_smooth(method = "rlm",aes(Strategy = "Blue"), alpha = 0.1) +
scale_alpha(guide = 'none') + colScale

scatter + labs(x = "Fixation Rate (count/s)", y = "Path Deviation (m)")
+ scale_x_continuous(limits = c(0, 20)) +
  scale_y_continuous(limits = c(0, 200))
s1 <- scatter + labs(x = "Fixation Rate (count/s)", y = "Path Deviation
(m)") + scale_x_continuous(limits = c(0, 20)) +
scale_y_continuous(limits = c(0, 200))
ggsave("scatterPathFixation.png")

scatter <- ggplot(ldat, aes(SpatialMemory,PathEucDev, colour = Strategy,
alpha = 0.1))
scatter <- scatter + geom_point(aes(shape = Strategy), position =
"jitter", size = 2) +
  geom_smooth(method = "rlm",aes(Strategy = "Blue"), alpha = 0.1) +
scale_alpha(guide = 'none') + colScale
scatter + labs(x = "Spatial Memory (a.u)", y = "Path Deviation (m)")
s2 <- scatter + labs(x = "Spatial Memory (a.u)", y = "Path Deviation
(m)")
ggsave("scatterPathMemory.png")

#####
scatter <- ggplot(ldat, aes(FixationRateTime,TimeTravelled, colour =
Strategy, alpha = 0.1))
scatter <- scatter + geom_point(aes(shape = Strategy), position =
"jitter", size = 2) +
  geom_smooth(method = "rlm",aes(Strategy = "Blue"), alpha = 0.1) +
scale_alpha(guide = 'none') + colScale
scatter + labs(x = "Fixation Rate (count/s)", y = "Travel Time (s)") +
scale_x_continuous(limits = c(0, 20)) +
  scale_y_continuous(limits = c(0, 200))
s3 <- scatter + labs(x = "Fixation Rate (count/s)", y = "Travel Time
```

```

(s)") + scale_x_continuous(limits = c(0, 20)) +
scale_y_continuous(limits = c(0, 200))
ggsave("scatterTimeFixation.png")

scatter <- ggplot(ldat, aes(SpatialMemory,TimeTravelled, colour =
Strategy, alpha = 0.1))
scatter <- scatter + geom_point(aes(shape = Strategy), position =
"jitter", size = 2) +
  geom_smooth(method = "rlm",aes(Strategy = "Blue"), alpha = 0.1) +
scale_alpha(guide = 'none') + colScale
scatter + labs(x = "Spatial Memory (a.u)", y = "Path Deviation (m)")
s4 <- scatter + labs(x = "Spatial Memory (a.u)", y = "Travel Time (s)")
ggsave("scatterTimeMemory.png")

grid.arrange(s2,s4, ncol=2)
grid.arrange(s1,s3, ncol=2)

grid.arrange(s1,s2,s3,s4, ncol=2)
ggsave("scatterx4.png")

#####
scatter <- ggplot(ldat, aes(fittedmlm1,PathEucDev, colour = Strategy,
alpha =0.1))
scatter <- scatter + geom_point(aes(shape = Strategy), position =
"jitter", size = 2) +
  geom_smooth(method = "rlm",aes(Strategy = "Blue"), alpha = 0.1) +
scale_alpha(guide = 'none') + colScale
scatter + labs(x = "Predicted Values", y = "Path Deviation (m)")
s5 <- scatter + labs(x = "Predicted Values", y = "Path Deviation (m) ")
+ scale_x_continuous(limits = c(250, 600)) +scale_y_continuous(limits
= c(0, 2000))
s5
ggsave("scatterFittedPath.png")

scatter <- ggplot(ldat, aes(fittedmlm2,TimeTravelled, colour = Strategy,
alpha = 0.1))
scatter <- scatter + geom_point(aes(shape = Strategy), position =
"jitter", size = 2) +
  geom_smooth(method = "rlm",aes(Strategy = "Blue"), alpha = 0.1) +
scale_alpha(guide = 'none') + colScale
scatter + labs(x = "Predicted Values", y = "Time Travelled (s)")
s6 <- scatter + labs(x = "Predicted Values", y = "Time Travelled (s) ")
+ scale_x_continuous(limits = c(0, 80)) +scale_y_continuous(limits =
c(0,200))
s6
ggsave("scatterFittedTime.png")

grid.arrange(s5,s6, ncol=2)

```

```
#####
scatter <- ggplot(ldat, aes(SpatialMemory,FixationRateTime, colour =
"Blue", alpha = 0.5))
scatter <- scatter + geom_point(aes(), position = "jitter", size = 2) +
  geom_smooth(method = "rlm",aes(), alpha = 0.1) + scale_alpha(guide =
'none') + colScale
scatter + labs(x = "Spatial Memory", y = "Fixation Rate")
s7 <- scatter + labs(x = "Spatial Memory (a.u)", y = "Fixation Rate
(count/s)") + scale_x_continuous(limits = c(0, 1)) +
scale_y_continuous(limits = c(0,15))
s7
ggsave("scatterMemTime.png")
```

```
#####
```

```
# Change line color and fill color
ggplot(ldat, aes(x=TrialSuccess))+
  geom_histogram(color="darkblue", fill="lightblue")
```

```
ldat$TrialSuccess <- factor(ldat$TrialSuccess, levels = c(0,1),
labels = c("fail", "success"))
```

```
bp <- ggplot(data
= ldat, aes(x = TrialSuccess, y = ..prop.., group = 2,
alpha =0.1, size = 2)) +
  geom_bar( fill = "lightblue") +
  xlab("Navigation Outcome") +
  ylab("Relative Frequency")
bp
```

```
#####
```

```
mindat2 <- subset(ldat, subset =
(Trial > 5))
```

```
mindat1 <- subset(ldat, subset =
(Trial < 5.5))
```

```
table(mindat1$TrialSuccess)
table(mindat2$TrialSuccess)
```

```
bp1 <- ggplot(data
= mindat1, aes(x = TrialSuccess, y = ..prop.., group = 2,
alpha =0.1, size = 2)) +
  geom_bar( fill = "lightblue") +
  xlab("Navigation Outcome") +
```

```

  ylab("Relative Frequency")
bp1

bp2 <- ggplot(data
              = mindat2, aes(x = TrialSuccess, y = ..prop.., group = 2,
alpha =0.1, size = 2)) +
  geom_bar( fill = "dodgerblue3") +
  xlab("Navigation Outcome")      +
  ylab("Relative Frequency")
bp2

#####

t1 <- cbind(mindat1$TrialSuccess,mindat2$TrialSuccess) t1
<- table(t1)
chisq.test(t1)

```