VR for Cognition and Memory



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Abstract This chapter will provide a review of research into human cognition through the lens of VR-based paradigms for studying memory. Emphasis is placed on why VR increases the ecological validity of memory research and the implications of such enhancements.

Keywords Virtual reality · Cognition · Memory · Cognitive enhancement · Memory enhancement · Cognitive assessments · Memory assessments · Cognitive rehabilitation · Memory rehabilitation · Embodied cognition · Embodied memory · Extended cognition · Extended memory · Environmental enrichment

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1 Introduction

As the scientific community strives to understand the inner workings and neural correlates supporting cognition, it is of paramount importance that it be studied as naturalistically as possible. Otherwise, findings may not extend to real-world settings. Additionally, if studied outside a holistic perspective, researchers run the risk of deeming sets of findings as incongruent with the scientific corpus when they may indeed be complementary. Readers may find this concept reminiscent of the parable of the blind men and an elephant: since each man only felt one part of the elephant, each was quick to doubt the others when their reports were not congruent. Just as it would be erroneous to say an elephant *is* the way its tusk feels, it would be wrong to conclude about the real-world (RW) nature of cognition based on tests conducted in a sterile laboratory environment. To increase their generalizability to the RW (i.e., veridicality), studies of cognition should be conducted in verisimilar contexts (i.e., contexts appearing as the RW). Such frameworks inherently beget ecological validity.

To study cognition holistically means investigating interconnections between its rich repertoire of functions, including attention, reasoning, language, and memory. Memory is a particularly crucial facet, as it supports and subserves all other aspects of cognition; no cognitive task can be accomplished without memory. We cannot even conceive of the framing and timeline of our own experiences (i.e., autonoetic consciousness) without memory. As such, rigorous investigations of memory can serve as a fulcrum for understanding cognition, akin to equipping one of the blind men with extra limbs.

Fortunately, investigations of memory are arguably most ecologically valid if tobe-remembered information is situated in a spatial context – something virtual environments (VEs) can readily provide. Brain systems supporting memory are responsible for helping from the mental representations used to acquire, code, store, recall, and decode information about the relative locations and attributes of phenomena in everyday and metaphorical spatial environments (Tolman 1948). Such representations of an individual's personal knowledge for guiding behavior have been aptly named "cognitive maps" (O'Keefe and Nadel 1978). Since memory for personally experienced events is always backdropped by a spatio-temporal context (Tulving 1983), VEs serve as a ripe medium with which to present cognitive tasks. Indeed, the environmental customization afforded by VR makes it an ideal tool for studying cognition in an ecologically valid fashion. Through the lens of memory studies, this chapter aims to showcase the ways in which VR has advanced a meaningful and applicable understanding of cognition.

2 Enhancing the Ecological Validity of Memory Research with VR

There exist inherent limitations to generalizing laboratory findings, ripe with deliberate memorization tasks, to the processes normally occurring in people's everyday lives (Parsons 2015). VR offers a powerful means to enhance the ecological validity of memory research by providing realistic VEs in which participants can encode and retrieve information under naturalistic circumstances (Reggente et al. 2018). By utilizing stimuli and paradigms that echo RW demands, VR memory studies stand to more accurately capture the requisite insight to construct holistically grounded neurocognitive models of memory – a necessary first step in developing useful neuropsychological assessments. Given that the Diagnostic and Statistical Manual of Mental Disorders often list "interference with everyday activities" as criteria for diagnosing memory disorders, it follows that ecologically valid neuropsychology should leverage assessments that approximate real-world experiences.

The importance of prioritizing ecological validity goes beyond unveiling the true nature of how healthy and aberrant brains process memories. For example, only ecologically valid memory research can reveal robust and quantifiable signatures of retrieval that can be informative in a criminal justice context. In a recent study, for instance, after committing an RW mock crime, participants were shown laser-scanned, photorealistic models of the crime scene and objects via VR or as 2D images. Detection of concealed recognition was 25% more accurate in the VR condition (Norman et al. 2020), suggesting that VR may enhance stimulus recognition and salience so much that it prevents a criminal's capacity for concealment.

Investigations into validating VR-based tests of memory by comparing outcome distributions with traditional tests have yielded mixed results (Parsons and Rizzo 2008). Such inconsistencies do not necessarily indicate that VR is an unreliable medium for benchmarking traditional memory tests. On the contrary, these outcomes could be an indication that traditional tests are less reliable. Indeed, traditional tests do not typically predict RW behavior (Schultheis et al. 2002), whereas performance on VR tasks correlates with self-reports (Plancher et al. 2012; van der Ham et al. 2010) and observer assessments (Allain et al. 2014) of memory function in daily life. While corroboration with RW reports and studies may indeed be the gold standard when authenticating memory metrics captured by VR, it is also useful to investigate the features of VR that have a relationship with the neural underpinnings of memory.

2.1 Primacy of Space and Context

Both philosophers and psychologists alike postulate that brains have evolved solely to support purposeful and predictable movement (Dennett 1993; Llinas 2002). Glenberg and Hayes (2016) posit that the ontogeny of episodic memory relates to the onset of locomotion during infancy that scales with Hippocampal (Hipp.)

development (which also provides a mechanism for infantile amnesia and age-related episodic memory loss). One source of evidence to support this proposition is in the life cycle of the bluebell tunicate. This filter feeder begins to digest a substantial chunk of its cerebral ganglion once identifying a suitable undersea perch to spend the rest of its existence. This phenomenon suggests that once it has served its purpose as a neural network supporting movement, the cerebral ganglion yields greater utility to the organism as nutrition (Mackie and Burighel 2005). From chemotaxis to cognitive maps, a representation of space is necessary for meaningful movement (Llinas 2002). A neural instantiation of a map that provides spatial bookmarks of an organism's experiences, demarcating the locations of nutrition and enemies within an environment, is a fundamental component of brains (O'Keefe and Nadel 1978).

Indeed, there is a primacy of spatial content in the neural representation of events (Robin et al. 2018). Spatial information is often recalled earliest in the retrieval process (Hebscher et al. 2017), and the degree to which individuals report confidence in their autobiographical memories is predicted by their knowledge of the spatial layout of the setting in which the memory occurred (Rubin et al. 2003). The Method of Loci (a.k.a. Memory Palace) mnemonic has long been appreciated for its ability to increase memory by imagining to-be-remembered information placed at familiar locations. Reggente et al. (2020) used a VR implantation of this technique to suggest that the principal component behind mnemonic efficacy is the explicit binding of the objects to a spatial location and revealed a tight relationship between spatial memory (SM) and free recall of encoded objects. These observations showcase that space and memory are inextricably linked at conceptual and neuronal levels – a notion that has become entrenched in popular culture; the phrase "out of space" is often used when indicating a computer's memory is full.

2.1.1 Context Dependence

If space is the inescapable wallpaper that serves as the backdrop for all experience, then it follows that as our spatial or environmental context changes, so should the neural activity underlying diverse cognitive processes (Lester et al. 2017; Willems and Peelen 2021). Early research on learning and memory focused on ways in which encoding and retrieval contexts impacted memory. For example, in a seminal RW study, underwater and dry-land environments were used to reveal that similarity between encoding and retrieval contexts yielded the best memory – a phenomenon referred to as contextual reinstatement (Godden and Baddeley 1975). VR has provided an opportunity to study such effects with a much wider, rapidly accessible (teleportation), and safer contextual repertoire. Parker et al. (2020) used photorealistic underwater and grassy field VEs to effectively replicate the effects seen by RW Godden and Baddeley (1975). Shin et al. (2021) elaborated on the effect by showing that items deemed to be of high utility within each environment were remembered even more effectively, suggesting that context-dependent memory effects may depend on items being integrated into an active schema.

As VEs become more distinct from one another, so do the neural correlates representing them. This allows for single-context-specific information to be recalled without interference from information encoded in other VEs. During recall, the reinstatement of VE-specific brain activity patterns can act as proxy for the degree to which contextual information was bound to learned information. Essoe et al. (2022) showed that the fidelity of contextual reinstatement during recall (as measured by comparing BOLD activity patterns during recall to those collected when participants were instructed to mentally imagine themselves in the VE) was associated with improved recall performance. Conversely, spatial memory is impacted when Hipp. neural codes are representative of competing environments instead of the current environment (Kyle et al. 2015).

Visual context fidelity also moderates spatial information. If a previously encoded VE is perceptually impoverished by removing landmarks and making the walls and ground uniform, efficiency and accuracy of route retrieval decrease (Rauchs et al. 2008a). Moreover, perceptual elements are not the only modulators of context's impact on memory. Brown et al. (2010) found that successful navigation through virtual mazes that had discrete starting and ending locations but overlapping hall-ways (i.e., spatial disambiguation) required the retrieval of contextual information relevant to the current navigational episode (i.e., where the subject started the current trial).

Given that internal and environmental cues become bound to learnt information (S. M. Smith 1988), cues presented during both learning and recall facilitate recall – a phenomenon known as contextual support. Meaningfully leveraging contextual support for learning in the RW is difficult since only so much information can be contextually encoded within a single environment and regularly visiting multiple environments can be prohibitive for many learners. Furthermore, change-induced forgetting can also occur when recall fails due to a context change – a phenomenon that is only partially mitigated with mental reinstatement to the learning environment (S. M. Smith 1979). VR's ability to expose users to new contexts positions it as an ideal platform for utilizing contextual support during learning. However, VR researchers must carefully balance the benefit it affords by creating a scaffolding of context for the rich encoding of material with the potential drawback of change-induced forgetting when an individual exits the VE.

2.2 Impact of Immersion and Presence

Immersion is the sense of "being there" in an environment (Steuer 1992). Immersion can be subdivided into engagement and presence (the experience of being in one place while physically situated in another) and captured by questionnaires (Fox et al. 2009; Slater et al. 1994). Immersiveness of an environment is determined by objective characteristics of the VR system (e.g., field of view (FOV), multimodal sensory information, headset type; see Reggente et al. (2018); S. A. Smith (2019)), whereas presence refers to the subjective response to immersion, as if feeling

"transported" to the VE. Presence can be increased with interaction, volition, and actions that suspend the disbelief that one is in a digital setting (Dede 2009).

Attempts to mimic RW perception in VR have narrowed in on which facets of sensory experience impact memory. For instance, providing an illusory sense of depth with stereoscopy does not appear to impact memory (S. A. Smith 2019). However, a greater VR FOV does seem to enhance procedure memorization when tested both in a VE and the RW (Ragan et al. 2010). Notably, the impact of FOV on memory is not exclusive to VR – Mania et al. (2003) showed equal memory across groups where subjects either encoded in VR or the RW while wearing custom-made goggles designed to match their FOV with the VR.

Incorporating tactile, olfactory, and/or locomotive cues into what is typically a visually dominant VR experience can help mirror RW experience and bolster memory. For example, 360 VR that allowed subjects to place their hands on RW bicycle handlebars vs. simply watching 2D videos of a motorcycle ride almost doubled recognition scores (Schöne et al. 2019). Triggering RW fans to blow when encountering virtual ones or emitting coffee scents when near virtual pots has improved recall performance (Dinh et al. 1999; Tortell et al. 2007). Given the importance of idiothetic signals in bolstering a sense of presence (Taube et al. 2013), increasing ambulatory movement, even by using tricks like foot pedals in Parkinson's disease studies (Matar et al. 2019), should help to increase immersion (Topalovic et al. 2020). Indeed, using an omnidirectional treadmill and Head Mounted Display (HMD) while learning to navigate a virtual rendition of a campus building can increase RW navigation performance (Hejtmanek et al. 2020) compared to using joystick/mouse/keyboard controls. However, SM performance (specifically judgments of relative direction) in VR did not benefit from the concurrent use of a treadmill and HMD while also increasing motion sickness compared to simply using a joystick and monitor (Huffman and Ekstrom 2019, 2021).

Immersion can also impact neural response profiles. Simple environments that do not foster immersion can permit for memory performance that depends more so on stimulus-response associations (and non-Hipp. processes), whereas highly immersive environments can encourage spatial associations (and thus Hipp. recruitment) (Burgess et al. 2002). For instance, in a simple maze with few distinctive landmarks, an individual may remember to turn left at the first intersection, right at the second intersection, and so on. In contrast, in a complex and highly immersive maze with many distinctive landmarks, an individual might remember that the exit is behind the statue, which is located to the right of the pond, and use this spatial information to form a cognitive map of the maze and navigate to the exit, without relying on a specific series of turns or stimulus-response associations. Indeed, fully immersive 3D VR has been shown to induce a higher sense of presence, enhance success rate of spatial navigation, and increase midline EEG theta during encoding compared to 2D (Slobounov et al. 2015). Increased presence also yields a greater recruitment of regions associated with attention (Kober and Neuper 2012), whereas the cerebellum is more active when immersion is low, suggestive of more reflexive processing and less higher order cognition (Gomez et al. 2014; Hartley et al. 2003). On the other hand, participants recognized more environment-consistent items and showed more confidence in their recognition in quick visits to RW environments compared to VE replicas (Flannery and Walles 2003), suggesting that brief exposures to VEs may not induce immersion necessary to overcome the baseline advantage of RW encoding. Waller et al. (1998) made a similar claim following their observation that short periods of VE training were not more effective than map training when solving a maze in the RW. However, they also found that sufficient exposure to VEs eventually surpassed RW training.

In addition to the impact of exposure duration, somatic cues also influence the efficacy of VR in tasks that involve memory. For instance, memory for dance sequences does not seem to be impacted by whether instruction was delivered via immersive VR or nonimmersive videos (LaFortune and Macuga 2018), suggesting that motor learning may already be maximally attuned to observing bodily movement. Likewise, when tested on map drawing and a computer pointing task, participants that did route-learning in the RW outperformed those that learned the same routes in a VE. However, there was no difference in landmark recognition, estimation of route distance, or object locations (van der Ham et al. 2015), suggesting that VEs reasonably approximate a majority of important SM components – a gap that could be lessened with the insertion of body-based locomotion cues (e.g., with a virtual treadmill).

Finally, context-dependent memory effects have also been linked to immersion in VR-based studies. Participants tasked with learning overlapping sets of words in two foreign languages across two VEs performed better when each language was learned in its own context relative to those who learned both languages in the same context – however, this advantage was only apparent in participants reporting high presence in the VEs (Essoe et al. 2022). The sense of "being there" during an experience directly translates to the recruitment of neuronal populations that have the dual purpose of representing an individual's discrete location in space and encoding memories. Indeed, when participants recall information that was originally encoded in VEs, their performance is associated with the degree to which fMRI patterns of brain activity that represent the VE are reinstated (Essoe et al. 2022). Additionally, this study showed that if there were higher representational similarities between trials when participants imagined themselves in a particular VE and the recall periods for information that was encoded in that VE, participants had improved recall performance. Relatedly, Miller et al. (2013) showed that when retrieving information that was encoded in a VE by driving in a virtual city, the place cells that fired at specific locations during encoding were also activated during recall of the item associated with that location. Such an observation is inherently contingent on the elicitation of a sense of embodiment in the individual.

2.3 Impact of Embodiment, Enactment, and Extension

2.3.1 Embodied Cognition

A twenty-first century shift within the cognitive sciences has caused researchers to focus increasing attention on the role of embodied representations as the foundation of cognition. In this view, our cognitive abilities are fundamentally grounded in our capacities for purposeful perception and action. Further, all cognition is inherently situated (Foglia and Wilson 2013). Indeed, all sensory organs are situated in discrete locations on the body and provide a grounding perspective (e.g., sight is only toward the front of the body) that inevitably tags every experience with a sensorimotor component (Varela et al. 1992; Wilson 2002). Given that VR permits for egocentric points of view coupled with volitional movement, it contains the crucial ingredients for the embodiment recipe (Repetto et al. 2016).

In keeping with the idea that many aspects of higher order human cognition, such as long-term memory functions, are fundamentally linked to sensorimotor experience, it has been demonstrated that signals produced by self-motion cues (i.e., idiothetic signals) affect encoding fidelity; subjects encode objects and their position better if they move around a table vs. the table moving (Frances Wang and Simons 1999) – a finding that was extended to improving reaction time (RT) in VR even with only simulated movement (Christou and Bülthoff 1999). Participants who use an HMD and physically walked through a VE made 38% fewer errors than those who physically turned, but moved using a joystick (Ruddle et al. 2011).

Further, active locomotion in VEs, compared to stationary periods, enhances directional sensitivity in the entorhinal and retrosplenial cortices and boosts SM (Nau et al. 2020). Similarly, active navigation enriches SM (Brooks 1999b), source memory (Sauzéon et al. 2016), object recognition (Hahm et al. 2007) compared to passive tours and yields enhanced recall of central and allocentric spatial information as well as binding (Plancher et al. 2012). Even merely watching an experimenter actively search a VE was more effective for learning target locations compared to participants observing the environment from a fixed position (Thomas et al. 2001). Scene recognition, however, does not seem to differ as a function of active vs. passive encoding in VR (Gaunet et al. 2001). The effect of action is present in non-visual modalities as well. Audio-VR provides iconic and spatialized sound cue updates with each step, allowing for an update of heading direction and place in the actual RW environment. Such setups have been used to train blind participants to navigate toward (away from) rewards (predators) in VEs, revealing that ludic (i.e., undirected and playful) exploration yield better shortcut-finding performance than guided tours when tested in an RW analog of the VE they were trained in (Connors et al. 2014). Decision making seems to be the primary component for the acquisitions of topological graph knowledge, whereas idiothetic information is crucial for metric survey knowledge (Chrastil and Warren 2015).

Bréchet et al. (2020) showed that the presence of self-related bodily cues (e.g., virtual hands and legs appearing in the VE when the participant moves their RW

counterparts) increases object recognition compared to when these cues are absent. Amazingly, recognition of objects in a scene that was originally encoded without self-related bodily cues was retroactively enhanced by subsequent visits to the same scene where self-related bodily cues were present. It appears the degree to which these virtual renditions of the body have RW fidelity have substantial ramifications. VR manipulation of experienced self-location relative to one's real body (e.g., using the output of a camera placed behind a participant as the input to their HMD) can elicit an "out of body" experience that results in catastrophic EM impairments and decreased Hipp. activity during retrieval (Bergouignan et al. 2014).

When participants see an avatar looking in a particular direction toward an object, they are primed to that perspective and perform better and faster on target displacement tasks when they take that perspective as compared to no avatar conditions (Sulpizio et al. 2016) – an effect theorized to be due to spatial computation being conducted in advance via imagination (Burgess 2006). Deepening this perspective taking, the projection of oneself onto a virtual avatar can also yield consequences on memory. For example, in a study conducted by Ganesh et al. (2012), gamers were asked to rate the extent to which trait words described different aspects of themselves, their long-term avatar, close others, and familiar distant others. A surprise recognition test for the trait words showed that avatar-referent memory was superior to familiar distant other-referent memory. Activity in regions of the brain associated with self-identification (e.g., Inferior Parietal Lobe) was shown on avatar trials (even more than self-trials!) and correlated with an individual's self-reported propensity to incorporate external body enhancements (e.g., prosthetics) into one's bodily identity.

2.3.2 Enacted Cognition

The observation that long-term memory abilities increase with active navigation could also be related to the enactment effect – that is, the finding that participants who perform an action are more likely to recall the event compared to subjects who listen to the action phrase or watch an experimenter do the task (Madan and Singhal 2012). For instance, actively rotating objects vs. passively observing their rotation increases speed of recognition (James et al. 2002). Virtually manipulating body parts vs. watching another do the manipulation increases anatomical memory with greater benefit for individuals with lower baseline spatial abilities (Jang et al. 2017). "Running" in a VE using a joystick evoked a faster understanding of foot-action verbs, but not hand or mouth action verbs (Repetto et al. 2015). Simple interaction with to-be-remembered material also seems to enhance SM for where that information was encountered, but not necessarily the rest of the VE – suggesting a role of proximity to body in the upregulation of encoding during interaction (Reggente et al. 2020).

2.3.3 Extended Cognition

Extended cognition posits that facets of the external environment are *part* of cognitive processes as extensions of mind outside the brain. Draschkow et al. (2021) showed that participants made frequent eye movements (indicative of reliance on the visual scene and not WM) when performing naturalistic tasks in VR like collecting objects and arranging them according to a template. This use of the environment was present even if the number of objects were well within WM range, supporting the idea that there exist a fundamental preference and dependence for memory on external information during goal-directed behavior. The same study revealed that as demands on locomotion increased (i.e., they need to see information that's out of sight), so does reliance on WM. Given the limits of human WM in the context of the expansive workspace within VR, it is not surprising that many VR productivity tools contain easy-to-access visuospatial sketchpads that supplant the need for WM (e.g., sticky notes, whiteboards).

2.4 Impact of Environmental Enrichment

Environmental enrichment was originally observed when mice were given toys and larger, more complex cages, leading to enhanced dendritic arborization and improved learning (van Praag et al. 2000). Relatedly, the use of fantastical and erotic environments increases the efficacy of spatial mnemonic techniques in humans (Bower 1970). Virtual exploration that closely approximates RW factors (e.g., 3D vs. 2D) is a core aspect of enrichment (Clemenson et al. 2015; Freund et al. 2013) and why RW variables like sound in VE can increase Hipp. activity (Andreano et al. 2009). The complexity of structures built in Minecraft scaled with memory improvements (Clemenson et al. 2019), making such mediums far more approachable than similar construction efforts in the RW (Kolarik et al. 2020). Prolonged exposure to enriched virtual environments also appears to confer benefits for RW memory. Video gamers who prefer 3D video games over 2D games performed better on recognition tasks unrelated to the game – a phenomenon that was expanded to naïve gamers who underwent training (Clemenson and Stark 2015).

3 VR Bridges the Gap Between RW and Lab-Based Memories

Given that laboratory and RW stimuli tend to evoke different behavior (Snow et al. 2014) and brain activation profiles (Chen et al. 2017; Chow et al. 2018; Roediger and McDermott 2013), researchers put considerable energy into ensuring they are capturing ecologically valid metrics, especially when memory can be multi-faceted.

For example, the phenomenon of recognition (the ability to recognize previously encountered events, objects, or people) reflects the contribution of both recollection (retrieval of details associated with previous experiences) and familiarity (the feeling that the event was previously experienced) (Yonelinas et al. 2010). VR experiences appear to be retrieved via recollection-based processes similar to those that support autobiographical/recollection memory, whereas retrieval of conventional screen experiences seems more similar to familiarity (Kisker et al. 2021). Elaborating on this point, Schöne et al. (2019) suggest that VR experiences become a part of the autobiographical associative network, whereas conventional presentations remain as episodic events. Support for this comes from the observation that individuals with highly superior autobiographical memory tend to recognize the same number of laboratory events as age and education matched controls (LePort et al. 2012), suggesting that laboratory memory tests are often not ecological tests of recognition else these unique participants would outperform controls.

VR stands to serve as a cost-effective middle-ground that balances the experimental control of a laboratory with ecological validity. A proof of concept for how VR can bridge the gap between RW and lab-based memories comes from two VR-based route-navigation studies (Janzen and Weststeijn 2007; Wegman and Janzen 2011) that showed comparable behavioral and neuroimaging results to an RW study involving the creation of a 3-km outdoor walking course through Philadelphia (Schinazi and Epstein 2010). While RW task paradigms will likely always remain valuable, VR can provide follow-up studies to tease apart nuances. For example, the seminal study that examined static structural correlates in the Hipp. of London taxi drivers that scaled with experience (Maguire et al. 2000) was extended by a study that recorded functional activity in the same population *during* virtual navigation around London, revealing the recruitment of a more distributed network (Woollett et al. 2009). Furthermore, virtual renditions of familiarized RW environments can be used to probe memory for the location of RW objects from precisely positioned frames of reference (Schindler and Bartels 2013) and examine the neural activations supporting recollection of goal location found in familiar RW environments (Retrosplenial and Posterior Hipp.) vs. recently experienced RW environments (Hipp. only; Patai et al. 2019). Being a passenger in a virtual car as it navigates about a VE replica of an RW environment elicits the same SM performance as being an RW passenger (Lloyd et al. 2009). A virtual version of a common false memory test, where participants encountered objects from vendor stands instead of words on a screen replicated some of the findings of the original lab-based study - namely, that younger adults recalled and recognized more correct elements than older adults. However, it also showed that the typically-observed gap between younger and older adults groups in their susceptibility to perceptually and semantically related false recognitions went away – a finding the authors attribute to the use of a naturalistic context in keeping with the idea that VR may provide more "age-fair" and ecological tests of memory (Abichou et al. 2021).

VR can also induce cognitive-impacting situations that may not be commonplace, ethical, or safe in the RW. For example, Martens et al. (2019) showed that despite producing a strong physiological stress response, memory performance was not

impacted by asking participants to step off a tall building. The ability to create convincing simulations in a safe and operationalized fashion holds promise in shedding light on how memory works in stressful RW situations (e.g., is there high accuracy in eye witness testimonies of a violent crimes?) while simultaneously supporting investigations and treatment of stress-related disorders.

3.1 Human Analogs of Non-human Research

Feasibility and ethical limitations have prevented human analogs of many non-human research paradigms. For example, the Morris Water Maze (MWM), which places animals in a pool of water and tests their SM based on their ability to find a hidden platform, would be onerous with human subjects. VR's ability to provide precise control over task features has permitted for investigations into the nuances of memory by utilizing the MWM in humans. For example, BOLD activations in the parahippocampus, precuneus, and fusiform (and surprisingly not the Hipp.) were greater during trials where the platform was hidden as opposed to visible (Shipman and Astur 2008). Using a single distal cue (more allocentric) vs. multiple cues (more egocentric) allowed for investigators to reveal how the parietal cortex helps with translating between allocentric coordinates and egocentric directions (Rodriguez 2010).

VR-based MWM investigations have also revealed that higher circulating levels of testosterone (Driscoll et al. 2005), Hipp. volume size (Moffat et al. 2007), and ratios of finger length (2D:4D – an indicator of hormonal ratio in utero; Müller et al. (2018)) are positively correlated with task performance. Pharmacological disruption of the Hipp. with scopolamine allowed for the identification of striatal-based memory systems as a compensatory mechanisms for MWM completion (Antonova et al. 2011). Similarly, it was shown that an intact Hipp. is not necessary for leveraging distal cues to perform well on the MWM (Kolarik et al. 2016).

The Radial Arm Maze (RAM), whose design is a circular central platform that radiates out corridors (arms) that contain rewards not visible from the center, now also has VR variations where the location of the reward will stay in the same place (win-stay; Cyr et al. (2016)) or switch places (win-shift; Demanuele et al. (2015). VR RAMs have been used to differentiate between spatial learners (using landmarks; Hipp. dependent) and response learners (using sequences of turns; caudate dependent) by removing distal landmarks between learning and testing (Bohbot et al. 2004, 2007; Iaria et al. 2003). Similar to the RAM, the hole-board maze (holes instead of arms) has been translated into VR as an evaluation of human place learning that contains facets of working memory (repeat visits to explored locations) and reference memory (prioritized visits to rewarded locations) (Cánovas et al. 2008). This and similar inspired location-based memory task have been validated based on their ability to reproduce commonly observed learning rates and the sexual dimorphism in which men outperform women in spatial memory tasks (Cánovas et al. 2008; Tascón et al. 2017).

Where Leutgeb et al. (2007) created a physical contraption that morphed a square environment to a circular one to investigate changes in rodent behavior, pattern separation, and place-cell remapping, Steemers et al. (2016) created a virtual analog that allowed for two distinct environments to be visually morphed along a continuum – an elegant design that showed changes in reward-finding behavior based on which environment participants thought they were in and also provided support for an attractor dynamic model of pattern completion in the hippocampus, supporting mnemonic processing and decision making.

While visual input seems sufficient for conducting tests of spatial memory in VR without the accompanying RW elements (e.g., swimming in water in the MWM), some task designs may require non-VR elements. For example, in studying associative learning tasks like fear conditioning, there may not be a common visual element that evokes the same response across all participants. In order to utilize the tried-and-true method of instilling fear in rodents, Alvarez et al. (2008) replicated classic fear conditioning experiments by delivering foot shocks to participants as they explored VEs, revealing more Hipp. and Amygdala activity in the VE that was paired with the shock.

A separate analog of non-human research that can be applied to human subjects with the use of VR is the collection of implicit or passively derived metrics. Given that non-humans are incapable of explicit reporting, researchers must rely on behavioral observations to infer cognition and memory which are often remarkably informative and detailed, even sometimes more so than subjective reporting. The ability to extract a plethora of detailed datapoints about a subject's behavior is unprecedented in VEs; real-time position, orienting directions, interactions with objects, and many other metrics can all be used to create derived metrics like time spent in a location, attentional focus, and to eventually yield objective measures of memory.

For instance, much like how freezing behavior exhibited by rodents in particular environments can indicate a contextually based fear memory in the absence of subjective reporting, an individual's behavior in a VE can reveal facets of memory. While technically feasible with RW object tracking, automated classification of learned reward/fear-based behavior through computational ethology is substantially easier and more accurate in VEs and can extract individualized ethograms such as thigmotaxis (tendency to remain close to walls), panic errors, and approach/avoidance/intermittent locomotion (Mobbs et al. 2021). For example, place aversion in open field tests can indicate a fearful memory originally encountered in that place. Computational analyses of VR behavior shed light on an amnesic MTL patient, revealing deficits in spatial precision rather than spatial search strategy, suggesting that an intact Hipp. is not necessary for representing multiple external landmarks during spatial navigation of new environments (Kolarik et al. 2016).

3.2 Studying Different Types of Memory with VR

VR affords memory researchers with an unprecedented ability to design paradigms that balance the benefits of RW verisimilitude with the laboratory rigor of isolating variables of interest. Such affordances have significantly advanced the field of memory research by providing an observational lens that can focus in on specific elements without necessarily disrupting the observation of the cohesive whole. For example, researchers have been able to dissociate visual scenes from events, an important tool for examining the binding of/separation of components that make up complex phenomena like EM (Burgess et al. 2001; S. A. Smith 2019). VR has also facilitated the implementation of mnemonic techniques, such as the Method of Loci, which previously relied solely on an individual's imagination of previously visited environments. By utilizing template virtual environments (VEs), VR allows for standardization of the size, detail, and exposure time of environments. This standardization helps control for individual differences in real-world experience (Legge et al. 2012; Reggente et al. 2020).

Additionally, VR exclusively permits for the creation of infinitely large-scale and novel environments, insertion of invisible barriers, event-based rendering of objects, teleportation between locations, impositions of visual route guidance, and interactions with other agents. Such features have bred designs that can disentangle cognitive decision making from other processes of interest (Marsh et al. 2010) or tease apart place-based vs. sequence-based strategies of spatial encoding (Igloi et al. 2015). VR can also present scenes outside of conscious awareness, which has revealed that conscious perception is not mandatory for spatial EM formation (Wuethrich et al. 2018). While VR can allow for visual perspective shifts (e.g., first-person vs. third-person viewing angles), it can also foster perspective taking (e.g., role-playing a skilled scientist) which can help to unbound "trapped intelligence" in poor-performing students by allowing them to step out of their real-world identity and build confidence while embodying another (Dede 2009). The sections that follow describe different types of memory, the ways in which they have been studied traditionally, and how VR paradigms provide a more ecological investigation. Table 1 highlights some particularly potent examples of the ways in which the affordances of VR have uniquely extended the understanding of different types of memory.

3.2.1 Spatial Memory (SM)

SM is defined as the storage and retrieval of information that is needed to remember and plan routes to locations of objects and events. In traditional tests of SM (e.g., finding matching pairs of face-down cards arranged in a grid), the use of egocentric or allocentric processing cannot be distinguished, as the two frames coincide. Furthermore, scenes, objects, and landmarks are encoded differently when discovered during 3D navigation as compared to 2D presentations. While both

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VR affordance	Citation(s)
Rapid teleportation to unique VEs to foster context facilitated learning	Essoe et al. (2022), Parker et al. (2020), Shin et al. (2021)
Creating invisible blockades or targets that impact function but not visual percepts	Shipman and Astur (2008), Kolarik et al. (2016)
Providing participants with interactive perspec- tives that are not egocentric (i.e., first-person point of view) such as third person or bird's eye points of view	Morganti et al. (2013), Serino and Riva (2015), Bergouignan et al. (2014), Serino et al. (2015), Weniger et al. (2009)
Overlaying toggled route guidance to dissociate the processes responsible for true wayfinding vs. path-following	Hartley et al. (2003)
Maintaining proximal environmental fidelity while altering distal cues to differentiate between spatial and response learning	Bohbot et al. (2004, 2007), Iaria et al. (2003)
Exposing participants to multiple distinct VEs and then computationally blending the visuo- spatial components of those environments to observe evidence of Hipp. pattern completion and attractor dynamic processes	Steemers et al. (2016)
Create duplicate instantiations of environmental transgressions during route-finding while iter- ating on other variables (e.g., passive vs. active movement) to isolate differences between mul- tiple navigational pursuits	Janzen and Weststeijn (2007), Wegman and Janzen (2011), Plancher et al. (2012), Gaunet et al. (2001)
Inserting realistic "events" that impact naviga- tional pursuits (e.g., lava blocking a path) as a probe of RW spatial memory and path integra- tion processes	Javadi et al. (2019)
Leveraging VEs as a common, universal tem- plate of spatial environments to investigate the mechanisms supporting the Method of Loci – a mnemonic which is typically conducted using mental imagery of familiar locations which vary meaningfully across subjects	Legge et al. (2012), Reggente et al. (2020), Krokos et al. (2019)
Use VEs to impart cognitive-impacting situa- tions mimicking RW situations (e.g., being on a ledge of a tall building, driving a large truck, being chased by a predator) that would be unethical or impractical to induce non-virtually	Martens et al. (2019), Unni et al. (2017), Faul et al. (2020), Mobbs et al. (2007)
Testing the efficacy of procedural memory training in situations where real-life examples are not readily available or practice like surgical procedures or mining expeditions	Siu et al. (2016), Zhang (2017), Wang et al. (2020), Mantovani et al. (2003)
Create VR replicas of RW environments with varying levels of detail to observe the impacts of learning prior to subsequent RW environ- ment exposure	Wallet et al. (2011), Mania et al. (2010), Larrue et al. (2014), Coleman et al. (2019), Brooks (1999b)

 Table 1
 Highlighted studies of memory that showcase affordances unique to VR

(continued)

VR affordance	Citation(s)
Crafting VEs that become iteratively similar to an individual's feared context like the scene of a victim's road accident or a soldier's battlefield while also substantiating extinguishment over multiple environments	Foa and Kozak (1986), Maples-Keller et al. (2017), Beck et al. (2007), Bohil et al. (2011), Gerardi et al. (2008), Reger and Gahm (2008), Wood et al. (2008), Dunsmoor et al. (2014)

Table 1 (continued)

presentations may suffice for recognition, 3D affords participants with the ability to decide upon novel shortcuts or forecast unseen points of view (Burgess et al. 2002).

VR allows for a suite of more ecologically valid measures of SM when tasking participants with navigating from one location to another. During such tasks, critical environmental features can be changed (Dhindsa et al. 2014; Wegman et al. 2014), tests of perspective-based orientation can be conducted (Brown et al. 2014; Dimsdale-Zucker et al. 2018; Gomez et al. 2014; Stokes et al. 2015; N. A. Suthana et al. 2009), and covert tasks can be embedded so as to observe implicit acquisition of object-location memories (Wong et al. 2014). Altering exposure to first-person and/or bird's eye views (e.g., small aerial map overlays) of an environment can also reveal how SM is encoded and retrieved (Serino and Riva 2015). Following navigation, participants can be tasked with pinpointing locations on maps of environments. Such a task requires egocentric-to-allocentric transformation and yields precise quantification of error through measurement of the Euclidean distance between the actual and subject-provided coordinates (Pine et al. 2002; Reggente et al. 2020). VR paradigms have also revealed a sustained neural "memory" of position in VE akin to the classic function of 2D (Hassabis et al. 2009) and 3D (Kim et al. 2017) place cells.

VR has also elucidated the role of sleep on replaying and consolidating SM processes. Perhaps the most salient traditional exemplar of this phenomenon is that the temporal order of place-cell firing in rodents during NREM sleep mirrors that of sequentially visited RW place fields (i.e., a path) before sleep (Davidson et al. 2009). Peigneux et al. (2004) demonstrated in humans that the degree to which hippocampal areas that showed fMRI activation during virtual navigation were also detectable via EEG during subsequent slow wave sleep accounted for individual differences in performance on route retrieval the next day. From a different approach, Rauchs et al. (2008b) made clever use of VEs to demonstrate that post-learning sleep deprivation modulates the neural substrates of both spatial and contextual memories in a way that accounts for individual differences in place-finding efficiency.

Successful navigation to learned locations from different start points, which requires an interplay across memory for environmental maps and routes, is also a straightforward and ecologically valid test of SM. "Optimality of trajectory" (Howett et al. 2019), improvement over runs (Cyr et al. 2016; N. Suthana et al. 2011), time spent on task (Migo et al. 2016), distance traveled (Salgado-Pineda et al. 2016), use of shortcuts (Caglio et al. 2012), and adjusting to events (e.g., lava blocking a learned path (Javadi et al. 2019) or newly precluded landmarks (Wolbers et al.

2004)) are all creative ways in which SM can be objectified in VR. Chapter "VR for Spatial Navigation and Action Science" of this text discusses this topic at length.

3.2.2 Short-Term Memory (STM)

STM is an umbrella term used to describe a capacity for keeping small amounts of information on top of mind, with the ability to regurgitate said information (via recall or recognition) shortly after its initial presentation. The next sections focus on VR research that sheds new light on the mechanisms underlying components of short-term memory such as working memory.

Working Memory (WM)

WM involves the manipulation of information held in STM and can take the form of visuospatial (e.g., remembering the color and location of your drink at a party), verbal (e.g., repeating a phone number in a phonological loop), and/or kinesthetic (e.g., repeating another's hand gestures). WM is usually tested using tools such as the N-back task, where participants are tasked with making a button press when a current presentation of an item (e.g., a word) is the same as one presented N items back in the presentation stream (K. M. Miller et al. 2009) or the List Sorting Test (Tulsky et al. 2014), where participants are tasked with recalling and sorting (e.g., largest to smallest) a list of objects.

In VR, visual-spatial WM has been studied by asking individuals to navigate a previously shown route - a design that permitted researchers to compare epochs of encoding and retrieval and identify that encoding requires more cerebral effort than retrieval (Jaiswal et al. 2010). Similar demarcation of epochs during virtual navigation permitted for the discovery of WM EEG signatures. Weidemann et al. (2009), for instance, observed that frontal theta power was high during navigational efforts and was released when participants released the goal state (and no longer had to utilize their WM). Plancher et al. (2018) extended such work by examining the role of WM in the integration of episodic memories. Participants were tasked with memorizing as much contextual content as they could while navigating a VE and performing a concurrent task that barraged either of two cognitive scaffolds that support WM: the phonological loop (e.g., keeping track of the number of garbage containers colored yellow) or visuospatial sketchpad (memorize a spatial pattern composed by the garbage containers). Results revealed that WM is crucial for EM; blocking the phonological loop impacted the encoding of central elements in the VE and blocking the visuospatial sketchpad interfered with the encoding of temporal context and relational binding.

Researchers have been able to develop more realistic N-back-style tasks like viewing streams of letters on a blackboard in a replica classroom (Coleman et al. 2019) or counting moving fish in a virtual aquarium (Climent et al. 2021). Such developments have equipped researchers with more realistic paradigms for assessing

the efficacy of learning aids, especially compared to traditional laboratory tests. For instance, Jang et al. (2021) found that ADHD drugs in children can improve accuracy and RT on an n-back task in a realistic classroom VE – a finding that was accompanied by decreased default mode network activity during high working memory load.

Prospective Memory (PM)

PM is remembering to carry out a previously planned action like taking medication at specific times (time-based) or starting your fitness tracker before a mountain bike ride (event-based). PM is typically tested by giving participants RW time-based (e.g., ask the experimenter for a newspaper after 20 min) and event-based (e.g., change pens after completing seven assignments) instructions before embarking on an intellectually demanding filler task (Groot et al. 2002). In VR, PM can be probed more meticulously and even incidentally by examining if an individual makes stops at instructed spots along virtual routes (Lecouvey et al. 2019) or gathers the right grocery items from virtual stores (Dong et al. 2019). This latter effort elicited significantly more activity in rostral prefrontal cortex than an analogous non-VR version of the task, which corroborates the RW deficits in PM observed in patients with lesions to that area (Volle et al. 2011) and evidences ecological validity of VR-based PM tasks. VR also stands to serve as an encoding environment to upregulate RW PM. Kalpouzos and Eriksson (2013) were able to show that selfefficacy beliefs modulate intentional encoding on delayed real-life intentions by collecting fMRI data while subjects mentally imagined executing tasks (e.g., mail a letter) in VEs that were based on RW environments.

3.2.3 Long-Term Declarative Memory: Semantic Memory

Semantic Memory is the explicit knowledge of general words, concepts, and facts like remembering the name of objects surrounding you or the punch line to a joke. Semantic Memory is typically tested with a picture naming task – a paradigm that has been extended with VR using standardized sets of 3-D objects which carry increased semblance to actual objects compared to pictures (Peeters 2018). Encoding semantics in VR is particularly advantageous for repetitive field training where RW counterparts would be more costly and less readily accessible (e.g., flight simulations for pilots, emergency rooms for health care professionals (Mantovani et al. 2003)). Such utilizations have the additional benefit of increasing motivation, engagement, and retention scores compared to didactic instruction (Chang et al. 2019; Ryan and Poole 2019).

Experiences with virtual routes can provide quantifiable measures of semantic memory (e.g., knowing whether or not you can reach point A from point B without turning). After encoding VEs, tests of semantic memory and survey knowledge

revealed a dorsal (survey)/ventral (semantic) dissociation, supporting the putative "where" (dorsal)/"what" (ventral) streams (Aguirre and D'Esposito 1997).

3.2.4 Long-Term Declarative Memory: Episodic

An episode, much like a proper journalistic summary, encapsulates information about the "who," "what," and "where" of an event. As such, EM holds information about temporal-spatial relations among events (Tulving and Thomson 1973); abstract features of an episode are like individual nodes in a network whose temporal linkage forms a collective representation of an event (Eichenbaum and Cohen 2001). An innovative RW test of EM strength has been recognition tasks of stimuli captured from participants' wearable cameras (Chow et al. 2018; Rissman et al. 2016).

The spatio-temporal nature of VR allows for a multitude of experiments conducted in VR to be considered tests of EM (S. A. Smith (2019)). A quintessential study had subjects navigate about a VE and encounter avatars (who) in discrete locations (where) that dispensed objects (what) (Burgess et al. 2001), permitting for discrete probes of EM's constituent components: spatial context (where the object was received), temporal context (which object was received first), which person was involved, and object recognition. Neuroimaging revealed that the Parahipp. was recruited during spatial probes whereas object memory elicited parietal and prefrontal activity. The same task was also utilized in temporal lobectomy patients (Spiers et al. 2001a). The task's ability to precisely target core components of EM revealed that L Temporal patients were impaired on context-dependent memory questions whereas R Temporal patients were impaired on topographical memory and object recognition, suggesting that the R Temporal lobe is more involved in SM, whereas the context-dependent aspects of EM are dependent on the L Temporal lobe. A similar paradigm employed by Buchy et al. (2014) revealed activation of ventrolateral prefrontal cortex during external source memory that scaled with selfreflectiveness.

It should be noted that studies of autobiographical memory in VR may lack some ecological validity because there is currently a richer diversity and temporal separation in actual streams of life events. Such a notion could explain the increase in prefrontal activity during VR-based studies of EM as compared to RW studies (Burgess et al. 2002). Without rigorous design, VEs have higher potential to be self-similar than RW environments which may increase the likelihood of interference and subsequent recruitment of prefrontal regions to disentangle them.

3.2.5 Long-Term Nondeclarative/Procedural Memory

When learning a new skill or routine, memory for the process is typically declarative (e.g., consciously remembering which note comes next when learning to play a new song) before it becomes nondeclarative (i.e., procedural or implicit – as in the case of unconsciously playing the song without thinking about the constituent notes). A

classic test of nondeclarative memory is the weather prediction task (Knowlton et al. 1994), where participants use feedback to learn which cues are associated with weather outcomes and improve on the task despite not being able to declare the information that is guiding their behavior.

In VR, procedural memory can be probed by showing and then testing multistep procedures like grasping and moving a series of objects from to specific locations (Ragan et al. 2010). This is particularly useful for testing the efficacy of training in situations where real-life examples are not readily available nor practical (e.g., surgical procedures (Siu et al. 2016) and mining safety (Zhang 2017)). Wang et al. (2020) showed a 12% improvement in learning how to erect scaffolds when using a personalized VR tool vs. conventional methods.

3.2.6 RW Memory Modulators in VR

In addition to creating life-like episodes and providing templates for memory manipulation, it is also possible to bring other components of the RW (e.g., stressful scenarios) into VR, further increasing the ecological validity of research paradigms, while also unveiling the dynamic nature of memory under specific mindsets and settings (e.g., affective states).

3.2.7 Impact of Emotion

Given that the neural architecture supporting SM can become completely remapped once the environment is associated with fear (Moita et al. 2004), the impact of emotion on the encoding of information within VEs can be revelatory. Showing participants task-irrelevant images of negative scenes while they completed an object-location task elicited an increase of Parahipp. activity and faster RTs when later viewing rooms within the VE compared to positive images (Chan et al. 2014). The integration of fearful stimuli into schemas appears to be sensitive to an individual's physical proximity to the stimuli; how close individuals were to an RW bank robbery determined their likelihood of developing PTSD (Frans et al. 2018). VR provides a safe medium with which to dissect this phenomenon. Faul et al. (2020) showed that profiles of neural activity during fear acquisition that occurred within peri-personal space showed recruitment of reactive fear circuits vs. cognitive fear circuits for threats acquired further away. Mobbs et al. (2007) also revealed proximity-based functional differences when participants were far away (ventromedial prefrontal) vs. close to (periaqueductal gray) a virtual predator.

3.2.8 Cognitive Load/Attention

Studying cognitive load and attention in VEs is crucial for understanding how people interact with and respond to complex and dynamic situations, such as driving or navigating unfamiliar environments. Unni et al. (2017) created a realistic driving simulator where participants drove down a virtual highway while monitoring speed signs that appeared every 20 s. Participants were tasked with matching their speed to the sign that appeared N signs back. This putative WM load significantly impacted safety relevant driving behaviors (e.g., variability of brake pedal position and RT). Blondé et al. (2021) had participants passively encode an urban VE while they were randomly probed for reports of mind wandering. Results suggested that attention coupled with a moderate degree of mind wandering creates a hospitable medium for encoding processes by helping to avoid the distraction of inner thoughts while also preventing individuals from being overly focused on the environment. Familiarity with a VE mitigates errors that typically accompany increased cognitive demands (Tascón et al. 2021). Electrodermal, subjective, and behavioral measures of cognitive load as participants carried out simple tasks in RW train stations and their virtual replicas revealed an increased load in novice travelers compared to experts implying that domain expertise can ease situational cognitive load (Armougum et al. 2019). Taken together, these results suggest that simulating RW situations in VR can permit for the development of protocols that detect (and limit) WM load, encourage moderate mind wandering, and develop environmental familiarity to bolster RW safety and performance.

3.2.9 Impact of Volition

Volitional control can improve memory due to the interplay between neural systems related to planning, attention, and item processing (Voss et al. 2011). VR allows researchers to vary volition along component (i.e., stationary or motoric) and degree (e.g., high vs. low-motor control) axes of the interaction being considered (S. A. Smith 2019). This technique has revealed that making itinerary choices or having motor control over a vehicle during virtual navigation enhances SM compared to merely being a passenger (Plancher et al. 2013) – an enhancement more pronounced in older adults (OA; Meade et al. 2019). Further, feature binding is also enhanced for virtual passengers both in cases of itinerary choosing and after experiencing low navigational control (e.g., moving a car along a rail instead of steering), revealing a need for balance between cognitive load and volition when optimizing for memory encoding (Jebara et al. 2014). Likewise, granting participants the ability to place objects along a route resulted in greater recall and SM for those objects compared to having no control over placement (Reggente et al. 2020).

Interestingly, the belief that an avatar was expressing human-based volition (i.e., is controlled by a person and not an algorithm) yielded better factual memory than when participants believed the avatar was a computer program (Okita et al. 2008). Such benefits stand to be increased if human-controlled avatars are attentive – an attribute that promoted emotional security in threatening VEs (Kane et al. 2012).

Finally, virtual navigators seem to activate the anterior Hipp. during wayfinding and the caudate when following routes (Hartley et al. 2003). This outcome can be viewed as a modern extension of early RW work showing the R Hipp. to be

associated with knowing places and getting between them, whereas the R caudate was associated with getting there quickly (Maguire et al. 1998).

3.3 VR to RW Transfer

VR to RW transfer is the successful RW recall of VR encoded information. Neural activity patterns expressed during recall remain relatively similar despite encoding in RW vs. equivalent VEs (Spiers and Maguire 2006). When considering the real-world implications of VR-based learning protocols, it would behoove VE designers to carefully balance detail with abstraction and realism with fantasy while also considering other RW components (e.g., bodily information) to increase the likelihood of VR to RW transfer.

High-fidelity VR replicas of RW settings yielded better wayfinding in the RW compared to replicas that removed color and textures (Wallet et al. 2011). Following exposure to a high-detail version of a VE replica of an academic office, participants showed an increase in object recognition compared to when exposed to a low-detail wireframe version (Mourkoussis et al. 2010). Interestingly, the results only held for objects that were consistent with the office (e.g., phone and not a cash register). However, not all detail is created equal – object recognition in the RW was better after encoding low-fidelity flat-shaded (no textures used, but color tone preserved) virtual objects compared to those rendered with radiosity (color blending intended to suggest the presence of a realistic light source) (Mania et al. 2010). The authors suggest that variations from the RW could recruit stronger attentional resources.

Encoding routes in a VE replica of an RW environment with access to full bodybased information (treadmill with rotation) promoted better transfer of SM to the actual RW environment over encoding done without body-based information (joysticks or treadmills without rotation) (Larrue et al. 2014). Reciprocally, early studies have shown a reliable transfer of RW spatial knowledge to VE replicas (Ruddle et al. 1997; Wesley Regian and Yadrick 1994; Witmer et al. 1996), emphasizing the ability to create hybrid studies that can be seeded with RW experience and enhanced in VEs. Similarly, differences in SM and wayfinding between OA and YA found in RW environments were also found in their virtual replicas (Taillade et al. 2016). Learning locations in either a familiar or novel RW settings or virtual equivalents show bi-directional RW/VR transfer of SM (Clemenson et al. 2020).

Children with attention disorders who completed 5 weeks of memory training using a "virtual classroom continuous performance task" showed substantial improvement in what the authors describe as a "real-life scenario" of classroom learning, making transfer far more likely (Coleman et al. 2019). Procedural memory supporting an object movement sequence task can also be transferred to the RW (Ragan et al. 2010). Other exemplars of VR/RW transfer are discussed in the section on memory rehabilitation.

4 VR-Based Memory Assessments

Conventional measures of memory typically focus on core content (i.e., the "what") instead of the true binding that happens in actual episodes (i.e., "what," where," and "when"). They also often use verbal materials, which makes the test sensitive to performance in non-memory domains (Helmstaedter et al. 2009), permitting for compensatory strategies which could erroneously reveal normal "memory."

Subjective reports rarely scale with performance on traditional memory tests, warranting criticism that such measures wrongly estimating memory capacities for everyday situations. For example, patients reporting topographical memory deficits have preserved ability in tabletop tests of spatial or geographical knowledge (Habib and Sirigu 1987). Cognitive complaints in amnesiacs typically show little correlation with verbal memory tests used in clinical settings (Chaytor and Schmitter-Edgecombe 2003). Pflueger et al. (2018) designed a VR version of a common verbal memory test and found that the gap between age groups in memory performance was smaller than the traditional assessment, again positioning VR as a more "age-fair" medium. Taken together, clinical cognitive assessments should leverage the affordances of VR paradigms: personalized, objective, reliable, and ecologically valid assessments that are impervious to subjectivity or compensatory strategies and yield behavioral metrics that capture subjective reports (Bohil et al. 2011; Parsons 2015; van Bennekom et al. 2017).

Remembering information and events while completing tasks in a complex environment is one of the crucial abilities needed for the preservation of autonomy in individuals with cognitive impairment (Perneczky et al. 2006). Practicality, however, precludes assessment in standardized RW surroundings (Cushman et al. 2008). "Serious games" have the potential to be effective tools in the prognosis, management, and potentially treatment of cognitive impairments, especially in scenarios that simulate daily activities (Zucchella et al. 2014). VR tests of memory that emphasize feature binding and recall/recognition tests of VE details following virtual executions of everyday life tasks tend to show strong relationships with selfreports (Plancher et al. 2010; Widmann et al. 2012). Likewise, a VR kitchen can capture the RW impairment in Alzheimer's disease (AD); patients performed virtual tasks like preparing a cup of coffee with the same aptitude as in the RW and the objective measures scaled with caregiver reports (Allain et al. 2014).

Virtual supermarkets have been shown as a viable tool for measuring executive function in patients with mild cognitive impairment (MCI) and healthy older adults (OAs; Werner et al. 2009; Zygouris et al. 2015), making it an effective screening tool that can be done at-home over multiple periods – a benefit that increases classification accuracy, sensitivity, and specificity (Zygouris et al. 2017). Tasks in grocery stores can also probe spatial orientation performance that can discriminate AD and frontotemporal dementia groups. Grocery tasks that test prospective memory (PM; e.g., return to pharmacist when hearing your number) and retrospective memory (e.g., securing items from a learned shopping list) are not susceptible to compensatory benefits of executive function, allowing such tools to be specific and reliable

assessors (Parsons and Barnett 2017). Similarly, using a fire evacuation task that is sensitive to subtle errors can serve as a tool for both dementia screening (Tarnanas et al. 2013) and MCI prognosis (Tarnanas et al. 2014).

PM memory strength in life-like VR scenarios such as carrying out errands can differentiate OA and mild AD while also ascertaining an individual's ability to be trusted with such tasks in the RW (Knight and Titov 2009; Lecouvey et al. 2019). VR-based memory tests of cognition that are sensitive to population-specific behaviors and deficits are helping with clinical classification (Déjos et al. 2012; La Corte et al. 2019), permitting for early interventions that may dampen disease impact. A seminal VR study showed that an MCI patient had recall deficits when changing viewpoints (King et al. 2002), despite normal recognition of topographical scenes (Spiers et al. 2001b). Intact performance when using egocentric navigation strategies vs. depreciated performance when using allocentric strategies in a VR MWM was also crucial for dissociating another amnesic from controls (Goodrich-Hunsaker et al. 2010) and amnestic MCI (aMCI) from AD (Laczó et al. 2010). A reduction in ability to leverage solutions shown from a bird's eye view perspective when later navigating a first-person VR maze navigation (i.e., allo- to egocentric spatial memory [SM]) is pronounced in AD patients (Morganti et al. 2013) who also show SM and non-verbal EM impairment when navigating to a temporally ordered series of goal locations (Kalová et al. 2005).

VR researchers have also designed diagnostically-sensitive tasks that necessarily recruit the Entorhinal cortex – a region contributing to remembering and navigating to learned places along novel paths and one of the first to exhibit neurodegeneration in AD (Howett et al. 2019). Paired with fMRI, Agosta et al. (2020) postulate that such tasks can identify compensatory mechanisms during performance on memory tasks even if outcome is matched to controls. Skouras et al. (2020) cleverly approached assessment from a neurofeedback angle: individuals were tasked with mentally increasing their velocity in a VE (yoked to downregulation of Hipp. CA1 activity), revealing a reliable functional signature that was characteristic of advanced AD stages evident in high-risk individuals that were cognitively unimpaired. Showing decreased grid-cell like representations during navigation in VEs has also been shown in adults with a genetic risk for AD (Kunz et al. 2015). Similarly, since the neural response of the VR radial arm maze (RAM) is so well known, compensatory mechanisms can be used to predict risk or severity in a variety of psychiatric disorders despite normal task performance (Astur et al. 2005; Migo et al. 2016; Wilkins et al. 2017).

4.1 Profiling Memory-Impaired Populations

Given that both AD and aMCI are characterized by episodic memory impairment, it can be difficult to differentiate the two. Spatial navigation disturbances can provide robust neural signatures of MCI and AD like recruitment of lower-order, task-irrelevant cerebral systems (Drzezga et al. 2005). VE landmark and object

recognition tasks show less mistakes while showing more confidence in foils – an impairment that was more pronounced in AD than aMCI (Zakzanis et al. 2009). Serino et al. (2015) showed a deficit in aMCI and AD patients in ability to encode and store allocentric viewpoints, but that AD had difficulty storing allocentric viewpoints and syncing them with viewpoint-dependent representation. Individual differences on allocentric memory assessments following a driving task where patients were either passengers or drivers were capable of dissociating aMCI, AD, and OA (Plancher et al. 2012). Showing SM impairment on the RAM has also been shown to be predictive of which aMCI patients will convert to AD (Lee et al. 2014). Cushman et al. (2008) showed close correlations between RW and virtual navigational deficits that distinguished between controls, MCI, and early AD. AD can also be identified amidst aging, aMCI, and frontotemporal lobar degeneration by poorer performance on temporal memory tests that are void of environmental cues like asking participants to reproduce a virtual route using only body-turns (Bellassen et al. 2012).

VR has also been used to determine the impact of lesions and brain damage on RW memory demands, revealing specific profiles of damage and benchmarking recovery (e.g., impacts on egocentric but not allocentric memory (Weniger et al. 2009) or transfer between the two (Carelli et al. 2011)). Epilepsy patients were shown to recruit the MTL contralateral to their seizure focus during VR objectlocation tasks (Frings et al. 2008). van der Ham et al. (2010) identified deficits in temporal vs. SM in patients with R parieto-occipital damage when doing navigation tasks in a VE replica of Tübingen. Testing for recall of object locations in RW VEs has also been used to quantify and track memory-impaired Traumatic Brain Injury (TBI) patients (Matheis et al. 2007) and differentiate them from other memoryimpaired populations (Arvind Pala et al. 2014) – a metric that can be useful to determine ecological readiness like with normally-appearing athletes following injury (Slobounov et al. 2010). Using a VR version of the MWM, Livingstone and Skelton (2007) also found that TBI patients do worse than controls when force to rely on distal features (i.e., allocentric strategy) vs. using proximal cues (i.e., egocentric strategy).

5 VR-Based Cognitive Rehabilitation and Enhancement

VR tasks have been used to quantify memory enhancement following deep-brain stimulation (Suthana et al. 2012). However, VR can also upregulate encoding through its embedding of to-be-remembered information within spatial, episodic, and embodied contexts. For example, in a virtual navigation study, Kessels et al. (2011) showed that AD patients had higher implicit memory for objects encountered at key decision points. Could VR experiences be explicitly designed to take advantage of such observations with the goal of enhancing memory in patient populations? Can VR be used to repurpose intact functionality to compensate for deficits?

My grandfather's SM was impressive – he could take me through a detailed Google Maps tour of his childhood neighborhood in Italy while completely forgetting that we had shared the same experience mere minutes ago. Can we use VR to drape non-spatial information over the inherently stronger scaffolds that support SM? Indeed, instructions that favor the link between content and its context serve as an effective compensatory strategy for deficient memory processing (Luo and Craik 2008). Empirically driven designs of VR paradigms can provide engaging opportunities to practice tasks, learn compensatory strategies, or intentionally upregulate depreciating brain regions.

5.1 Healthy Aging

Severity of age-related SM decline is correlated with the use of response over spatial strategies (see "Impact of Immersion and Presence" section above) when navigating a virtual maze and is hallmarked by reduced Hipp. gray matter (Konishi and Bohbot 2013), suggesting that the use of spatial encoding could mitigate deviant aging deficits. VR allows older adults to become unbound from the small and often monotonous spaces that their limited mobility confines them to while receiving meaningful, movement-focused mental stimulation in enriched environments that encourages stronger encoding. Benoit et al. (2015) showed that VR is well tolerated by older adults and stimulates autobiographical recollection and conveys scene familiarity – positioning VR as a reminiscence therapy tool (Repetto et al. 2016). Long-term training of OAs also appears viable: 6 months of VR training powerfully increased long-term recall (Optale et al. 2010).

In older adults, active encoding during virtual navigation (Sauzéon et al. 2016) or walking (Tascón et al. 2018) and deciding the itinerary/actively controlling VR navigation (Diersch and Wolbers 2019; Jebara et al. 2014) strengthen distinctive memory traces, enrich source memory, and enhance EM. Training on tasks that mimic daily life yields upticks in visual memory, attention, and cognitive flexibility in older adults (Gamito et al. 2019). Even simple, fun, and engaging tasks like playing Super Mario 64 can increase Hipp. gray volume in both older and younger adults (Kühn et al. 2014; West et al. 2017). A realistic room-scale VR task where OAs with memory complaints needed to memorize a list of grocery objects, engage in conversation mid-task, and then gather the items amongst semantically similar distractors showed marked improvement in auditory recall (Boller et al. 2021).

5.2 Back to Baseline

Where memory for an event is the crux of a disorder (e.g., PTSD), VR can be used to create stimuli that are maximally similar to an individual's feared stimuli (Foa and Kozak 1986; Maples-Keller et al. 2017), as has been shown in cases of road accident

victims (Beck et al. 2007) and soldiers (Bohil et al. 2011; Gerardi et al. 2008; Reger and Gahm 2008; Wood et al. 2008) in order to support extinguishment over multiple environments (Dunsmoor et al. 2014).

The use of VR in brain damage rehab can help to train cognitive functioning for everyday activities (Rose et al. 2005). Vascular brain injury patients have shown enhanced SM after VR training (D. Rose et al. 1999). A TBI patient showed memory improvement and increased activation of Hipp. regions following a virtual navigation task that they genuinely enjoyed (Caglio et al. 2012). By using realistic event-based PM tasks, Acquired Brain Injury patients showed significant improvement in both VR and RW PM (Yip and Man 2013).

Amnesic patients were able to learn routes through their hospital after training in a virtual reconstruction of the same environment (Brooks 1999a) and an AD case study showed that relearning cooking activities in VR transfers to real life and remains stable over time (Foloppe et al. 2018). For more information, see Chapter "VR for Spatial Navigation and Action Science" of this volume, D'Cunha et al. (2019), García-Betances et al. (2015), Clay et al. (2020), and Larson et al. (2014).

5.3 Above Baseline

The pursuit of cognitive enhancement, especially through extending the breadth of memory, is a perennial modus operandi. Virtual makeovers of the ancient, highly effective mnemonic technique known as the Method of Loci can increase recall by 28% within a single session (Reggente et al. 2020), and its benefits increase as a function of subjective immersion (Krokos et al. 2019). Simply navigating novel VEs has increased motivation during Hipp. dependent measures of memory (Schomaker et al. 2014). Mere hours playing a racing game can yield microstructural changes supporting localized neuroplasticity in the Hipp. of both humans and rats (Sagi et al. 2012). While this chapter has emphasized the importance of context for memory, encoding multiple times in the same environment (e.g., RW classroom) can induce "contextual crutch" and interference (S. M. Smith and Handy 2016) – phenomena that VR can mitigate with multiple distinctive VEs (Perfect and Lindsay 2013; Smith and Handy 2014; Essoe et al. 2022).

High-gamma oscillations during exploration of novel VEs are crucial for successful encoding (Park et al. 2014). Such biomarkers could be utilized to trigger stimuli presentation when individuals are in more impressionable states. Similarly, VR could embed emotionally valent material during encoding to bolster memory strength (Chan et al. 2014). VEs can also help encode information passively. For example, an individual could rapidly encode an environment that has two rooms: one with an elephant in it and then a door to another with a monkey in front of a car that has two balloons on it. By subsequently revealing a "key" (e.g., take the first letter of each object, let each door be an equal sign, and use balloons as exponents), individuals will realize they have passively encoded $E = MC^2$.

6 Outro

This chapter has positioned VR as a potent environmental simulator in which cognition can be measured and modified with unparalleled granularity. Given the intimate relationship between memory and spatial processing, VEs have served as a ripe medium for ecologically valid investigations into memory and the facets of cognition it subserves. If the blind men from the parable in the introduction are researchers looking for the veridical underpinnings of cognition, then VR studies of memory have equipped them with dozens of highly sensitive hands.

The portability of VR in conjunction with other easily accessible data devices (e.g., activity trackers) sets the stage for conducting at-home crowd-sourced studies. Such non-laboratory-based efforts can still be financially incentivized while remaining anonymized with blockchain technology. Proceedings would allow for the creation of large, longitudinal normative databases that permit for investigations of how lifestyle attributes like sleep quality, activity levels, and drug use impact memory. The inherently engaging qualities of VR, coupled with its ability to implicitly quantify and enhance memory, make it a powerful tool in populations spanning from pediatrics to the elderly. As the era of "quantified self" is continually ushered into the collective, the evolution of VR and its incorporation into daily routines will provide pervasive upregulation of encoding processes as well as lifelong benchmarks of function that can identify and prevent insidious descents of cognition.

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