Cognitive Ageing of the Medial Temporal Lobe across Cultures: A Digital Neuropsychological Approach

Aminette D'Souza

Supervised by Prof. Andrew D. Lawrence and Prof. Kim S. Graham

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School of Psychology, Cardiff University

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Thesis Summary

In the context of a rapidly ageing global population, understanding the influence of age on cognitive functioning becomes imperative. The Medial Temporal Lobe (MTL) is widely acknowledged to be important for memory. This thesis applies a novel digital neuropsychological tool - Memory in Neurological Disorders (MiND) tablet-based application - which is informed by recent advancements in our understanding of MTL function (Graham et al., 2010) to investigate age-related changes in MTL-dependent cognition and assess if these effects generalise across cultures (UK and India).

Episodic memory - which is thought to be supported by the hippocampal operation of pattern separation - is known to be particularly vulnerable to age-related cognitive decline. In *Chapter 2*, I use a novel translational task on MiND to assess spatial pattern separation. I find that this hippocampal-dependent operation is not sensitive to age-related decline in middle-to-older aged adults. My results suggest that education may act as a protective factor, while culture-specific factors may contribute to risk.

Beyond memory, the hippocampus is specialised for scene representations which support various cognitive functions. In *Chapter 3*, on MiND, I test the boundary extension phenomenon which depends upon scene construction ability. Results show that boundary extension is universal but constrained by age and stimulus characteristics.

Finally, in *Chapter 4*, I examine the broader specialisations of MTL sub-regions for higher-order perception across representational categories. I use the MiND Oddity perceptual discrimination task to study age effects across stimulus categories. I find that age impairs MTL-dependent higher-order conjunctive processing. Importantly, object perception is more vulnerable to age-related cognitive decline than scenes across cultures.

Taken together, this thesis contributes towards a deeper theoretical understanding of cognitive ageing of the MTL and offers valuable insights for the early detection of cognitive decline, cognitive assessment of culturally diverse populations, and advancement of digital assessments in global health research.

To my dear grandmothers -

Catherine, who lost her memory but still remembered to dust the shelves;

and Katherina, with whom I hope to spend more time once I submit this thesis.

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My friends, near and far – I feel lucky to have shared this four-year journey of successes, struggles, and growth with incredible friends and fellow PhD students. Teddy and Abi, I look forward to celebrating together soon. All my other friends, I promise to return your calls as soon as I finish writing.

My family, my support system – Mummy and Daddy, words cannot express my gratitude for everything you have done for me. My dear sister, Kimi, you have helped me through this PhD in more ways than I can acknowledge here. And Alex, thank you for being by my side through the ups and downs of this journey. I feel so grateful to have such a remarkable support system in my life – I owe my achievements to all of you.

Lastly, all the participants in my studies – Even during a pandemic, thank you very much for generously contributing your time and support to my work. I value your contribution far beyond the research data you have provided.

Table of Contents

List of Abbreviations

ACE	Addenbrooke's Cognitive Examination
AD	Alzheimer's Disease
AIC	Akaike Information Criterion
ALSPAC	Avon Longitudinal Study of Parents and Children
APOE	Apolipoprotein E
AT	Anterior-Temporal network
ANOVA	Analysis of Variance
BE	Boundary Extension
bvFTD	Behavioural-variant Frontotemporal Dementia
COVID-19	Coronavirus Disease 2019
cTUNL	Continuous Trial-Unique Non-match to Location
CUBRIC	Cardiff University Brain Research Imaging Centre
DG	Dentate Gyrus
DOF	Depth of Field
EAM	Evolutionary Accretion Model
EM	Episodic Memory
ERC	Entorhinal Cortex
fMRI	Functional Magnetic Resonance Imaging
GDPR	General Data Protection Regulation
GLMM	Generalised Linear Mixed Model
HC	Hippocampus
HIC	High Income Country
hTUNL	Human Trial-Unique Non-match to Location
IES	Inverse Efficiency Score
IT	Inferior Temporal cortex

LASI	Longitudinal Ageing Study in India
LME	Linear Mixed Effects model
LMIC	Low-to-Middle Income Country
MCI	Mild Cognitive Impairment
MiND	Memory in Neurological Disorders
MMSE	Mini Mental State Examination
MRI	Magnetic Resonance Imaging
MST	Mnemonic Similarity Task
MTL	Medial Temporal Lobe
NFT	Neurofibrillary Tangles
NIMHANS	National Institute of Mental Health And Neurosciences
PART	Primary Age-Related Tauopathy
PCC	Posterior Cingulate Cortex
PHC	Parahippocampal Cortex
PM	Posterior-Medial network
PMAT	Posterior-Medial Anterior-Temporal framework
PRC	Perirhinal Cortex
PS	Pattern Separation
RSC	Retrosplenial Cortex
RSVP	Rapid Serial Visual Presentation
RT	Response Time
SC	Scene Construction
SD	Semantic Dementia
TUNL	Trial-Unique Non-match to Location
UF	Uncinate Fasciculus
vmPFC	Ventromedial Prefrontal Cortex
WEIRD	Western, Educated, Industrialized, Rich, and Democratic

Preface

In the history of medicine, it has long been recognised that an elevation in body temperature (i.e., a fever) is a marker of an infection. The subsequent development of a thermometer to objectively measure a change in body temperature was a significant milestone which made it possible to accurately detect, monitor, and treat infectious diseases. This instrument was built upon the "ground truth" that normal human body temperature - established from a database of patients in Germany in the 19th century - is 37°C (Wunderlich, 1871). Recent research, however, has refuted the idea of a universal normal body temperature, showing that mean body temperature has decreased by 0.03°C per birth decade since the Industrial Revolution (Protsiv et al., 2020). The COVID-19 global pandemic (which played an influential role in this PhD project) revealed that immune responses to infections, usually associated with an increased body temperature, can vary between individuals of different ages, cultural or environmental exposures, or genetic vulnerabilities (Bajaj et al., 2021; Melenotte et al., 2020; Ovsyannikova et al., 2020; Samadizadeh et al., 2021). The accuracy of measurement may also be limited by the type of thermometer (Niven et al., 2015). These findings highlight two key considerations in health research: i) the identification of valid and measurable correlates of health (or, biomarkers), and ii) the application of measurement tools sensitive to these biomarkers across diverse populations. The field of cognitive ageing - a relatively new focus in this period of global population ageing - faces similar challenges.

Chapter 1: General Introduction

1.1. Understanding Cognitive Ageing

The global demographic landscape is currently undergoing a notable transformation, marked by a substantial rise in the number of older individuals. According to recent projections, by 2050, the world's population above 60 years of age will rise to 2.1 billion, nearly doubling current figures (United Nations Department of Economic and Social Affairs, 2017). More strikingly, by 2050, it is estimated that 80% of the global population over 60 will be living in developing countries[1] (United Nations Department of Economic and Social Affairs, 2017). This demographic shift presents a complex challenge for societies worldwide, particularly in developing regions such as India. In this context, the issue of cognitive decline associated with normal ageing emerges as a pressing concern. As individuals age, a decline in cognitive functions may affect their ability to actively contribute to their communities, placing pressure on social and economic systems. Adding to this challenge, population ageing is associated with a rise in age-related neurodegenerative diseases, such as dementia (Fleming et al., 2020), which further exacerbates the cognitive health crisis. To address these concerns, it is imperative for health research to develop cognitive assessments which are sensitive to age-related cognitive decline and to expand these efforts to cross-cultural populations.

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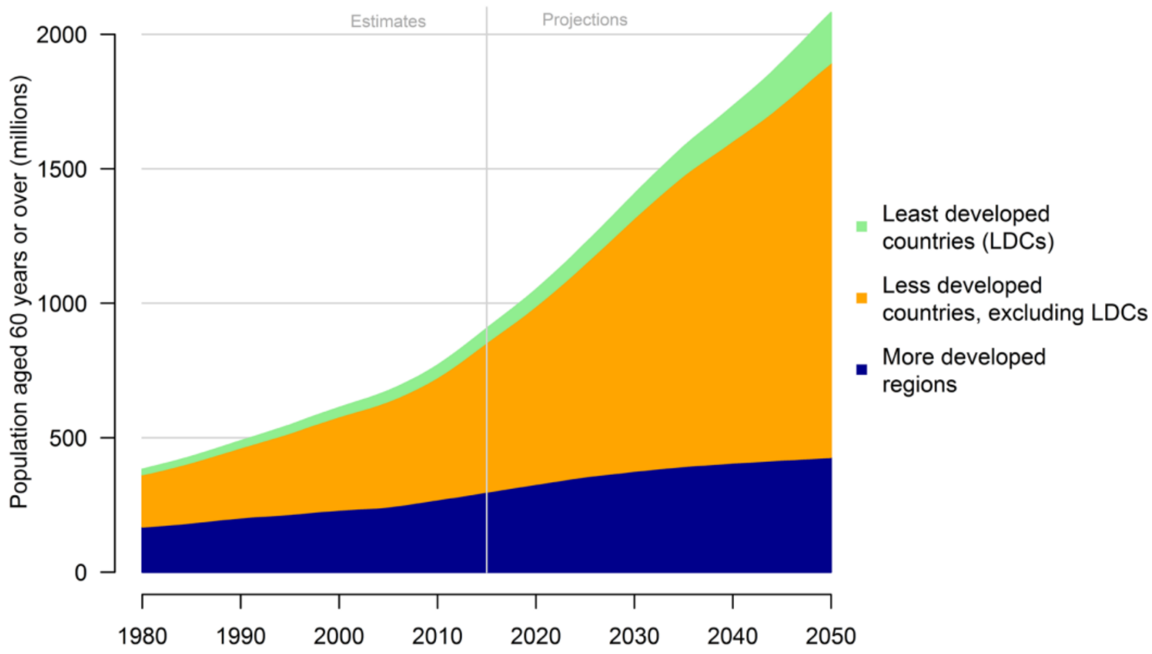
[1] As reported in the United Nations Department of Economic and Social Affairs (2017) population ageing statistics, the term "developed" regions encompasses Europe, Northern America, Australia, New Zealand, and Japan, whereas "developing" countries includes all other areas globally. The use of these terms in this thesis does not intend to imply a hierarchy or make any assessment regarding the current developmental stage of specific regions. It is important to recognise that labels such as developed/ developing, West/ East, or HIC/ LMIC tend to oversimplify complex socio-economic dynamics and may perpetuate misconceptions. However, given the lack of suitable alternatives, this thesis adopts this terminology while acknowledging challenges in accurately representing diversity. For relevant discussions on terminology applied in global health research and implications, see Khan et al. (2022) and Lencucha & Neupane (2022).

Figure 1: Estimates and Projections of the global population aged 60 years or over between 1980 - 2050 (reprinted from United Nations Department of Economic and Social Affairs, 2017)



Cognitive decline is a normal part of the ageing process - yet there is still variability in the influence of age on specific cognitive functions - some cognitive functions become increasingly impaired with age, while others are relatively spared (Wisdom et al., 2012). Among these functions, episodic memory (EM) - which refers to the ability to recall and remember specific events in time and space (O'Keefe, 1990; Tulving, 1985) - is found to be particularly susceptible to the effects of age (Grady, 2012; Maass et al., 2018; Tromp et al., 2015). Longitudinal studies have revealed that age-related impairments in EM may manifest as early as 60 years of age (Nyberg et al., 2012; Rönnlund et al., 2005). A surge of studies has emerged to investigate the underpinnings of age-related cognitive decline in the brain and explore the factors contributing to variability in EM (Bishop et al., 2010; Christensen et al., 2001; for a review, see Deary et al., 2009).

1.2. Role of the Medial Temporal Lobe (MTL)

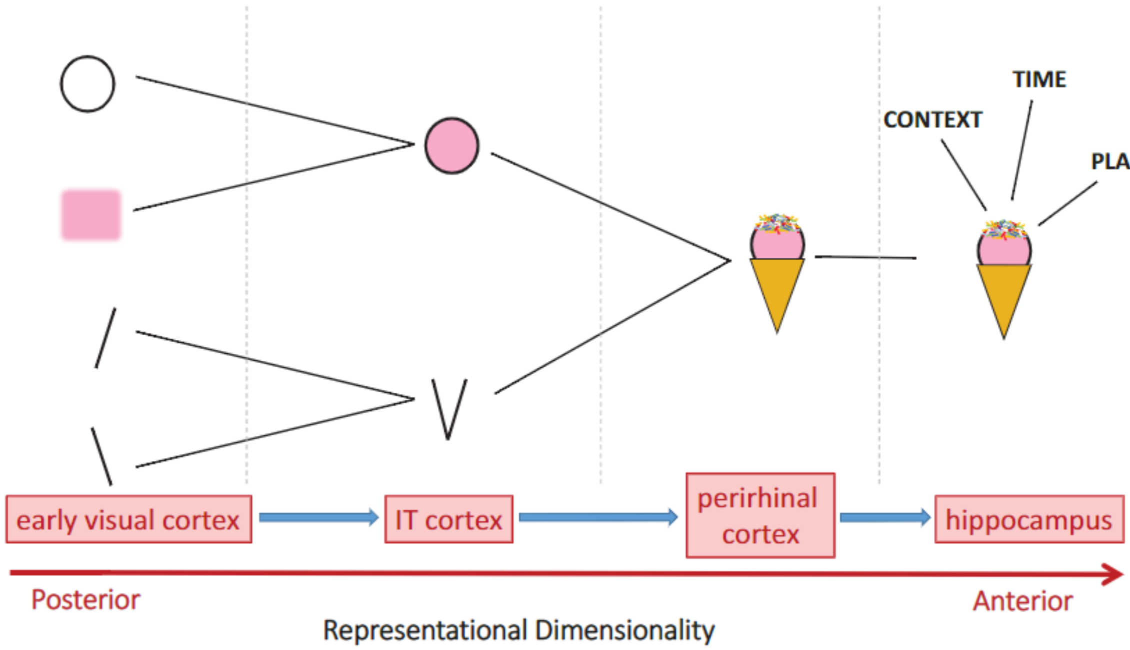
1.2.1. Theoretical Advances

It is well established that the Medial Temporal Lobe (MTL) brain region - comprised of the hippocampus (HC), entorhinal cortex (ERC), perirhinal cortex (PRC), and parahippocampal cortex (PHC) - plays a critical role in the formation and retrieval of episodic memories (Easton & Eacott, 2010; Eichenbaum et al., 2012; Nyberg et al., 1996; Scoville & Milner, 1957). Over the years, several proposals have been put forward to explain how this key brain region, and the structures it is composed of, support episodic memory (Aggleton & Brown, 1999; Eichenbaum et al., 2007; Graham et al., 2010; Maguire & Mullally, 2013; Ranganath, 2010; Saksida & Bussey, 2010; Yonelinas, 2013).

In episodic memory research, a long-standing view has been that there are two separate processes involved: recollection and familiarity (Aggleton & Brown, 2006; Yonelinas et al., 2010). Recollection involves the retrieval of information from memory without external cues, while familiarity refers to the identification of a previously encountered item from novel items. Both processes are thought to dissociate within the MTL - the HC is proposed to be critical for recollection, while the PRC is implicated in familiarity (Aggleton & Shaw, 1996; Baddeley, 2001; Hirsh, 1974; Moscovitch et al., 2006; Turriziani et al., 2019). However, this dual-process conceptualisation of the MTL functions (Aggleton & Brown, 2006; Yonelinas et al., 2010) is inconsistent with findings which have shown that associative recognition (involving item-context relationships) is selectively impaired in patients with hippocampal lesions, while item recognition is relatively normal (Bird & Burgess, 2008; Cipolotti et al., 2006; Lacot et al., 2017; Mayes et al., 2004). Thus, emerged frameworks conceptualising MTL sub-regions in terms of the content they process and bind together (Diana et al., 2007; Ranganath, 2010; Shimamura, 2010). Beyond memory processes, extensive work with animal models revealed a specialisation for the HC in spatial navigation (O'Keefe & Nadel, 1978), leading to the idea that the HC was important for representations of spatial scenes (Bird et al., 2010). Encompassing these seemingly disparate views of the HC, proposals by Maguire and Mullally (2013) and Hassabis and Maguire (2009) assign a central role for the HC in scene construction. But how does this integrate with a broader understanding of MTL specialisations?

A more holistic view is offered by contemporary representational accounts of MTL function, such as the representational-hierarchical model (Saksida & Bussey, 2010), the emergent memory account (Graham et al., 2010) and, more recently, the evolutionary accretion model (Murray et al., 2017). These have emerged from findings that MTL sub-regions involved in memory also play a role in supporting perception (Buckley et al., 2001; Bussey & Saksida, 2005; Graham et al., 2010). At the core of these contemporary models lies the shared premise that brain regions, such as the MTL, are organised in a hierarchical continuum of representations (or, patterns of neural firing). Lower levels of the hierarchy represent basic sensory information (such as features), and higher levels represent more complex, abstract information (such as feature conjunctions). As information passes through the ventral visual-perirhinal-hippocampal pathway (Cowell et al., 2010), the level or complexity of representations increases: beginning from early visual areas, sensory information is represented as lower-level features e.g. colour and shape, moving to more anterior regions such as PRC where complex conjunctions or combinations of features are represented and, finally, spatial associations and context are represented and resolved in the hippocampus. The specialisations of brain regions, therefore, are for the level of representation, and each region plays a role in various cognitive processes which rely on these representations, e.g. memory, perception, and attention (Graham et al., 2010; A. C. H. Lee & Rudebeck, 2010; Ruiz et al., 2020). Moreover, research has revealed specialisations within MTL regions for processing different types of stimulus representations i.e., scenes in HC and objects in PRC (Buckley et al., 2001; Bussey & Saksida, 2005; A. C. H. Lee, Buckley, et al., 2005; A. C. H. Lee, Bussey, et al., 2005; A. C. H. Lee et al., 2006).

Figure 2: Illustration of the Representational Hierarchical Framework (reprinted from Cowell et al., 2019)



1.2.2. Evidence for a Representational-Hierarchical View

Strong support for representational hierarchical models (Graham et al., 2010; Murray et al., 2017; Saksida & Bussey, 2010) comes from applications of the Oddity perceptual discrimination task, in both animal and human studies. The Oddity paradigm involves the presentation of an array of visual stimuli, from which two are identical and the other is perceptually similar but a different stimulus - the goal is to identify the "odd-one-out". Buckley et al (2001) were amongst the first to develop and apply the Oddity task in a study investigating the role of the perirhinal cortex in perceptual processing in macaques. They compared the performance of controls and macaques with PRC lesions on a series of Oddity tasks, each presenting different stimuli involving either simple feature discriminations (such as colour, shape, and size) or more abstract discriminations of conjunctions of features or objects (such as objects, degraded objects, scenes, human faces, and monkey faces). It was found that macaques with PRC lesions did not show significant performance impairments on the former but were significantly impaired on the tasks that required processing at the conjunction level. Furthermore, these impairments were more pronounced when these stimuli (i.e., objects and faces) were also presented from different viewpoints. These results support the hypothesis that the PRC plays a selective role in the perceptual processing of stimuli which involves complex conjunction- or object-level discriminations. Furthermore, the authors suggest that the impairments observed on scene processing could be because the monkeys perceived these stimuli as objects or images of objects.

Stark and Squire (2000) applied the same stimuli used with monkeys in a study with amnesic patients who had damage to PRC regions. In contrast to results from the animal study, they found that patients performed all tasks at par with controls. But performance was still found to be lower on the face Oddity in some patients. Building upon this, the Oddity task was adapted by Lee, Buckley et al. (2005) with the application of trial-unique stimuli, thereby reducing any reliance on memory. They tested four types of stimuli on their Oddity task (same-view scenes, different-view scenes, same-view faces, and different-view faces) with patients who showed selective hippocampal damage and a group with damage to wider MTL regions including the PRC. Results revealed that HC patients were selectively impaired only on the different-view scene condition, while patients with wider MTL (including HC and PRC) damage were impaired on both different-view scenes and faces on the perceptual discrimination task. Importantly, no differences were found on the same-view stimuli between patients and controls, suggesting that MTL regions such as the HC and PRC are necessary for viewpoint-independent perception. These results in human participants strengthened the proposal that MTL sub-regions such as the HC and PRC are involved in perception, and they are selectively involved in processing complex representations of scenes and faces, respectively. Lee et al. (2006) also found striking evidence for a double dissociation on the Oddity task: AD patients - who show predominantly HC atrophy - were selectively impaired on a scene Oddity task; SD patients - who have greater PRC atrophy - showed impairments only on a face Oddity task but not a scene Oddity task. Converging evidence for scene Oddity specificity to the HC and object/ face specificity to the PRC comes from neuroimaging studies (Barense et al., 2009; A. C. H. Lee et al., 2008).

Localised structures of the MTL, such as the hippocampus and perirhinal cortex, are now understood to operate within large-scale neurocognitive networks (Mesulam, 1990) which are specialised for generating specific and dissociable types of representations, such as for scenes and objects. The evolutionary accretion model (EAM) proposed by Murray and colleagues (2017) describes two distinct cortical networks which contribute to memory: a medial network, which includes an extended hippocampal navigation system; and a lateral network, which includes a feature system. The former network consists of the hippocampus (HC), parahippocampal cortex (PHC), retrosplenial cortex (RSC), posterior cingulate cortex (PCC) and is connected via the cingulum bundle; the latter includes the perirhinal cortex (PRC), various prefrontal regions, anterior temporal regions, and is connected via the uncinate fasciculus. A related 'PMAT' framework described by Ranganath and Ritchey (2012), identifies the Posterior Medial (PM) and Anterior Temporal (AT) networks, which closely map on to the medial and lateral networks respectively. The PM network includes the parahippocampal cortex (PHC), retrosplenial cortex (RSC), cingulum bundle tract, and is involved with scene or spatial representations; the AT network comprises of the perirhinal cortex (PRC), prefrontal regions, uncinate fasciculus tract, and is associated with object-level feature representations, including semantic concepts and categories. These networks extend towards the entorhinal cortex (ERC) – the posterior-medial ERC is involved with scene content, while the anterior-lateral ERC is strongly connected with the PRC and plays a greater role in object processing (Knierim et al., 2014; Maass et al., 2015; Reagh & Yassa, 2014). Corresponding network distributions and distinctions are also identified by Catani and colleagues (2013) in their limbic system model. Their model includes the hippocampal-diencephalic and parahippocampal-retrosplenial network and dorsomedial default network, which covers structures and functions that are comparable to the medial network (Murray et al., 2017) or PM network (Ranganath & Ritchey, 2012) described earlier.

Using a diffusion MRI approach in combination with the Oddity task, Hodgetts, Postans et al. (2015) identified functionally dissociable MTL neurocognitive networks for scene and face perception i.e., fornix (white matter tract connecting HC) and inferior longitudinal fasciculus (connecting PRC) respectively. Given connections between the PRC and frontotemporal regions via the uncinate fasciculus (UF) tract, Coad et al. (2020) applied the face Oddity and a novel face emotion Oddity task to isolate the functional contributions of the UF to emotion perception. Results revealed an involvement of right UF microstructure in emotion perception, but not face perception tasks. Performance on the Oddity task is also associated with genetic AD risk: Shine and colleagues (2015) showed that young adult carriers of the APOE-e4 allele were impaired on scene perceptual discrimination but not face or object discrimination. Performance on scene perception was linked with lesser ability to modulate the posteromedial cortex, which is implicated in episodic memory (Buckner et al., 2008) and is part of the spatial processing brain network (Ranganath & Ritchey, 2012). Taken together, these findings provide strong support for a representational-hierarchical view of the MTL, which conceptualises this brain region in terms of its specialisations for processing different types/ categories of complex conjunctive representations, which support diverse functions such as memory and perception (Graham et al., 2010; Saksida & Bussey, 2010).

Returning to EM processes such a recall and recognition, Cowell et al. (2019) argue that by focusing on these high-level mental phenomena, one may overlook the underlying components which may actually drive certain behaviours. This may explain the difficulties faced by earlier MTL models, which focused on recall and recognition, in explaining contradictory findings (Aggleton & Brown, 2006; Yonelinas et al., 2010).

Instead, Cowell et al. (2019) propose that cognitive processes can be broken down further into "operations" and "representations". Operations can be defined as algorithmic computations performed by the brain, such as pattern separation, which involve the generation of neural signals corresponding with memory strength; while representations consist of patterns of neural firing for a particular stimulus or event (Cowell et al., 2019). A process such as recollection, therefore, involves both an operation and representation - identifying and treating these components in isolation allows for a deeper understanding of the mechanisms underlying memory and age-related cognitive decline.

1.3. Influence of Age on MTL Function

As part of normal ageing, there are significant structural and functional alterations within the MTL (Berron et al., 2018; Fjell et al., 2009, 2014; Raz et al., 2004; Stoub et al., 2012), which are associated with age-related deficits (Head et al., 2009; Van Petten, 2004; Wolf et al., 2001). EM, as a result, is particularly susceptible to age-related cognitive decline (Nyberg et al., 2003; Rönnlund et al., 2005). In this section, to understand the mechanisms underlying these age-related impairments, I will decompose memory into its underlying components i.e., operations and representations (Cowell et al., 2019), and examine evidence for specific age-related changes.

An example of an operation performed within the HC is pattern separation (Bakker et al., 2008) - this involves the differentiation of similar inputs or patterns of neural activation to create distinct, non-overlapping inputs before storage (Marr, 1971; for a review, see Yassa & Stark, 2011). In simpler terms, when we are presented with new information/ events which need to be stored in memory, the process of encoding involves differentiating this information from already stored memory of similar information/ events to avoid interference at a later point of retrieval. It has been argued that pattern separation (PS) is a crucial component of episodic memory and a failure to pattern separate results in episodic memory impairments in normal ageing (Yassa & Stark, 2011). PS has been linked with the dentate-gyrus (DG) sub-field of the hippocampus (Marr, 1971; O'Reilly & McClelland, 1994). Age-related changes in this structure may contribute to the deficits observed in PS with age (Bennett et al., 2015; Yassa et al., 2010; Yassa, Mattfeld, et al., 2011). Since PS occurs at the cellular level and is not possible to directly study in humans, one approach that has been taken in the literature is to use a proxy behavioural measure such as a mnemonic discrimination paradigm. On this task, participants are required to differentiate between previously encountered stimuli and new, but perceptually-similar stimuli. Successful performance on this task involves the correct identification of "similar" items (as opposed to categorising them as "old"). Several studies have found evidence for a significant age-related decrease in performance on such tasks (Huffman & Stark, 2017; Leal & Yassa, 2015; S. M. Stark et al., 2015; S. M. Stark & Stark, 2017) - in this case, older adults are more likely to confuse similar stimuli with previously encountered stimuli, thereby resulting in false memories or false alarms.

An increase in false memories, such as those observed on behavioural pattern separation tasks (S. M. Stark et al., 2013, 2015; Yassa, Lacy, et al., 2011), is a common observation in ageing literature (Devitt & Schacter, 2016; Gellersen et al., 2021; Jacoby & Rhodes, 2006). It has been linked with age-related changes in the MTL (Devitt & Schacter, 2016). A specific type of false memory which is linked with the HC is called boundary extension (BE). The BE error is demonstrated when recalling a visual scene - for certain close-up images, it has been observed that viewers recall a wider context surrounding the scene than what was actually shown to them (Intraub & Richardson, 1989). The memory error has been linked with scene construction ability in the HC (Maguire & Mullally, 2013; Mullally et al., 2012). Paradoxically, it offers an adaptive advantage in integrating views and predicting spatial layout (Gottesman, 2011). Although studies have found that healthy adults across the lifespan commit the BE error

(Intraub & Richardson, 1989; Quinn & Intraub, 2007; Seamon et al., 2002; Spanò et al., 2017), some report that the BE error increases with age (H. Te Chang et al., 2021; Seamon et al., 2002).

From a representational lens (Graham et al., 2010; Murray et al., 2017; Saksida & Bussey, 2010), it has been suggested that high-feature ambiguity between conjunctive representations is associated with poorer performance in ageing (Gellersen et al., 2021; Newsome et al., 2012; Ryan et al., 2012). In participants with memory impairments due to PRC damage, Newsome et al. (2012) found that increasing the degree of perceptual interference reduced task performance. Following up on this, Ryan et al. (2012) conducted a neuroimaging study to compare the performance of healthy young and older adults on an object perceptual discrimination task previously shown to be sensitive to PRC lesions (Barense et al., 2012). Ryan et al. (2012) used an object matching paradigm which consisted of pairs of complex blob-like objects and relatively simpler squares. They found that older adults, relative to young adults, were impaired at object discrimination when the stimuli were more complex/ more perceptually-similar i.e., blob-like objects which involved discrimination of more overlapping features than simpler square stimuli. These behavioural deficits were related to lower levels of activation of the left anterior PRC in older adults compared to young adults, suggesting that age-related changes in PRC function cause impairments in complex object perceptual discrimination – a finding that is supported by animal research (Burke et al., 2010, 2012).

Gellersen (2021) applied high-ambiguity scene and object Oddity trials in a study with young and older adults. They found that older adults exhibited a notably greater decline in performance compared to young participants. This is in line with findings from the application of memory discrimination tasks with older individuals, where age-related performance deficits have been observed on conditions involving a high degree of perceptual similarity between stimuli (Gusten et al., 2021; Reagh et al., 2016; Reagh & Yassa, 2014; S. M. Stark & Stark, 2017). In fact, numerous studies have found that older adults perform more poorly when asked to recall specific details, such as the spatio-temporal context of an event, rather than gist-based details (Addis et al., 2008; Cansino, 2009). Leal & Yassa (2015) explain that age-related reductions in representational quality of scene/ spatial details in the HC and object details in the PRC could underlie decline in EM observed in normal ageing. However, further research is still required to understand the drivers of episodic memory decline in ageing. Using a fine-grained approach of testing the integrity of specific MTL-based operations and representations in ageing may provide greater clarity.

1.4. Variation in Cognitive Ageing of the MTL

1.4.1. Cross-cultural Evidence

Trajectories of age-related cognitive decline are found to be heterogeneous (Mungas et al., 2010) - many factors have been identified which may contribute to this variation (Deary et al., 2009; Lenehan et al., 2015; Mortensen & Høgh, 2001; T. A. Salthouse, 2009). In this thesis, I explore one possible source of variation i.e., culture. While several studies discussed so far in the cognitive ageing literature have shown evidence for age-related changes in MTL-dependent cognition, it must be noted that most of this research arises from High-Income Countries (HICs)/ developed nations/ Western societies/ WEIRD societies (Henrich et al., 2010; for discussions on terminology, see Khan et al., 2022; Lencucha & Neupane, 2022). As limited research has examined these changes in Low-to-Middle-Income Countries (LMIC)/ developing nations/ non-Western societies, the question of whether cognitive ageing is a byproduct of neurobiological processes or shaped by cultural experiences is still largely unexplored. As ageing is associated with several neurobiological changes (Erickson & Barnes, 2003; Kelly et al., 2006; Lacreuse et al., 2020), this is a unique opportunity to probe the age-old debate of nature versus nurture within the realm of cognitive ageing.

Brain measures associated with age-related cognitive decline largely reveal similar effects of ageing across culturally diverse populations. Loss of brain volume, particularly in temporal lobe regions such as the hippocampus, has been found in healthy older adults (Fjell et al., 2009, 2014), and this is strongly associated with cognitive decline in an ethnically and educationally diverse population in the U.S. (Fletcher et al., 2018). Chee et al. (2011) report a broadly similar pattern of age-related reduction in total cerebral and hippocampal volume in an elderly East Asian sample as compared to findings from studies conducted in the West. Early autopsy studies comparing neuropathological changes revealed that the mean ages of onset of neurofibrillary tangles (NFTs i.e., abnormal accumulations of tau protein) in non-demented individuals – which is found to be associated with age-related cognitive impairments in object processing (Maass et al., 2019) – are similar between three geographically distinct populations i.e., Brazil, Germany, and Japan (Dani et al., 1997). Furthermore, NFT depositions are qualitatively and quantitatively similar between age-matched non-demented cases in East Africa and USA (Ogeng'o et al., 1996).

In India, autopsy studies with non-demented older adults have found that the incidence of age-related changes in NFTs reported in HICs is comparable with studies conducted with small samples in North-west India (S. K. Mohanty et al., 2004), and South India (Yasha et al., 1997). Despite the similarities reported in these studies, direct cultural comparisons are often challenging due to limitations in the size and characteristics of the samples compared, and the use of different research protocols. Purohit et al. (2011) attempted to address this by recruiting a larger sample and employing strict protocols to directly compare non-clinical autopsy cases in India with age- and gender-matched cases in USA for AD-related pathology such as NFTs. After excluding any cases with a diagnosis of AD, results indicated no significant differences in the mean density and counts of NFTs between both geographical samples. These studies suggest that biological processes associated with age-related cognitive decline (such as reduction in brain volume and tau accumulation) may be largely generalisable, but whether culture also influences the trajectory of cognitive decline is yet to be determined.

In the context of cognition, Park et al. (1999) provided a framework to understand the combined influences of culture and age. They propose a distinction between fundamental cognitive processes (hardware) and culturally acquired knowledge (software) in cognitive ageing research. From this perspective, any cultural differences observed in culturally acquired knowledge may magnify with age. On the other hand, differences in basic cognitive processes may reduce with age as neurobiological changes in ageing may reduce capacity and limit flexibility in mental processes, thereby resulting in cross-cultural similarities in age effects.

Chee et al. (2009) compared the performance of young and older cohorts in Singapore on basic cognitive processes such as processing speed, executive function, attention, and visuospatial measures. They report similar patterns of age-related cognitive decline in older adults as found in Western populations. Similarly, Hedden (2002) found that patterns of age-related performance decline on visuospatial measures of processing speed and working memory were comparable between Chinese and American participants. However, a different pattern emerged on the verbal tasks – while this may indicate cultural differences in this function, it could also be attributed to the characteristics of the measurement tool – translating or equating the properties and difficulty level of linguistic stimuli across diverse groups is a common challenge with verbal assessments. When cross-cultural differences are observed in performance on such cognitive tasks, it is difficult to determine whether this reflects differences in the underlying cognitive abilities or if it is due to the cultural in-appropriateness of the task. Category fluency is another area known to decline with age due to changes in the semantic network (Levine et al., 2002) – it has been found that older adults across cultures show a similar decline in free recall (Gutchess et al., 2006). Interestingly, even though East Asians used less categories than Americans in this study, these differences in categorisation did not result in differences in the number of words recalled. Neuroimaging evidence from Goh et al. (2007) has indicated that, irrespective of cultural background, ageing uniformly results in decreased activation of the hippocampus. Research in the area of cross-cultural differences across the lifespan seems to indicate that, despite differences in strategies or content of recall, the trajectory of age-related decline is comparable across cultures.

A few recent investigations have focused on understanding MTL-dependent mechanisms underlying memory across cultures. Previous studies on memory have found some evidence for cross-cultural behavioural differences in memory specificity i.e., memory of specific object features or events. Millar et al. (2013) showed that Western populations tend to remember more object details than Eastern populations, suggesting that culture may influence the quantity/ quality of representations encoded/ retrieved in memory. Building on this, Leger & Gutchess (2021) compared pattern separation performance between North Americans and East Asians and tested whether any differences were related to cultural values often studied in the context of cognitive differences (see Masuda & Nisbett, 2001). On the first experiment, they predicted that both cultural groups would show similar performance when distinguishing between old and new stimuli (or, general memory), but North Americans would be better than East Asians when discriminating old stimuli from similar-looking new stimuli (or, specific memory). Interestingly, a main effect of culture was observed across conditions - North Americans performed better than East Asians on both, discriminations of old and new stimuli as well as old and similar-looking new stimuli. Moreover, personal values (Schwartz, 1992; Singelis, 1994) were not strongly correlated with pattern separation ability. These results indicate that North Americans may have more detailed representations of previously studied stimuli, and this may be partly attributed to pattern separation ability as well as broader memory mechanisms such as memory resolution for stimuli previously encoded.

From a representational-hierarchical view, Leger et al. (2023) expanded previous work to evaluate whether the representational component of memory may explain cultural differences observed in earlier studies (Leger & Gutchess, 2021; Millar et al., 2013). They tested memory for higher-level feature conjunctions (i.e., objects) and lower-level features (i.e., shape, colour, size). Similar to Leger & Gutchess (2021), they found a general effect of culture, with North American participants performing better across representational levels. Taken together, these results support the idea that culture influences memory, and adds novel insights by showing that MTL-dependent operations and representations do not fully explain these cultural differences. However, based on the framework provided by Park et al. (1999) for understanding cross-cultural cognitive ageing, it can be argued that MTL-dependent operations and representations are the "hardware" of higher-level cognitive phenomena. From this perspective, one may expect to see greater convergence with age in terms of cognitive decline. It is possible to gain a deeper understanding of memory in ageing by testing these basic MTL components.

1.4.2. Considerations in Cross-cultural Research

Cross-cultural research is far from straightforward - a recent article by Fischer & Poortinga (2018) identifies several methodological issues in the literature. I focus on three key issues here, which I have attempted to address in my research. First, the most apparent issue - and yet the most overlooked - is the difficulty in defining 'culture'. The concept is usually used in reference to the core values and beliefs shared by a group (Faulkner, 2003) - yet, in practice, this is difficult to measure. Therefore, several proxy measures have been utilised e.g., language (Laesser et al., 2014) or geographical location (Brewer & Venaik, 2012; Taras et al., 2016). Another difficulty arises in trying to determine the relative cultural distance between studied groups. As Fischer & Poortinga (2018) point out, in ethnography, the concept of culture was traditionally applied to an isolated group of people with a unique lifestyle different from other groups. In such conditions of isolation, cultural characteristics of the group were believed to be relatively homogeneous, unique, and persisting over time. Today's globalised world, however, presents a very different picture - cultural and geographical borders are increasingly blurred and it is extremely unusual to come across a group of people who live in complete isolation. Nonetheless, in cross-cultural comparative research, Fischer & Poortinga (2018) concede that there needs to be an acceptance of some degree of "essentialism" between groups i.e., the idea that there are some traits and characteristics that are specific to a particular culture and not shared with other cultures (e.g, Fuchs, 2001).

The majority of research in cross-cultural psychology, so far, has focused on the East-West divide (i.e., comparing East Asian populations with North Americans). Therefore, little is known about the cognitive performance of South Asian populations, such as Indians, in the context of ageing. On the cultural dimension of individualism-collectivism, Indian culture is found to fall in the middle of the spectrum, between typically studied Western cultures (e.g., United States) and East Asian cultures (e.g. China) respectively (Hofstede, 1984, 2011). More recently, Muthukrishna et al., (2020) adopted a data-driven approach in systematically quantifying the cultural distance and psychological distance between countries (http://www.culturaldistance.com/). By applying the fixation index, a concept from population biology, to the World Values Survey (2005 – 2014), they calculate and visualise on a scale the relative distance between countries. For reference, the distance between two Western/ HIC societies (i.e., US and UK) is 0.056 (a larger value indicates a larger distance), while the distance between typically compared Western and Eastern countries (i.e., North America and China) is 0.170, and the distance between lesser compared countries (i.e., UK and India) is 0.141 (Muthukrishna et al., 2020). In my thesis, I diverge from other cross-cultural studies in the field by comparing UK and India. As revealed by the cultural distance scale (Muthukrishna et al., 2020), these two cultures are closer to each other on average than the East-West/ China-North America focus in cross-cultural research, thus providing novel insights into cultural differences. To define culture, I have applied a combination of language and geographical proxies to determine group belonging.

A second issue relates to the cultural bias of cognitive measures and constructs developed in the West and then implemented in other societies (Rosselli & Ardila, 2003; van de Vijver & Tanzer, 2004). Many cognitive tasks used in cross-cultural research were developed and validated in Western societies, so they need to be adapted and translated to be applied in other countries. However, translation can result in subtle changes in the task's meaning and difficulty. For example, some cultures may not have exact linguistic equivalents for certain concepts. In this thesis, to avoid the influence of such effects, I have applied tasks which use non-verbal and computer-generated stimuli designed to be "culture-free" (as per software parameters). Though it can be argued that cultural bias is an inherent characteristic of cognitive assessments transferred from one group to another, this is a first step towards addressing these issues in research.

The third issue is that of drawing direct comparisons between cultural groups. It is challenging to equate groups on different dimensions, so any observation of group differences may actually arise from unaccounted factors. Historically, cross-cultural studies have primarily centered around highlighting group "differences" (Fischer & Poortinga, 2018). However, there are alternative approaches, such as a focus on generalization - this involves identifying universal principles or patterns that apply across diverse cultural contexts. Ultimately, the choice between these contrasting approaches depends on the specific research aims i.e., whether the goal is to understand mechanisms underlying different group behaviours (e.g., Leger et al., 2023; Leger & Gutchess, 2021) or to uncover overarching principles that transcend cultural boundaries (see Haeffel & Cobb, 2022). In this thesis, I was interested in understanding how the trajectory of age-related cognitive decline generalises across cultures, and not how culture influences performance levels within particular age groups. Hence, I have adopted a generalisation approach in my analysis and interpretation of findings.

1.5. Aims of Thesis

In this section, I have traced developments in our understanding of the role of the MTL, culminating in the formulation of the representational-hierarchical account of MTL function (Graham et al., 2010; Murray et al., 2017; Saksida & Bussey, 2010). By reviewing literature in the area of cognitive ageing and cross-cultural psychology, I have identified several research gaps which I aim to address in my thesis. While a large body of literature has examined how age influences EM and underlying cognitive processes, an understanding of the specific components of memory processes - operations and representations (Cowell et al., 2019) - which are susceptible to age requires further attention. Furthermore, population ageing is a global phenomenon - it is imperative to bridge the gap in our understanding of how cognitive ageing generalises cross-culturally. Previous cross-cultural research has predominantly compared two distinct cultural groups along the East-West divide. It is yet to be understood how populations closer on the cultural distance scale (Muthukrishna et al., 2020), such as UK and India, compare in terms of trajectories of cognitive ageing.

To expand cognitive ageing studies to wider global populations, the use of digital technologies is emerging as a potential solution. Over recent years, there has been an increased interest in the application of digital assessments with older adults (Öhman et al., 2021; Rienzo & Cubillos, 2023; Staffaroni et al., 2020; Zygouris & Tsolaki, 2015). More recently, researchers at Cardiff University and Ounce Technology (https://ouncetech.co.uk/) have developed the Memory in Neurological Disorders (MiND) tablet-based application. MiND is a novel digital cognitive tool for the assessment of MTL-based cognitive function such as memory and perception. The tasks on MiND draw upon latest insights into the role of the MTL and specialisations of its sub-regions (Graham et al., 2010). Moreover, tasks on the MiND app are designed to be visual rather than verbal, thereby facilitating cross-cultural transferability. In this thesis, I have applied the MiND App with healthy young and older adults cross-culturally (*Study*

A: UK and *Study B: India*) to examine age effects on paradigms known to be sensitive to MTL function.

In *Chapter 2*, I aim to understand the influence of normal ageing on the hippocampal-dependent operation of spatial pattern separation, and I will expand this study to a different cultural context (i.e., India) to examine whether patterns of ageing observed in spatial pattern separation generalise more broadly.

In *Chapter 3,* I turn towards the representational component of memory processes. I focus on the specialisation of the HC for scene representations. Here, I aim to investigate whether age influences scene construction ability by testing the phenomenon of boundary extension (Intraub & Richardson, 1989). I ask whether boundary extension is demonstrated across age groups and whether any changes are observed with increasing age. I then apply this task with an Indian sample to understand how this generalises.

In *Chapter 4*, I take a broader view by studying different MTL-dependent representational specialisations (e.g., scenes and objects) in complex perception. I apply a perceptual discrimination task assessing multiple content categories to test whether age influences complex perception. I also ask whether vulnerabilities differ between representational content, and I aim to replicate these findings with an Indian sample.

Finally, in *Chapter 5*, I discuss how findings from *Chapters 2 - 4* enhance our understanding of the vulnerabilities of the MTL in normal ageing, and how this generalises cross-culturally. I will reconcile my findings with existing theoretical accounts of memory and MTL function; and I will discuss implications for the early detection of cognitive decline, development of digital cognitive assessments, and the wider application of these tools cross-culturally.

Chapter 2: Influence of Age on Pattern Separation across Cultures

2.1. Introduction

The hippocampus (HC) is known to play an important role in episodic memory (Eichenbaum & Cohen, 2004; Squire et al., 2004; Squire & Zola-Morgan, 1991; Vargha-Khadem et al., 1997), which involves memory of previous experiences and events in time and space (Tulving, 1983, 2002). The key operation of pattern separation (PS) within the hippocampus is proposed to underlie episodic memory (Leal & Yassa, 2018; for a review, see Yassa & Stark, 2011). Pattern separation involves the transformation of similar inputs into unique, non-overlapping representations to reduce interference (O'Reilly & McClelland, 1994; Yassa & Stark, 2011). In other words, this operation distinguishes between similar experiences and events to allow for the formation of unique traces in memory which are not confused with existing memories. By creating distinct representations, PS is crucial for maintaining the specificity and detail which is important for EM. In normal ageing, a marked decline is observed in EM (Grady, 2012; Hedden & Gabrieli, 2004), and this may be associated with an attenuation in the pattern separation ability in the HC (Yassa & Stark, 2011). The development of cognitive tasks specifically targeting PS is crucial as it would provide insight into how age impacts this hippocampal operation and whether age-related changes in PS generalise across cultures.

Within the hippocampal formation, the dentate gyrus (DG) sub-field is proposed to be the neural substrate for pattern separation (Marr, 1971; O'Reilly & McClelland, 1994). Evidence for this comes from electrophysiological studies in rodents - Leutgeb et al. (2007) found that dentate granule cells, compared to cells in other hippocampal sub-fields, are particularly sensitive to small differences between stimuli. This sensitivity is crucial for discriminating between similar inputs - a key aspect of PS. Furthermore, lesion studies with rats have shown that the DG is necessary for pattern separation(Gilbert et al., 2001; Kesner et al., 2004). An fMRI investigation in humans by Bakker et al. (2008) found support for activity consistent with pattern separation in the DG, compared to other hippocampal sub-fields, and this was supported by a more recent 7T fMRI study by Berron et al. (2016). These findings from both animal and human studies underscore the importance of the DG sub-field of the hippocampus for pattern separation.

In ageing, the dentate gyrus sub-field is found to be particularly vulnerable - electrophysiological studies in rats have shown reduced synaptic activity in the DG, pointing towards a decline in functional capacity with age (Barnes, 1979; Barnes et al., 1980). While it is not possible to directly measure PS at the cellular level in human studies, indirect behavioural measures of PS such as mnemonic discrimination paradigms also find supporting evidence for an age-related decline (Gellersen et al., 2021; Rizzolo et al., 2021; S. M. Stark et al., 2015; S. M. Stark & Stark, 2017). A behavioural tool which is commonly applied to measure PS is the Mnemonic Similarity Task (Kirwan & Stark, 2007; S. M. Stark et al., 2013, 2019). On this task, participants are shown a series of items in the study/ encoding phase and later tested on their memory of these items. In the test phase, participants are presented with three types of images: repeats (identical to previously presented images, also referred to as ‘targets’ in the literature), novel images (not shown before, also referred to as ‘foils’), and lures (perceptually similar to previously shown images but not identical). Participants are asked to respond to each test item with “old”, “new” or “similar” judgments. In the context of PS, the key measure is the identification of lures as “similar” images rather than “old”. Successful PS would involve the discrimination of similar inputs from existing traces in memory. Several studies have shown that ageing is associated with impairments in lure discrimination performance in older adults (Huffman & Stark, 2017; S. M. Stark et al., 2015; S. M. Stark & Stark, 2017), and this is correlated with structural and functional age-related changes in hippocampal regions such as the DG (Yassa et al., 2010; Yassa, Lacy, et al., 2011).

Evidence discussed so far indicates that the observation of an age-related decline on PS measures converges across species (Cès et al., 2018; Leal & Yassa, 2015; S. M. Stark et al., 2013, 2015; Yassa & Stark, 2011). Within our own species, however, there is a dearth of research examining how the influence of age on PS generalises to other cultures. Leger and Gutchess (2021) applied the MST (Kirwan & Stark, 2007; S. M. Stark et al., 2013) across a series of experiments to compare pattern separation performance in two cultures, North Americans and East Asians. They found some evidence for cultural differences in PS, with North Americans showing higher performance than East Asians at the identification of similar items as similar (indicating successful PS), but they did not find significant correlations between value measures (Schwartz, 1992) and pattern separation performance. Interestingly, Leger and Gutchess (2021) also found that North American participants performed better on other task conditions which do not assess PS per se. These results demonstrate a general effect of culture on the task rather than a specific effect on conditions which tax pattern separation, suggesting that other influences may be at play. However, the question as to whether the trajectory of age-related changes in PS is similar across cultures remains largely unanswered.

A notable criticism of the application of discrimination paradigms such as the MST for the assessment of PS is that performance may not reflect pattern separation per se, but may reveal complex memory processes which depend upon pattern separation (Aimone et al., 2011; Leal & Yassa, 2018; for discussions, see Yassa & Stark, 2011). Recent studies have revealed that mnemonic discrimination tasks are not ‘process-pure’ and may also rely on cognitive control (Gellersen et al., 2021; Pishdadian et al., 2020). Furthermore, stimuli on mnemonic tasks such as the MST (Kirwan & Stark, 2007; S. M. Stark et al., 2013) involve everyday objects which may not be appropriate to apply cross-culturally. For the development of cognitive assessments of PS, Hunsaker and

Kesner(2013) put forward two key requirements that must be met by pattern separation paradigms: i) the level of interference (or, overlap) between stimuli should be systematically varied; and ii) there should be a way of measuring how behaviour changes as a function of the level of interference. A key attribute of pattern separation is that it occurs at the encoding phase (Marr, 1971; McClelland et al., 1995), and tasks assessing PS should manipulate the degree of interference at this stage.

In line with the guidelines provided by Hunsaker and Kesner (2013), Talpos et al. (2010) developed a paradigm which was originally applied to investigate hippocampus-dependent pattern separation ability in rodents, called 'Trial-Unique Non-matching-to-Location' (TUNL). The experiment begins by presenting a single rectangular stimulus on a touchscreen. Following a brief interval, the original stimulus reappears with a novel target stimulus in a new location on the screen, and the subject must touch the new stimulus location on every trial. The location of target stimuli is varied across trials (i.e., trial-unique), and the spatial separation between the original and target stimuli (or, interference) is manipulated with small (highest interference), medium, and large (lowest interference) spatial distance conditions. This design can be used to probe spatial working memory and spatial pattern separation ability (i.e., the ability to differentiate between similar spatial locations on a screen); smaller spatial separation distances (or greater similarity between original and target stimuli locations) increase the demand on pattern separation operations. Talpos et al. (2010) found that performance accuracy decreased as spatial distance decreased, and rodents with hippocampal lesions demonstrated a greater impairment than controls in smaller separation conditions. These results reveal the sensitivity of the TUNL paradigm to hippocampal lesions. Moreover, McAllister et al. (2013) found that lesions of the medial prefrontal cortex – a region associated with working memory (Courtney et al., 1998) – do not contribute to separation-dependent deficits observed on the TUNL task, suggesting that PS performance on the TUNL task is specific to hippocampal integrity. To probe specific hippocampal sub-fields implicated in PS, Oomen and colleagues (2015) developed a variation of this paradigm called continuous TUNL (cTUNL). In this modification, the novel target location on a previous trial is carried forward as an incorrect location on a subsequent trial beside a new novel stimulus location. This combines the original presentation and test phases, creating a continuous test paradigm, which allows for spatial separation to be manipulated at encoding and retrieval stages. It also allows for the number of stimuli on the screen to be increased, thereby increasing spatial working memory load. Oomen et al. (2015) found that, in rodents, cTUNL performance was sensitive to damage in the dentate gyrus sub-region of the hippocampus, which is regarded as the key neural substrate for pattern separation in rodents and humans alike (Bakker et al., 2008; Berron et al., 2016; Leutgeb et al., 2007).

More recently, researchers at Cardiff University have adapted the cTUNL task for implementation with human subjects i.e., human Trial-Unique Non-match to Location (hTUNL). In the present study, I apply this novel translational task as part of the MiND tablet-based app (introduced in *Chapter 1*) with healthy young and older adults in the UK and India. First, I aim to understand how normal ageing influences hippocampal-dependent spatial pattern separation. A growing body of animal and human literature has shown that ageing impairs pattern separation performance (Bakker et al., 2008; Burke et al., 2010; Dillon et al., 2017; for a review, see Holden & Gilbert, 2012). Similarly, on mnemonic discrimination tasks - a behavioural proxy measure for PS (Kirwan & Stark, 2007; S. M. Stark et al., 2013) - age-related impairments are commonly observed (Leal et al., 2014; Reagh et al., 2014; S. M. Stark et al., 2015). On hTUNL - a spatial pattern separation measure - I expect to see similar age-related declines, with older adults demonstrating lower accuracy than young adults, particularly on small spatial separation distances (high interference condition which increases demand on fine pattern separation). Second, I investigate how age effects on pattern separation generalise across cultures, specifically in the UK and India. I do not test an a priori hypothesis here as the present study is the first to apply a spatial pattern separation paradigm with an Indian population to study cognitive ageing.

2.2. Methods

2.2.1. Participants

Study A: UK

For this study, data collection was carried out in Cardiff, UK, after the study received approval from the Cardiff University School of Psychology Research Ethics Committee. Young adults were recruited through Cardiff University School of Psychology's undergraduate student participant panel. For the older group, participants were recruited from the wider Cardiff University population using University mailing lists and message boards, and from the pool of volunteers in the Cardiff University School of Psychology Community Panel.

The inclusion and exclusion criteria for all participants were: (i) Must be between 18 – 25 years of age (for the young sample), or 50 – 70 years of age (for the older sample), (ii) Must have normal or corrected-to-normal vision (e.g., glasses), (iii) Must not have any known memory impairments, neurological conditions, or brain injury, (iv) Must not be taking any psychoactive or neuroactive medications, (v) Must speak English or Welsh as a first language. It should be noted that inclusion criterion (v) was added retrospectively, as it was recognised that the student and staff community at Cardiff University came from diverse cultural and linguistic backgrounds. To avoid an overlap in cultural characteristics between the samples tested in *Study A* and *Study B,* first language was used as a proxy definition for culture. Furthermore, due to the difficulty in recruiting participants in the older group, the pre-determined age range was wider than that of the young sample. As this study was disrupted by the COVID-19 pandemic, the sample size was determined and limited by travel, time, and resource constraints. While the initial sample tested included 164 adults, after applying the language criterion (v), 23 adults (21 young and 2 older) were excluded from the study, and an additional young adult was excluded due to incomplete task data. The final sample size for *Study A* after exclusions was $N = 140$ ($n = 71$ young adults, $n = 69$ older adults). These sample characteristics are summarised in *Table 1*.

Study B: India

Data collection for this study was initially carried out in Bangalore, India. However, due to travel restrictions during the COVID-19 pandemic, a part of the sample was recruited and tested in Vadodara, India. This study received ethical approval from the National Institute of Mental Health and Neurosciences (NIMHANS) Research Ethics Committee, India. In Bangalore, participants were identified and contacted with help from study collaborators at NIMHANS. Young adults were recruited from the Psychology postgraduate student community at Bangalore University. The older adults were either volunteers from local community groups, or teachers at the Mahila Seva Samaja Senior Secondary School in Bangalore. In Vadodara, participants were identified and contacted with help from the Navrachana Education Society and the Vadodara Psychology Club. Young adults were recruited either from the student population at Navrachana University, or the student members database at Vadodara Psychology Club. Participants were studying different University disciplines (i.e., Journalism, Sociology, and Business Administration), and degree levels (i.e, Bachelor's and Master's). Older adults tested in this study were either teachers based at the Navrachana Education Society institutions (i.e., Navrachana International School Vadodara, Navrachana University, Navrachana Vidyani Vidyalaya, and Neev Prep School), or community members of the Vadodara Psychology Club.

The inclusion and exclusion criteria (i), (ii), (iii), and (iv) were similar to *Study A*. Additionally, the language criterion (v) for this study was that participants must speak English or Kannada fluently (as the MiND app was only available in both these languages at the time of testing). In this study, it was not possible to include participants based on a shared first language/ majority language due to the wide heterogeneity in linguistic backgrounds that exists in India. As this study was delayed by the COVID-19 pandemic, the sample size was determined by the maximum number of participants who met the criteria above and could be tested within the limited time-frame. From the initial sample tested (152 adults), two participants from the young group were excluded due to errors in data recording, one young participant did not complete all the tasks, and one participant from the older group chose to withdraw from the study. After these exclusions, the final sample size for *Study B* was $N = 148$ ($n = 76$ young adults, $n = 72$ older adults). The sample characteristics are summarised in *Table 3*.

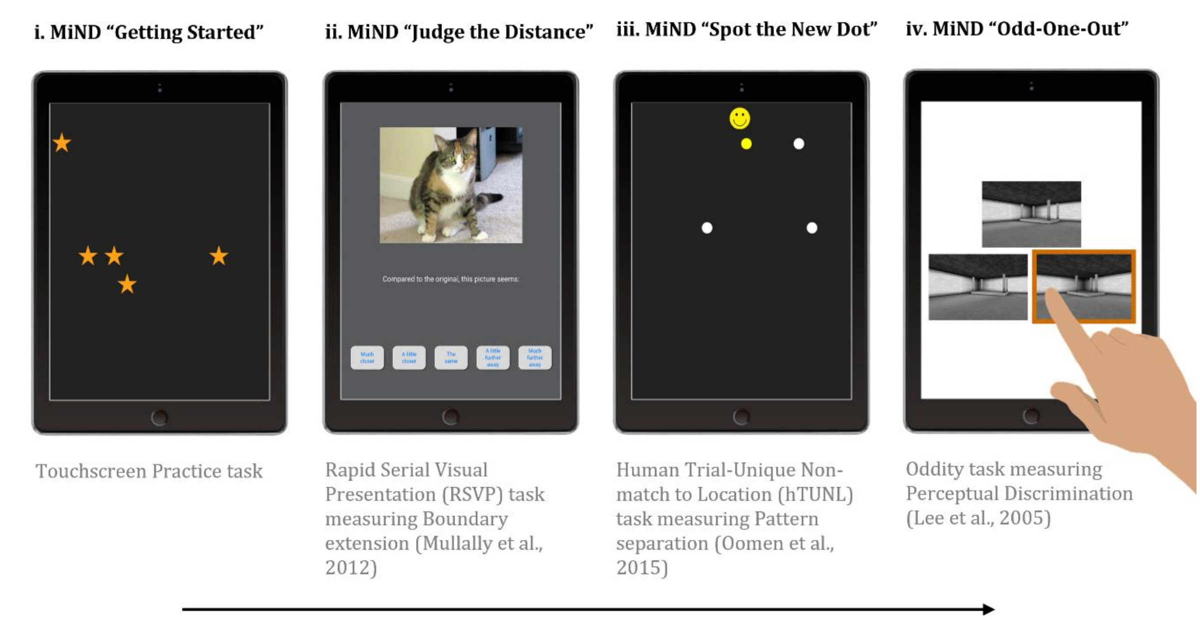
2.2.2. Procedure

Participants were invited to attend in-person testing sessions where they were asked to complete a series of tasks. In *Study A: UK*, data collection was carried out with each participant individually at the Cardiff University Brain Research Imaging Centre (CUBRIC) cognitive testing labs. In *Study B: India*, data collection was carried out at multiple locations (i.e., during university, school, or home visits). Testing was carried out either individually or in groups of 2 - 6 participants in this study, to accommodate for time, travel, and room availability restrictions set by the host institutions or arising from the COVID-19 pandemic. Care was taken to avoid interruptions and limit environmental distractions during testing. In both studies, the testing room and equipment was set up in a similar manner, and the test administration was kept constant. In *Study A: UK*, with all participants, the test was administered in English using the original English version of the MiND app. In *Study B: India*, participants were given the option to complete the study either in English or Kannada (a commonly spoken language in Bangalore, India). Kannada translations (and back translations) for the study instructions and tasks were written and piloted by collaborators at NIMHANS, India, before implementing it on MiND.

At the start of the study, participants were provided with an information sheet and consent form, and given the opportunity to clarify any doubts before deciding to provide their written consent. For the rest of the study, a tablet device was used to carry out all the tasks. The device used was an Apple© (Apple Inc, 2023) iPad 6th generation with a 9.7-inch (diagonal) screen size, and a 2048-by-1536-pixel screen resolution. The operating software used was iOS 11 - 15, depending on the latest available version at the time of testing with each participant. Following each software update, rigorous piloting was carried out to ensure that the app functions and task presentation remained constant for all participants. The iPad was set-up on a tablet stand with an approximately 45^{o} recline angle measured by eye.

On the tablet, participants were administered the following tasks on the MiND application (introduced in *Chapter 1*) in a fixed order: i) Touchscreen practice task (called “Getting Started” on MiND), (ii) Rapid Serial Visual Presentation (RSVP) task (“Judge the Distance” on MiND), (iii) Human Trial Unique Non-Match to Location task or hTUNL (“Spot the New Dot” on MiND), and (iv) Oddity perceptual discrimination task (“Odd-One-Out” on MiND). After attempting the tasks on the MiND app, participants were asked to complete a Demographics and Digital Experience survey which was administered on the Qualtrics online survey platform (Qualtrics, 2022). Task (i) was a digital training task to give participants an opportunity to get familiar with the tablet and practice responding on it by touching the screen. They were simply asked to touch stars on the screen until they disappeared. The design and results for task (iii) and the Qualtrics survey will be discussed further in this chapter. At the end of the study, participants were debriefed, given an opportunity to ask any questions, and reimbursed for their time. On average, each study session took 72 minutes to complete. See *Figure 3* for a summary of the MiND app tasks and presentation order. Also see *Appendix A* for a screenshot of the MiND app home screen with the task menu.

Figure 3: Summary of tasks on the MiND tablet-based application



Note. Screenshots of the four tasks on the MiND application administered on a tablet device. Each of these tasks is selected from the MiND home screen to commence; at the end of each task, an option appears to return to the MiND home screen and select the next task in the sequence. The four tasks were presented in a fixed order on the home screen, and participants were instructed to follow this sequence. Participants had to respond on each task by touching an option or stimulus on the screen. In the current chapter, task (iii) will be described further; see *Chapter 3* for task (ii) and *Chapter 4* for task (iv).

2.2.3. Materials

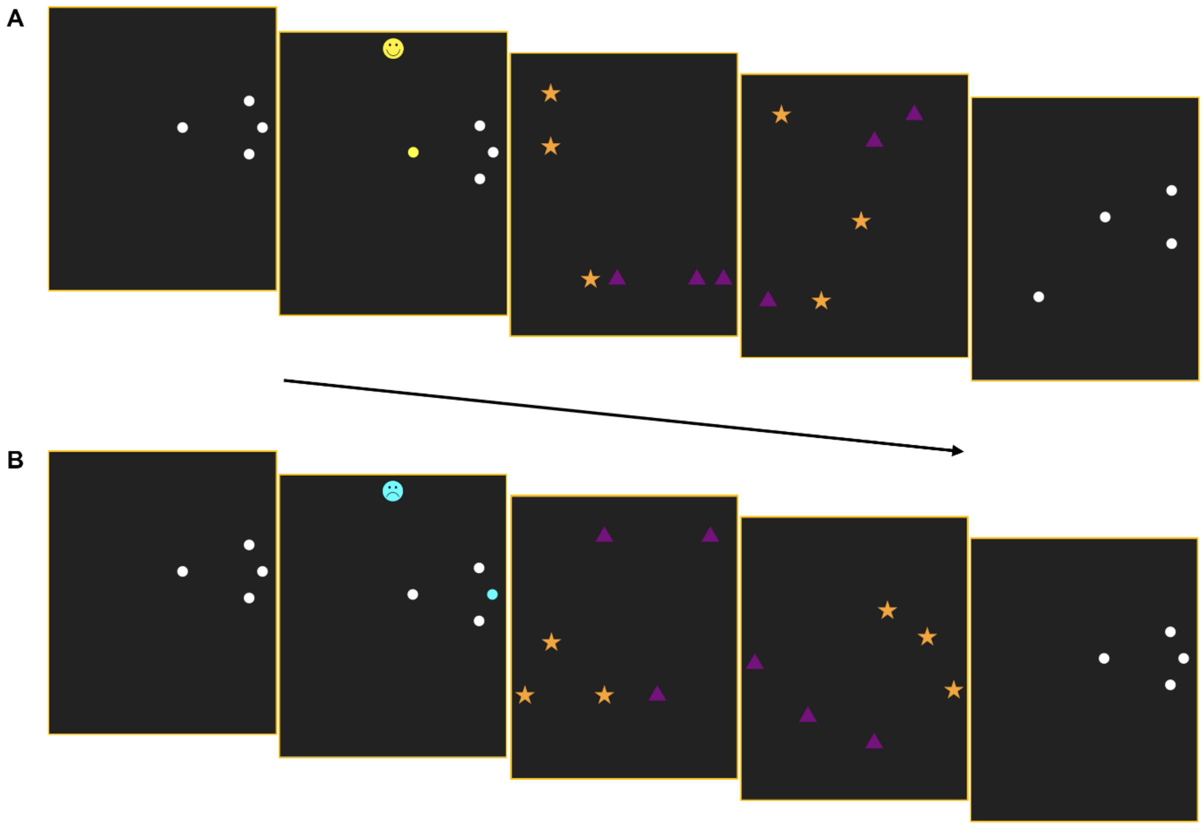
MiND human Trial-Unique Non-matching to Location (hTUNL) Task

This is a novel translational task adapted from paradigms designed to study working memory and spatial pattern separation in rodents i.e., the continuous trial-unique non-matching to location (cTUNL; Oomen et al., 2015) and, an earlier version, the trial-unique non-matching to location (TUNL; Talpos et al., 2010) tasks. In the present study, human participants were tested using a modified version of cTUNL (Oomen et al., 2015), referred to as human Trial-Unique Non-match to Location (hTUNL; Postans et al., in prep; Palmer et al., 2021).

To increase the complexity of hTUNL for humans compared to earlier paradigms used with rodents, the number of stimuli presented on the screen and the complexity of the visual array have been increased, and a distraction task has been introduced. The task began with the presentation of a single white dot location on a black screen, and participants were instructed to touch the dot in order to proceed. Following this initial stimulus, a 10 secs distractor screen involving orange stars and purple triangles randomly distributed across the screen would appear - participants were asked to touch all the stars and ignore the purple triangles (the orange stars used here were similar to the stimuli used in the touchscreen practice task on MiND i.e., Getting Started). The distractor task involved two screens of stars and triangles to respond to, with each screen lasting either 5 secs or the time taken to touch all the stars and complete the task (whichever was longer). Following this delay, participants were shown two white dot locations on the screen - this time, one dot was the previously touched location (S -), and the other was in a novel/ target location (S +); participants were asked to touch the new dot (S +). There was no time limit applied, and the stimuli remained on the screen until a response was given. If the participant responded correctly, a happy smiley face would appear at the top of the screen, and the task would proceed to the distractor task, after which a new trial would appear. If an incorrect response was provided (i.e., participant touched the old dot location (S -), a sad smiley face would appear, and the task would proceed to the distractor task, after which it would repeat the same trial (correction trial) until the participant provided the correct response. Once the trial and distractor screens were successfully resolved, a new trial would appear with three white dot locations on the screen, including the previously touched location (S -), the target from the earlier trial (S - -), and a novel dot location (S +). Once more, participants had to successfully select the new dot (S +) to trigger the next trial (correction trials if wrong, and distractor screens before every new trial or correction trial applied for all trials).

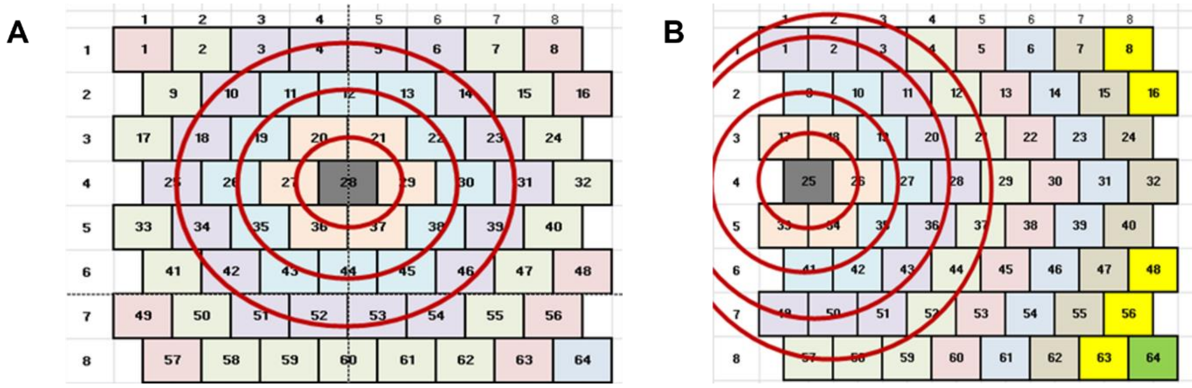
A 3- and 4-stimulus version of hTUNL were piloted with young participants, before selecting the 4-stimulus design for this study as there were no ceiling effects in performance on this version. In this version, the number of dot locations on the screen increased until there were 4 presented at a single time i.e., the previously touched location (S -), the earlier target location (S - -), the target prior to that (S - - -), and the novel location (S +). Once the task reached this point, all subsequent trials involved the simultaneous presentation of 4 stimuli, with one of these being the target dot location. See *Figure 4* for the task sequence on correctly and incorrectly answered trials with 4 stimuli. This task always began with a practice round where detailed instructions were provided to participants at every step until participants reached a point where 4 stimuli were presented to them on the screen and they were able to successfully resolve the trial. There was also an opportunity to repeat practice trials before proceeding to the test phase which involved a total of 48 trials with new dots appearing on the screen. The location of the novel dot on every trial (S +) was assigned randomly from a screen grid of 6 options of separation distances from the previous target location on the screen (S -) i.e., 1 - 2 spaces were assigned as a small separation distance, 3 - 4 spaces were medium, and 5 - 6 were large. This breakdown of separation distances met Hunsaker and Kesner's (2013) criteria for parametric alteration of the degree of interference, and behavioural responses would be expected to scale with this interference. This screen grid was used to break down task performance by levels of separation distance at retrieval (or, separation at retrieval) i.e., small, medium, or large. Moreover, combining the six separation distances to form three levels also served to maximise power in each condition. See *Figure 5* for a diagram of how the screen was divided into a grid composed of equal separation spaces. It was hypothesized that accuracy on this task would scale with the level of retrieval separation for each novel dot location (S +) from a previous dot location (S -) on every trial.

Figure 4: MiND human Trial-Unique Non-matching to Location (hTUNL) Task Schematic for (A) Correctly answered trials and (B) Incorrectly answered trials



Note. (A) Four dots are presented on the screen, one of these was not presented on the previous trial and is a new/ target dot location. The participant has to identify the new dot location (S +) by non-matching to previously rewarded dot locations (S -/ S --/S ---). The distance between S + and S - was manipulated as either small, medium, or large spatial separation at retrieval. If the participant correctly touches the new dot, a smiley face appears to indicate that it was the correct option. Two distractor screens will then appear, where the participant has to touch all the orange stars and ignore the purple triangles to continue. Each distractor screen lasts for 5 secs or the time taken for the participant to touch all the stars, whichever is longer. The next trial will then begin where one older dot will disappear and a new target dot will appear in place of it, and the participant needs to touch the new dot once again. (B) Four dots are presented on the screen, one of these is new and was not presented on the previous trial. If the participant selects the incorrect dot, a sad face appears to indicate that it was the incorrect option. The distractor task will then appear, followed by the same presentation of dots again - this is a correction trial. This correction trial sequence is repeated until the participant provides the correct response.

Figure 5: Screen Grid applied for separation distances between dots on the hTUNL Task (Reprinted from Postans et al., in prep)



Note. This grid demonstrates how the spatial separation distance between stimulus S - (i.e., the target location on the previous trial) and stimulus S + (i.e., target dot location on the current trial) is randomly assigned on the screen. The grey box 28 in (A) and box 25 in (B) represent stimulus S - on different trials. On a given trial, the location of S + will be either 1, 2, 3, 4, 5, or 6 spatial separation distances away. This is randomly selected from the corresponding distance circles e.g., the smallest circle around box 28 represents all grid locations which are 1 spatial separation distance away, the second circle represents distances which are 2 spatial separation distances away, and so on. Locations of target stimulus S + are not repeated across trials.

Demographics and Digital Experience Survey

This survey was used to collect basic demographic information on participants, their previous experience/ familiarity with using digital devices (with the aim to ascertain whether this may be a potential confound), and qualitative user experience feedback on the tablet assessments. This self-report survey was designed using Qualtrics XM Platform (Qualtrics, 2022), and participants responded to it on the tablet after completing the MiND cognitive tasks. Multiple-choice, short text entry, or Likert scale style questions were used on the survey. As per GDPR guidelines, providing responses was not mandatory on any of the questions, and participants could skip a question if they wished to. However, the questionnaire completion rate for all participants was 100%. The design of survey items is described here:

(i) Demographics: There were 7 demographic questions which asked participants about their age, gender, education, current employment status, whether they resided in an urban or rural area, their first language, and how many languages they could speak. For education, participants were asked to select the current/ highest degree or level of school completed from a list of options. Halfway through the study, an additional question was added for education – participants were also asked how many years of formal education they had completed. However, data collected with this additional question was not analysed due to the following reasons: the missing data for earlier participants, the unreliability of self-report estimates for this question (as older participants, in particular, did not always remember exactly how many years they had spent in formal education), and due to the difficulty in equating diverse educational backgrounds, schooling systems, or countries of schooling that participants had been a part of (e.g., part-time vs. full-time, repeated qualifications, school starting age). The rural vs. urban residence question was used as a proxy measure for socioeconomic status. However, data from this question was not included in analyses due to the lack of clear, objective socioeconomic or geographic demarcations between urban and rural areas. The 'first language' question was only used to perform sample exclusions (as explained in *Chapter 2.2.1*). All other demographic questions were analysed further.

(ii) Digital Experience: First, participants were asked whether they used their own smartphone. If they responded "yes", this was followed by a set of 5 questions asking them whether their device had a touchscreen, approximately how long they had been using their device, what purpose(s) they usually used their device for, and their rating for how comfortable they are with a smartphone on a scale from 1 - 10 (1 = Not at all comfortable; 10 = Extremely comfortable) and how competent they would say they are with a smartphone (1 = Beginner; 10 = Expert). If participants answered "no" to the initial question, they were presented with 3 questions asking them whether they had any experience with using a smartphone, and their ratings for their comfort and perceived competence with a smartphone. Finally, all participants were asked whether they had experience with using any other digital devices. As this experiment was carried out with participants from different age groups and countries (in *Study A: UK* and *Study B: India*), this part of the questionnaire was used to quantify and further analyse the variable levels of experience that participants may have had with digital devices. As most participants reported that they extensively used their own smartphones with touchscreens, the rating scale questions on comfort and perceived competence were found to be more informative about the quality of their digital experiences. Therefore, only these two measures were analysed further.

(iii) Feedback: Participants were asked a set of 4 questions to understand how their experience was with using the tablet to perform the tasks, whether all the task instructions were clear to them, if there were any technical issues with the tablet and/ or applications while completing any of the tasks, and whether they had any additional comments or suggestions. The data collected from this set of questions was not included in any analyses reported in this thesis but was used to check data quality and participant engagement with the tasks, and to identify any issues in the experimental setup, equipment, or paradigms.

2.2.4. Analysis

All data cleaning and statistical analyses reported in this thesis were conducted with R version 4.2.2 (R Core Team, 2022) using R Studio (RStudio Team, 2022). Descriptive statistics, outlier identification, statistical tests, and effect sizes were calculated using the rstatix package (Kassambara, 2021) and coin package (Hothorn et al., 2006). Where appropriate, linear mixed effects models (LME) and Generalised linear mixed effects models (GLMM) were built using the lme4 package (Bates et al., 2015).

The lmerTest package (Kuznetsova et al., 2017) was applied with LME models to calculate p-values for model fits using Satterthwaite's degrees of freedom method. For GLMM, the car package (Fox & Weisberg, 2019) was used to produce ANOVA tables for model effects. Estimated marginal means for main effects, trends, and comparisons of slopes were analysed using the emmeans package (Lenth, 2022), and model predictions using marginal means were calculated using the ggeffects (Lüdecke, 2018) package. The level of significance for all statistical tests was set at $p < .05$. Where Cohen's d effect sizes are reported, they have been interpreted according to Cohen's (1988) criteria: 0.20 - 0.50 is a small effect, 0.50 - 0.80 is a medium effect, and 0.80 or greater is a large effect. For correlations, the strength of association between variables is interpreted as low for correlations between 0.30 - 0.50, medium for correlations between 0.50 - 0.70, and high for correlations which are 0.70 and above. It should be noted that the order or direction of all comparisons run on R is alphabetical by default, and coefficients should be interpreted accordingly - in the present analysis, performance of older adults was evaluated against young adults. For data visualisations in R, the packages ggplot2 (Wickham, 2016) and plotly (Sievert, 2020) were used. The methods described here were independently applied to both, *Study A – UK* and *Study B – India.*

Data for this task was first aggregated at the participant level (i.e., combined by calculating means or sums for trial-level variables for each participant) before carrying out any cleaning and analysis steps. As this task involved correction trials which would be triggered if a participant provided a wrong response on any given trial, and the correction trials would be repeated until the participant was able to provide the correct response (i.e., choose the new dot location) on that particular trial, it is possible that participants who did not follow the instructions appropriately, were distracted, or found the task very challenging had an unusually high number of correction trials across the task. To avoid the influence of such anomalies on the analysis, the boxplot method was applied separately in each study and with each age group to identify any extreme outliers (high outliers which fall outside the "whiskers" of a box plot) in the total number of correction trials on the task for each participant. This method uses the Interquartile range (IQR) and identifies extreme points as values which are above Quartile 3 + 3 x IQR or below Quartile 1 - 3 x IQR. In *Study A: UK*, two participants were identified, one from the young and one from the older sample, who had extremely high numbers of correction trials. By investigating the trial-level data for these participants, it was found that the young participant performed corrections on 33 of 48 trials with new dot locations, and up to 9 corrections on a single trial in the small separation condition (which was designed to be the highest difficulty condition). The older participant performed corrections on 31 of 48 trials, and up to 14 corrections on a single trial in the small separation condition. Two extreme points were also identified in *Study B: India*: a young participant who performed corrections on 37/48 trials, and up to 8 corrections on a single trial in the small separation condition, with none correct on the first attempt in this condition; a participant from the older sample had corrections on 39/48 trials, with up to 29 corrections on a single trial in the small separation condition. These participants were excluded from both studies respectively before further cleaning was applied. Further inspection of accuracy (i.e., trials where participants correctly identified the new dot location (S +) from an array of older dot locations on the first attempt) was carried out to identify participants who may have performed at or below chance. As this task employed a 4-choice design, the probability of selecting the target response on each trial was 25%, so the probability of answering at or below chance was 25%. Mean task accuracy was calculated for each participant to identify any participants who may have responded randomly throughout the task. This criterion identified 4 participants from *Study B: India* (n = 1 young, n = 3 older adults) who performed at or below chance on this task, and these participants were excluded from further analysis. Interestingly, the participants with low mean accuracy also had quicker mean RTs, suggesting that there might have been a speed accuracy trade-off at play. Further checks were conducted with mean response time for correctly answered trials only. An absolute minimum mean RT threshold of 200 ms was applied on this task to filter any responses which may have been provided randomly (Ashby & Townsend, 1980; see Gusten et al., 2021 for a similar implementation of RT cut-off; Whelan, 2008) – however, no exclusions had to be made based on this criterion. Since the task did not enforce an upper time limit or time-out, the box plot method was applied in both studies to identify any extreme outliers. Four participants (n = 2 healthy young, n = 2 healthy older) were identified from *Study B: India* with extremely high mean RTs. However, these participants also had mean accuracy scores which were well over chance, possibly due to a speed-accuracy trade-off, so they were not excluded from the analysis at this stage.

Finally, a combined speed-accuracy measure - Inverse Efficiency Scores (IES) (Bakun Emesh et al., 2022; also see Bruyer & Brysbaert, 2011; Townsend & Ashby, 1978) - was also calculated. IES is calculated as Mean RT of correct responses (Liesefeld & Janczyk, 2019) divided by Proportion Correct. Townsend and Ashby (1983) explain that IES can be best interpreted as “the average energy consumed by the system over trials” (p.204) - or a measure of inefficiency. It uses the same unit of measurement as RT and is useful in cases where a speed-accuracy trade-off may be suspected i.e., slower RTs associated with higher accuracy, and faster RTs associated with lower accuracy. A further step of cleaning was carried out here by applying the box plot method with IES scores in both studies. In *Study B: India*, two extreme points were found (n = 1 healthy young, n = 1 healthy older) with high IES scores, and these participants were excluded from the dataset. The cleaning steps described here resulted in the exclusion of 2 participants (n = 1 healthy young, n = 1 healthy older) from *Study A: UK;* and 8 participants (n = 3 healthy young, n = 5 healthy older) from *Study B: India*.

For analysis, participant-level outcome measures were aggregated by retrieval separation distances/conditions (i.e., small, medium, and large distances). Earlier iterations of the TUNL paradigm have similarly grouped participant performance by spatial separation distance as performance is expected to decline with reductions in spatial separation distance (e.g. Oomen et al., 2015). I focus on three outcome measures here: i) Mean Accuracy (calculated as proportion correct) by Retrieval Separation, ii) Mean Response Time (RT) by Retrieval Separation, and iii) Inverse Efficiency Scores (IES) by Retrieval Separation. i) Mean Accuracy was calculated by taking the sum of all correct responses on each separation condition and dividing it by the sum of all correct and incorrect responses on that particular condition. ii) Mean RT was RT averaged across all correctly answered trials on each separation condition. iii) Mean IES was calculated by dividing the Mean RT of correct responses on each separation condition by the Mean Proportion Correct. Speed-accuracy correlations were also calculated by separation group to determine whether IES was an appropriate measure for the data. The relationship between speed and accuracy may vary between spatial separation distances of varying difficulty, such as there may be a more evident trade-off on a harder condition such as the small separation distance; hence, a combined performance measure may provide additional insights here.

Statistical Tests and Modelling

The distributions of the data were checked before running further tests. To compare performance measures between age groups, Welch independent sample *t*-tests were used. Performance differences between age groups were investigated further using linear mixed effects (LME) models to understand which variables were significant predictors. Compared to traditional regression models, an LME approach offers several advantages, such as it is better at accounting for variability in data as it combines fixed effects (similar to predictor variables in linear regression models) with random effects (e.g., individual- and group-level differences which may influence measures such as RT). The model estimation is also better at handling unbalanced data, where in the number of observations varies between groups being compared in the same model (e.g., due to outlier exclusions). Finally, the LME model is relatively robust to violations of normality in a dataset, compared to simple linear models (Brown, 2021; Schielzeth et al., 2020). This is an important advantage, especially when working with Response Time data which typically follows an Ex-Gaussian distribution (Balota & Spieler, 1999). The lme4 package (Bates et al., 2015) and the lmerTest package (Kuznetsova et al., 2017) on R (R Core Team, 2022) were used to model the data and test the significance of effects. For all outcome measures, fixed effects and a random participant-level effect were added to the model; the latter is useful to account for individual variation in the data (Gellersen et al., 2021; for a similar analysis, see Gusten et al., 2021). The models were fitted using the Restricted Maximum Likelihood method as it reduces bias in estimates. In *Study A: UK*, the following equation was used to build each model: *Outcome measure = Retrieval Separation Group*Age + Education + Digital experience score + (1 | Participant ID).* The Education variable was not included in *Study B: India* as it did not differ significantly between age groups and there was only one participant in this sample who had an education below University-level. The modelling equation applied in *Study B: India* was: *Outcome measure = Retrieval Separation Group*Age + Digital experience score + (1 | Participant ID).*

For the separation condition, which is a categorical variable with three levels, the deviation method was applied to contrast-code each level of the factor with values which represent deviations from the overall mean. This allows for coefficients to be interpreted as how much each level differs from the mean of the variable. To make the interpretation of effects more practical in terms of original units of measurement, variables were not standardised or rescaled before entering them into the model. Age was treated as a continuous variable to capture the variability in performance across the age spectrum studied here (for a similar analysis, see Gusten et al., 2021). A group by age interaction is tested as age is expected to impair performance particularly on the small spatial separation condition (Yassa & Stark, 2011). Where appropriate, education was entered into the model as a binary variable to maximise power i.e., education “At/ Above

University-level" and "Below University-level"; Digital experience was entered as a continuous numeric variable. To avoid overfitting, Gender and Number of Spoken Languages were not included in the models as they did not differ significantly between age groups, and the addition of these variables did not improve the fit of the models. All models built using the parameters described here met the assumptions of model diagnostic tests, and any outliers which were identified as influential points based on Cook's distance cut-off of 1 were investigated further. Finally, using the emmeans package (Lenth, 2022) on R (R Core Team, 2022), post-hoc tests with a 95% confidence level were run to contrast age trends between spatial separation groups (i.e., pattern separation difficulty levels) after correcting for multiple comparisons using the Tukey method.

2.3. Results

2.3.1. Study A: UK

Sample Characteristics

The final sample for this study comprised of 140 participants (n = 71 young and n = 69 older adults). The characteristics of this sample are summarised in *Table 1* by age group. The age of the young participants ranged from 18 to 24 years (M = 19.35, SD = 1.22), while the older participants had a broader age range between 50 and 70 years (M = 60.74, SD = 6.22). The number of women outnumbered the men, with a gender ratio of 3.73:1 in the young group and 2.83:1 in the older group. A Pearson Chi-squared test showed that both groups did not differ significantly by gender ($\chi^2(1) = 0.24$, p = .623). See *Figure 6* for a histogram displaying the age and gender distribution.

As the young group was recruited from a University population, it was largely homogeneous as 100% of participants had an education level at or above University-level and were enrolled in University degrees at the time of testing. On the other hand, the older group was characterised by a comparatively greater variation in education and employment. In this group, 73.91% of participants had an education level at or above University-level, while 26.09% were below University-level. As the age range of this group overlapped with retirement age, 37.68% of participants reported that they were not employed/ retired at the time of the study. Since the data were non-parametric, a Wilcoxon-Mann-Whitney test was run and the results indicated that the young group had a significantly higher education level than the older group (z = -4.58, $p < 0.001$). A Pearson Chi-squared Test showed that the group differences for the employment status were also statistically significant ($\chi^2(2) = 128.48$, $p < 0.001$). On the other hand, the linguistic background of the young and older groups did not differ significantly (z = -1.27, p = .201). The number of spoken languages in both groups was between 1 and 4, with 66.20% of young adults and 76.81% of older adults reporting that they were monolingual. The digital experience score, which was calculated as an average of the digital comfort and digital competence self-ratings in the survey, differed significantly for both groups (z = -4.95, $p < 0.001$), with the young group demonstrating higher digital experience (M = 8.78, Mdn = 9) than the older group (M = 7.63, Mdn = 8).

Table 1: Sample Characteristics by Age Group in *Study A: UK*

	Age Group	
Characteristic (N = 140)	**Young (n = 71)**	**Older (n = 69)**
Age (years)		
M (SD)	19.35 (1.22)	60.74 (6.22)
Range	18 - 24	50 - 70
Gender		
Women	56 (78.87%)	51 (73.91%)
Men	15 (21.13%)	18 (26.09%)
Highest/ Current Education level * [a]		
At/ Above University	71 (100.00%)	51 (73.91%)
Below University	0 (0.00%)	18 (26.09%)
Employment Status *		
Student	71 (100.00%)	3 (4.35%)
Employed/ Self-employed	0 (0.00%)	40 (57.97%)
Not employed/ Retired	0 (0.00%)	26 (37.68%)
No. of Spoken Languages		
M (SD)	1.41 (0.64)	1.32 (0.67)
Mdn [IQR]	1 [1, 2]	1 [1, 1]
Digital Experience Score * [b]		
M (SD)	8.78 (1.09)	7.63 (1.44)
Mdn [IQR]	9 [8.25, 9.50]	8 [7, 8.50]

Note. Values represent the number of participants and percentage (in parentheses) in each category, the mean and standard deviation (in parentheses), or the median and interquartile range (in parentheses). *M* = Mean, *SD* = Standard Deviation, *Mdn* = Median, IQR = Interquartile Range.

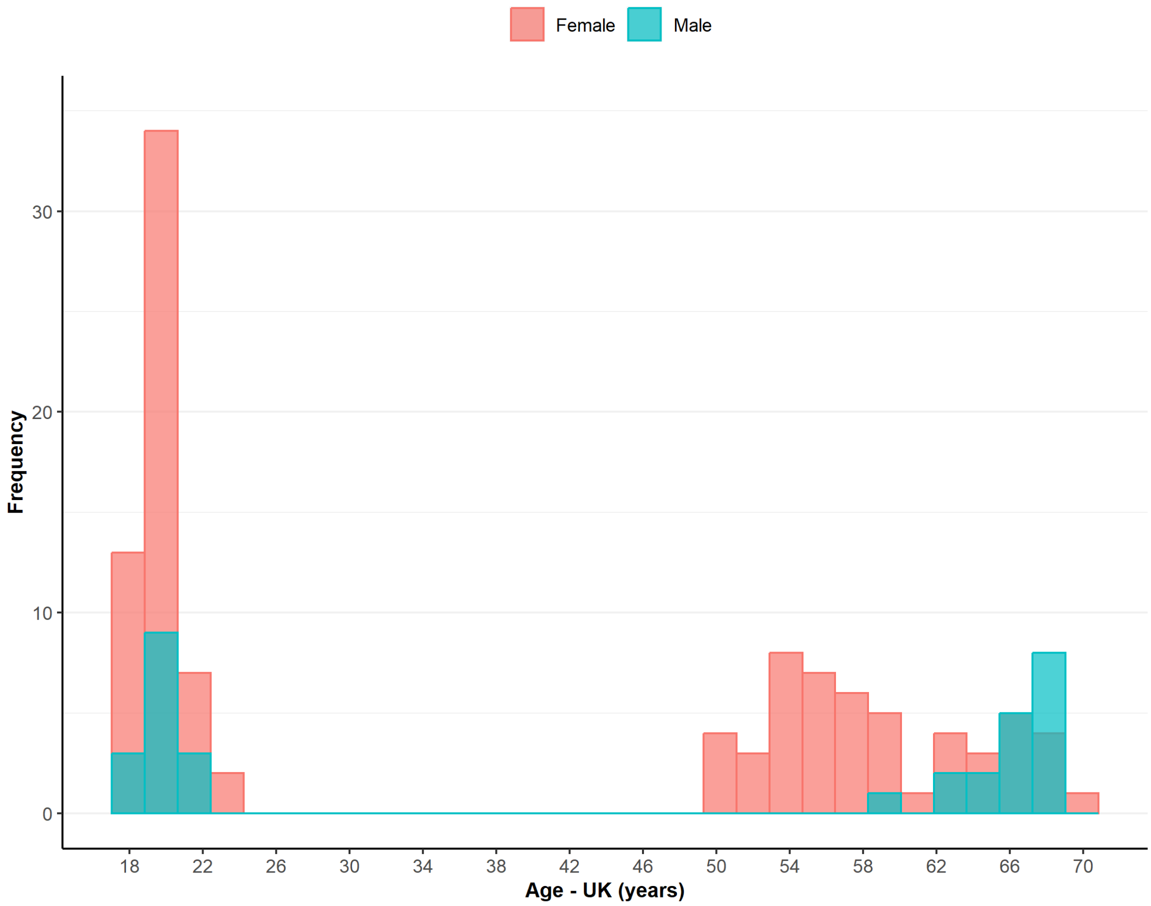
* Statistically significant differences between age groups ($p < .05$).

[a] The Highest/ Current Education Level was measured as a categorical variable with 10 education levels in the survey. As there was limited representation in this sample for levels below University, to maximise statistical power, the survey levels have been collapsed into a binary variable consisting of "At/ Above University" and "Below University" levels.

[b] The Digital Experience Score was calculated as the average of the Digital Comfort and Digital Competence self-ratings provided by participants in the survey. Digital Comfort was measured on a scale

from 1 (Not at all comfortable) to 10 (Very comfortable), and Digital Competence was measured on a similar scale from 1 (Beginner) to 10 (Expert). In cases where self-ratings were reported only for one of the two scales and missing for the other, the reported value was assigned as the Digital Experience Score. In cases where self-ratings were missing for both scales because participants did not own a smartphone but had experience with other digital devices (e.g., laptop), the minimum calculated group (age by country) mean for the Digital Experience Score was assigned to each of these cases.

Figure 6: Histogram displaying the Age and Gender distribution of the sample in *Study A: UK*



Note. The histogram bars represent the number of participants within each age bracket in the study sample. Overlapping bars display the gender distribution within each age bracket. The age criteria for recruitment to the healthy young group was 18 - 25 years, and 50 - 70 years of age in the healthy older group.

Human Trial-Unique Non-matching to Location (hTUNL) Task Performance

Table 2 provides a summary of the mean values and standard deviations for all the outcome measures presented in this section, including Accuracy, Response Time, and Inverse Efficiency Scores across spatial separation conditions and age groups. *Figure 10* graphically displays the model estimates for each of these outcome measures.

Table 2: Group Descriptive Statistics for hTUNL Task Performance in *Study A: UK*

	Young Adults		Older Adults	
Proportion Correct (0 – 1)	***M***	***SD***	***M***	***SD***
Small Separation at Retrieval	0.74	(0.14)	0.71	(0.16)
Medium Separation at Retrieval	0.80	(0.13)	0.77	(0.13)
Large Separation at Retrieval *	0.83	(0.11)	0.77	(0.14)
Response Time (ms)	***M***	***SD***	***M***	***SD***
Small Separation at Retrieval ***	4336.04	(775.05)	5027.95	(1177.78)
Medium Separation at Retrieval ***	4049.81	(726.39)	4773.34	(1136.34)
Large Separation at Retrieval ***	3972.69	(570.06)	4549.62	(1042.26)
Inverse Efficiency Score (ms)	***M***	***SD***	***M***	***SD***
Small Separation at Retrieval **	6103.13	(1535.13)	7502.02	(2493.73)
Medium Separation at Retrieval **	5251.08	(1421.41)	6319.11	(1592.06)
Large Separation at Retrieval ***	4898.16	(1095.23)	6207.34	(2377.35)

Note. M and *SD* are used to represent Mean and Standard Deviation, respectively.

* Indicates the level of significance of age differences at $p < .05$, ** $p < .01$, *** $p < .001$.

Proportion Correct

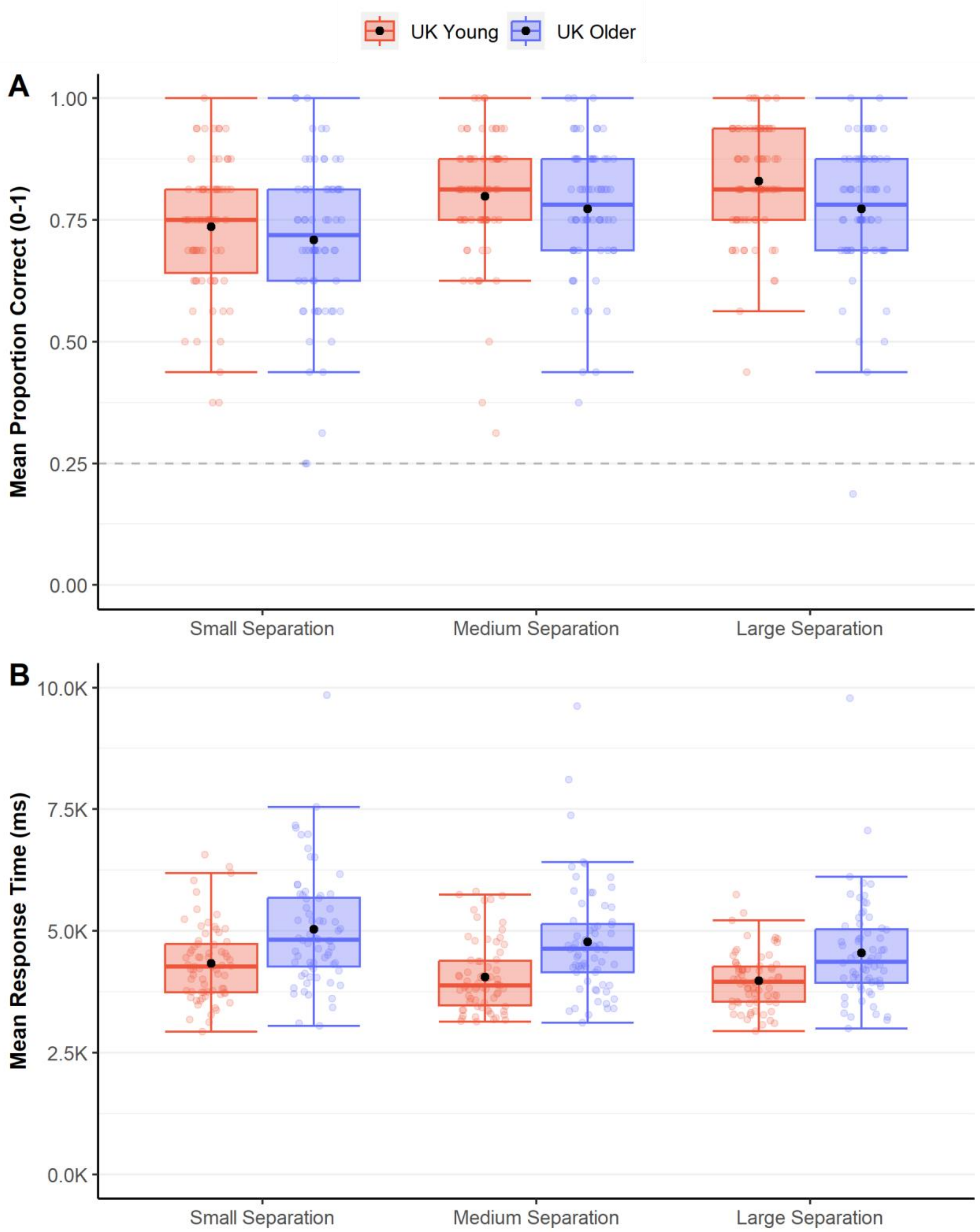
Mean accuracy, measured as proportion correct on a scale of 0 - 1, was significantly above chance (0.25) with large effect sizes for the healthy young adults on the small ($t(69) = 29.45$, $p < .001$, Cohen's d = 3.52), medium ($t(69) = 34.83$, $p < .001$, Cohen's d = 4.16), and large ($t(69) = 42.32$, $p < .001$, Cohen's d = 5.06) spatial separation conditions. Similarly, the healthy older adults also performed well above chance, with large effect sizes, on all spatial separation conditions: small ($t(67) = 23.15$, $p < .001$, Cohen's d = 2.81), medium ($t(67) = 32.19$, $p < .001$, Cohen's d = 3.90), and large ($t(67) = 31.19$, $p < .001$, Cohen's d = 3.78). Between age groups, young adults demonstrated higher accuracy than older adults on all spatial separation distances, but these group differences were significant only on the large separation distance with a small effect size ($t(130.02) = -2.61$, $p = .010$, Cohen's d = -0.44), and not significant on the small ($t(130.88) = -1.01$, $p = .313$, Cohen's d = -0.17) or medium ($t(135.71) = -1.12$, $p = .267$, Cohen's d = -0.19) conditions. *Table 2* shows that mean accuracy was highest on the large separation condition and lowest on the small separation in the young group, and highest on the large and medium separations, and lowest on the small separation in the older group. *Figure 7* displays proportion correct across spatial separation categories and age groups as box plots.

The linear mixed effects model built to predict Accuracy (i.e., Proportion Correct) had a significant main effect of Spatial separation condition ($F(2, 272) = 9.63$, $p < .001$), but not Age ($F(1, 134) = 1.22$, $p = .272$), or the interaction between Separation condition and Age ($F(2, 272) = 1.57$, $p = .210$). Post-hoc comparisons using estimated marginal means showed that the age trend for performance on all separation groups was characterised by a slightly negative slope, and the gradient on the large separation condition was steeper than other categories (i.e., a greater decline in performance on this condition over age), possibly driving the main effect of Separation group seen in the model. However, there were no significant differences between the age trends for the Large and Small separation ($t(272) = -1.59$, $p = .253$), Large and Medium ($t(272) = -1.48$, $p = .303$), or the Small and Medium ($t(272) = -0.11$, $p = .993$) separation groups. See *Figure 10* for a visualisation of these age trends. Interestingly, there was a significant main effect of Education in the mixed effects model ($F(1, 134) = 5.66$, $p = .019$), and further examination revealed that Education below University-level had a significantly negative effect on Proportion Correct ($\beta = -0.07$, $SE = 0.03$, $t(134) = -2.38$, $p = .019$). As only a small sub-sample of healthy older adults had an education below University-level (all young adults had an education level of University or above), the main effect of

Education seen here should be interpreted with caution as there is limited power to investigate this variable.[2] However, as shown in *Figure 8*, the mean accuracy for these participants across separation categories was lower than healthy older participants with education above University-level (plotted only for UK Older adults group). Finally, Digital experience was not a significant predictor of Accuracy on this task ($F(1, 134) = 0.29$, $p = .592$).

[2] An exploratory model was built with a subset of participants, all of whom who had an education level of University and above, to check whether the lower Education level was influencing the Age effect observed in the full model. Results of this model showed that there was a significant main effect of Separation condition for IES ($F(2, 238) = 9.39$, $p < .001$), but still no effect of Age ($F(1, 119) = 1.45$, $p = .230$) or the interaction between Separation condition and Age ($F(2, 238) = 1.24$, $p = .290$), similar to the effects seen in the full model.

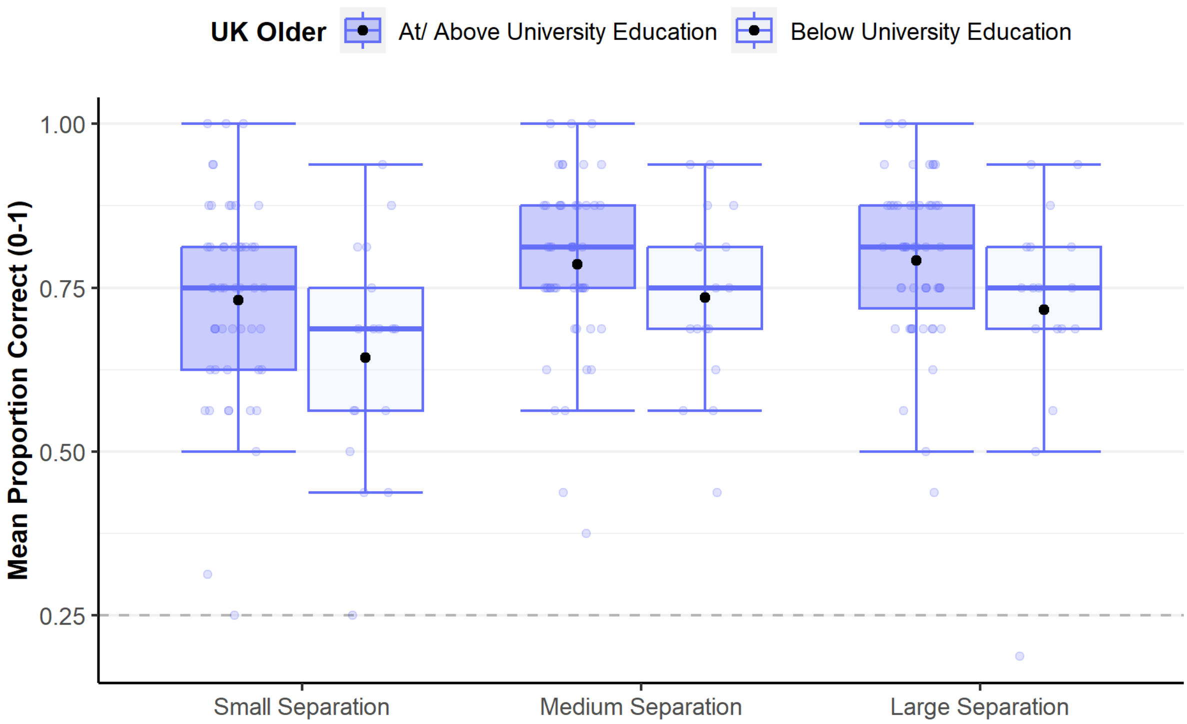
Figure 7: Box and whisker plots displaying (A) Mean Proportion Correct, and (B) Mean Response Time compared across Spatial Separation at Retrieval and Age groups in *Study A: UK*



Note. Boxes represent the Interquartile Range (i.e., the middle 50% of values), with a horizontal line drawn within each box to mark the Median value. The whiskers, or the lines extending from either side of the

box, display the dispersion of data, with the error bars representing the 95% confidence interval. Raw data points have been added to the plots, with a small amount of jitter. The black dot on each box shows the Mean value. An intercept has been added to plot (A) to display performance at chance (0.25 or 25% accuracy).

Figure 8: Box and whisker plot displaying Mean Proportion Correct compared across Spatial Separation at Retrieval and Education groups in the *Study A: UK* Older adults sample



Note. Boxes represent the Interquartile Range (i.e., the middle 50% of values), with a horizontal line drawn within each box to mark the Median value. The whiskers, or the lines extending from either side of the box, display the dispersion of data, with the error bars representing the 95% confidence interval. Raw data points have been added to the plots, with a small amount of jitter. The black dot on each box shows the Mean value. An intercept has been added to plot (A) to display performance at chance (0.25 or 25% accuracy).

Response Time

In terms of mean response time for correctly answered trials, young adults had lower RTs (i.e., quicker responses) than older adults on all separation conditions. These differences were significant with moderate effect sizes on the small ($t(76.03) = 3.48$, $p < .001$, Cohen's d = 0.66), medium ($t(77.26) = 3.60$, $p < .001$, Cohen's d = 0.69), and large ($t(81.91) = 3.69$, $p < .001$, Cohen's d = 0.70) spatial separation distances. As shown in *Table 2*, in both age groups, mean RT was highest on the small separation condition, and lowest on the large separation condition. See *Figure 7* for a box plot displaying RT across categories and age.

In terms of predictors of RT in a Linear Mixed Effects model, a significant main effect was found for the Separation condition ($F(2, 272) = 3.41$, $p = .034$) and Age ($F(1, 134) = 19.25$, $p < .001$), but not for the interaction between Group and Age ($F(2, 272) = 0.76$, $p = .470$). Post-hoc analyses showed that, across all separation conditions, the age trend for RT was positive i.e., there was an increase in RT as age increased - see *Figure 10*. The gradient of the age trend was comparatively flatter for the large separation condition, but this was not significantly different from the small ($t(272) = -0.91$, $p =.634$) or medium ($t(272) = -1.17$, $p = .471$) conditions; differences were also not significant between the small and medium conditions ($t(272) = 0.26$, $p = .963$). Additionally, the effects of Education ($F(1, 134) = 0.13$, $p = .718$) and Digital experience ($F(1, 134) = 0.0004$, $p = .985$) were not significant predictors of RT in the model.

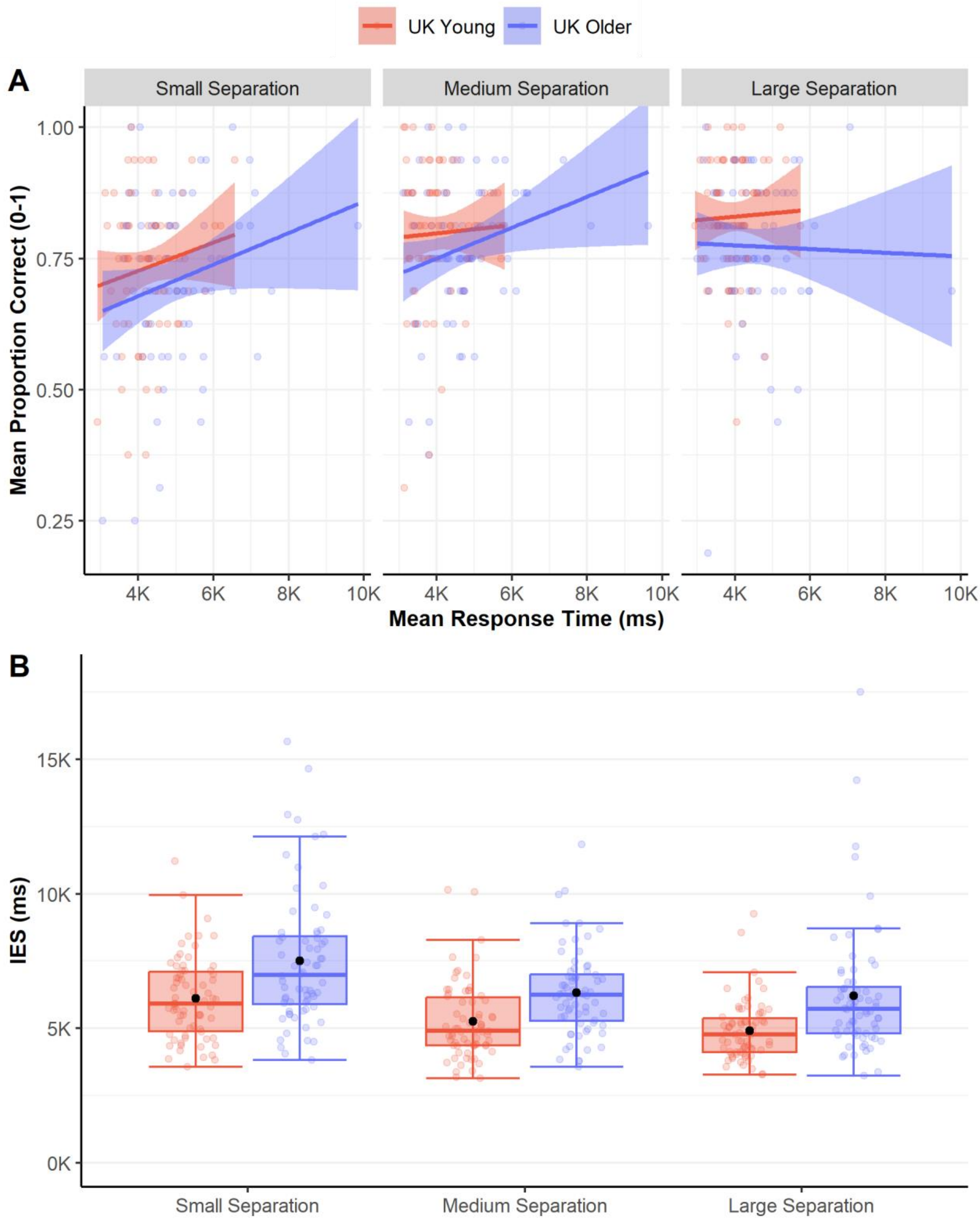
Inverse Efficiency Score

Results from correlation tests run between accuracy and RT revealed no significant correlations in the young adults group: small separation distance ($r = 0.15$, $p = .211$), medium ($r = 0.04$, $p = .722$), and large ($r = 0.03$, $p = .788$). In the older adults group, there were small correlations on the small ($r = 0.23$, $p = .104$), medium ($r = 0.21$, $p = .140$), and large ($r = -0.10$, $p = .472$) separation conditions, but none of these reached statistical significance. See *Figure 9* for a graphical display of the correlations. These results suggest that a speed-accuracy trade-off may have been unlikely on this task. However, in order to get a complete picture of performance on this task, results for a combined speed-accuracy measure - Inverse Efficiency Score - will be described here.

Young adults showed better performance (indicated by lower IES) than older adults on all separation distance conditions. All differences were statistically significant with moderate effect sizes on the small separation (t(81.35) = 2.95, p = .004, Cohen's d = 0.56), medium (t(98.53) = 3.15, p = .002, Cohen's d = 0.58), and large (t(80.72) = 3.50, p < .001, Cohen's d = 0.66) conditions. In both age groups, IES scores were lowest on the large separation condition (indicating better performance), and highest on the small separation condition (indicating poorer performance). These results are consistent with findings from accuracy and RT, where performance was better on the large separation condition and lower on the small separation condition. In line with the hypothesis, these results show that performance declines as spatial separation at retrieval decreases between dots. See *Figure 9* for a visualisation of results for IES.

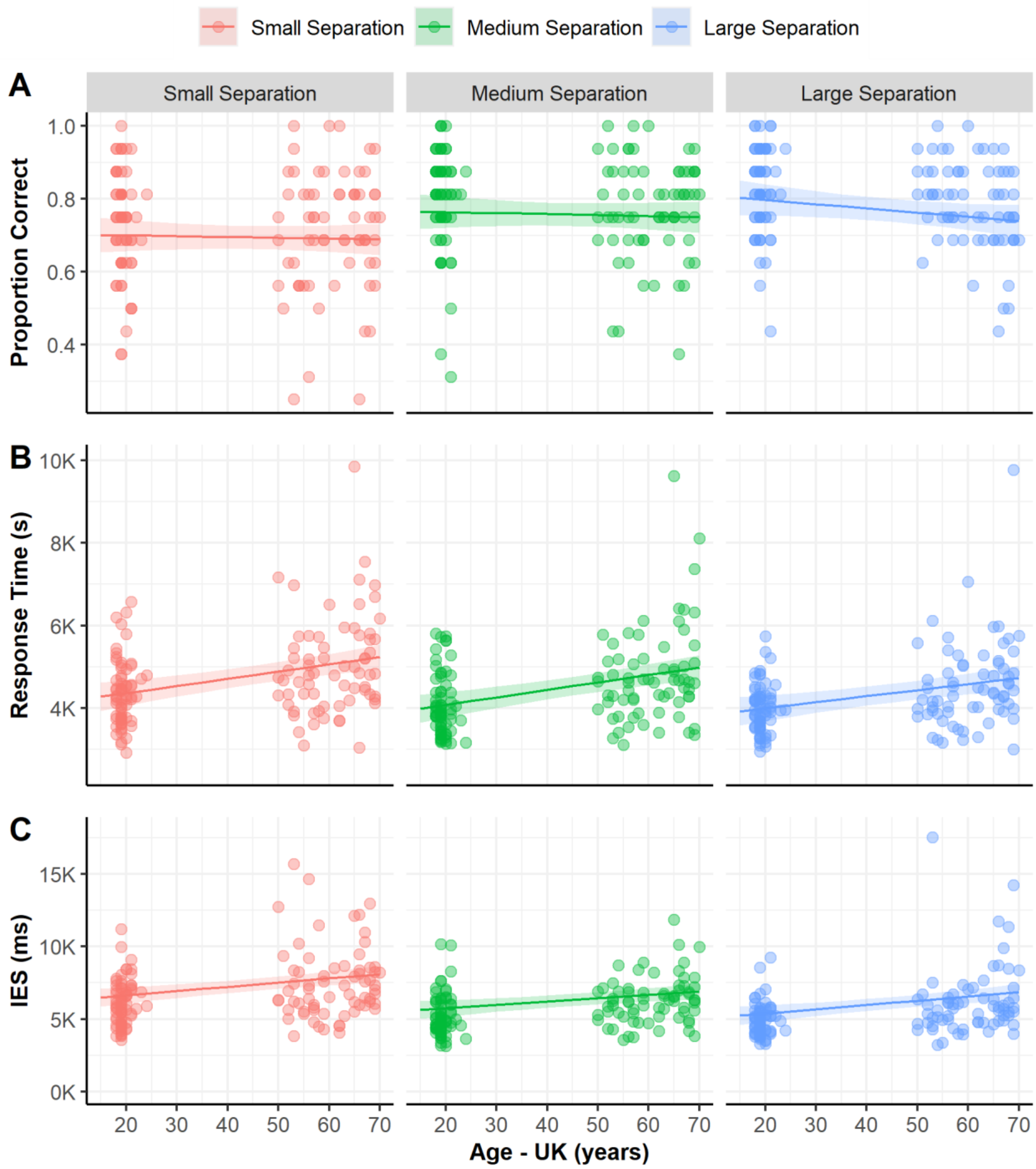
In the LME model for Inverse Efficiency Score, there was a significant main effect of Separation group (F(2, 272) = 6.62, p = .002) and Age (F(1, 134) = 17.66, p < .001), but not the interaction term (F(2, 272) = 0.43, p = .653). Estimated marginal trends revealed that, across separation groups, IES had a positive association with age - in other words, inefficiency increased with age. No significant differences were seen between the age trends for the small and large (t(272) = 0.03, p = .9996), small and medium (t(272) = -0.79, p = .712), and medium and large (t(272) = -0.81, p = .695) separation distances. Similar to the pattern observed with Accuracy, there was a significant main effect of Education (F(1, 134) = 7.98, p = .005) in the model predicting IES. A positive association was found between Education below University-level and higher IES/ poorer performance (β = 1118.16, SE = 395.91, t(134) = 2.82, p = .005). Finally, there was no significant effect of Digital experience (F(1, 134) = 1.18, p = .279) for IES.

Figure 9: (A) Scatter plot visualising the relationship between Mean Response Time and Mean Proportion Correct, and (B) Box and whisker plot displaying Mean Inverse Efficiency Scores compared across Spatial Separation at Retrieval and Age groups in *Study A: UK*



Note. The scatter plot in (A) displays the raw data points with regression lines (formula = y ~ x) drawn through them, and the bands represent the 95% confidence interval. In the box plot in (B), boxes represent the IQR, horizontal line within boxes = Median, Error bars = 95% confidence interval, coloured dots = jittered raw data points, black dots = Mean.

Figure 10: Line plots visualising the effect of Age on (A) Mean Proportion Correct, (B) Mean Response Time, and (C) Mean Inverse Efficiency Scores compared across Spatial Separation at Retrieval groups in *Study A: UK*



Note. The line plots display the mixed effects model predictions of the marginal means (i.e., averaged over different levels of the fixed effects Age and Spatial Separation condition, and adjusted for Education and Digital experience) for each of the outcome measures in (A), (B), and (C). The bands represent the 95% confidence intervals for the predicted values. These calculations were done using the 'ggemmeans' function in the R 'ggeffects' package. The raw data points have been added to each of the plots. As seen from the dispersion of the data points, the age range of the participants tested in the older group was wider than the young group; no jitter has been added to these points. Outliers displayed here were not removed as they did not change the model results.

2.3.2. Study B: India

Sample Characteristics

This study had a final sample of 148 participants (n = 76 young and n = 72 older adults). *Table 3* summarises the characteristics of this sample for both age groups. The young participants recruited in India were between 18 and 25 years (M = 21.34, SD = 1.72), while the older group was between 50 and 69 years (M = 55.57, SD = 4.87). In both groups, there was a greater representation of women than men (a gender ratio of 3.47:1 in the young group and 6.2:1 in the older group). There was no significant difference in the gender distribution between the young and older groups ($\chi^2(1) = 1.26$, $p = .262$). *Figure 11* graphically displays the age and gender distribution.

In the young group, all participants had an education level at or above University-level. Of these, 75 (98.68%) participants were currently enrolled in degrees and 1 participant was in employment. Whereas, in the older group, 71 (98.61%) older participants had an education level at or above University-level and only 1 participant had an education level below University-level education. Additionally, 68 (94.44%) participants were employed or self-employed at the time of testing. Due to the selection bias in the recruitment of these participants (through Schools and Universities in India), the present sample is characterised by high levels of education and employment. The difference between education levels of the young and older participants is not statistically significant in this sample (z = -1.03, p = .304). However, there is a significant difference between the employment status of the young and older groups ($\chi^2(2) = 144.06$, $p < 0.001$). The number of spoken languages also did not differ significantly between both groups (z = -0.03, p = .979), with 100% of participants in both groups reporting that they were bilingual i.e., could speak two or more languages (A. K. Mohanty, 1994). Finally, the young group had higher digital experience scores (M = 8.32, Mdn = 8.5) than the older group (M = 7.53, Mdn = 8), and the difference between both groups was statistically significant (z = -2.67, p = .008) for this measure.

Table 3: Sample Characteristics by Age Group in *Study B: India*

	Age Group	
Characteristic (N = 148)	**Young (n = 76)**	**Older (n = 72)**
Age (years)		
M (SD)	21.34 (1.72)	55.57 (4.87)
Range	18 - 25	50 - 69
Gender		
Women	59 (77.63%)	62 (86.11%)
Men	17 (22.37%)	10 (13.89%)
Highest/ Current Education level [a]		
At/ Above University	76 (100.00%)	71 (98.61%)
Below University	0 (0.00%)	1 (1.39%)
Employment Status *		
Student	75 (98.68%)	0 (0.00%)
Employed/ Self-employed	1 (1.32%)	68 (94.44%)
Not employed/ Retired	0 (0.00%)	4 (5.56%)
No. of Spoken Languages		
M (SD)	3.50 (0.87)	3.56 (1.15)
Mdn [IQR]	3 [3, 4]	3 [3, 4]
Digital Experience Score * [b]		
M (SD)	8.32 (1.22)	7.53 (1.73)
Mdn [IQR]	8.5 [7.5, 9.12]	8 [6.5, 9.00]

Note. Values represent the number of participants and percentage (in parentheses) in each category, the mean and standard deviation (in parentheses), or the median and interquartile range (in parentheses). *M* = Mean, *SD* = Standard Deviation, *Mdn* = Median, IQR = Interquartile Range.

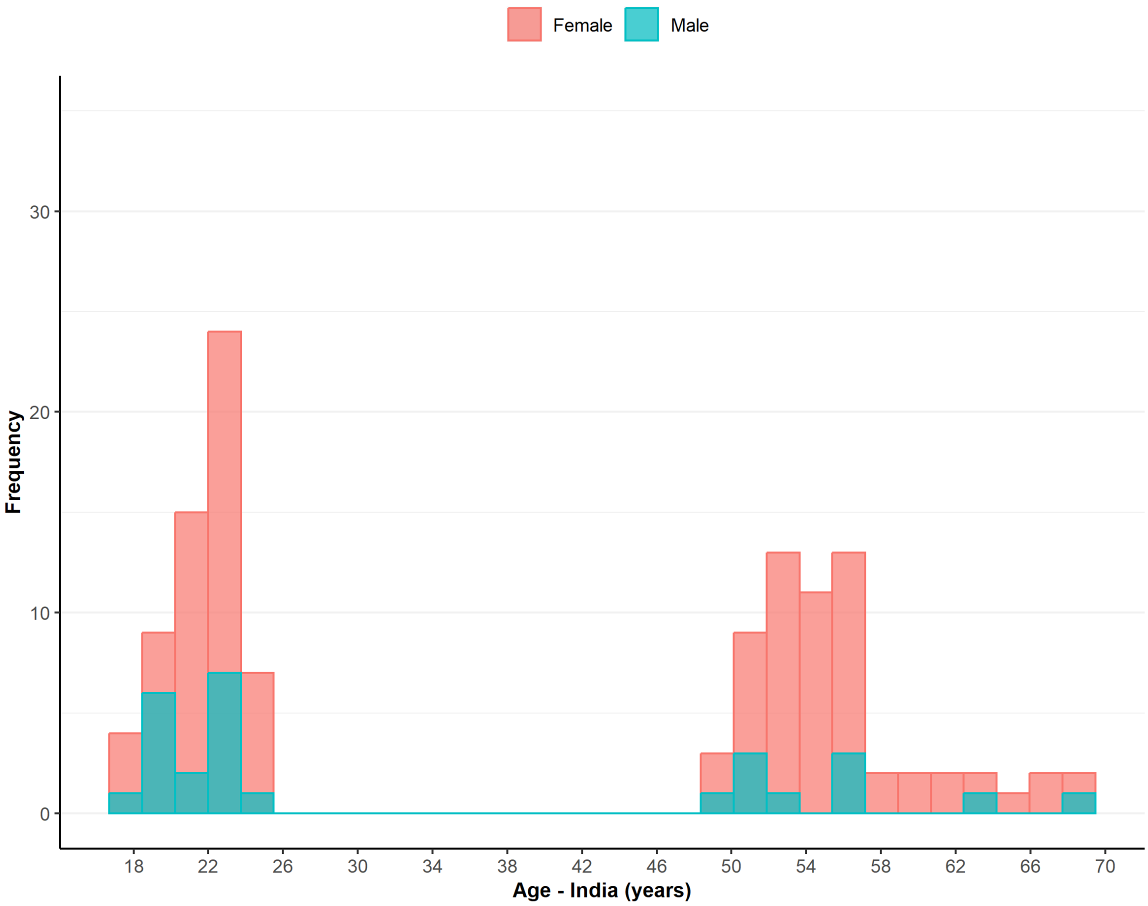
* Statistically significant differences between age groups ($p < .05$).

[a] The Highest/ Current Education Level was measured as a categorical variable with 10 education levels in the survey. As there was limited representation in this sample for levels below University, to maximise statistical power, the survey levels have been collapsed into a binary variable consisting of "At/ Above University" and "Below University" levels.

[b] The Digital Experience Score was calculated as the average of the Digital Comfort and Digital Competence self-ratings provided by participants in the survey. Digital Comfort was measured on a scale

from 1 (Not at all comfortable) to 10 (Very comfortable), and Digital Competence was measured on a similar scale from 1 (Beginner) to 10 (Expert). In cases where self-ratings were reported only for one of the two scales and missing for the other, the reported value was assigned as the Digital Experience Score. In cases where self-ratings were missing for both scales because participants did not own a smartphone but had experience with other digital devices (e.g., laptop), the minimum calculated group (age by country) mean for the Digital Experience Score was assigned to each of these cases.

Figure 11: Histogram displaying the Age and Gender distribution of the sample in *Study B: India*



Note. The histogram bars represent the number of participants within each age bracket in the study sample. Overlapping bars display the gender distribution within each age bracket. The age criteria for recruitment to the healthy young group was 18 - 25 years, and 50 - 70 years of age in the healthy older group.

Human Trial-Unique Non-matching to Location (hTUNL) Task Performance

In *Table 4*, you will find a summary of the average values and standard deviations for all the outcome measures reported in this chapter, namely Accuracy, Response Time, and Inverse Efficiency Score across spatial separation conditions and age groups. Furthermore, *Figure 14* visualises the model estimates for each of these measures.

Table 4: Group Descriptive Statistics for hTUNL Task Performance in *Study B: India*

	Young Adults		**Older Adults**	
Proportion Correct (0 – 1)	***M***	***SD***	***M***	***SD***
Small Separation at Retrieval ***	0.67	(0.16)	0.57	(0.17)
Medium Separation at Retrieval **	0.71	(0.13)	0.62	(0.18)
Large Separation at Retrieval ***	0.77	(0.13)	0.67	(0.18)
Response Time (ms)	***M***	***SD***	***M***	***SD***
Small Separation at Retrieval *	4589.48	(962.89)	5218.53	(1875.78)
Medium Separation at Retrieval	4513.75	(1111.45)	4968.14	(1603.48)
Large Separation at Retrieval	4367.85	(967.25)	4733.37	(1239.91)
Inverse Efficiency Score (ms)	***M***	***SD***	***M***	***SD***
Small Separation at Retrieval **	7610.24	(4981.44)	10122.78	(5286.31)
Medium Separation at Retrieval ***	6715.25	(2879.92)	8859.57	(4124.71)
Large Separation at Retrieval ***	5860.92	(1696.55)	7645.24	(3122.54)

Note. M and *SD* are used to represent Mean and Standard Deviation, respectively.

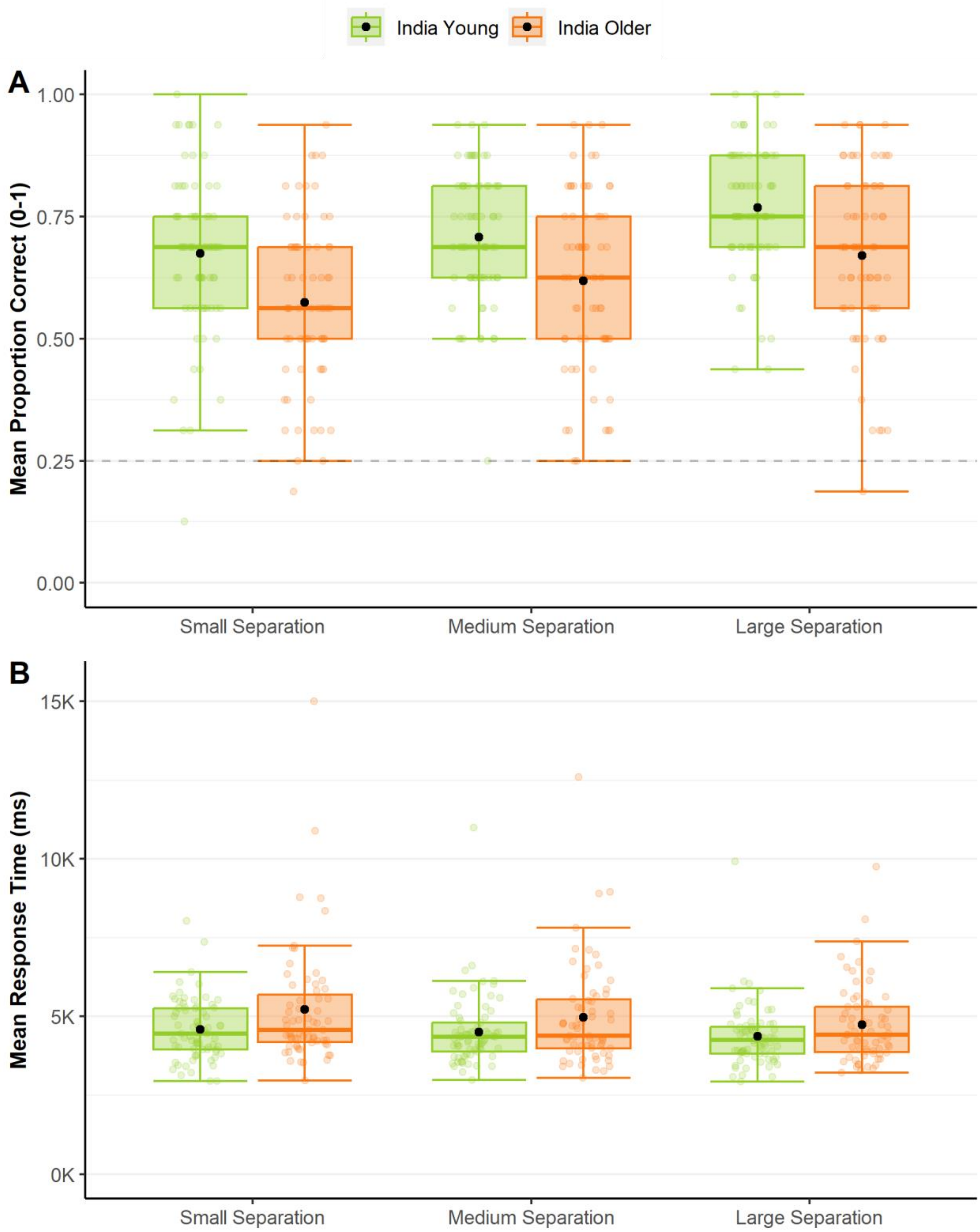
* Indicates the level of significance at $p < .05$, ** $p < .01$, *** $p < .001$.

Proportion Correct

In the healthy young adults group, mean proportion correct was significantly above chance (0.25) with large effect sizes on the small ($t(72) = 22.21$, $p < .001$, Cohen's d = 2.60), medium ($t(72) = 29.70$, $p < .001$, Cohen's d = 3.48), and large ($t(72) = 35.38$, $p < .001$, Cohen's d = 4.14) spatial separation conditions. The healthy older adults group also demonstrated performance which was statistically above chance with large effect sizes on the small ($t(66) = 15.63$, $p < .001$, Cohen's d = 1.91), medium ($t(66) = 16.74$, $p < .001$, Cohen's d = 2.05) and large ($t(66) = 19.53$, $p < .001$, Cohen's d = 2.39) separation conditions. Young adults scored significantly higher than older adults, with moderate effect sizes, in all separation groups: small ($t(135.83) = -3.54$, $p < .001$, Cohen's d = -0.60), medium ($t(120.18) = -3.33$, $p = .001$, Cohen's d = -0.57), and large ($t(118.12) = -3.77$, $p < .001$, Cohen's d = -0.64) distances. Across both age groups, accuracy was highest on the large spatial separation condition, and lowest on the small separation condition. See *Figure 12* for a box plot of proportion correct (on a scale of 0 - 1) across separation condition and age groups.

Turning towards the predictors of Accuracy in this study, the linear mixed effects model showed that Separation condition ($F(2, 276) = 3.30$, $p = .038$) and Age ($F(1, 137) = 15.80$, $p < .001$) had significant main effects on Accuracy, but not the interaction term between Separation condition and Age ($F(2, 276) = 0.18$, $p = .839$). Further investigation with estimated marginal means showed that the age slope for all separation conditions was characterised by a negative gradient (i.e., decrease in accuracy with age) and the slope was steepest on the small separation condition. However, there were no significant differences between the age trends for small and large ($t(276) = 0.50$, $p = .873$), small and medium ($t(276) = 0.53$, $p = .857$), or medium and large ($t(276) = -0.03$, $p = .9994$) separation conditions. *Figure 14* presents these age trends graphically. Furthermore, no significant effect was noted for Digital experience ($F(1, 137) = 1.08$, $p = .301$) in this model.

Figure 12: Box and whisker plots displaying (A) Mean Proportion Correct, and (B) Mean Response Time compared across Spatial Separation at Retrieval and Age groups in *Study B: India*



Note. Boxes represent the Interquartile Range (i.e., the middle 50% of values), with a horizontal line drawn within each box to mark the Median value. The whiskers, or the lines extending from either side of the

box, display the dispersion of data, with the error bars representing the 95% confidence interval. Raw data points have been added to the plots, with a small amount of jitter. The black dot on each box shows the Mean value. An intercept has been added to plot (A) to display performance at chance (0.25 or 25% accuracy).

Response Time

Across all spatial separation conditions, healthy young adults performed faster than older adults, but these group differences were only significant on the small separation condition with a small effect size ($t(96.60) = 2.46$, $p = .015$, Cohen's d = 0.42). Performance differences between young and older adults did not reach statistical significance on the medium ($t(116.31) = 1.93$, $p = .056$, Cohen's d = 0.33), and large ($t(124.67) = 1.93$, $p = .055$, Cohen's d = 0.33) separation conditions. In both age groups, mean RT was quickest on the large separation condition, and slowest on the small separation condition. *Figure 12* provides a box plot visualising RT across separation condition and age groups.

In the LME model for RT, there was a significant main effect of Age ($F(1, 137) = 6.30$, $p = .013$), but not of Separation condition ($F(2, 276) = 0.14$, $p = .867$), or the interaction term ($F(2, 276) = 1.70$, $p = .184$). Post-hoc comparisons with estimated marginal means showed that there was a positive age slope for RT (i.e., longer RTs with age) across all separation categories, and this slope was steepest for the small separation condition - see *Figure 14*. The differences between age trends, however, were not significant between small and large ($t(276) = -1.78$, $p = .177$), small and medium ($t(276) = -1.30$, $p = .394$), or medium and large ($t(276) = -0.48$, $p = .880$) separation conditions. Finally, there was no significant effect of Digital experience on RT ($F(1, 137) = 0.46$, $p = .500$).

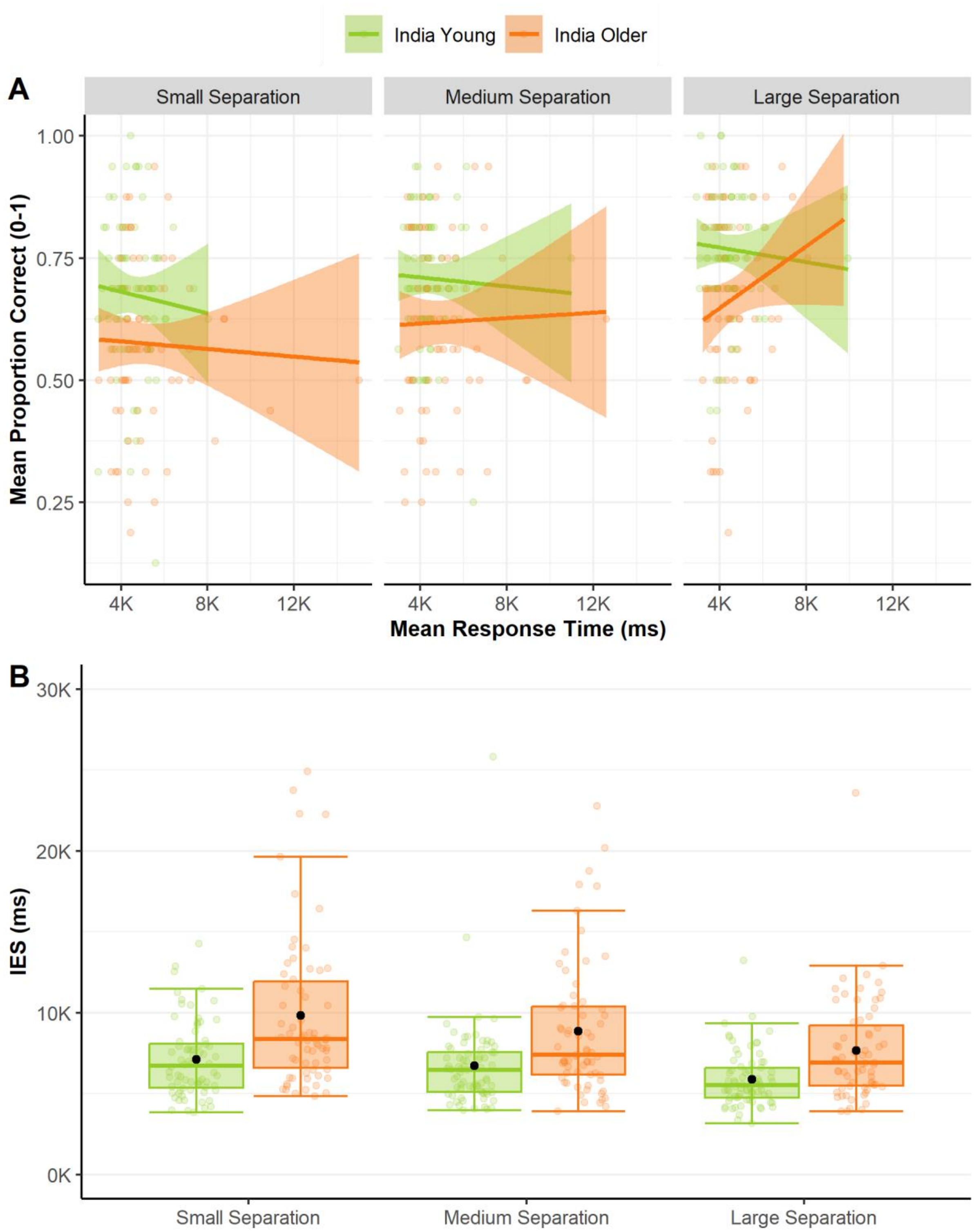
Inverse Efficiency Score

Correlations between accuracy and RT in the young adults groups showed negligible and non-significant associations between both measures on the small (r = -0.06, p = .585), medium (r = -0.04, p = .744), and large (r =-0.06, p = .629) separation conditions. In the older group, a small but non-significant correlation was seen on the large separation condition (r = 0.22, p = .070), and negligible correlations were found on the small (r = -0.04, p = .730), and medium (r = 0.02, p = .843) conditions. *Figure 13* displays these associations graphically. As no significant relationships have been found between accuracy and RT in either of the groups, a speed-accuracy trade-off may be unlikely. However, there is still added value of calculating a combined speed-accuracy measure, as it would give further insight into performance, allowing for direct comparisons using a single metric. It may also be sensitive to individual differences in performance efficiency not picked up by average measures (i.e., accuracy and RT) used to calculate correlations here.

As shown in *Table 4*, on all spatial separation conditions, young adults performed more efficiently (demonstrated by lower IES) than older adults. These group differences were significant and characterised by a moderate effect size on the small (t(135.14) = 2.89, p < .001, Cohen's d = 0.56), medium (t(116.83) = 3.54, p < .001, Cohen's d = 0.59), and large (t(99.89) = 4.15, p < .001, Cohen's d = 0.66) separation distances. Between separation at retrieval distances, both groups showed higher performance on the large condition and lowest performance on the small condition, thereby mirroring the pattern of results observed on accuracy and RT. As hypothesized, this shows that performance declines as the spatial separation between dots decreases. For box plots showing IES between conditions and age groups, see *Figure 13.*

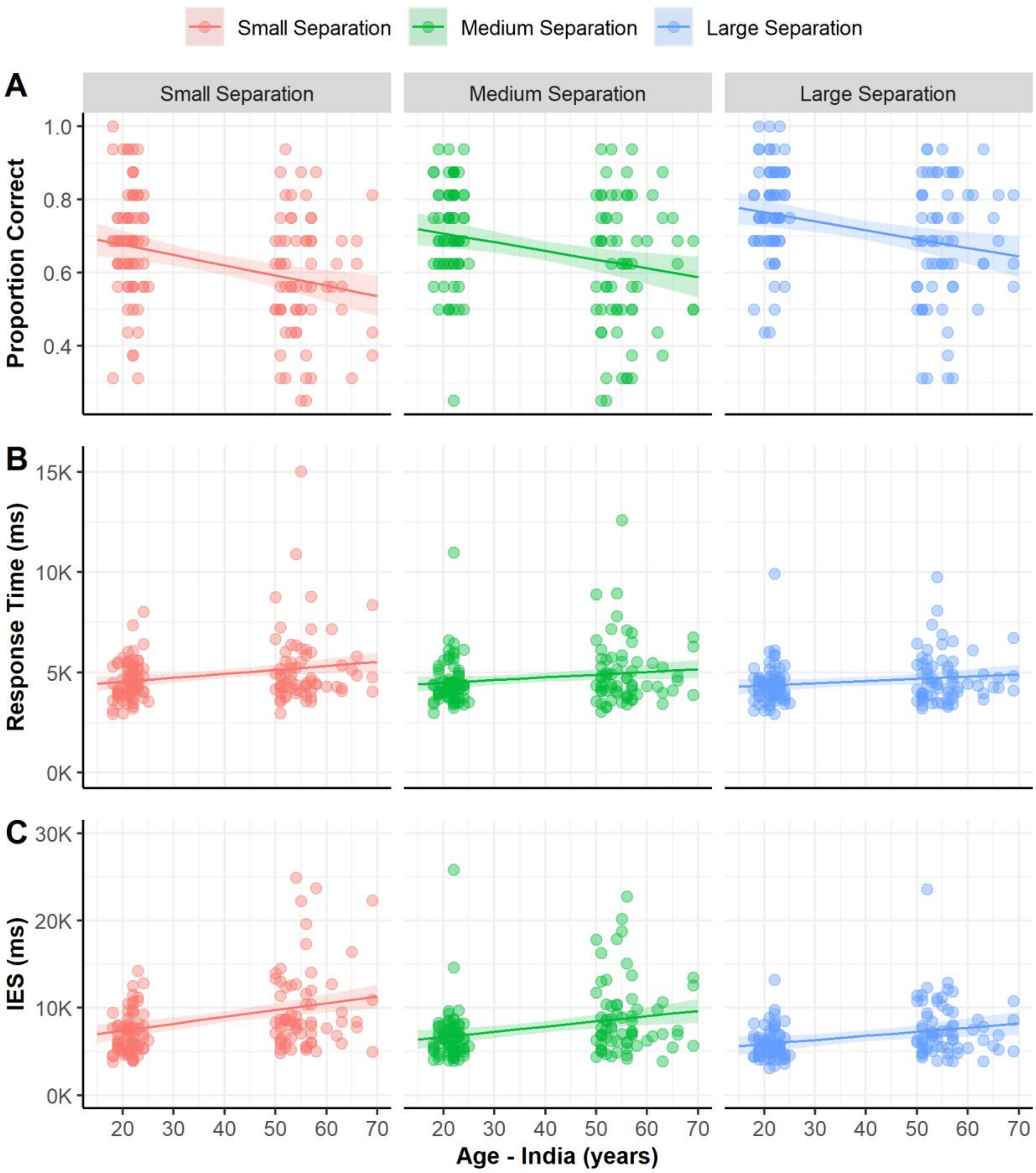
The main effect of Age was significant in this model (F(1, 137) = 16.51, p < .001), but Separation group (F(2, 276) = 0.65, p = .521) and the interaction between Separation group and Age (F(2, 276) = 1.20, p = .303) were not significant effects. Post-hoc analysis of estimated marginal means showed a positive age slope for all separation conditions, indicating an increase in inefficiency with age, especially on the small separation condition. Similar to performance patterns observed on Accuracy and RT, no significant differences were found between age trends on the small and large ($t(276) = -1.54$, $p = .273$), small and medium ($t(276) = -0.90$, $p = .639$), and medium and large ($t(276) = -0.64$, $p = .798$) separation conditions. For completeness, it should be reported that Digital experience ($F(1, 137) = 0.0001$, $p = .991$) was not a significant predictor of IES.

Figure 13: (A) Scatter plot visualising the relationship between Mean Response Time and Mean Proportion Correct, and (B) Box and whisker plot displaying Mean Inverse Efficiency Scores compared across Spatial Separation at Retrieval and Age groups in *Study B: India*



Note. The scatter plot in (A) displays the raw data points with regression lines (formula = y ~ x) drawn through them, and the bands represent the 95% confidence interval. In the box plot in (B), boxes represent the IQR, horizontal line within boxes = Median, Error bars = 95% confidence interval, coloured dots = jittered raw data points, black dots = Mean.

Figure 14: Line plots visualising the effect of Age on (A) Mean Proportion Correct, (B) Mean Response Time, and (C) Mean Inverse Efficiency Scores compared across Spatial Separation at Retrieval groups in *Study B: India*



Note. The line plots display the mixed effects model predictions of the marginal means (i.e., averaged over different levels of the fixed effects Age and Spatial Separation condition, and adjusted for Digital experience) for each of the outcome measures in (A), (B), and (C). The bands represent the 95% confidence intervals for the predicted values. These calculations were done using the 'ggemmeans' function in the R 'ggeffects' package. The raw data points have been added to each of the plots. As seen from the dispersion of the data points, the age range of the participants tested in the older group was wider than the young group; no jitter has been added to these points. Outliers displayed here were not removed as they did not change the model effects.

2.4. Discussion

By applying a novel translational task of spatial pattern separation (PS) - human Trial-Unique Non-match to Location (hTUNL) - with healthy young and older adults, I aimed to understand how age influences PS and whether effects of age generalise cross-culturally. Across both cultures studied, I found that healthy young and older adults could perform the task at levels which were well above chance across all conditions of spatial separation distance at retrieval (which can be understood as levels of interference). Between conditions, as expected, task performance scaled with the level of interference - participants in both studies demonstrated a pattern of lowest mean accuracy and longest mean RTs on the small spatial separation condition which was designed to place highest demands on PS, and performance was highest on the large separation condition. The influence of age, however, was less consistent between both cultures. In *Study A: UK*, young adults generally showed better PS performance than older adults, but task accuracy did not show a significant decline with age. Interestingly, education was found to be a significant predictor of accuracy in this study; a lower level of education was associated with poorer PS accuracy across interference conditions in older adults. Contrastingly, *Study B: India* revealed significant age-related deficits across all spatial separation distances, with young participants consistently performing better than older adults at discriminating between old and new dot locations on this task across all spatial separation conditions. In both studies, I did not find an interaction between age and spatial separation condition, the age-related performance deficit was not greater on the small separation condition than in conditions with lower interference. Here, I will reconcile these findings with previous literature on PS, offer plausible explanations for the differing pattern of age effects observed between cultures, and discuss broader implications for the assessment of behavioural PS.

In human cognitive ageing literature, previous studies which have found age-related impairments in PS have typically tested older adults aged 60 and above e.g., mean age of 71 years in Yassa et al. (2011), 74.4 years in Toner et al. (2009) and Holden et al. (2013), and 72.9 years in Stark et al. (2015). In *Study A: UK,* the mean age of older participants was 60.74 years ($SD = 6.22$ years) - the comparatively younger sample in my study may partly explain why a main effect of age was not observed. Clark et al. (2017) also failed to replicate an age effect on spatial pattern separation performance in their sample consisting of older adults with a mean age of 67 years. Contrastingly, Stark et al. (2013) recruited participants from across the adult lifespan in their study (including the often-overlooked middle age category in cognitive ageing research) and found striking evidence for a linear decrease in PS performance between 20 to 60 years of age. A distinction, however, should be made here between tests of spatial and object pattern separation. Stark et al. (2013) apply an object PS paradigm, which may show greater sensitivity to age than spatial PS - consistent with recent studies which have found that performance on mnemonic discrimination of objects shows a greater age-related decline compared to scenes (Gusten et al., 2021; Reagh et al., 2016). It is possible that spatial pattern separation is sensitive to the influence of age only later in life (Clark et al., 2017).

On the other hand, I found a significant age-related decline in spatial PS in *Study B: India,* which is comparable to previous findings (Holden et al., 2013). Notably, older participants were significantly impaired on PS compared to young participants in *Study B: India* even though the mean age of older adults in this group was 55.57 years (lower than *Study A: UK*). One explanation for these inconsistencies is the variability observed in the age of onset of episodic memory decline. In healthy ageing, it is widely agreed that EM is particularly sensitive to the influence of age (Nyberg et al., 1996), but the question of when impairments begin to appear is still a matter of debate. Some studies have claimed that EM decline appears as early as in young adulthood (T. A. Salthouse, 2003), but longitudinal studies have found a significant reduction in EM in adults aged 60 years or over (Josefsson et al., 2012; Rönnlund et al., 2005). It should be highlighted, however, that there is large inter-individual variability in this decline (Habib et al., 2007; Josefsson et al., 2012). Pattern separation, which is thought to be a core component of EM (Leal & Yassa, 2018; Yassa & Stark, 2011), may show similar individual variability in terms of the age of onset. Furthermore, the progression of decline is not necessarily linear, and longitudinal approaches are required to gain further insight on ageing trajectories. Interestingly, in their lifespan study of PS, Stark et al. (2013) found that performance reached a plateau at 60 years of age and did not continue to decline further. However, this should not be mistaken for stability of age effects upon entering old age - Stark et al. (2013) suggest that other cognitive factors may contribute to variability in this age group.

One such factor could be education - my results showed that older adults with education at University-level or above had better PS accuracy than those with education below University-level, and education had a significant effect on performance in *Study A: UK*. Similarly, the older adults' sample in Clark et al. (2017) was also characterised by higher levels of education compared to earlier studies (Holden et al., 2012), but this was not investigated as a potential predictor of spatial PS performance in their study. The relationship between education and cognitive performance has been extensively explored, with findings showing that higher education is linked with better cognitive performance on a variety of tasks (Opdebeeck et al., 2016; Strenze, 2007). In normal ageing, Stern (2002; 2012) suggests that educational attainment may act as a protective factor against cognitive decline, but the mechanisms are still to be fully elucidated (for reviews, see Lenehan et al., 2015; Lövdén et al., 2020; Seblova et al., 2020). On the other hand, older adults in *Study B: India* were vulnerable to age-related decline in PS performance even though all participants in this sample were University-level educated. There may be other risk factors at play here - recent results from the Longitudinal Ageing Study in India (LASI) have shown that lower socioeconomic status (Muhammad, 2023), female gender (Angrisani et al., 2020; J. Lee et al., 2014), and lower social capital (Pandey et al., 2023) can contribute to cognitive decline. While a broader investigation of cognitive risk and protective factors influencing PS performance was beyond the scope of the present work, it certainly warrants further investigation. Cross-cultural cognitive ageing studies, in particular, should consider that the populations they study may be characterised by diverse cognitive, sociocultural, and health variables, making direct comparisons problematic. Depending on research aims, a generalisation approach - as I have applied in *Study B: India* - may be more appropriate.

A notable limitation of the present research is that a standardised memory test, such as for word learning, was not used to account for differences in memory ability in healthy adults. This approach has previously been applied in human and rodent studies to split older participants into aged 'impaired' and 'unimpaired' groups, to gain further insight into sources of variation within the group (Gallagher et al., 2006; Holden et al., 2012; Reagh et al., 2016; S. M. Stark et al., 2013). Holden et al. (2012) showed that when older adults were divided into 'impaired' and 'unimpaired' groups, only the 'impaired' group performed significantly differently from the young adults on the spatial pattern separation task. However, to apply this approach in cross-cultural studies, one also needs to consider the challenge of identifying, adapting, or translating verbal standardised assessments so that they are culturally appropriate for a given population. Another limitation is that participants in both studies were characterised by high levels of education, as most participants were recruited from educational institutions. Although education has been analysed as an independent effect in *Study A: UK*, there was limited power due to the small group of older adults who had an education below University-level in this sample; in *Study B: India*, only one participant had an education below University-level, so it was not possible to analyse the effect of education on PS performance. Future studies should aim to recruit more heterogeneous community samples to gain a better picture of how education impacts hippocampal operations.

Unlike rodent studies which offer more precise insights into hippocampal operations such as pattern separation, human performance is characterised by greater complexity. While my findings do not consistently reveal age effects on PS in a middle-to-older aged sample, it is crucial to consider the influence of education, and individual and cultural variation in the study of PS. Behavioural assessments of PS - such as the hTUNL task applied here - are only indirect measures of the integrity of hippocampal sub-fields and circuity in ageing (for further discussions, see Hunsaker & Kesner, 2013; Liu et al., 2016), and further work is needed to validate the neural basis of behavioural performance on this task. Nonetheless, the hTUNL task holds potential for further application in the study of ageing and age-related neurodegenerative diseases - it draws upon years of evidence from rodent models where similar paradigms have been applied (Oomen et al., 2015; Talpos et al., 2010), it meets the criteria proposed by Hunsaker & Kesner (2013) for the design of PS assessments, various task parameters can be manipulated to meet research requirements, and it is non-verbal and involves simple dot stimuli which are unlikely to carry semantic associations if applied cross-culturally.

Chapter 3: Influence of Age on Boundary Extension across Cultures

3.1. Introduction

In "The Hippocampus: A Manifesto for Change", Maguire and Mullally (2013) advocate for a reconceptualisation of the role(s) of this MTL sub-region in cognitive functions. Several theoretical accounts place the representation of scenes as central to hippocampal function (Gaffan, 1991; Maguire et al., 2016; Maguire & Mullally, 2013; Murray et al., 2018; Robin et al., 2018). It is now acknowledged that the hippocampus (HC) plays a crucial role in scene construction (Hassabis et al., 2007), and this ability supports diverse cognitive functions such as recall, imagination, and navigation (Hassabis & Maguire, 2007). One line of evidence supporting the significance of the HC for scene representation comes from the boundary extension (BE) phenomenon (Intraub & Richardson, 1989; Mullally et al., 2012). Boundary Extension is a well-established cognitive phenomenon displayed by healthy individuals where in observers confidently recall seeing more of a scene than what was actually viewed. In drawing tasks, for example, participants draw elements beyond the boundaries of the image originally shown to them (Intraub & Richardson, 1989); or, when comparing the viewpoint of a new photo which is identical to a target photo which was briefly viewed before, participants perceive the new photo as appearing closer to them, suggesting that their memory of the target photo was broader (Intraub & Dickinson, 2008). Several studies have found evidence for the BE effect in healthy individuals (Bainbridge & Baker, 2020; De Luca et al., 2018; Mullally et al., 2012; Seamon et al., 2002). Yet, the impact of normal ageing on this phenomenon and how this generalises across cultural contexts is yet to be understood.

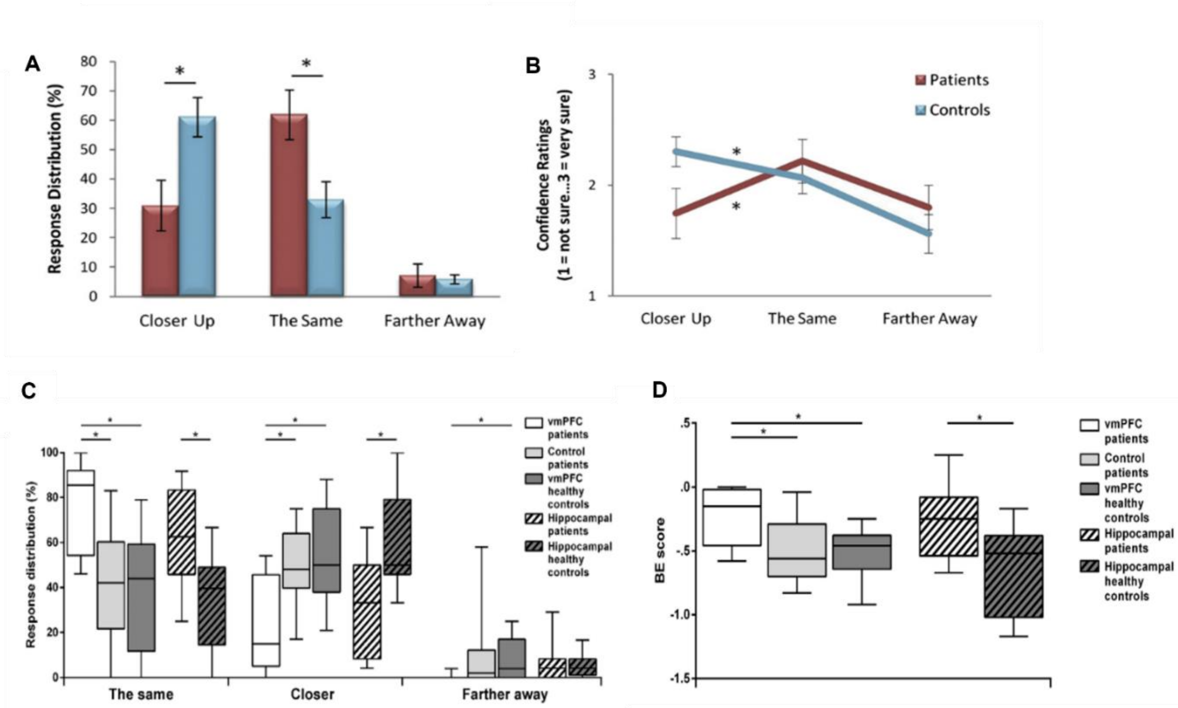
According to the multi-source model (Intraub, 2010, 2012), scene perception is a constructive process which does not correspond with the visual input alone, but instead integrates multiple sources of information. This includes the actual visual input received, but also expectations, past knowledge, and prior experiences - the internal representation of a scene, therefore, includes more information than what is viewed. This is revealed when individuals are asked to recall a scene, and incorrectly recall the extended representation (Intraub & Richardson, 1989). Through this framework, BE can be viewed as a source monitoring error i.e., a misattribution of the origin of visual information in memory (Johnson et al., 1993). However, it is important to emphasize that although BE is characterised as a memory error, it offers adaptive value as the integration of internal and external sources allows a viewer to make predictions about the broader spatial context of a scene, which facilitates tasks such as spatial navigation (Gottesman, 2011).

The Boundary extension effect relies upon the integrity of scene construction (SC) ability in the hippocampus and related regions, as demonstrated by studies with patients who have suffered damage to brain regions involved in this function (De Luca et al., 2018; Mullally et al., 2012). Mullally et al. (2012) administered a range of tasks designed to test the BE phenomenon in patients with bilateral hippocampal damage and amnesia who showed clear deficits in scene construction ability as measured with an established paradigm (Hassabis et al., 2007). Importantly, tasks used to test BE with memory-impaired patients in this study were modified to allow for immediate recall following stimulus presentation, thereby eliminating the need for long-term memory. In a drawing task (Intraub & Richardson, 1989), participants were shown photographs of scenes, and then immediately asked to draw these from memory. In a different modality, a haptic/ tactile task, Intraub (2004) asked participants to study the dimensions of scene arrangements presented within a wooden border using touch alone; the border was then removed and participants had to recall the location of each border. Compared to controls, Mullally et al. (2012) found that patients showed a reduced boundary extension effect on these tasks i.e., they did not recall an extended representation, but recalled the scene more accurately than controls. Even more strikingly, this attenuated BE effect in patients was also demonstrated on a modified version of the Rapid Serial Visual Presentation

(RSVP) paradigm (Intraub & Dickinson, 2008). On this task, participants were shown two scenes in rapid succession, separated by a visual noise mask (250ms interval). They were then asked to rate whether the second picture was a "closer-up", "same", or "further away" view compared to the first picture; unknown to participants, both pictures were identical (i.e., "the same"). Healthy adults were more likely to rate the second picture as closer-up, demonstrating the BE error. Contrastingly, patients performed significantly more accurately (i.e., less BE error). In terms of response distribution, Mullally et al. (2012) found that patients with bilateral hippocampal damage (n = 7, M_{age} = 41.43) provided "the same" responses most frequently, "closer-up" responses less frequently (indicating less BE), and "further away" responses only occasionally. Conversely, healthy controls (n = 12, M_{age} = 42.67) in their study showed a different pattern: "closer-up" responses were most common (indicating more BE), followed by "the same" responses, and "further away" was least common. Authors conclude that this is due to a scene construction deficit in patients with HC damage, which impairs the construction of extended representations of scenes, thereby making performance less prone to the BE error.

It is now recognised that the hippocampus does not function in isolation but is part of a wider network involved in scene processing (Murray et al., 2017; Ranganath & Ritchey, 2012). Functional neuroimaging studies have found activity consistent with boundary extension in the HC and related circuitry such as the RSC (Chadwick et al., 2013; S. Park et al., 2007). The HC is also found to interact with other brain regions such as the ventromedial prefrontal cortex (vmPFC) which support scene construction ability (Bertossi et al., 2016). More recently, De Luca et al. (2018) applied the RSVP task from Mullally et al. (2012) and have shown that the finding of attenuated BE error extends to patients with damage to the vmPFC region. In their study, they tested patients with vmPFC damage (n = 8, M_{age} = 59.25 years) and found their performance was similar to the hippocampal patients in Mullally, Intraub & Maguire (2012), while control participants with occipital lesions sparing vmPFC (n = 10, M_{age} = 59.30) and healthy participants (n = 10, M_{age} = 56.50) were comparably more susceptible to the BE effect. This replicates the pattern of performance observed in Mullally et al. (2012) with patients and healthy controls. These studies indicate that both the hippocampus and supporting regions such as the vmPFC are needed to automatically construct scene representations involving boundary extensions.

Figure 15: Results adapted from Mullally et al. (2012) in A and B; and De Luca et al. (2018) in C and D



Note. Both studies use the Rapid Serial Visual Presentation task paradigm and identical stimuli to test participants. In (A) and (C), the frequency of incorrect "closer-up" distance judgments, when comparing two rapidly presented images which were exactly the same, was higher than incorrect "further away" responses in healthy controls, compared to patients (Mullally et al., 2012; De Luca et al., 2018). Confidence ratings in (B) mirror the response pattern in (A) - with healthy controls showing higher confidence on incorrect "closer up" responses compared to patients (Mullally et al., 2012). The former error indicates boundary extension (Mullally et al., 2012), while the latter is argued to signify boundary contraction (Bainbridge & Baker, 2020). In (D), the boundary extension (BE) score demonstrates the direction and degree of bias towards a particular response type - a mean score of 0 represents no effect, while a negative score is linked with BE. Healthy controls demonstrate a significantly larger BE effect (i.e., more negative score) than patients (De Luca et al., 2018).

In the context of normal ageing, there is a limited number of studies investigating whether there are age-related changes in boundary extension. The HC is vulnerable to age-related reductions in structural and functional integrity, and this is associated with cognitive decline in normal ageing (for a review, see Bettio et al., 2017). Yet, healthy older adults demonstrate a significantly larger BE effect (i.e., more BE error) than patients with damage to regions involved in SC (De Luca et al., 2018; Mullally et al., 2012). Furthermore, Seamon et al. (2002) found that all age groups demonstrate a BE effect on a drawing paradigm, but older adults demonstrate an observably larger BE effect than young adults. In this study, however, it is important to note that performance between age groups was not compared statistically. Multhaup et al. (2018) and Ménétrier et al. (2019) statistically compared age groups in their studies and, in contrast to Seamon et al. (2002), their results indicated that both young and older adults demonstrated BE, but there was no age-related increase in BE in older adults. Boundary extension has also been demonstrated by older adults in work by Kim et al. (2015) and middle-to-older aged healthy controls in Mullally et al. (2012) and De Luca et al. (2018), but performance has not been compared with young adults in these studies. The gaps and inconsistencies in this literature leaves the question of whether age influences the BE effect still unanswered.

BE is argued to be a universal phenomenon, demonstrated across ages, developmental stages, and even certain disorders (Intraub & Richardson, 1989; Quinn & Intraub, 2007; Seamon et al., 2002; Spanò et al., 2017). However, it is yet to be established whether this effect generalises across cultural contexts. Till date, a study by Chang et al. (2021) with participants in Taiwan is the only investigation of the boundary extension phenomenon beyond the West. In an adaptation of the Intraub and Richardson (1989) BE task, they found that both healthy young and older participants demonstrated the boundary extension effect, but the effect was more pronounced in healthy older compared to young adults. This age trend, crucially, is similar to what has been observed by Seamon et al. (2002) with American young and older adults. While these results suggest that age effects on BE may be cross-culturally invariant, further research in a different cultural context is needed to strengthen this proposal.

In the present study, I will test the boundary extension effect in healthy young and older adults across two cultures - UK and India - using the Rapid Serial Visual Presentation task (Mullally et al., 2012) administered on the MiND app (introduced in *Chapter 1*). I use the same RSVP task stimuli as Mullally et al. (2012) and De Luca et al. (2018) to facilitate direct comparisons of performance with healthy controls in these studies. First, I aim to determine whether the BE error is made by both young and older adults - I hypothesise that all groups will demonstrate BE, consistent with previous literature (H. Te Chang et al., 2021; Intraub & Richardson, 1989; Ménétrier et al., 2019; Multhaup et al., 2018; Seamon et al., 2002). Second, I aim to understand how age influences performance on this task. Although some studies have suggested that the BE error increases with age (H. Te Chang et al., 2021; Seamon et al., 2002), other studies have found no age-related differences (Ménétrier et al., 2019; Multhaup et al., 2018), so I do not make a prediction here as previous research has produced conflicting results. Third, I aim to understand whether the BE effect and an increase in BE with age is replicated in an Indian sample - I do not test an a priori hypothesis here as no study has previously investigated the BE phenomenon in this cultural context.

3.2. Methods

3.2.1. Participants

Described in *Chapter 2.2.1.*

3.2.2. Procedure

Described in *Chapter 2.2.2*.

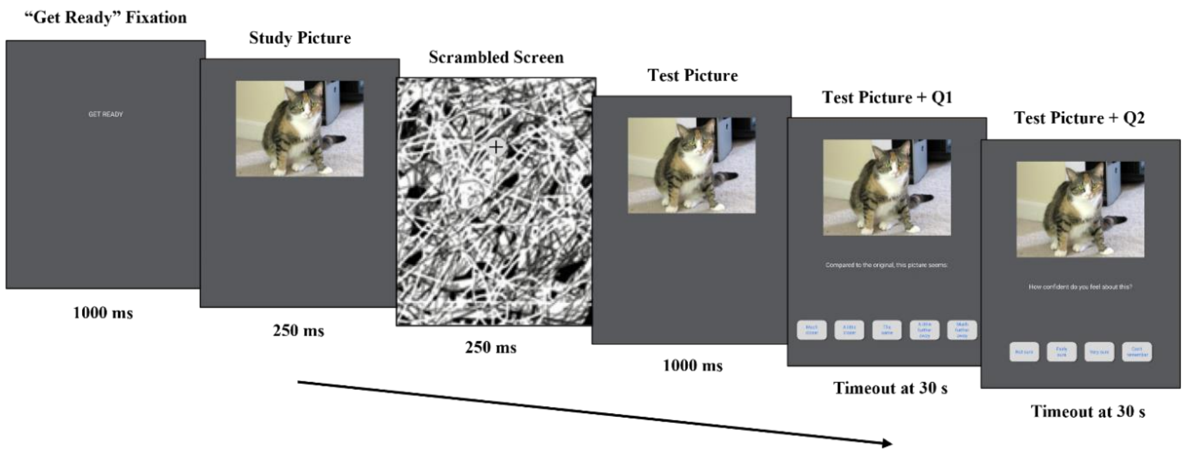
3.2.3. Materials

MiND Rapid Serial Visual Presentation Task

This task is an adaptation of the Rapid Serial Visual Presentation (RSVP) task used by Mullally et al. (2012) to test whether a boundary extension (BE) effect is displayed when participants are rapidly presented with exactly the same scene twice, with a brief distraction in between, and asked to judge the distance of the second presentation compared to the first. A boundary extension effect is an error in judgment, where in participants inaccurately recall the first presentation of a scene to include an extended boundary/ environment surrounding it and, compared to their memory of the first image, the second presentation of the identical scene appears closer to them.

The MiND RSVP task uses identical stimuli as Mullally et al. (2012), with minor adjustments to the task design for presentation on a tablet device. All images of scenes are composed of a close-up of a single, centrally-located every-day object, such as a bowl of oranges or a cat. Only close-up images of scenes were used as previous research has shown that identical close-ups elicit a significantly greater BE effect than pairs of wide-angle pictures which reveal little or no BE effect (Intraub & Dickinson, 2008). The task design involved the initial presentation of a stimulus for 250 ms on the screen, followed by a visual noise mask/ scrambled screen with a fixation cross for 250 ms, and then the same stimulus presented again for 1000 ms. Following this, two consecutive questions appeared, and participants had to respond to these by touching the relevant option on the screen. The first question asked participants to judge whether the second presentation of the stimulus was “much closer”, “a little closer”, “the same”, “a little further away”, or “much further away” than the original presentation. Importantly, on all trials, the second presentation of the scene was exactly “the same” (i.e., correct response) as the first presentation, but participants were not aware of this. In the second question, participants were asked to estimate whether their level of confidence in their first response was “not sure”, “fairly sure”, “very sure”, or “can’t remember”. If participants did not provide a response to either of the questions within 30 seconds, the screen was set to time-out and move to the next question or trial. There was an inter-trial interval of 1000 ms, during which a “Get Ready” fixation message was displayed before every trial. See *Figure 16* for an example of a trial. A total of 24 trials were presented to participants, and the order of stimuli was randomised for all participants. There was no practice trial for this task. It was hypothesized that healthy adults would commit the boundary extension “error” on this task by providing “much closer” or “a little closer” responses more frequently than other response choices. In terms of confidence in their responses, a higher level of confidence would be expected with the “much closer” or “a little closer” responses based on findings from Mullally et al. (2012).

Figure 16: MiND Rapid Serial Visual Presentation Task Schematic



Note. An example of the trial order: the task begins with a “Get Ready” text fixation on the screen for 1000 ms, followed by the first presentation of the “study” image (a close-up image) presented for 250 ms, then a scrambled/ visual noise screen with a fixation cross for 250 ms, and a second presentation of the “test” image for 1000 ms. The “study” and “test” images are always exactly the same on every trial. The “test” image remains on the screen while the first question is presented: “Compared to the original, this picture seems:”. There are five response choices for this question: “much closer”, “a little closer”, “the same”, “a little further away”, and “much further away”. Once the participant responds to this question, or the screen is timed-out if no response is provided in 30 seconds, the second question appears while the "test" image continues to remain on the screen: "How confident do you feel about this?". Four response choices are provided here: "Not sure", "Fairly sure", "Very sure", "Can't remember". All 24 trials follow a similar order.

Demographics and Digital Experience Survey

Described in *Chapter 2.2.3*.

3.2.4. Analysis

MiND Rapid Serial Visual Presentation Task

Details about the software and software packages used for data cleaning, analyses, and visualisations are reported in *Chapter 2.2.4*. All steps described here were independently implemented with the datasets for *Study A: UK* and *Study B: India.*

The RSVP task consisted of 24 trials - on each of these, the first image of the trial was presented on the screen for 250 ms, followed by a visual noise screen for 250 ms, and then the same image for 1000 ms before the test questions. However, due to an error in the MiND algorithm which was only discovered at the end of the study, the visual noise screen was not presented for the required duration for some participants on the first trial, and it was not possible to retrospectively check which participants were not shown this screen. Furthermore, due to the rapid presentation of images, some participants were not prepared for the speed on the first trial and reported missing the first presentation of the scene on Trial 1 (despite the "Get ready" reminder at the start of the trial). While an additional practice trial at the start of the task could have been used to prepare participants (see De Luca et al., 2018), this was not included on MiND to prevent deviations from the original task design (Mullally et al., 2012). Consequently, due to the presentation error and participant self-reports of being unprepared for the rapid presentation of images on Trial 1, this trial was excluded entirely from the analysis for all participants - only 23 trials were analysed here.

Due to the rapid presentation of stimuli on this task, it was important for participants to be attentive, and any trials where participants missed a picture due to being unprepared or distracted would have resulted in a random response on the test questions - on both questions, an option was not provided for “missed image” or “did not see image”. To avoid incorrectly including such trials in the overall calculation of boundary extension scores, rigorous data cleaning criteria were applied. Trials in which participants failed to provide a response on either or both of the test questions (distance and confidence judgments), resulting in a time-out after 30 seconds, were excluded entirely from the analysis for that particular participant. There were 4 trials in *Study A: UK*, and 23 trials in *Study B: India* which were excluded after applying this criterion. For the same reason, any trials where participants responded “Can’t Remember” to the confidence judgment question were also excluded - see De Luca et al. (2018) for a similar data cleaning approach. This resulted in the exclusion of 37 trials in *Study A: UK* and 74 trials in *Study B: India*. Confidence judgments provided by participants in *Study B: India* were generally more conservative (i.e., lower confidence). Due to the ambiguity of the response choices, it is possible that participants in this sample interpreted the responses differently, thereby differing in decision criterion (see Kim et al., 2015).

After applying the strict cleaning criteria outlined here, checks were run to see whether more than 50% of trials were excluded for any single participant or stimulus. One participant from *Study A: UK* was identified for whom more than half of the trials had been excluded - this participant had answered “can’t remember” on 16/24 recorded trials. As it was possible that the participant may have misunderstood the task and/ or performed it incorrectly, and only 8 trials were eligible for analysis, this participant was excluded from the analysis for this task. Reassuringly, no stimuli were identified for which more than half trials had to be excluded, also suggesting that no single stimulus was substantially more difficult than the others. The response selection position was also examined to check whether any participants clicked in the same location repeatedly, hence providing the same response (all test choices were always presented in the same location/ order). There were 5 participants in the *Study A: UK* sample, and 1 participant from the *Study B: India* sample who clicked "The Same" response on the distance judgment question 100% times. As this was the correct response on all trials (i.e., both pictures were always exactly the same), these participants were not excluded to avoid inaccurately inflating boundary extension scores - however, the possibility that these participants repeatedly selected the same response at random cannot be ruled out. Finally, the RT distribution of participants was investigated - plots revealed a typical Ex-Gaussian RT distribution with a long right tail. As trials automatically timed-out after 30 seconds if a response was not given, no further upper threshold was applied for RT. For the lower bound, an absolute minimum response limit of 200 ms was applied, but no trials were identified that fell below this threshold. After applying all cleaning measures described here, there were 3173 trials available in the UK sample (187 omitted - 5.56%), and 3306 trials in the Indian sample (246 omitted - 6.93%) for further analysis.

Similar to the analysis conducted by Mullally et al. (2012), the 5-choice distance judgments were converted to a 3-choice scale as follows to maximise power: "Much closer up" and "A little closer-up" responses were combined under the "Closer-up" category; "Much farther away" and "A little farther away" were combined as "Farther away", and "The same" option was maintained. A larger number of incorrect "closer-up" responses reflects boundary extension (Mullally et al., 2012). The three response types were used to group participant performance across different measures: i) Response Type Distribution, ii) Response Time by Response Type, and iii) Confidence by Response Type. Additionally, De Luca et al. (2018) calculate a boundary extension (BE) score which indicates which response type a participant is biased towards. iv) The BE score was computed on a scale of -2 to 2 by assigning numeric values to each level of the distance judgment: "Much closer-up" = - 2; "A little closer-up" = 1; "The same" = 0; "A little farther-away" = 1; "Much farther-away" = 2. While a mean score of 0 is thought to reflect no boundary extension effect (as responses are biased towards "the same"), a negative score would indicate that a participant is exhibiting boundary extension (De

Luca et al., 2018).

Statistical Tests and Modelling

T-tests were used to compare performance on each of the outcome measures between age groups, and a one-tailed *t*-test was used to determine whether mean BE scores were significantly lesser than 0 (i.e., BE effect). Mean BE scores were also calculated and compared as a function of stimulus/ image type in each age group, as studies have argued that the boundary extension effect may vary as a function of image characteristics (Bainbridge & Baker, 2020; Gandolfo et al., 2023). For modelling, the BE effect was converted to a binomial scale, such that a score < 0 signified a boundary extension effect and > 0 indicated no BE effect. To analyse whether age was a significant predictor of BE, a generalised linear mixed effects model (GLMM) of the logistic type was employed. A GLMM is appropriate with this task dataset as it is capable of handling non-Gaussian distributions, such as the binomial distribution (in this context, a boundary extension effect or no effect) which underlies a logistic regression. Furthermore, this analysis was run with BE trial-level data, and the dataset involved a hierarchical structure, such that lower-level variables such as image type were nested within higher-level variables such as age. A mixed effects approach is better here at accounting for heterogeneity/ variability within and between groups, provides increased flexibility with modeling population level trends (e.g., fixed effects) and deviations from these trends (e.g., random effects), and provides improved estimates for fixed effects accounting for random variance. Using the lme4 package (Bates et al., 2015) in R (R Core Team, 2022), a generalised linear mixed effects model was built via Maximum Likelihood method, with the binomial distribution specified with the logit link (i.e., logarithm of odds). The ANOVA function in the car package (Fox & Weisberg, 2019) was applied with the model to check the significance of predictors. Variable selection and model building followed a similar approach as the hTUNL task analysis in *Chapter 2*. In *Study A: UK*, the GLMM model used the following equation: *Boundary extension effect = Age + Education +*

Digital experience score + (1 | Participant ID) + (1 | Image). In *Study B: India*, the education variable was not included in the model due to the lack of variation in this variable; the following equation was used in this study: *Boundary extension effect = Age + Digital experience score + (1 | Participant ID) + (1 | Image).*

Age was entered as a continuous variable in the model (see Gusten et al., 2021) to capture the variability of its influence over the lifespan. Two random effects were added to the model: a participant term and an image term (Judd et al., 2012). The former accounts for variance introduced by individual differences in this study, while the latter accounts for stimulus/ image influences on the age effect on BE. It should be noted that image type was not investigated as a fixed effect as this study did not manipulate the stimulus set or design parameters of each image, but the variation that the stimuli introduce in terms of age effects can be accounted for as a random effect term in a GLMM. The Akaike Information Criterion (AIC) was used to compare the fit of this model with an exploratory model built without the image random effect, to determine whether the addition of this parameter significantly changed model fit - a smaller AIC indicates a better model fit for the observed data. Diagnostic tests were run to check that the models met the required assumptions.

3.3. Results

3.3.1. Study A: UK

Sample Characteristics

Described in *Chapter 2.3.1.*

Rapid Serial Visual Presentation (RSVP) Task Performance

See *Table 5* for a summary of the descriptive statistics for all outcome measures presented in this section, including Response Distribution, Response Time, Confidence Rating, and Boundary Extension (BE) Score between age groups.

Table 5: Group Descriptive Statistics for RSVP Task Performance in *Study A: UK*

	Young Adults		Older Adults	
Response Distribution	%		%	
Closer**	22.03		31.53	
The Same	58.97		59.54	
Further Away**	19.00		8.93	
Response Time (ms)	***M***	***SD***	***M***	***SD***
Closer**	2082.36	(1559.65)	2780.09	(2157.81)
The Same**	1773.89	(1811.22)	2155.30	(1886.96)
Further Away	1933.65	(1743.04)	2725.04	(2785.13)
Confidence Rating (0 to 3) [a]	***M***	***SD***	***M***	***SD***
Closer	2.02	(0.66)	1.98	(0.60)
The Same	2.22	(0.70)	2.18	(0.57)
Further Away	2.02	(0.63)	1.85	(0.64)
Boundary Extension Score (-2 to 2) [b]	***M***	***SD***	***M***	***SD***
Scaled Responses***	-0.04	(0.70)	-0.25	(0.64)

Note. M and *SD* are used to represent Mean and Standard Deviation, respectively. For each of these outcome measures, trial-level responses for each participant have been averaged at the group level by response type, where appropriate.

* Indicates the level of significance of age differences at $p < .05$, ** $p < .01$, *** $p < .001$.

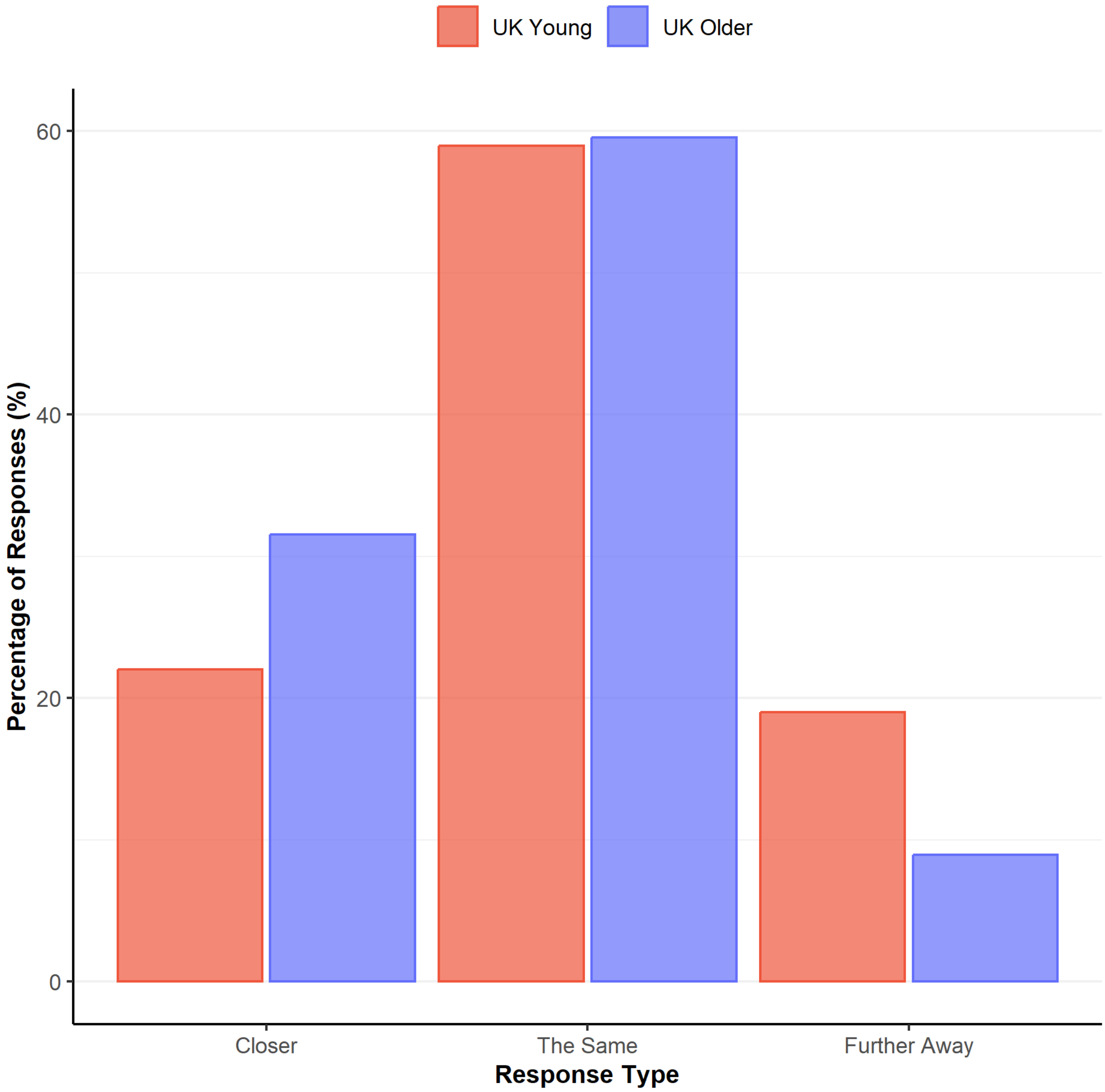
[a] Confidence responses converted to a numeric scale as follows: "Can't Remember" = 0, "Not Sure" = 1, "Fairly Sure" = 2, "Very Sure" = 3. A higher confidence rating indicates greater confidence.

[b] Distance responses converted to a numeric scale as follows: "Much Closer" = -2, "A Little Closer" = -1, "The Same" = 0, "A Little Further Away" = 1, "Much Further Away" = 2. A more negative score indicates a greater boundary extension effect.

Response Distribution

A boundary extension (BE) effect is demonstrated by a disproportionately larger number of incorrect ''closer-up'' responses to the test image in the present task (Mullally et al., 2012). Both age groups provided "the same" responses most frequently, followed by "closer-up", and then "further away" responses. *Figure 17* visually presents the distribution of response types by age group. Comparing the distribution of response types in the young group, there was no significant difference between the proportion of incorrect "closer-up" and incorrect "further away" responses (t(109.97) = 0.12, p = .908, Cohen's d = 0.02), but differences were significant between incorrect "closer-up" and correct "the same" responses (t(126.19) = -10.72, p < .001, Cohen's d = -1.83) and "the same" and "further away" responses (t(124.87) = -9.96, p < .001, Cohen's d = -1.76) with large effect sizes. In the older group, response proportions were significantly different between all response types: "closer-up" and "further away" (t(101.54) = 5.92, p < .001, Cohen's d = 1.13), "closer-up" and "the same" (t(127.27) = -6.12, p < .001, Cohen's d = -1.07), and "the same" and "further away" (t(106.03) = -12.22, p < .001, Cohen's d = -2.23). Between age groups, older adults gave significantly more "closer-up" responses than the young group (t(110.68) = 3.11, p = .002, Cohen's d = 0.55) and significantly fewer "further away" responses (t(95.97) = -3.03, p = .003, Cohen's d = -0.61), but differences were not significant on "the same" category (t(132.02) = 0.23, p = .819, Cohen's d = 0.04).

Figure 17: Bar Plot displaying Percentage of Responses by Response Type compared between Age groups in *Study A: UK*



Note. Bars represent the mean percentage of responses for a specific response type within its corresponding age category. Mean response percentage is calculated by dividing the total number of responses in each category by the sum of all responses and multiplying it by 100.

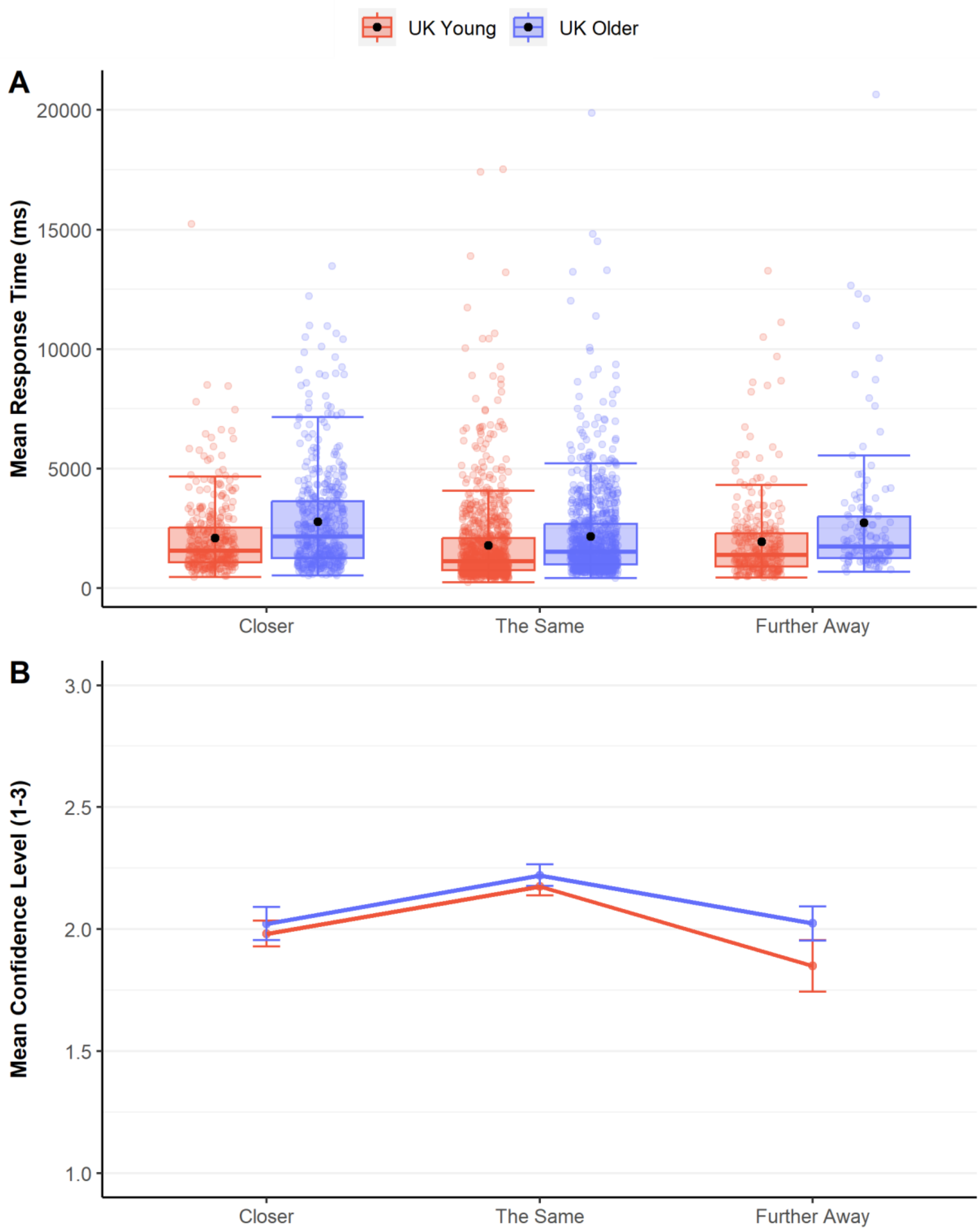
Response Time

Turning towards mean RTs for each of the three response types, the slowest responses were provided when choosing the "closer-up" option and the quickest responses were given on "the same" option in both age groups (see *Table 5*). In the young group, RT on "closer-up" responses was not significantly different from "further-away" responses (t(106.36) = 0.16, p = .869, Cohen's d = 0.03), but the "closer-up" responses had a significantly slower RT than "the same" responses with a small effect size (t(121.51) = 2.43, p = .049, Cohen's d = 0.42). In the older group, after adjusting for multiple comparisons, there were no significant differences between RT for "closer-up" and "further away" responses (t(72.34) = 0.02, p = .982, Cohen's d = 0.005), or "closer-up" and "the same" responses (t(124.12) = 2.09, p = .116, Cohen's d = 0.37). Comparing between age groups, mean RTs in the older group were significantly slower (with small effect sizes) than the young group for "closer-up" (t(112.37) = 2.72, p = .008, Cohen's d = 0.48) and "the same" responses (t(114.78) = 2.71, p = .008, Cohen's d = 0.46), but slowing for "further away" responses failed to reach statistical significance (t(69.24) = 1.90, p = .062, Cohen's d = 0.40).

Confidence Rating

Consistent with the pattern observed for RT, *Table 5* shows that there was a lower confidence rating associated with "closer-up" responses, and a higher confidence rating associated with "the same" responses - these differences were significant (after adjusting for multiple comparisons) with a small effect size in the young group (t(131.62) = -2.48, p = .043, Cohen's d = -0.43), but not the older group (t(127.96) = -1.59, p = .342, Cohen's d = -0.28). On the other hand, differences between "closer-up" and "further away" responses were not significant in the young (t(112.89) = -0.04, p = .968, Cohen's d =) or older group (t(81.04) = -0.03, p = .979, Cohen's d = =-.005). Between ages, there were no significant differences between confidence ratings associated with each response type: "closer-up" (t(123.17) = -0.16, p = .871, Cohen's d = -0.03), "the same" (t(136.81) = -1.13, p = .259, Cohen's d = -0.19), "further away" (t(91.71) = -0.14, p = .888, Cohen's d = -0.03).

Figure 18: Box and whisker plots displaying (A) Mean Response Time, and (B) Mean Confidence Rating compared across Response Type and Age groups in *Study A: UK*



Note. In plot (A), boxes represent the Interquartile Range (i.e., the middle 50% of values), with a horizontal line drawn within each box to mark the Median value. The whiskers, or the lines extending from either side of the box, display the dispersion of data, with the error bars representing the 95% confidence interval. Raw data points have been added to the plots, with a small amount of jitter. The black dot on each box shows the Mean value. In plot (B), dots represent the mean confidence rating for each response type, the error bars represent the 95% confidence interval, and a line has been drawn through these points for each age group.

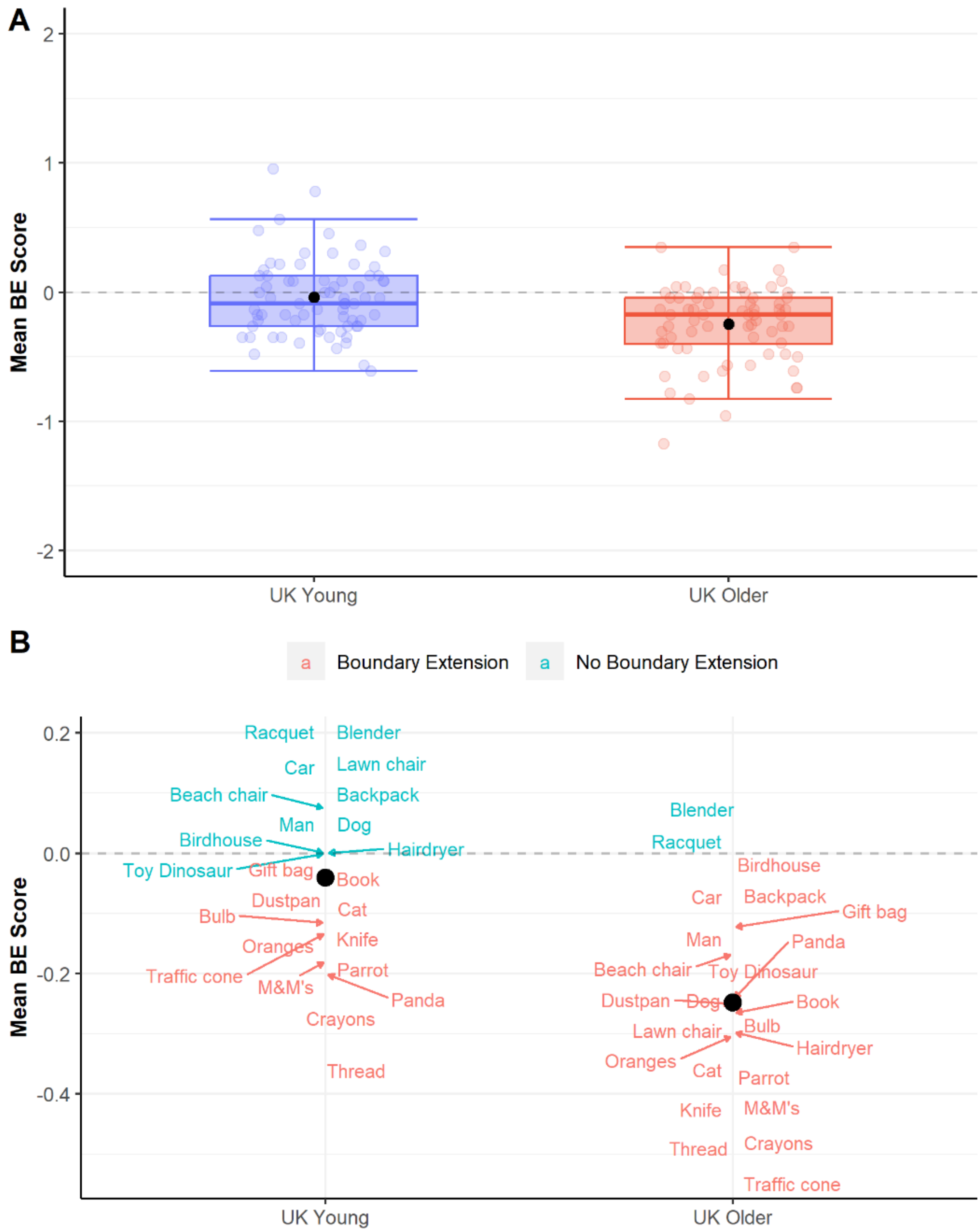
Boundary Extension Score

The boundary extension (BE) score combines the response types on a single numeric scale - a more negative score on this scale indicates more "closer-up" responses i.e., a boundary extension effect (Mullally et al., 2012). As 0 on this scale corresponds with "the same" response, a score equal to 0 is not thought to reflect a BE response, while a score greater than 0 is argued to reflect boundary contraction instead (Bainbridge & Baker, 2020). Both age groups in this study showed a mean BE score below 0 (see *Table 5*), but to understand whether these scores were significantly different from 0, one-tailed *T*-tests were run. In the young group, mean BE score was not significantly different from 0 ($t(70) = -1.12$, $p = .134$, Cohen's d = -0.13), while the older group demonstrated a statistically significant boundary extension effect with a large effect size ($t(67) = -6.90$, $p < .001$, Cohen's d =-0.84). This BE error performed by the older group was also significantly larger than the young group with a moderate effect size ($t(136.69) = -4.16$, $p < .001$, Cohen's d = -0.71).

The BE error also varied as a function of the stimulus/ image on which distance was judged (See *Appendix B* for the stimulus set used in the RSVP task by Mullally et al. (2012) applied in the present study). As shown in *Figure 19*, the mean BE score by image was not below 0 (i.e., no boundary extension effect) for 11/24 (45.83%) of images in the young group and 2/24 (8.33%) images in the older group. BE scores by image ranged between 0.19 (SD = 0.58) for 'Blender' to -0.39 (SD = 0.82) for 'Thread' in the young group; and 0.05 (SD = 0.54) for 'Blender' to -0.54 (SD = 0.66) for 'Traffic cone' in the older group. Although some images, such as 'Blender' and 'Racquet' had mean BE scores above 0 (i.e., no BE effect) in both age groups, they were not excluded from the analysis as the variation between participants, indexed by SD, was high. To account for this variation in the effect of Age on the probability of BE, the stimulus type as well as a subject-level term were modelled as random effects in the model presented below.

In the generalised linear mixed model fitted to predict the probability of a BE effect (i.e., score below 0), a significant main effect was found for Age ($X^2(1) = 7.99$, $p = .005$). The effect of Education did not reach statistical significance ($X^2(1) = 3.08$, $p = .079$), but it is relevant to report that this was driven by the Education below University-level, for which a negative but non-significant effect on BE probability was observed ($\beta = -0.61$, $SE = 0.35$, $z(3172) = -1.75$, $p = .079$). In other words, probability of BE was lower in the low education group, but this did not reach significance in the current sample. Finally, there was no significant effect of Digital experience on BE ($X^2(1) = 0.71$, $p = .400$). In terms of the variance explained by the image variable, including this parameter in the model as a random effect significantly improved the fit as compared to a model without image entered as a random effect ($AIC_{NoImage} = 3353.2$, $AIC_{Image} = 3262.7$; $X^2(1) = 92.49$, $p < .001$). See *Figure 20* for a visualisation of the age trend for BE effect with fixed and random effects. As depicted, the image random term partly accounts for the variance in the model. Nonetheless, the age trend is observably similar across all images - there is an increase in BE error probability with age.

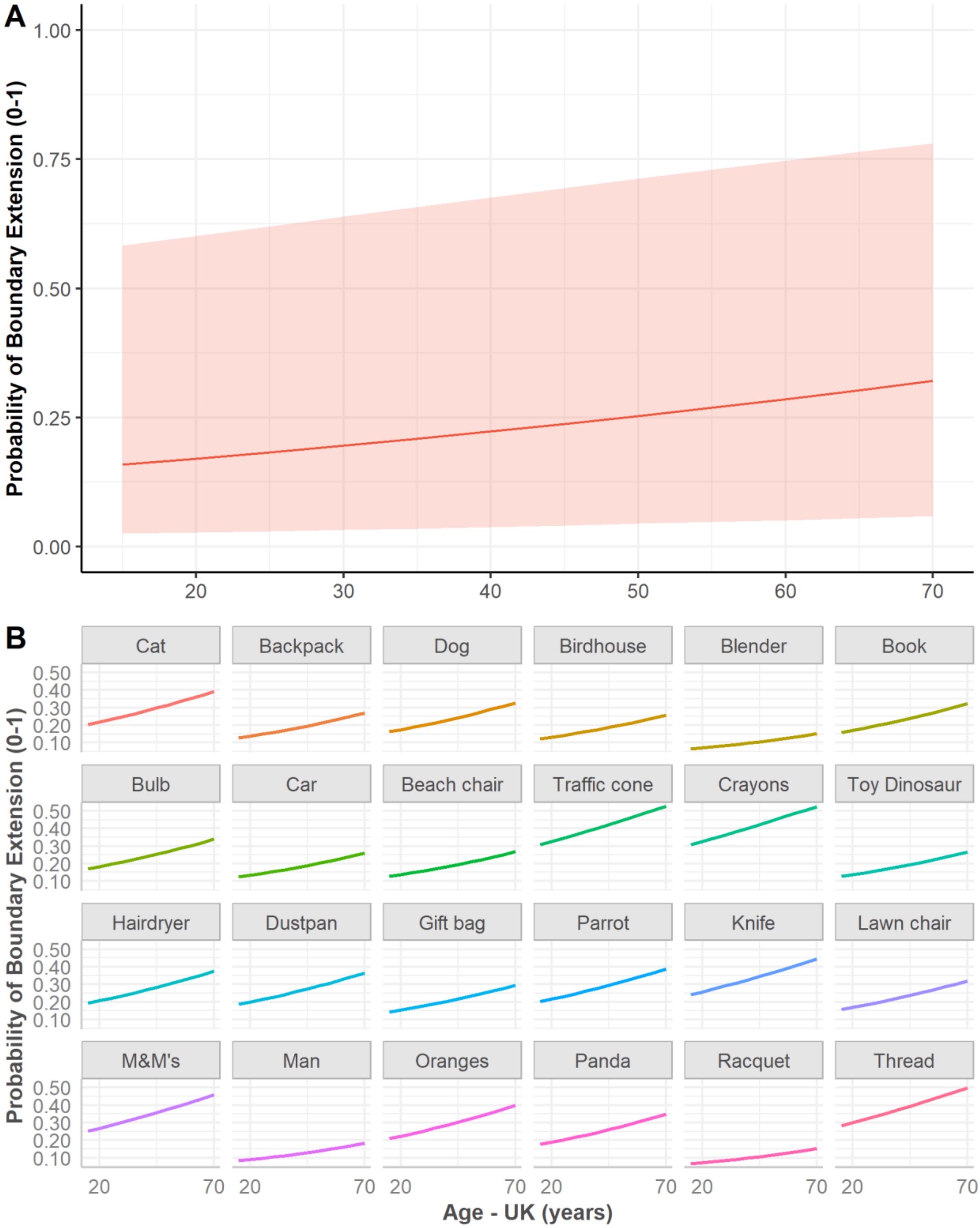
Figure 19: (A) Box and whisker plot displaying Mean Boundary Extension Score, and (B) Mean Boundary Extension Score by Image Type compared between Age groups in *Study A: UK*



Note. A y-axis intercept has been added to both plots at 0 - a score below 0 reflects boundary extension (Mullally et al., 2012), while a score above 0 is argued to reflect boundary contraction (Bainbridge &

Baker, 2020). In box plot (A), boxes represent the IQR, horizontal line within boxes = Median, Error bars = 95% confidence interval, coloured dots = jittered raw data points, black dots = Mean. In (B), the position of image names on the y-axis (arrows added so that text does not overlap) corresponds with mean BE scores for each image. Text in blue indicates images for which mean BE score was above the intercept of 0 (i.e., no BE effect), and red words indicate images with a BE score below 0 (i.e., BE effect). The black dot represents the mean BE score for each age group.

Figure 20: Line plots visualising Marginal effects on the Probability of Boundary Extension over (A) Levels of the fixed effect Age including variance by Random effects, and (B) Levels of the Random effect Image by the fixed effect Age in *Study A: UK*



Note. The y-axis represents the probability (0 - 1) of a boundary extension error being demonstrated (i.e., a BE score below 0). The line plots display the mixed effects model predictions of the marginal means in

(A) averaged over different levels of the fixed factor Age, adjusted for Education and Digital experience, and accounting for the variance of random effect terms Subject and Image, hence depicting large prediction intervals for marginal effects. In plot (B), marginal effects are conditioned on each level of the random effect 'Image' i.e., 24 images used in the RSVP task (taken from Mullally et al., 2012). See *Appendix B* for the stimulus set. These calculations were done using the 'ggpredict' function in the R 'ggeffects' package with 'type' specified as "random".

3.3.2. Study B: India

Sample Characteristics

This has been described in *Chapter 2.3.2*.

Rapid Serial Visual Presentation (RSVP) Task Performance

Table 6 provides a summary of the means and standard deviations for all outcome measures analysed here i.e., Response Distribution, Response Time, Confidence Rating, and Boundary Extension Score between age groups.

Table 6: Group Descriptive Statistics for RSVP Task Performance in *Study B: India*

	Young Adults		**Older Adults**	
Response Distribution	%		%	
Closer**	31.84		40.42	
The Same	43.06		44.20	
Further Away	25.10		15.38	
Response Time (ms)	***M***	***SD***	***M***	***SD***
Closer*	4386.88	(3989.20)	5555.21	(4501.39)
The Same	3065.73	(3604.77)	3578.59	(3702.20)
Further Away**	4637.42	(4280.06)	6058.62	(5123.93)
Confidence Rating (0 to 3) [a]	***M***	***SD***	***M***	***SD***
Closer	2.41	(0.63)	2.43	(0.59)
The Same	2.60	(0.56)	2.53	(0.59)
Further Away	2.48	(0.61)	2.21	(0.58)
Boundary Extension Score (-2 to 2) [b]	***M***	***SD***	***M***	***SD***
Scaled Responses***	-0.10	(0.97)	-0.36	(0.97)

Note. *M* and *SD* are used to represent Mean and Standard Deviation, respectively. For each of these outcome measures, trial-level responses for each participant have been averaged at the group level by response type, where appropriate.

* Indicates the level of significance of age differences at $p < .05$, ** $p < .01$, *** $p < .001$.

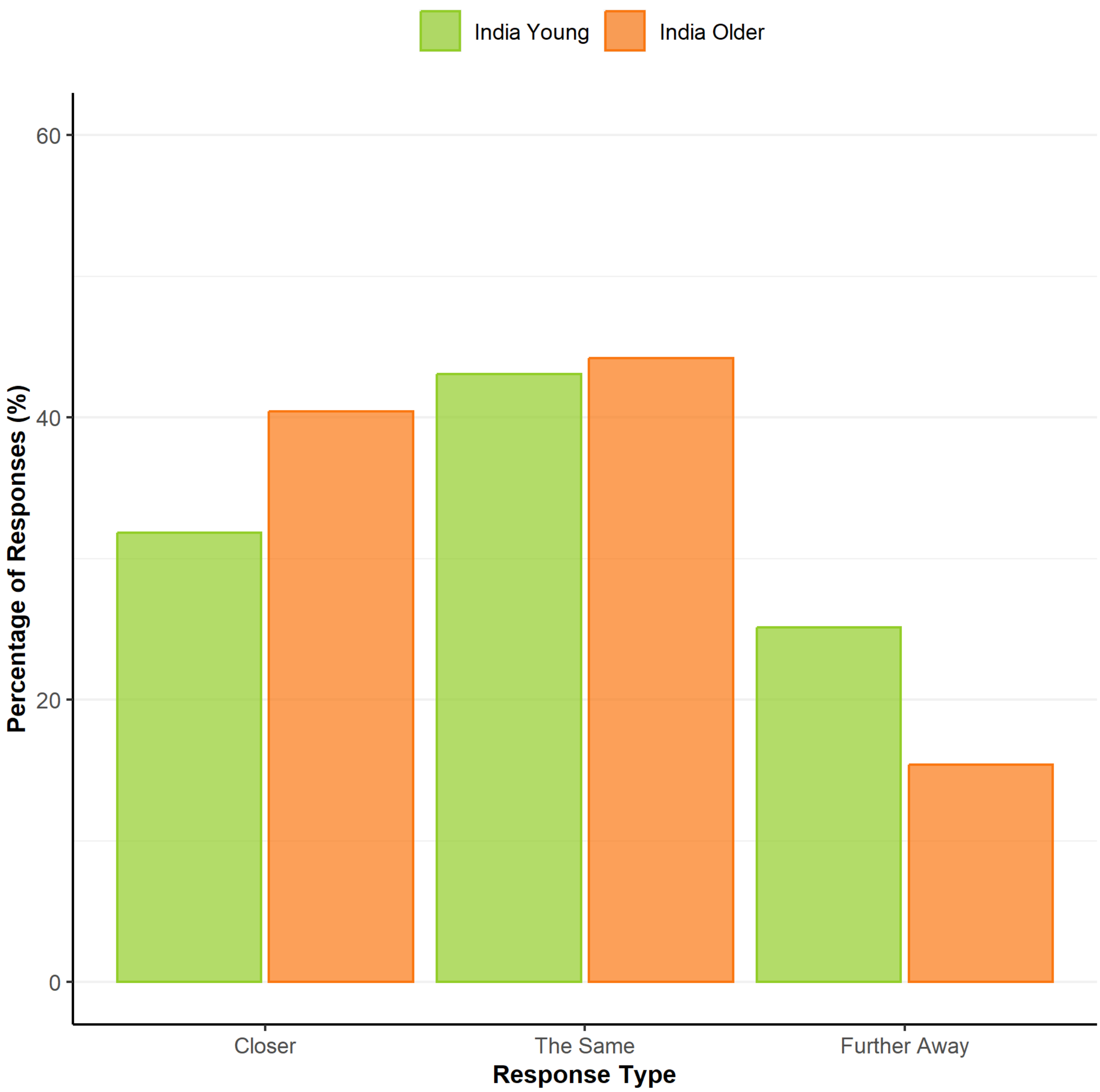
[a] Confidence responses converted to a numeric scale as follows: “Can't Remember” = 0, “Not Sure” = 1, “Fairly Sure” = 2, “Very Sure” = 3. A higher confidence rating indicates greater confidence.

[b] Distance responses converted to a numeric scale as follows: “Much Closer” = -2, “A Little Closer” = -1, “The Same” = 0, “A Little Further Away” = 1, “Much Further Away” = 2. A more negative score indicates a greater boundary extension effect.

Response Distribution

On this task, a larger number of incorrect “closer-up” responses to the second presentation of the image is thought to reflect the boundary extension error (Mullally et al., 2012). In both age groups, “the same” responses were provided most frequently on this task, followed by “closer up”; “further away” responses were least frequent. In the young group, there were significant differences between “closer-up” and “the same” responses ($t(135.37) = -3.71$, $p < .001$, Cohen's d = -0.61), and “the same” and “further away” responses ($t(132.10) = -5.26$, $p < .001$, Cohen's d = -0.88), but not between “closer-up” and “further away” responses ($t(143.99) = 1.76$, $p = .080$, Cohen's d = 0.29). On the other hand, in the older group, differences were significant between all categories: “closer-up” and “further away” ($t(119.79) = 5.31$, $p < .001$, Cohen's d = 0.95), “closer-up” and “the same” ($t(126.16) = -2.06$, $p = .042$, Cohen's d = -0.36), and “the same” and “further away” ($t(110.51) = -7.03$, $p < .001$, Cohen's d = -1.30). Between age groups, older adults gave significantly more “closer-up” responses than young adults ($t(131.37) = 2.65$, $p = .009$, Cohen's d = 0.44). The percentage of responses was slightly higher for older adults on “the same” category but not significantly different from young adults ($t(126.45) = 1.23$, $p = .219$, Cohen's d = 0.21); group differences were also not significant for “further away” ($t(108.38) = -1.64$, $p = .105$, Cohen's d = -0.30). See *Figure 21* for a graphical presentation of the response distribution for both age groups.

Figure 21: Bar Plot displaying Percentage of Responses by Response Type compared between Age groups in *Study B: India*



Note. Bars represent the mean percentage of responses for a specific response type within its corresponding age category. Mean response percentage is calculated by dividing the total number of responses in each category by the sum of all responses and multiplying it by 100.

Response Time

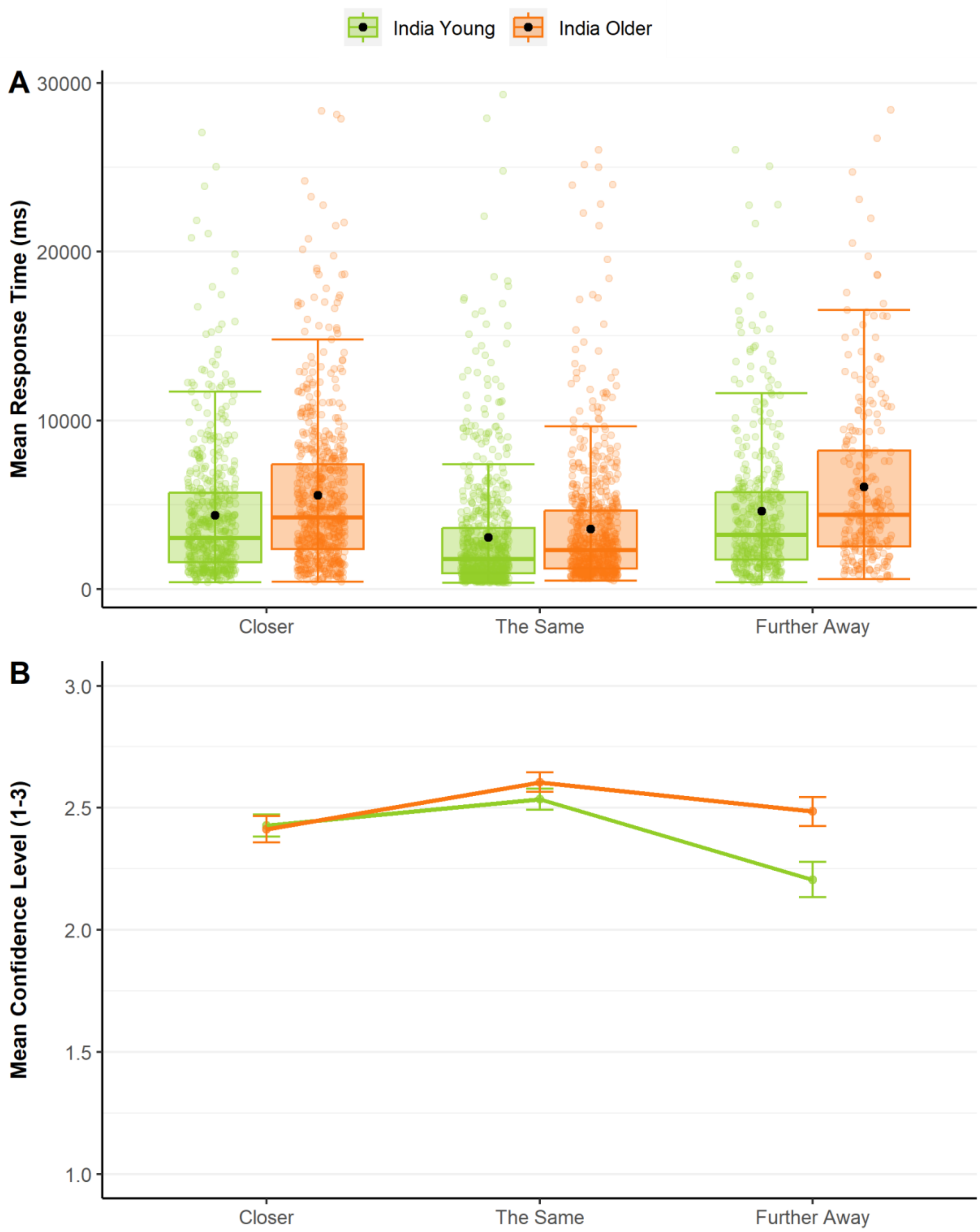
In this study, "closer-up" responses were associated with higher RTs than "the same" responses - these differences had a small effect size but did not reach statistical significance after adjusting for multiple comparisons in the young ($t(144.86) = 1.99$, $p =$

.125, Cohen's d = 0.33) or older age groups (t(119.37) = 2.21, p = .058, Cohen's d = 0.39). The "same" responses were the quickest in both age groups. On the other hand, "further away" responses were associated with the highest mean RT in both groups but did not differ significantly from "closer-up" responses in the young (t(143.54) = -0.09, p = .927, Cohen's d = -0.15) or older (t(96.57) = -0.86, p = .393, Cohen's d = -0.16) groups. Compared to the young group, RTs were significantly higher in the older group for "closer-up" (t(137.04) = 2.58, p = .011, Cohen's d = 0.43) and "further away" (t(87.05) = 2.86, p = .005, Cohen's d = 0.53) responses, but not for "the same" responses (t(108.69) = 1.36, p = .175, Cohen's d = 0.24).

Confidence Rating

In both age groups, the mean confidence rating was highest for "the same" responses, but this was not significantly different from confidence for "closer-up" responses in the young (t(144.59) = -2.19, p = .090, Cohen's d = -0.36) or older groups (t(125.65) = -1.05, p = .494, Cohen's d = -0.18). In the young adults sample, the confidence rating was lower for "closer-up" responses compared to "further away", but this was not significantly different (t(137.39) = -0.55, p = .581, Cohen's d = -0.09). Conversely, in the older group, "further away" responses were associated with the lowest level of confidence, but this was not significantly different from confidence for "closer-up" (t(100.14) = 1.16, p = .494, Cohen's d = 0.21) after corrections for multiple comparisons. Between ages, the young adults had a higher confidence rating for "the same" responses, but this was not significantly different from the older group (t(124.23) = -1.27, p = .206, Cohen's d = -0.22). No significant differences were found between ages for confidence ratings on "closer-up" (t(141.18) = -0.46, p = .647, Cohen's d = -0.08) or "further away" (t(108.25) = -1.93, p = .056, Cohen's d = -0.35) responses.

Figure 22: Box and whisker plots displaying (A) Mean Response Time, and (B) Mean Confidence Rating compared across Response Type and Age groups in *Study B: India*



Note. In plot (A), boxes represent the Interquartile Range (i.e., the middle 50% of values), with a horizontal line drawn within each box to mark the Median value. The whiskers, or the lines extending from either side of the box, display the dispersion of data, with the error bars representing the 95% confidence interval. Raw data points have been added to the plots, with a small amount of jitter. The black dot on each box shows the Mean value. In plot (B), dots represent the mean confidence rating for each response type, the error bars represent the 95% confidence interval, and a line has been drawn through these points for each age group.

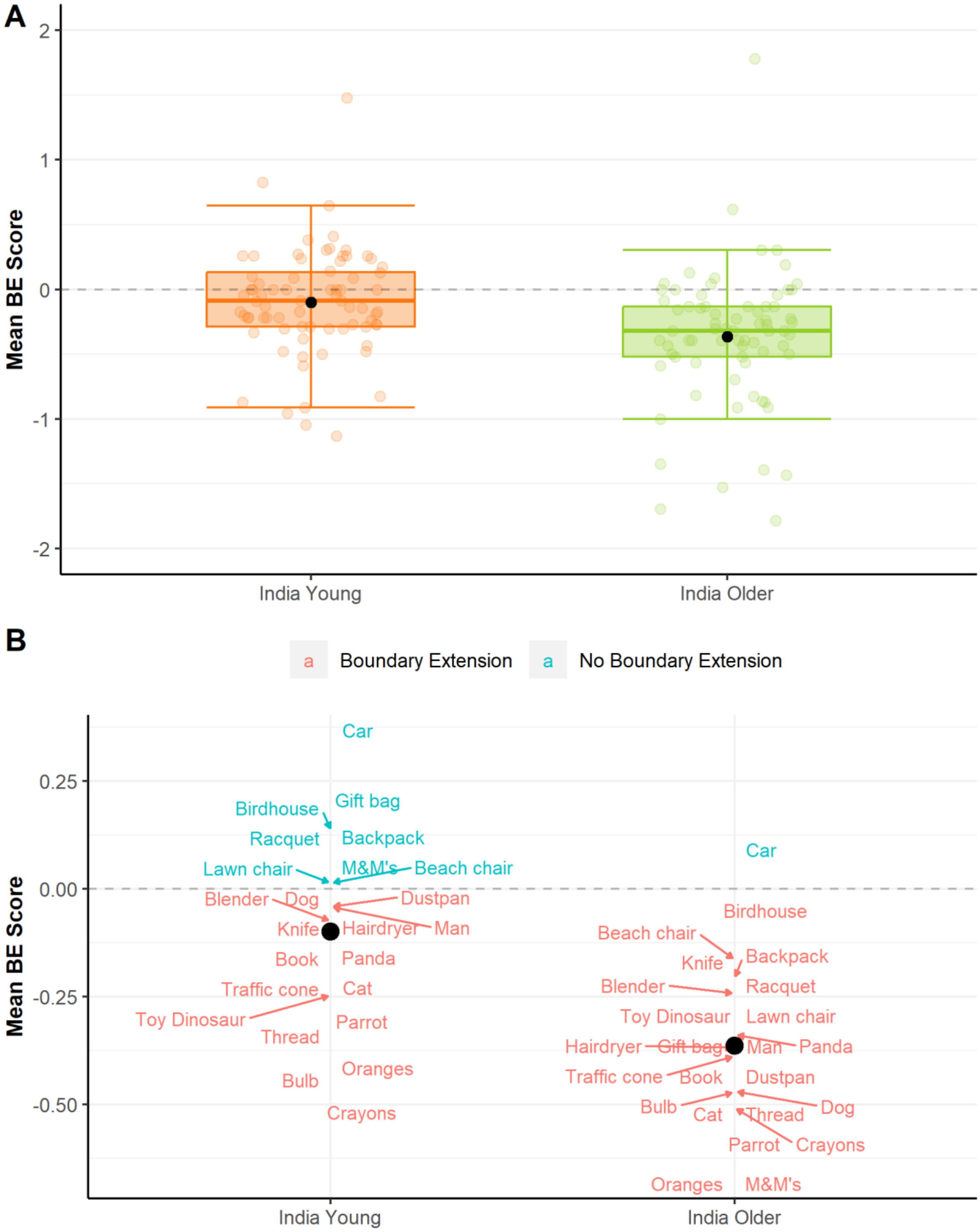
<u>Boundary Extension Score</u>

Both age groups demonstrated a boundary extension (BE) effect - mean BE scores were negative for both groups (See *Table 6* and *Figure 23*), and these scores were significantly different from 0 (i.e. correct "the same" response) for the young adults with a small effect size ($t(75) = -2.10$, $p = .019$, Cohen's d = -0.24) and older adults with a moderate effect size ($t(71) = -5.88$, $p < .001$, Cohen's d = -0.69). A more negative score indicates a greater boundary extension error (Mullally et al., 2012) - in this study, BE scores were significantly lower (i.e., greater BE error) in the older group compared to the young group ($t(133.68) = -3.43$, $p < .001$, Cohen's d = -0.57) with a moderate effect size.

Turning to stimulus/ image effects, *Figure 23* depicts the mean BE score calculated by image and age group in this study (see *Appendix B* for the full set of images used in this task). Mean BE scores by image were lower than 0 for 8 of 24 stimuli (33.33%) in the young group and 1/24 (4.17%) images in the older group. In the young group, BE scores by image ranged between 0.35 ($SD = 0.99$) for 'Car' to -0.48 ($SD = 0.99$) for 'Crayons'; in the older group, the range was between 0.06 ($SD = 0.98$) for 'Car' to -0.67 ($SD = 0.87$) for 'Oranges'. To capture the variance introduced by stimulus effects in the model predicting effects of Age on BE probability, the image type and participant ID were entered as random effects in the model below.

A generalised linear mixed model showed that there was a significant main effect of Age ($X^2(1) = 4.98$, $p = .026$), but not of Digital Experience ($X^2(1) = 0.20$, $p = .655$) on the probability of a boundary extension error being demonstrated. Including image type as a random effect in this model along with a participant term significantly improved the fit for the data, compared to a model with only a participant term as a random effect ($AIC_{NoImage} = 3959.90 > AIC_{Image} = 3928.90$; $X^2(1) = 32.95$, $p < .001$). *Figure 24* portrays the age trend for BE effect estimated over levels of the fixed and random effects. The probability of boundary extension varies between images, introducing variance in the model predictions for Age effects, but the pattern of increasing BE with age is consistently observed across the stimulus set.

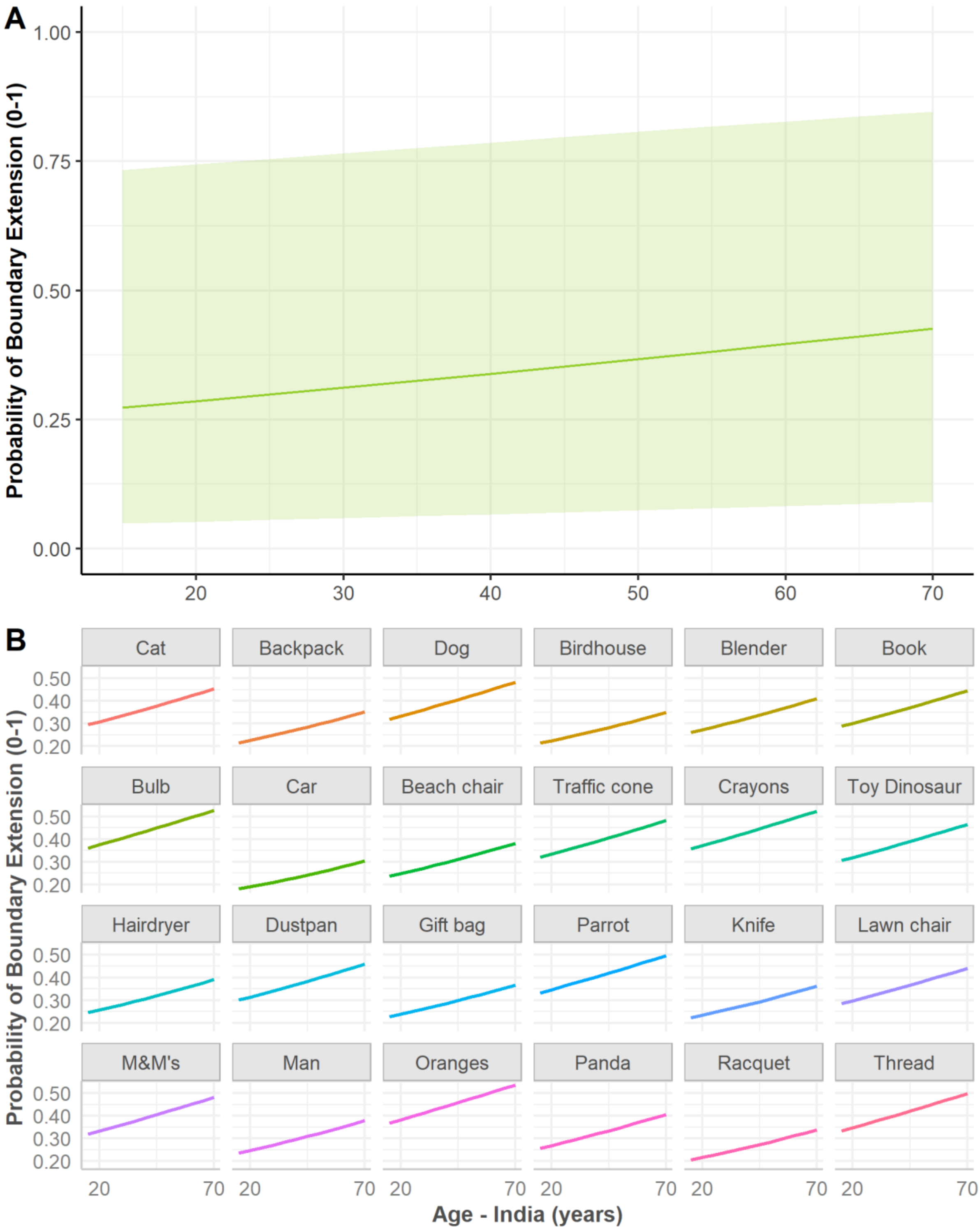
Figure 23: (A) Box and whisker plot displaying Mean Boundary Extension Score, and (B) Mean Boundary Extension Score by Image Type compared between Age groups in *Study B: India*



Note. A y-axis intercept has been added to both plots at 0 - a score below 0 reflects boundary extension (Mullally et al., 2012), while a score above 0 is argued to reflect boundary contraction (Bainbridge &

Baker, 2020). In box plot (A), boxes represent the IQR, horizontal line within boxes = Median, Error bars = 95% confidence interval, coloured dots = jittered raw data points, black dots = Mean. In (B), the position of image names on the y-axis (arrows added so that text does not overlap) corresponds with mean BE scores for each image. Text in blue indicates images for which mean BE score was above the intercept of 0 (i.e., no BE effect), and red words indicate images with a BE score below 0 (i.e., BE effect). The black dot represents the mean BE score for each age group.

Figure 24: Line plots visualising Marginal effects on the Probability of Boundary Extension over (A) Levels of the fixed effect Age including variance by Random effects, and (B) Levels of the Random effect Image by the fixed effect Age in *Study B: India*



Note. The y-axis represents the probability (0 - 1) of a boundary extension error being demonstrated (i.e., a BE score below 0). The line plots display the mixed effects model predictions of the marginal means in

(A) averaged over different levels of the fixed factor Age, adjusted for Education and Digital experience, and accounting for the variance of random effect terms Subject and Image, hence depicting large prediction intervals for marginal effects. In plot (B), marginal effects are conditioned on each level of the random effect ‘Image’ i.e., 24 images used in the RSVP task (taken from Mullally et al., 2012). See *Appendix B* for the stimulus set. These calculations were done using the ‘ggpredict’ function in the R ‘ggeffects’ package with ‘type’ specified as “random”.

3.4. Discussion

This experiment aimed to understand the effects of cognitive ageing on the boundary extension effect (Intraub & Richardson, 1989) and whether this phenomenon is similar across cultures. Consistent with evidence which suggests that the BE phenomenon is universal (Intraub & Richardson, 1989; Seamon et al., 2002; Spanò et al., 2017), my results have shown that participants across age and cultural groups demonstrate a BE effect. With increasing age, the probability of BE error also increases - notably, this pattern is consistent across cultures. However, my results fail to replicate BE performance patterns differentiating healthy controls from patients with damage to brain regions involved in scene construction (De Luca et al., 2018; Mullally et al., 2012). Specifically, I have found that the BE error demonstrated on the RSVP task by healthy adults is less frequent than what has been previously reported (De Luca et al., 2018; Mullally et al., 2012). In this section, I provide plausible explanations for this pattern of results, and discuss broader implications for our understanding of the BE effect and cognitive tasks designed to measure BE.

My results are consistent with findings of an age-related increase in BE in work by Seamon et al. (2002) and, more recently, Chang et al. (2021) in a non-Western culture. The multi-source model (Intraub, 2010, 2012) suggests that scene construction involves the integration of multiple sources, including visuo-sensory input and contextual information. In ageing, it has been argued that there is a bias towards greater semanticization i.e., a greater reliance on general or semantic memory, rather than specific details (Levine et al., 2002; Spreng et al., 2018). The increased probability of the BE error with age, therefore, can be explained as a greater dependence on less detailed information in pre-existing schemas which results in extrapolation or "filling in" of the boundaries of a scene based on expectations and general knowledge. On the other hand, boundary extension reductions observed in patients with damage to HC and regions involved in the wider scene network (De Luca et al., 2018; Mullally et al., 2012) can be interpreted as a loss in their core ability to integrate visual, spatial, and contextual information (i.e., scene construction), which is fundamental to boundary extension. This contrasts with age-related changes in scene construction, as healthy older adults may maintain their scene construction ability (revealed by the BE effect), but an age-related loss of integrity may create an imbalance in the sources of information used to extrapolate scenes, resulting in greater BE.

The age-related increase in BE is also compatible with the source monitoring error (Johnson et al., 1993), as older adults are less likely to distinguish between externally received and internally generated information, leading to an increase in false memory errors (Hashtroudi et al., 1989; McDaniel et al., 2008; Mitchell et al., 2003). This evidence is consistent with findings of an age-related increase in false memory errors in the broader cognitive ageing literature (for reviews, see Devitt & Schacter, 2016; Jacoby & Rhodes, 2006) - for example, in mnemonic discrimination tasks (Reagh et al., 2014; C. E. L. Stark et al., 2010; S. M. Stark et al., 2013; Yassa, Mattfeld, et al., 2011). Moreover, age-related changes in the MTL and prefrontal cortex are proposed to play an important role in false memories (Devitt & Schacter, 2016). It is relevant to point out that digital experience was not a significant predictor of boundary extension probability in the present research, suggesting that a greater BE effect in older groups was unlikely to be related to differences in experience with digital technologies compared to young groups.

Between cultures, my results reveal a similar pattern of age-related changes in BE amongst both British and Indian samples - an age-related increase in BE has also been found by Chang et al. (2021) in Taiwanese participants. Beyond the boundary extension error, a study on cross-cultural differences in categorical memory errors has also found similar age-related changes (Gutchess & Boduroglu, 2019) i.e., older adults across cultures were more prone to committing memory errors on a categorical recall task, of both semantically related and unrelated information. In my results, it should be noted that differences can be observed in terms of the magnitude of BE error between *Study A: UK* and *Study B: India*. A larger mean boundary extension effect is seen in the Indian samples compared to UK in both age groups. While it was beyond the scope of the present research to investigate factors which may underlie cross-cultural differences, Gutchess et al., (2006) have suggested that memory strategy may differ across cultures e.g., the reliance on categories for recall. It is important for future cross-cultural studies to compare memory errors such as BE in well-matched cross-cultural samples to gain an understanding of the mechanisms underlying differences. Nonetheless, my results provide support for the idea that the susceptibility to memory errors observed in normal ageing (Balota et al., 1999; Schacter et al., 1997) is cross-culturally invariant, possibly driven by universal neurobiological processes in ageing.

Previous applications of the Rapid Serial Visual Presentation task (Mullally et al., 2012) used here have detected a boundary extension effect across healthy older adults and patients with damage to the HC and vmPFC regions. Crucially, while all participants demonstrate BE, the degree of boundary extension error varies between healthy adults and patient populations (De Luca et al., 2018; Mullally et al., 2012). In my work, I have shown that all groups demonstrated BE, but both healthy young and healthy older adults perform BE less frequently than what is reported in previous studies. Across age groups and cultures, my results show that healthy adults provided “the same” responses most frequently on the RSVP task, followed by “closer up”, and then “further away” responses. Results for RT and confidence ratings by response type mirrored this distribution in both age and cultural groups, with the quickest and most confident ratings being provided on “the same” category, rather than “closer-up”. Most strikingly, this response pattern is comparable with vmPFC (De Luca et al., 2018) and HC patient groups (Mullally et al., 2012), rather than controls in previous studies. An important question is raised here regarding the frequency of boundary extension observed in earlier studies with healthy adults which is not replicated in my sample. Interestingly, Kim et al. (2015) also found that healthy older adults preferred to respond “the same”, similar to patient performance in Mullally et al. (2012). When Kim et al. (2015) manipulated the task design by telling participants that both images were different, they found a shift in the decision criterion: performance of both patients and healthy older controls was now biased towards the “closer” option, similar to performance of controls in Mullally et al. (2012), implying that the BE error (as measured on the RSVP task) may be sensitive to decision criteria. Cross-cultural research has also shown that response patterns on rating scales may vary between cultures (J. W. Lee et al., 2002).

Another contribution to the variability in reports of the BE error could be stimulus-level effects. In the present study, I used the same task design and stimuli from Mullally et al. (2012). My results showed that the magnitude of the BE error varied between stimuli and, interestingly, certain stimuli were more likely to elicit a boundary contraction effect instead (i.e., mean scores above 0). In the healthy young groups, a boundary contraction effect instead of BE was demonstrated on 45.83% of stimuli in *Study A: UK* and 33.33% stimuli on *Study B: India.* Certain images caused a boundary contraction effect in both age groups e.g., “blender” and “racquet” in *Study A: UK*, and “car” in *Study B: India.* Cross-culturally, a larger mean BE effect is seen across most stimuli in the Indian samples. As stimuli used in this study were not adapted for the Indian population, this difference could be attributed to culture-specific semantic associations with stimuli. However, if semantic associations drastically varied between cultural groups, one would not expect to see any cultural invariance in stimulus-specific effects. This was not the case as 25% of stimuli showed a boundary contraction effect across both cultures when comparing between young groups (namely, “car”, “beach chair”, “lawn chair”, “racquet”, “backpack”, “birdhouse”). Recent findings from Bainbridge & Baker (2020) and Gandolfo (2023) on the effect of image properties on the BE effect provide plausible explanations for these findings. In a large-scale online MTurk study, Bainbridge & Baker (2020) used the RSVP paradigm to test the BE phenomenon on a new, diverse set of 1000 images with 2000 participants. The set was composed of 500 images of naturalistic scenes from the Scene Understanding Database, and 500 naturalistic objects downloaded from Google Open Images; each image was randomly sampled from different categories within each database, and edits were made to ensure that the positioning and sizing of all images were similar. Remarkably, they found that object-oriented images primarily elicit a boundary extension effect, while the scene images show an equal tendency to cause a boundary extension or contraction effect.

A key difference between scene and object processing is that the former takes into account spatial and contextual relationships surrounding a single or multiple objects. In the stimulus set tested in the Mullally et al. (2012) RSVP task (applied in my study), all stimuli were designed to be images of single objects, but the amount of background content provided varied between images. In their supplemental information, Mullally et al. (2012) state that, in the 24 stimuli they used, the proportion of background contained within each image was manipulated to prevent learning effects. However, they do not report how the BE effects they observed varied as a function of the background proportion, and do not provide information on how they calculated background proportions in order for this variable to be included in the present analysis. Nonetheless, in my results, it can be qualitatively observed that images for which a mean boundary contraction effect was observed across cultural groups provided greater scene background (or, could be categorised as scene images) e.g., a beach chair on a gravel beach and the ocean in the background, or a car on the road and trees in the background. In contrast, images which showed a high BE effect in both cultures provided no or little contextual details (or, could be categorised as object images) e.g., a traffic cone, oranges, or crayons. Bainbridge & Baker (2020) also found that these scene and object dissociations in BE applied to memory as well as perceptual paradigms. Furthermore, Patel et al. (2023) reported that BE is greater for object images as compared to face images. These stimulus-level dissociations in BE effects may highlight the need to conceptualise the boundary extension phenomenon through broader representational accounts of MTL function, which propose that brain regions and networks involved in scene and object processing tasks are dissociable within the MTL (Graham et al., 2010; Murray et al., 2017; Saksida & Bussey, 2010). This idea may explain why different types of stimulus representations (i.e., scenes or objects) could be differentially vulnerable to memory errors such as boundary extension. Furthermore, the heterogeneity in BE stimuli used across studies could also contribute to inconsistencies observed in age effects.

In an additional task where Bainbridge & Baker (2020) collected subjective distance ratings for how far the main object appeared to viewers, they found that images which were composed of a main object which was subjectively closer were associated with greater BE on the RSVP task, while objects which appeared more distant were more likely to cause boundary contraction. This finding is consistent with the literature as a key characteristic of the boundary extension effect reported by earlier studies is that it is most pronounced for images of close-up scenes, and this effect reduces as more space/ context around the scene is made visible (Intraub et al., 1992; Intraub & Richardson, 1989). On the other hand, no boundary extension effect is observed on wide-angle compositions (Intraub et al., 1992). Bainbridge & Baker (2020) add to this understanding by highlighting that boundary contraction is, in fact, as common as boundary extension for naturalistic scene images. An alternative interpretation provided by Gandolfo et al. (2023) is that the BE effect depends upon depth of field (DOF) of an image as determined by camera aperture settings i.e., a large aperture reduces depth of field, causing the object to be more in focus and the background to be more out-of-focus (e.g., portrait view on a camera), while a small aperture increases depth of field and brings the background more into focus. A larger DOF is less characteristic of natural human vision and, therefore, less naturalistic. Gandolfo et al. (2023) rated the 1000-image set used by Bainbridge & Baker (2020) by DOF, and found that photographs with DOF within the normal human range of vision largely led to boundary extension, while boundary contraction was observed on images with an unnaturally deep DOF (i.e., background details clearly in focus). Results from this study suggest that, while BE effect may depend upon image properties as tested in a large sample of stimuli which are more representative of our visual experiences (Bainbridge & Baker, 2020), BE effect is still commonly observed when the composition of these images is more similar to how we perceive our environment (Gandolfo et al., 2023). While an in-depth analysis of specific image properties was beyond the scope of the present study, my results add to an emerging understanding of how task-specific characteristics constrain the boundary extension phenomenon, even across age and cultural differences.

Another reason for differences observed between my findings and earlier studies with healthy adults using the RSVP task by Mullally et al. (2012) may be the sample size. As previous studies recruited a small number of participants in each group, it is possible that the boundary extension error has been overestimated in healthy controls and underestimated in patients due to sample size limitations. It is well recognised that the field of psychology suffers from a replication crisis (Open Science Collaboration, 2015) - statistically significant results found in low powered studies often fail to replicate as they are characterised by greater variability in effects, leading to high cases of Type I and Type II errors i.e., false positives and false negatives respectively (Christley, 2010; Oakes, 2017). To address these concerns, my study recruited a comparatively larger sample than earlier studies in this area, statistically accounted for variance introduced by individual differences and stimulus effects, and reported effect sizes where relevant. Importantly, in terms of the main effect of interest in my study - ageing - I have shown that, despite variance introduced by sample and image characteristics on the BE effect, the age trend of BE is observably similar across stimuli. With increasing age, the probability of boundary extension increases across cultures, at the task-level and the stimulus-level.

A notable limitation of the present study is that a standardised memory test was not used in the present study to screen for MCI in the older group. While it is not possible to rule out effects of pathological changes on cognitive performance, it is unlikely that my results are confounded by memory impairments, as the performance of older adults with MCI would be expected to be more similar to amnesic populations who show an attenuated BE effect (Mullally et al., 2012) - this was not observed. In terms of cross-cultural comparisons, it should be noted that the RSVP task stimuli (Mullally et al., 2012) were not adapted for the Indian population. In order to understand whether the BE effect generalised in a new cultural context, it was important to keep test stimuli constant. However, it is possible that familiarity and/or semantic associations with stimuli varied across cultures, and this could partly explain the higher BE magnitude demonstrated in both Indian age groups, compared to UK. Future studies should validate a wider set of task stimuli across large-scale cross-cultural samples - this is best achieved using online testing methods as employed in Bainbridge & Baker (2020). Given significant stimulus-level variation observed in the present study, it would be important for further investigations to consider effects of specific image characteristics on RSVP task performance. While this was beyond the scope of the present study, one way to achieve this is the objective identification and quantification of low- and high-level visual image properties (e.g., Rouw et al., 1997) and the inclusion of these parameters in models predicting BE. This can be calculated using R packages such as 'imagefluency' (Mayer, 2021), as well as more advanced machine learning methods. It would be interesting for future research to explore how BE performance correlates with broader functions of the MTL, such as in memory and perception (Graham et al., 2010; Saksida & Bussey, 2010) - if boundary extension and contraction phenomena vary for object and scene stimuli (as implied by Bainbridge & Baker, 2020), this may provide justification to view these phenomena from a representational-hierarchical lens. Age effects may have differential influences upon boundary extension for different stimulus types.

The present study is the first to find support for the boundary extension phenomenon in the Indian cultural context, adding to the body of literature which shows that this adaptive memory error is universally demonstrated (Intraub & Richardson, 1989; Seamon et al., 2002; Spanò et al., 2017). In the context of ageing, I have found strong evidence for a cross-culturally consistent age-related increase in the BE error, consistent with the broader cognitive ageing literature which finds an increase in memory errors in older adults e.g., on mnemonic discrimination tasks (Reagh et al., 2014; C. E. L. Stark et al., 2010; S. M. Stark et al., 2013; Yassa, Mattfeld, et al., 2011). However, my results have also highlighted the fragility of the BE effect. I have shown that the boundary extension effect is less frequent than previously reported with healthy adults (De Luca et al., 2018; Mullally et al., 2012). The variation observed in the BE effect can partly be attributed to stimulus-level effects on tasks such as the Mullally et al. (2012) RSVP paradigm, suggesting that the BE effect is constrained by stimulus characteristics, in line with recent work by Bainbridge & Baker (2020) and Gandolfo et al. (2023). In this case, it is difficult to tease apart the cognitive phenomenon (i.e., BE) from constraints of the tool used to measure it (i.e., RSVP task and stimuli). It is important for future research to consider how different BE paradigms and task stimuli may mediate the finding of an age effect on boundary extension.

Chapter 4: Influence of Age on Complex Perception across Cultures

4.1. Introduction

Representational models of Medial Temporal Lobe function (Graham et al., 2010; Saksida & Bussey, 2010) propose that sub-regions, such as the hippocampus (HC) and perirhinal cortex (PRC), are functionally heterogeneous and dissociable – they play a role in both mnemonic and perceptual functions, and are specialised for the processing of different types of stimulus representations i.e., scenes in HC and objects in PRC. In the ventral visual-perirhinal-hippocampal pathway of information processing, brain regions are organised in a hierarchical continuum of representations: earlier/ lower levels represent basic features and later/ higher levels represent more complex feature conjunctions (Cowell et al., 2010). The MTL is responsible for the formation of these complex visual representations, which facilitate the differentiation of stimuli with high degrees of feature overlap (in complex perception) and the resolution of perceptual interference (in memory). Within the MTL, the level of operation in the representational hierarchy determines the involvement of structures with different representational content: object representation and resolution occur in the PRC, while the combination of object conjunctions with spatio-temporal context takes place in the HC (consistent with the key role it plays in episodic memory). Normal age-related structural and functional changes in MTL regions (Berron et al., 2018; Fjell et al., 2014; Leal & Yassa, 2015; Lockhart & DeCarli, 2014; Ryan et al., 2012) have been associated with deficits in cognitive functions which rely on the quality of these representations, such as in memory (Gusten et al., 2021; Reagh et al., 2016). However, it is presently unclear whether ageing can also lead to impairments in complex perception, and research is yet to examine age-related changes in this cognitive function across cultures (Leal et al., 2017).

Assessments of age-related changes in MTL-based representations have largely focused on mnemonic discrimination tasks, which test the ability to differentiate between events/ representations in memory which share similar features. Such tasks have found age-related impairments in complex conjunctive representations of scene/ spatial (Gusten et al., 2021; Reagh et al., 2016; Reagh & Yassa, 2014; S. M. Stark & Stark, 2017), object (Gusten et al., 2021; Holden et al., 2013; S. M. Stark et al., 2015; S. M. Stark & Stark, 2017; Toner et al., 2009), and emotion (Leal et al., 2017; Leal & Yassa, 2014) content, thereby indicating that the formation of high-fidelity mnemonic representations of visual stimuli is sensitive to ageing across representational content and task demands. However, the specificity of mnemonic discrimination measures may be limited e.g., the Mnemonic Similarity Task (Kirwan & Stark, 2007; S. M. Stark et al., 2013) is found to require involvement of cognitive control in addition to memory (Pishdadian et al., 2020). On the other hand, perceptual discrimination tasks, which assess the ability to differentiate between stimuli with high degrees of feature similarities, have received little attention in this context. They are known to tax similar MTL representations while also being specific to MTL processes (Graham et al., 2010). A perceptual task which relies on the complex representational functions of the MTL is the Oddity Perceptual Discrimination task (A. C. H. Lee, Buckley, et al., 2005).

The Oddity paradigm involves the simultaneous presentation of an array of visual stimuli from which one stimulus is slightly different from the others; participants are simply asked to identify the “odd-one-out” from these stimuli (A. C. H. Lee, Buckley, et al., 2005). Stimuli presented simultaneously depict the same representational content (e.g., an array of scenes or objects) and are trial-unique. This design allows for the manipulation of perceptual demands (i.e., degrees of feature overlap between similar stimuli), while reducing memory retrieval needs. In line with the representational view of the MTL, the task tests the assumption that discriminations of stimuli involving complex conjunctions of features (such as scenes, objects, faces, different viewpoints) place greater demands upon MTL representations, while discriminations which can be solved based on single features (e.g., size, shape, or colour) are unimpaired by MTL lesions or loss of integrity (Graham et al., 2010).

Over the past two decades, several studies have demonstrated the sensitivity of the Oddity perceptual task to MTL function and dysfunction in investigations of animal lesions, dementia patients, genetic risk for AD, healthy adults, and neuroimaging (Barense et al., 2007; Buckley et al., 2001; Erez et al., 2013; Hodgetts et al., 2015, 2017, 2019; A. C. H. Lee, Buckley, et al., 2005; A. C. H. Lee et al., 2006; Shine et al., 2015; for a review, see Graham et al., 2010). Furthermore, the task stimuli can be varied to test different categories of representational content which correspond with different MTL sub-regions and associated networks - Oddity scene stimuli/ representations are specialised within the HC, while object and face stimuli are processed with the perirhinal cortex (Barense et al., 2009; Hodgetts et al., 2015; A. C. H. Lee, Buckley, et al., 2005; A. C. H. Lee, Bussey, et al., 2005; A. C. H. Lee et al., 2006, 2008). Recently, the Oddity task has also been adapted to test emotion stimulus representations (Coad et al., 2020). This study found some evidence for tract dissociations between face and emotion representations - it should be noted that both stimuli involve faces, but the former tests discriminations of face identity while the latter focuses on emotions conveyed through facial expressions. Integrating these findings with a representational view (Cowell et al., 2010) suggests that there are further segregations along the ventral visual-perirhinal-hippocampal pathway, for which the Oddity task may be a useful assessment tool. Despite this large body of evidence linking the Oddity perceptual discrimination task with specialisations of the MTL, its application in the study of cognitive ageing of MTL-based representations has received limited attention so far.

A key finding from the implementation of the Oddity task is that a high degree of perceptual interference (i.e., high feature overlap/ perceptual similarity) between stimuli is associated with poorer task performance when there is a loss of MTL integrity, arising from lesions as well as normal age-related changes (Gellersen et al., 2021;

Newsome et al., 2012; Ryan et al., 2012). Ryan et al. (2012) compared the performance of young and older adults on an Object perceptual discrimination task consisting of complex blob-like objects and simpler squares. Results showed that older adults performed worse on the more complex blob-like objects, and this was linked to lesser activation in PRC regions in older adults compared to young adults. More recently, Gellersen et al. (2021) applied the Oddity task with a sample of young adults and cognitively unimpaired older adults matched in terms of education. Their Oddity task consisted of computer-generated scenes and novel objects (i.e., greebles) – the use of novel stimuli ensured that familiarity was matched across participants, and there were no pre-existing semantic associations. Moreover, previous studies have shown that performance deficits may be larger when the task involves novel stimuli such as greebles (Barense et al., 2007; Mason et al., 2017). Gellersen et al. (2021) used Oddity stimuli which were presented in two conditions of difficulty: a high ambiguity condition characterised by higher feature overlap which required processing of conjunctions of features and different viewpoints, and a low ambiguity condition where stimuli could be differentiated based on simple perceptual features. A decline in performance was observed as feature ambiguity increased – importantly, older adults demonstrated a significantly larger performance deficit on the high ambiguity condition compared to young adults. Taken together, these studies suggest that perceptual discrimination involving stimuli with high degrees of feature overlap such as complex scenes and objects viewed from different viewpoints, is sensitive to age-related changes in MTL regions; while perceptual processing of simpler features such as shape or size discriminations does not show age-related differences. Till date, cognitive ageing studies of perceptual discrimination have investigated two MTL-based representational categories i.e., -complex scenes and objects. It is yet to be determined whether similar age effects are observed in the perceptual discrimination of other complex conjunctions, such as faces (e.g., Lee et al., 2008) and emotions (Coad et al., 2020).

A further question to ask is whether the magnitude of age-related discrimination deficits differs between representational categories, which would reveal specific vulnerabilities of MTL networks in ageing. Although no studies on perceptual discrimination have compared category-specific vulnerabilities so far, recent research using mnemonic discrimination paradigms provide some support for greater object discrimination deficits than spatial impairments in healthy ageing (Gusten et al., 2021; Reagh et al., 2016, 2018). For example, Reagh et al. (2016) applied a mnemonic discrimination task involving images of common objects, which either differed by identity on the object task or by screen location in the spatial task. They tested young and older adults – the older adults were split into aged-impaired and aged-unimpaired groups based on performance on a standardised word-learning task thought to be sensitive to dysfunction in episodic memory regions in the MTL. They found that the aged-impaired group showed a lower performance in both categories, relative to the young adults group. However, the aged-unimpaired group only showed a lower performance on the object identity mnemonic discrimination task compared to the young adults' group, indicating that there is a greater age-related impact on object discrimination, even in healthy ageing.

In a further study, Reagh et al. (2018) applied an fMRI approach to investigate the neural mechanisms underlying object and scene performance using an adapted version of the mnemonic discrimination task used in Reagh et al. (2016). Behavioural results showed that older adults performed more poorly than young adults in both scene and object categories, but the difference in performance was greater on the object mnemonic discrimination task. This correlated with a lower level of activation of the anterolateral ERC in the older group during object discrimination – the PRC has connections with this region. In another functional neuroimaging study, Berron and colleagues (2018) designed an object-scene mnemonic discrimination task which comprised of computer-generated everyday indoor objects or empty indoor scenes. They found that lower performance on the object task in older adults was associated with significantly lower category-specific activity in the PRC relative to young adults. Interestingly, the behavioural results revealed that while older adults showed reduced ability to discriminate perceptually similar stimuli, this impairment was not specific to scenes or objects. Evidence from another mnemonic discrimination study with a different task design and stimuli also found that older adults, compared to young adults, showed an overall performance deficit on scene and object tasks (S. M. Stark & Stark, 2017). Berron et al. (2018) discuss that tasks that are used to investigate category-specific effects are generally not matched in terms of difficulty of stimuli tested across categories, making it difficult to determine whether any performance differences are due to category-specific effects or simply stimulus/ task effects. Another limitation identified by Gusten et al. (2021) is that the age groups recruited across studies is not consistent, and the inclusion of pre-clinical individuals can influence category-specific age effects.

Gusten et al. (2021) address these criticisms by testing a large-scale sample on a wide set of different stimuli. While they note that a larger stimulus set does not guarantee that difficulty is matched between scene and object tasks, the diversity of stimuli reduces the risk of obtaining stimulus- or task-specific effects unrelated to the category. They tested a large online sample of participants across the adult lifespan (18-77 years, $N =$ 1554) and across a demographically diverse group (Amazon MTurk population) to compare the age trajectory of scene and object mnemonic discrimination. The tasks involved a 2-back design, in which participants were shown a sequence of four stimuli (either scenes or objects) and asked to respond to each stimulus with old/ new judgments. The stimuli were computer-generated images of rooms or familiar indoor objects. In their analysis, notably, they modelled age as a continuous variable rather than categorical (i.e., young and older) to capture the variance in age which may be underestimated with a categorical modelling approach and, consequently, to address issues of generalisability seen in previous studies of category-specific effects. While results showed an age-related decline in performance on both stimulus categories, a stronger negative age trend was observed on the object task as compared to scenes. These results corroborate the view that object performance shows a greater age-related cognitive decline than scenes. To date, there are no studies which have employed perceptual discrimination tasks, such as the Oddity task, to directly compare performance in scene and object categories across the lifespan, but evidence from mnemonic discrimination tasks discussed here suggests that the object processing network is more vulnerable to ageing compared to scene processing.

Most cognitive ageing research discussed so far has focused on populations from Western or Higher-Income countries. One recent cross-cultural study tested mnemonic discrimination of stimuli involving higher-level conjunctions (i.e., objects from the Mnemonic Similarity Task (MST); Kirwan & Stark, 2007; Stark et al., 2015) and lower-level features (i.e., shape, colour, and stripes) in American and East Asian young adults (Leger et al., 2023). Results showed that the performance of American participants was higher than East Asians across levels of representation and task demands, but it should be noted that the MST task stimuli uses concrete/ everyday object stimuli which may carry different semantic associations between cultures. This research is yet to be expanded to older adults cross-culturally and, till date, no study has applied a perceptual discrimination paradigm with a non-HIC population. In the context of ageing, it is yet to be understood whether perceptual discrimination of MTL-dependent complex processing would be more sensitive to age than lower-level perceptual processing across cultures. Evidence from neuroimaging and neuropathological literature suggests that age-related changes in cognitive functions which depend upon the MTL may generalise cross-culturally. Healthy older adults often demonstrate age-related reductions in brain volume of MTL regions, such as the hippocampus (Fjell et al., 2009, 2014) - this finding has been replicated in studies with culturally, ethnically, and educationally diverse populations in North America (Fletcher et al., 2018) and East Asia (Chee et al., 2011).

Furthermore, Goh et al. (2007) have found that ageing results in decreased activation of the hippocampus across cultures - cognitive functions associated with hippocampal integrity, such as complex scene processing, may show similar trajectories of decline as a result. In the present chapter, I use a digital version of the Oddity perceptual discrimination task (A. C. H. Lee, Buckley, et al., 2005) on the MiND app (introduced in *Chapter 1*) to assess the influence of age on MTL-dependent complex perceptual representations across two cultures: UK and India. The MiND Oddity task - which uses a simple, non-verbal paradigm, and culture-neutral stimuli - provides an opportunity to address gaps identified here in the cognitive ageing literature.

First, I ask whether perceptual representations across representational categories are sensitive to age. Robust evidence for age-related deficits has been found using mnemonic discrimination tasks across complex representational categories (Gusten et al., 2021; Leal & Yassa, 2014; Reagh et al., 2016; S. M. Stark & Stark, 2017). Perceptual discrimination, which relies on similar MTL representations (Graham et al., 2010), may also show impairments in healthy ageing (Gellersen et al., 2021; Ryan et al., 2012). Compared to previous studies, I will be exploring age effects on a wider range of perceptual stimulus categories i.e., scene, face, novel object, emotion, square size (control) variations. Similar to Gusten et al. (2021), I will be modeling age as a continuous variable to capture the variability in age-related performance, particularly in healthy middle to older-aged adults (50-70 years). I predict that an age-related decline will be observed on stimulus categories for which discriminations involve complex conjunctive representations which depend upon MTL integrity e.g., high-ambiguity scenes, objects, faces and emotions. As the size Oddity requires simpler single feature comparisons to find the “odd-one-out”, I predict that this performance would not be sensitive to age-related changes (hence, a control task).

Second, I test whether vulnerabilities to age-related perceptual impairments vary by representational category. Recent research on differential content vulnerabilities using mnemonic discrimination tasks has found that object discrimination shows greater age-related impairments than scenes (Berron et al., 2018; Gusten et al., 2021; Reagh et al., 2016, 2018; S. M. Stark & Stark, 2017). In this study, I will be extending this hypothesis to perceptual discrimination of scenes and objects (i.e., greebles) - I focus here on these two categories as previous evidence has found clear dissociations between the MTL regions and networks associated with the processing of scenes and objects (A. C. H. Lee et al., 2006; Murray et al., 2017; Ranganath & Ritchey, 2012). I expect to see a steeper performance decline with age on object perceptual discrimination compared to scenes.

Third, I examine whether the pattern of age effects observed for MTL-dependent complex perception generalises to other cultures. Studies on age-related structural changes in MTL regions (such as reductions in brain volume) find similar trajectories across cultures (Chee et al., 2011; Fletcher et al., 2018), suggesting convergence with age. I focus here on two countries which, compared to the commonly used East-West divide, are closer on the cultural distance scale (Muthukrishna et al., 2020) i.e., UK (HIC) and India (LMIC). As no existing study compares British and Indian participants on the MTL-dependent function studied here, it is not possible to provide a prediction. These research questions will provide greater insight into how cognitive tasks can be applied cross-culturally to understand age-related decline of MTL functions, particularly in LMICs where there is a growing need for the development of culturally appropriate cognitive assessments.

4.2. Methods

4.2.1. Participants

Described in *Chapter 2.2.1.*

4.2.2. Procedure

Described in *Chapter 2.2.2.*

4.2.3. Materials

MiND Oddity Perceptual Discrimination Task

A 3-choice Oddity perceptual discrimination task (A. C. H. Lee, Buckley, et al., 2005) was used, which tested five representational categories: (i) Scene, (ii) Face, (iii) Novel Object, (iv) Emotion, and (v) Square Size (control category). On each trial, three images were presented on the screen simultaneously, arranged in a triad (top centre, bottom left, bottom right). Two of these images showed the same stimulus, while the third image was a different stimulus. Participants were asked to respond by touching the unique or odd-one-out image on every trial.

The task was separated into 5 blocks of 36 trials each, with each block consisting of a different representational category. At the start of every block, an instruction screen was shown to tell participants which stimulus category they were going to be tested on. This was followed by a practice phase of 3 trials for that stimulus category, and participants were given feedback on whether their responses were correct (smiley face) or incorrect (sad face). At the end of this, participants could choose to repeat the practice or to proceed to the test phase for that stimulus category. If they proceeded to the test phase, they were presented with 36 trials, and no feedback was given here. The time limit for each trial was set to 30 seconds – previous piloting with the task showed that this was sufficiently long to encourage participants to respond on every trial. Participants were also instructed to respond as quickly and accurately as possible. The task would proceed to the next trial as soon as the participant provided a response or the trial timed-out. The inter-trial interval was 1000 ms, where a blank screen was shown to prevent participants from using the location of previous stimuli to guide their choice. At the end of every block, participants were shown a progress bar with the percentage of total blocks they had completed, and they were given the opportunity to take a short break before continuing with the next block. The order of the 5 blocks was randomised for all participants, with the restriction that the Face Identity and Face Emotion Oddity blocks would not immediately follow each other. Furthermore, the presentation of trials within each block was also randomised.

Stimuli were computer-generated, greyscale, high ambiguity (i.e., different viewpoints), and presented on a white background. None of the stimuli were repeated across trials. See *Figure 25* for example images of each stimulus category; *Appendix C* shows the instructions provided to participants on each category. The design and presentation of stimuli for each of the blocks are described below:

(i) Scene Oddity: Participants were presented with three scenes – two images showed the same rooms from different viewpoints, and the third image showed a perceptually similar but different room also from a different viewpoint. Different viewing angles were used within each trial so that trials would not be easily solved by single feature matching but, instead, participants would be required to form representations of the images and process multiple features (Barense et al., 2010). The scene stimuli used in this experiment were images of three-dimensional, virtual reality, indoor rooms - these were created by Barense et al. (2010) using a video game editor. Each of the rooms differed with respect to the size, location, or orientation of one or more features e.g., windows, staircase, beams, walls. Viewpoint and position of the odd-one-out images were counterbalanced across trials.

(ii) Face Oddity: On this category, participants were shown two faces of the same person, but from different viewing angles, and one face of a different person also from a different viewpoint. The FaceGen Modeller 3.5 (Singular Inversions, 2022) software was used to randomly generate face stimuli for this category. As one of the aims of this experiment was to understand whether these tasks found similar effects when applied across populations, the race, gender, emotion, and age settings on the software were manipulated to avoid population-specific biases in stimulus design. These parameters were set to the same level for the triad of faces on every trial. This resulted in statistically culture-neutral, gender-neutral, and emotion-neutral faces, that were age-matched (ranging between 20 - 50 years) within trials. The genetic setting was used to reduce the similarity level of a single face on every trial i.e., the odd-one-out image. Consistent with viewing angles used in the Face Oddity task in Barense et al. (2010), a combination of 3 of 4 viewpoints were applied to all faces on each trial: Straight on, 45^{o} to the left, 45^{o} to the right and up, and straight up.

(iii) Object Oddity: The objects used in this experiment were "greebles" i.e., a set of novel computer-generated three-dimensional objects (Gauthier & Tarr, 1997). This was chosen as greebles are unfamiliar stimuli for which participants would not hold pre-existing semantic knowledge, unlike other real-world objects that could be familiar or meaningful and, thereby, confound task performance. Furthermore, as these were computer-generated, it was possible to manipulate the degree of feature ambiguity. Participants were shown two identical greebles presented from different viewing angles, and a third similar looking but different greeble. The stimuli were similar to those used by Barense et al. (2010). In the original images, the greebles were purple in colour, but this was changed to greyscale in this experiment to keep it constant with other stimulus categories. On each trial, greebles were selected to be from the same family, same gender, and same symmetry (symmetrical vs. asymmetrical). The odd-one-out greeble on every trial was selected so that it displayed the maximum amount of feature overlap that was possible with the other two identical greebles. As determined by previous piloting by Barense et al. (2010), the difficulty level of this category was matched with the Scene Oddity stimuli also taken from the same experiment.

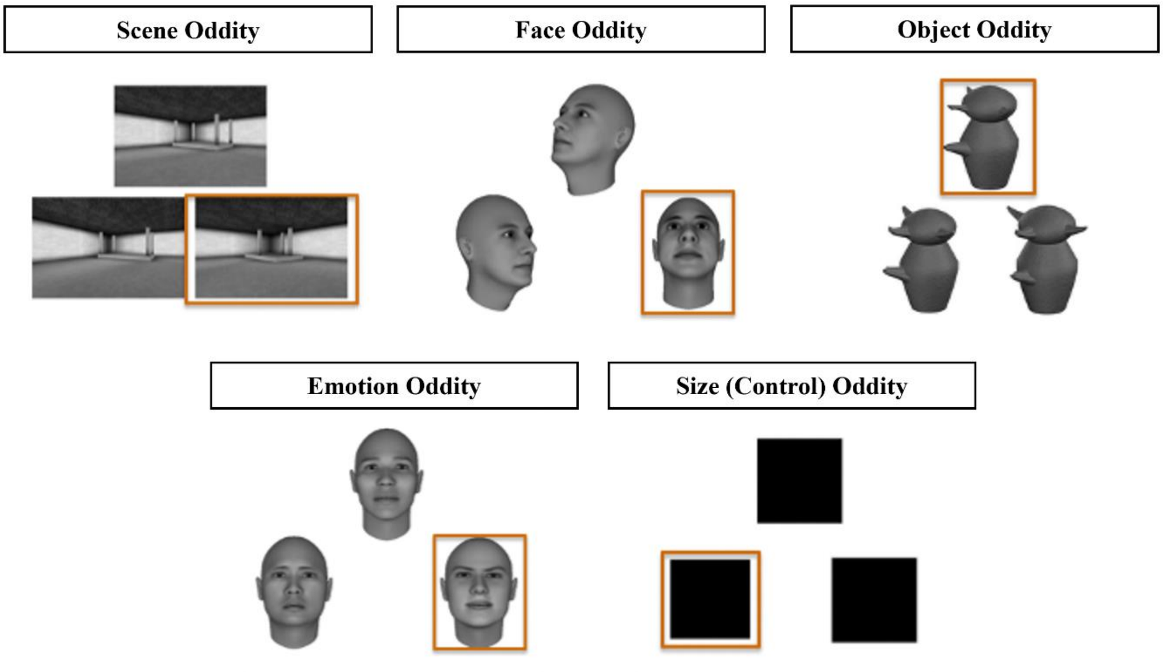
(iv) Emotion Oddity: For this category, three different faces were shown on every trial, with two displaying the same emotion and a third displaying a different emotion. The task design was adapted from the facial emotion expression discrimination tasks used in Coad et al. (2020) and Palermo et al. (2013). The stimuli were independently created for this experiment, using the FaceGen Modeller 3.5 software (Singular Inversions, 2022). To avoid cultural and gender biases in emotion recognition (e.g., "other race" effect in discrimination of similar face stimuli described by Chang et al. (2015), the race and gender settings were kept neutral for all faces. Furthermore, the viewpoint and age of faces was kept constant within trials. The emotion setting was used to generate faces with the six basic emotions of happiness, surprise, fear, sadness, disgust, and anger (Ekman, 1992). The emotion hexagon (Young et al., 2002) - which organises the basic emotions in a hexagon with neighbouring emotions being more perceptually confusable (i.e., happiness–surprise; surprise–fear; fear–sadness; sadness–disgust; disgust–anger; anger–happiness) - was used to assign a different but similar-looking 'neighbouring' emotion to the odd-one-out image on every trial. Viewpoint, emotion, emotion neighbours, and position of the odd-one-out images were counterbalanced across trials.

(v) <u>Size Oddity (Control):</u> For this category, participants were required to discriminate between the sizes of black squares. Two squares were of the same size, and one square was either bigger or smaller in size. The stimuli were designed by Barense et al. (2010). The difference in square sizes used in this experiment was between 9 and 15 pixels. The alignment of square positions was manipulated so that they did not line up either horizontally or vertically. This was particularly relevant for the bottom left and right images so that the vertical alignment would not be used as a reference for size discrimination.

Demographics and Digital Experience Survey

Described in *Chapter 2.2.3*.

Figure 25: MiND Oddity Perceptual Discrimination Task Stimulus Categories



Note. Examples of stimuli on the MiND Oddity task. Only three images from the same category are displayed on the screen at the same time. The goal is to find the “odd-one-out”. Orange boxes show the correct response on every triad.

4.2.4. Analysis

Details about the software and software packages used for data cleaning, analyses, and visualisations in this chapter are reported in *Chapter 2.2.4*. All steps described here were independently executed with the datasets for *Study A: UK* and *Study B: India.*

Due to the length of the Oddity task, it is possible that some participants got distracted or fatigued and responded randomly - this necessitates the implementation of rigorous data cleaning methods. To check for random clicks in the same location, the total number of clicks (not necessarily consecutive) in each selection position (Left/ Right/ Top) was calculated for each participant for each category. The presentation of targets in each location on every block was equal i.e., 12/36 trials; therefore, if participants clicked in the same position in any single block/ category more than 2/3 times i.e., more than 24/36 trials, the entire category was excluded for the subject. Applying this criterion resulted in the identification of 1 participant from the UK young group who clicked in the same selection position (right) 29 times – this particular category was excluded for this participant alone. Reassuringly, no other participant clicked in the same position more than 22 times on any category. Accuracy by trial stimuli in each stimulus category was also examined to check whether there were any trials where the average performance of all participants was below chance. Group average proportion correct was calculated for all stimuli triads used in each category (unique across trials). If, for any stimulus, the average accuracy was below chance i.e., below 0.33, that particular stimulus was excluded for all subjects in the study. This resulted in the exclusion of 1 stimulus on the Face category, and 1 stimulus on the Emotion category in *Study A: UK*. In *Study B: India*, three stimuli were excluded, one each from the Emotion, Face, and Object categories.

For response time, a minimum threshold of 200 ms was implemented across categories as the minimum amount of time for providing a physiological response (Ashby & Townsend, 1980; see Gusten et al., 2021 for a similar implementation of RT cut-off; Whelan, 2008). This resulted in the exclusion of 3 trials (1 from the Object Oddity and 2 from Size Oddity) in *Study A: UK*, and 1 trial (from the Object Oddity) in *Study B: India*. As the Oddity task on MiND had a time-out set at 30,000 ms (or, 30 secs) for each trial, beyond which the task would proceed to the next trial if a response was not given, no further upper threshold was applied so as not to exclude large amounts of data (e.g., other methods using SD/ median/ MAD, boxplot method would exclude 1 - 2% of data). Furthermore, time-outs were treated as 'False' accuracy and not exclusions (so that average accuracy was not inflated). In *Study A: UK*, 0.003% of the trials across categories were time-outs; and in *Study B: India*, 0.009% were time-outs. Checks were also conducted with the data to identify any potential effects arising from block order and target presentation position. The presentation order of the five Oddity blocks was randomised, rather than counterbalanced. Due to the sample size per group, the randomisation resulted in an uneven distribution of Oddity categories for each presentation order across groups. To account for any order effects, the block order of each Oddity category was included as a variable in the modelling approach discussed further. The presentation of target stimulus (correct Oddity choice in each trial) in either the left, right, or top location of the screen was equally distributed across trials i.e., 12/36 trials per location in each block. Mean accuracy and RT for targets presented in the top position were lower than targets presented in the left or right positions across categories and groups. For accuracy (True/ False) and RT, mixed effect models were run at the trial-level to check the effect of target position. Though it was found to be significant for both outcome measures, this effect was consistent across categories and did not change the model outcomes presented further, so it was not included in the final individual-level models which use accuracy and RT aggregated across categories for each individual. These outcome measures (described below) had to be calculated at the individual-level rather than the trial-level.

Three outcome measures were calculated for each individual on each of the stimulus categories on the Oddity task: i) Mean Accuracy (as proportion correct), ii) Mean Response Time (RT), and iii) Inverse Efficiency Scores (IES). i) Mean Accuracy was measured as proportion of correct responses on a scale of 0 - 1. This was done by calculating the sum of all correct responses divided by the sum of all correct and incorrect responses. Based on the values calculated for accuracy, further outlier exclusions were carried out at this stage. The probability of responding at chance or randomly on any 3-choice trial was taken to be below 0.33 or 33%. Participants who had average accuracy scores below chance on any of the stimulus categories were excluded for that stimulus category only. In *Study A: UK*, 4 participants were excluded for the Object Oddity ($n =$ 1 young, $n = 3$ older), and 1 young participant for the Size Oddity. In *Study B: India*, 2 participants were excluded for the Face Oddity ($n = 1$ young, $n = 1$ older), 31 for Object Oddity ($n = 14$ young, $n = 17$ older), 1 older participant for Scene Oddity, and 1 young participant for Size Oddity. After making these exclusions, further outcome measures were calculated. ii) The mean RT was calculated by averaging RT only for correct responses across all trials for each condition. iii) Finally, a combined speed and accuracy measure - IES (Townsend & Ashby, 1978) - was calculated by dividing Mean RT by Mean Accuracy (as proportion correct). On this task, IES would be a useful measure as performance strategies (e.g., speed over accuracy) may vary between Oddity categories and/ or age groups. Correlations were also calculated between speed and accuracy by Oddity category and age group.

Statistical Tests and Modelling

Performance means on each of the three outcome measures were statistically compared between young and older age groups using Welch independent sample *t*-tests. This test does not make the assumption of equal variances (i.e., standard deviations) between samples. To understand which variables significantly predicted performance on each of the outcome measures, linear mixed effects (LME) models were built using the lme4 package (Bates et al., 2015) and the lmerTest package (Kuznetsova et al., 2017) on R (R Core Team, 2022). The models included fixed main effects and a participant-level random effect; they were fitted using the Restricted Maximum Likelihood method. In *Study A: UK*, the equation for the model, with effects entered in this exact order, is given here: *Outcome measure = Oddity Category*Age + Education + Digital experience score + Block number + (1 | Participant ID).* In *Study B: India*, the Education variable was not included as only one participant had an education level below University. The modeling equation used in *Study B: India* is as follows: *Outcome measure = Oddity Category*Age + Digital experience score + Block number + (1 | Participant ID).* Contrast coding (using the deviation method) was applied with the Oddity category variable, as recommended for factors with multiple levels in an LME model. All predictors were entered as non-standardised variables in the model to make the interpretation of results more meaningful.

The main effects analysed were Oddity category and Age - both these were analysed as independent main effects and in interaction. Age was modelled as a continuous variable, similar to Gusten et al. (2021) - they argue that ageing is a gradual, continuous process and should be modelled accordingly. However, unlike Gusten et al. (2021), the present study did not include participants across the lifespan as it was beyond the scope of this research, but treating age as a continuous variable was useful to account for the greater age distribution (i.e., 50 - 70 years) in the older sample in both studies. As Digital experience differed significantly between young and older age groups in both studies, this was added as a fixed effect term. On the other hand, as Gender and the Number of Spoken languages did not differ significantly between Age groups and did not improve model fit, these were not included in the analyses. As explained earlier, the block order was also entered as a fixed effect term to account for any influence on performance of the order of presentation across categories. To account for individual variability in performance, a random effect term for each participant was added to the models (for a similar analysis, see Gellersen et al., 2021). Model diagnostic tests showed that all models met the required assumptions. To compare the model estimates for age trends/ slopes between the scene and object categories, post-hoc comparisons were run using the emmeans package (Lenth, 2022) on R (R Core Team, 2022). Corrections for multiple comparisons were applied using the Tukey method where appropriate. I also explored differences between age trajectories on other Oddity categories but did not have specific hypotheses for these. Additionally, a separate LME model was built in each study which only included data from the Scene and Object categories to directly compare age effects on both these categories.

4.3. Results

4.3.1. Study A: UK

Sample Characteristics

Described in *Chapter 2.3.1.*

Oddity Perceptual Discrimination Task Performance

For all outcome measures discussed in this Results section (i.e., Proportion Correct, Response Time, and Inverse Efficiency Scores), a summary of the mean values and standard deviations for each Oddity category and age group is presented in *Table 7.* All model estimates for each of the outcome measures are plotted in *Figure 28.*

Table 7: Group Descriptive Statistics for Oddity Task Performance in *Study A: UK*

	Young Adults		**Older Adults**	
Proportion Correct (0 – 1)	***M***	***SD***	***M***	***SD***
Scene Oddity	0.87	0.11	0.89	0.07
Face Oddity	0.79	0.12	0.76	0.11
Object Oddity	0.77	0.16	0.79	0.16
Emotion Oddity	0.82	0.11	0.80	0.10
Size (Control) Oddity***	0.76	0.14	0.85	0.12
Response Time (ms)	***M***	***SD***	***M***	***SD***
Scene Oddity***	5601.35	1815.31	9529.97	2156.34
Face Oddity***	3926.04	1393.88	7119.44	2118.59
Object Oddity***	4868.73	1626.02	8958.56	2147.01
Emotion Oddity***	3900.16	1107.67	6711.22	1858.67
Size (Control) Oddity***	2761.30	807.97	3828.87	1092.44
Inverse Efficiency Score (ms)	***M***	***SD***	***M***	***SD***
Scene Oddity***	6448.16	1963.46	10736.32	2529.11
Face Oddity***	5088.79	2032.61	9538.63	3072.00
Object Oddity***	6489.75	2599.74	11915.37	4082.48
Emotion Oddity***	4764.13	1207.78	8536.65	2465.69
Size (Control) Oddity***	3672.52	924.91	4570.56	1401.14

Note. M and *SD* are used to represent Mean and Standard Deviation, respectively.

* Indicates the level of significance of age differences at $p < .05$, ** $p < .01$, *** $p < .001$.

Proportion Correct

The mean accuracy of participants on the Oddity task, measured as the proportion correct on a scale of 0 - 1, was significantly above chance (0.33) for the healthy young participants on all stimulus categories (Scene: $t(70) = 40.09$, $p < .001$, Cohen's d = 4.76; Face: $t(69) = 33.01$, $p < .001$, Cohen's d = 3.95; Object: $t(69) = 23.54$, $p < .001$, Cohen's d = 2.81; Emotion: $t(70) = 36.04$, $p < .001$, Cohen's d = 4.28; and Size: $t(69) = 25.03$, $p < .001$, Cohen's d = 2.99). The older participants also showed above chance performance on all categories (Scene: $t(68) = 67.24$, $p < .001$, Cohen's d = 8.10; Face: $t(68) = 32.42$, $p < .001$, Cohen's d = 3.90; Object: $t(65) = 23.64$, $p < .001$, Cohen's d = 2.91; Emotion: $t(68) = 37.16$, $p < .001$, Cohen's d = 4.47; and Size: $t(68) = 36.72$, $p < .001$, Cohen's d = 4.42). Comparing between categories, the mean accuracy on the Scene Oddity was the highest in both age groups, with older participants scoring higher than young participants. The group differences, however, were not found to be statistically significant ($t(116.75) = 1.51$, $p = .132$, Cohen's d = 0.25). On the other hand, the young age group had the lowest mean accuracy on the Size (control) category, while the Older group demonstrated the second highest scores on this category, and performed significantly more accurately than the young group ($t(132.59) = 4.07$, $p < .001$, Cohen's d = 0.69). These results should be interpreted with caution as results for mean response time showed that the RTs of both age groups were highest on the Scene category and lowest on the Size category, with young participants performing faster than older participants on both categories. This indicates a possible speed-accuracy trade-off in performance on these categories and is analysed further in subsequent sections. Moving to the Face and Emotion categories, the mean accuracy of young participants was higher than their older counterparts, but these differences were not statistically significant (Face: $t(136.87) = -1.31$, $p = .193$, Cohen's d = -0.22; Emotion: $t(137.39) = -1.31$, $p =$

.194, Cohen's d = -0.22). Similarly, group differences were not significant on the Object category (t(133.54) = 0.56, p = .579, Cohen's d = 0.10), although older participants scored higher than young participants on average. *Figure 26* uses box plots to display mean accuracy (i.e., Proportion Correct) across categories and age groups.

In the linear mixed effects model predicting Proportion Correct, there was a significant main effect of Category (F(4, 541.62) = 10.28, p < .001), and of the interaction between Category and Age (F(4, 541.62) = 10.09, p < .001). However, the main effect of Age was not found to be significant (F(1, 131.43) = 0.83, p = .363). Post-hoc comparisons with estimated marginal means showed that the age trend for the Size category was characterised by a steeper slope than other categories, with the older adults performing higher than young adults. The gradient of this slope was significantly different from all other categories (Size and Scene contrast: t(545) = -3.19, p = .013; Face: t(545) = -5.59, p < .001; Object: t(547) = -4.20, p < .001; and Emotion: t(545) = -5.24, p < .001). Upon further investigation, it was found that the interaction effects observed here were partly driven by the Size category[3]. Although the Scene category was also characterised by a slightly positive slope (i.e., an increase in Proportion Correct over age), there was no significant difference between this age trend and what was observed for the Face (t(545) = -2.41, p = .114) and Object (t(546) = -1.04, p = .837) categories. Beyond this, there were no significant differences between the age trends of the Face category and Emotion (t(545) = 0.36, p = .996) and Object categories (t(547) = -1.35, p = .658). Finally, the demographic variables Education (F(1, 132.49) = 0.14, p = .706) and Digital Experience (F(1, 131.56) = 0.648, p = .422) did not have a significant effect on Proportion Correct.

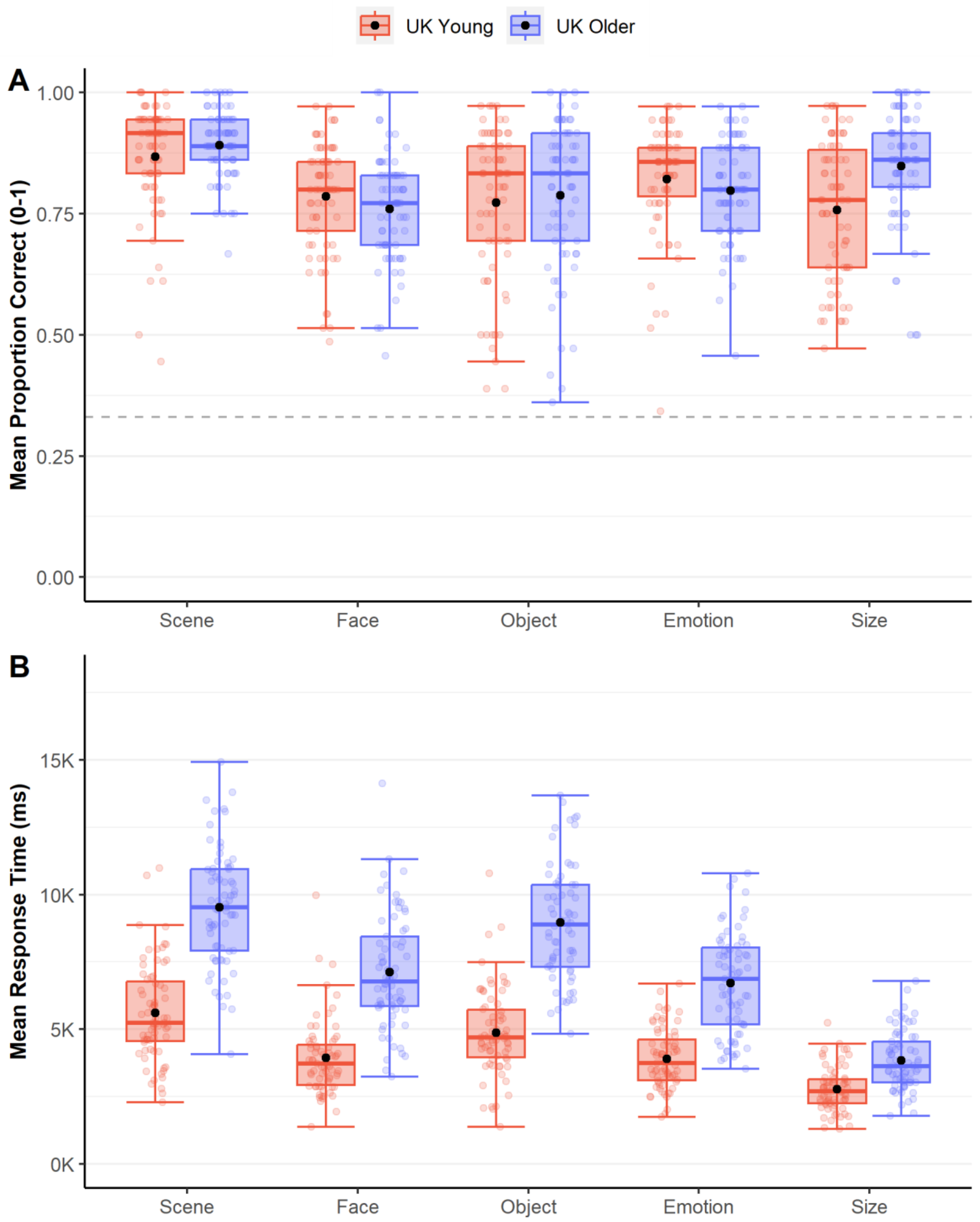
[3] When the Size category was excluded from the dataset in an exploratory model, the interaction between Category and Age was not significant for Proportion Correct (F(3, 405.92) = 2.56, p = .062).

Response Time

On all Oddity categories, the mean response time (calculated for accurately answered trials only) was significantly lower for young participants than older participants i.e., young participants made faster responses (Scene: $t(132.75) = 11.65$, $p < .001$, Cohen's d = 1.97; Face: $t(117.35) = 10.48$, $p < .001$, Cohen's d = 1.78; Object: $t(120.98) = 12.47$, $p < .001$, Cohen's d = 2.15; Emotion: $t(110.28) = 10.83$, $p < .001$, Cohen's d = 1.84; and Size: $t(125.22) = 6.54$, $p < .001$, Cohen's d = 1.11). These RTs were longest for the Scene Oddity and shortest for the Size Oddity (control category) in both age groups. The response time (correct trials only) across categories and age groups is displayed using box plots in *Figure 26.*

Results from the linear mixed effects model built for Response Time (fitted by Restricted Maximum Likelihood) showed a significant main effect of Age ($F(1, 135.14) = 157.56$, $p < .001$), thereby corroborating the group differences reported above - increasing age was associated with increasing RTs across all Oddity categories. Moreover, a significant main effect was found for Category ($F(4, 544.94) = 8.26$, $p < .001$), and the interaction between Category and Age ($F(4, 544.92) = 38.14$, $p < .001$). Post-hoc comparisons were conducted (corrected for multiple comparisons with the Tukey method where appropriate) to examine the slope of the relationship between Response Time and Age between categories. It was observed that the age trend of the Scene category differed significantly from Face ($t(545) = -3.05$, $p = .020$) and Emotion categories ($t(545) = -4.14$, $p < .001$), with the Scene category characterised by a slightly steeper slope i.e., a greater increase in RT over age. However, there was no significant difference between the age trend for the Scene and Object categories ($t(546) = 0.50$, $p = .987$). For the Face category, the pattern was significantly different from the Object category ($t(546) = -3.53$, $p = .004$) which had a steeper slope, while the difference in the age trend was not significant between the Face and Emotion categories ($t(545) = -1.07$, $p = .824$). The Response Time age trend for the Size (control) category was comparatively flatter than other categories - a smaller increase in RT over age was observed despite there being a significant difference between the performance of both age groups as reported earlier. This trend was significantly different from all other categories (Size and Scene contrast: $t(545) = 10.43$, $p < .001$; Face: $t(545) = 7.36$, $p < .001$; Object: $t(546) = 10.83$, $p < .001$; and Emotion: $t(545) = 6.30$, $p < .001$). Turning to the demographic variables added to the model, a significant effect was not observed for Education ($F(1, 135.80) = 0.10$, $p = .755$) or Digital Experience ($F(1, 135.23) = 0.17$, $p = .681$).

Figure 26: Box and whisker plots displaying (A) Mean Proportion Correct, and (B) Mean Response Time compared across Stimulus categories and Age groups in *Study A: UK*



Note. Boxes represent the Interquartile Range (i.e., the middle 50% of values), with a horizontal line drawn within each box to mark the Median value. The whiskers, or the lines extending from either side of the

box, display the dispersion of data, with the error bars representing the 95% confidence interval. Raw data points have been added to the plots, with a small amount of jitter. The black dot on each box shows the Mean value. An intercept has been added to plot (A) to display performance at chance (0.33 or 33% accuracy).

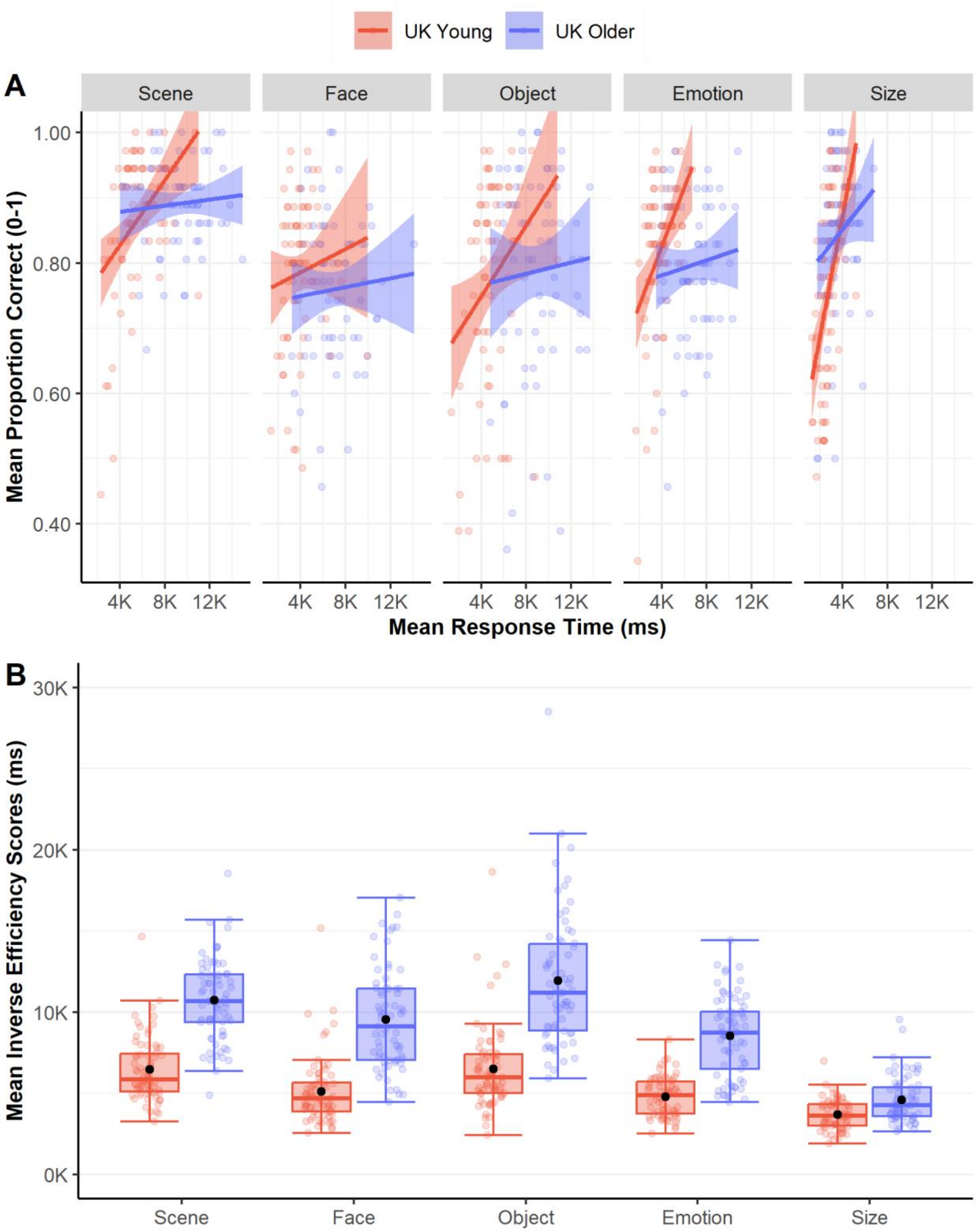
Inverse Efficiency Scores

As observed from the results obtained for Response Time and Proportion Correct, young adults demonstrated highest accuracy and slowest RT on the Scene category compared to other categories, and lowest accuracy and fastest RT on the Size category. In other words, decisions that were made more slowly tended to have higher accuracy and responses which were faster were associated with lower accuracy. The speed-accuracy trade-off suggested here was analysed further using correlation tests between proportion correct and response time on each of the categories (See *Figure 27* for correlation plots). It was found that, in the young group, there was a positive medium correlation between both outcome measures on the Scene category (r = 0.40, p < .001), and a large correlation on the Size category (r = .52, p < .001). Additionally, a medium correlation was also found on the Emotion category (r = 0.44, p < .001), and a small correlation on the Object (r = 0.28, p = .018) category. Interestingly, a significant relationship was not found between speed and accuracy for the Face category (r = 0.11, p = .373), implying that young participants did not prioritise either speed or accuracy at the expense of the other outcome on this category. On the other hand, a different pattern of results emerged with the older adults, suggesting that they may have employed a different performance strategy. There were no significant correlations between Response Time and Proportion Correct on the Scene (r = 0.07, p = .550), Face (r = 0.07, p = .594), Object (r = 0.06, p = .639), and Emotion (r = 0.10, p = .397) categories. On the Size category, a small correlation was observed, but this was not statistically significant either (r = 0.20, p = .092). To recall, older adults had low response times on the Size category, and yet maintained high accuracy and significantly outperformed young adults. Given evidence for a speed accuracy trade-off in the young sample, results from an integrated outcome measure, Inverse Efficiency Scores, are described here. However, it is best to take into consideration all outcome measures described so far when interpreting the results.

Similar to the pattern obtained with Response Time, the mean IES (which can be understood as mean Response Time for correct trials adjusted for the mean Proportion of Error) for young adults was significantly lower than for older adults on all categories (Scene: $t(128.25) = 11.18$, $p < .001$, Cohen's d = 1.89; Face: $t(117.74) = 10.06$, $p < .001$, Cohen's d = 1.71; Object: $t(109.17) = 9.18$, $p < .001$, Cohen's d = 1.59; Emotion: $t(98.22) = 11.44$, $p < .001$, Cohen's d = 1.94; and Size: $t(117.58) = 4.45$, $p < .001$, Cohen's d = 0.76). Between categories, IES was highest (i.e., least efficient performance) on the Object category, closely followed by the Scene category, and lowest on the Size category in both age groups. These results are visualised in *Figure 27* using box plots.

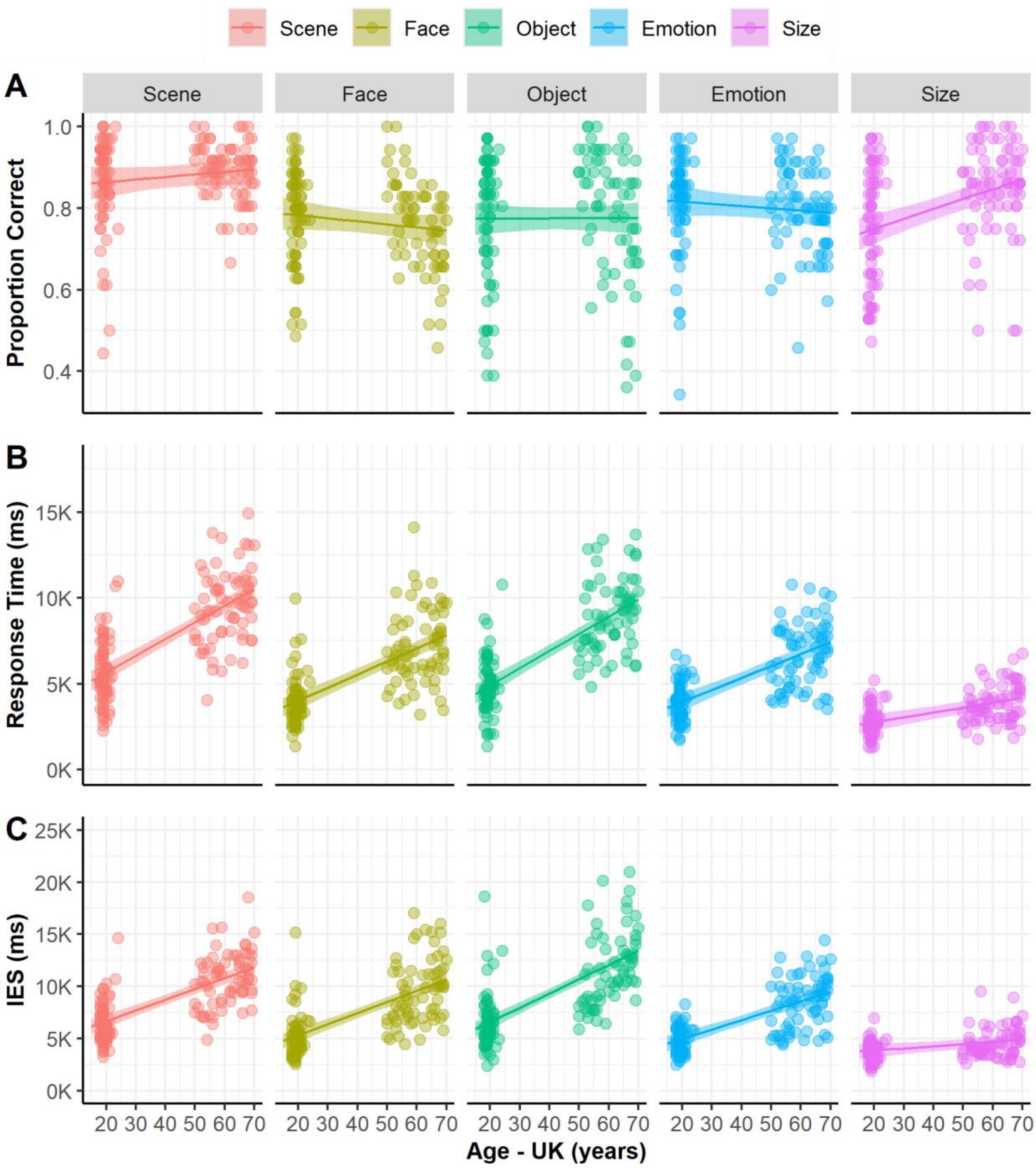
In a linear mixed effects model predicting IES, a significant main effect was found for Category ($F(4, 545.60) = 3.06$, $p = .016$), Age ($F(1, 135.14) = 175.49$, $p < .001$), and the interaction between Category and Age ($F(4, 545.61) = 31.64$, $p < .001$). As mentioned above, IES increased with age (characterised by a positive slope), but the gradient of the slope varied between categories. The trend for the Size (control) category was significantly flatter than the Scene ($t(546) = 6.50$, $p < .001$), Face ($t(545) = 7.97$, $p < .001$), Object ($t(547) = 10.67$, $p < .001$), and Emotion ($t(546) = 6.50$, $p < .001$) categories. Interestingly, the Object category had the steepest slope (higher increase in IES with an increase in age), and this was significantly different from the Scene ($t(547) = 3.08$, $p = .019$) and Face ($t(547) = -2.76$, $p = .047$) categories. However, no significant differences were found between the age contrasts of the Scene and Face ($t(545) = 0.32$, $p = .998$), and the Face and Emotion categories ($t(545) = -1.48$, $p = .576$). Returning to the main effects, it should be reported that there was no significant effect of Education ($F(1, 136.39) = 0.80$, $p = .372$), and Digital Experience ($F(1, 135.29) = 0.17$, $p = .679$) on IES. Focusing on just the scene and object contrasts, a model which only included data for these two Oddity categories revealed, once again, that performance on the object category showed a significantly greater decline with age than the scene category: $t(136) = 2.65$, $p = .009$. The comparison of IES age trends for scene and object categories is visualised in *Figure 29*.

Figure 27: (A) Scatter plot visualising the relationship between Mean Response Time and Mean Proportion Correct, and (B) Box and whisker plot displaying Mean Inverse Efficiency Scores compared across Stimulus categories and Age groups in *Study A: UK*



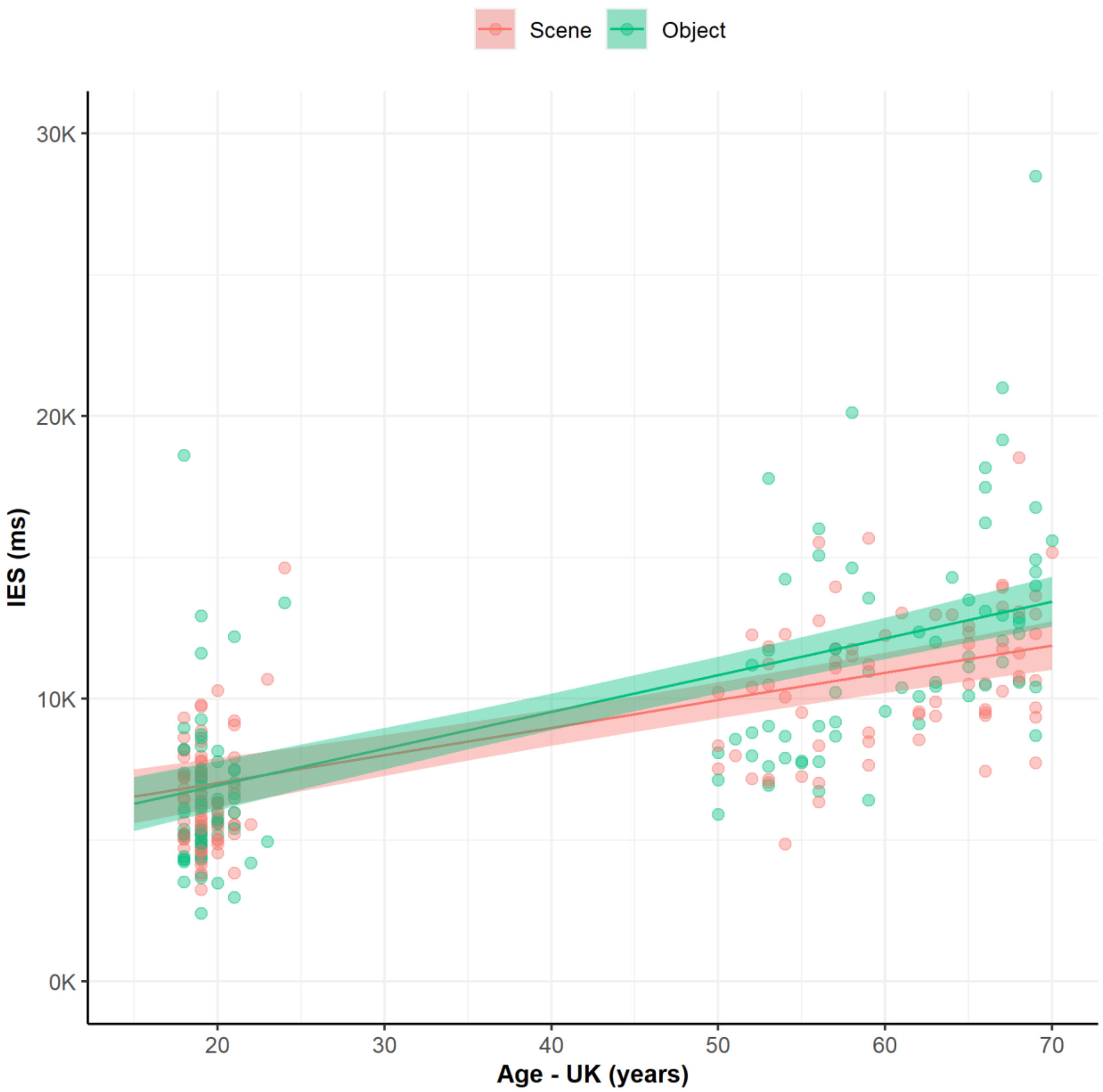
Note. The scatter plot in (A) displays the raw data points with regression lines (formula = y ~ x) drawn through them, and the bands represent the 95% confidence interval. In the box plot in (B), boxes represent the IQR, horizontal line within boxes = Median, Error bars = 95% confidence interval, coloured dots = jittered raw data points, black dots = Mean.

Figure 28: Line plots visualising the effect of Age on (A) Mean Proportion Correct, (B) Mean Response Time, and (C) Mean Inverse Efficiency Scores compared across Stimulus categories in *Study A: UK*



Note. The line plots display the mixed effects model predictions of the marginal means (i.e., averaged over different levels of the fixed effects Age and Oddity category, and adjusted for Education and Digital experience) for each of the outcome measures in (A), (B), and (C). The bands represent the 95% confidence intervals for the predicted values. These calculations were done using the 'ggemmeans' function in the R 'ggeffects' package. The raw data points have been added to each of the plots. As seen from the dispersion of the data points, the age range of the participants tested in the older group was wider than the young group; no jitter has been added to these points. Outliers displayed here were not removed as they did not change the model effects.

Figure 29: Focus Analysis for Scene and Object Oddity categories visualising the effect of Age on Mean Inverse Efficiency Scores in *Study A: UK*



Note. The model effects visualised here focused on data for the Scene and Object Oddity categories. The line plots display the mixed effects model predictions of the marginal means (i.e., averaged over different levels of the fixed effects Age and Oddity category, and adjusted for Education and Digital experience). The bands represent the 95% confidence intervals for the predicted values. These calculations were done using the 'ggemmeans' function in the R 'ggeffects' package. The raw data points have been added to each of the plots. No jitter has been added to these points. Outliers displayed here were not removed as they did not change the model effects.

4.3.2. Study B: India

Sample Characteristics

Described in *Chapter 2.3.2*.

Oddity Perceptual Discrimination Task Performance

A summary of the means and standard deviations for all performance measures across categories and age groups is provided in *Table 8*. See *Figure 32* for a visualisation of model predictions across categories.

Table 8: Group Descriptive Statistics for Oddity Task Performance in *Study B: India*

	Young Adults		**Older Adults**	
Proportion Correct (0 – 1)	***M***	***SD***	***M***	***SD***
Scene Oddity*	0.83	0.11	0.79	0.09
Face Oddity*	0.73	0.14	0.68	0.14
Object Oddity*	0.73	0.16	0.66	0.17
Emotion Oddity***	0.80	0.11	0.68	0.14
Size (Control) Oddity**	0.78	0.12	0.84	0.12
Response Time (ms)	***M***	***SD***	***M***	***SD***
Scene Oddity***	8304.07	2467.37	10916.05	2603.46
Face Oddity***	6119.97	2318.01	7735.38	2335.43
Object Oddity***	7418.06	2344.42	10098.85	2882.51
Emotion Oddity***	5787.41	1546.02	8296.72	2655.31
Size (Control) Oddity	4686.60	1419.55	4618.71	1344.21
Inverse Efficiency Score (ms)	***M***	***SD***	***M***	***SD***
Scene Oddity***	9969.10	2606.50	13828.73	3467.44
Face Oddity***	8552.11	3107.18	11865.08	4575.92
Object Oddity***	10616.02	3958.56	16177.39	6808.90

Emotion Oddity***	7320.79	1942.93	13027.13	6451.06
Size (Control) Oddity	6105.98	1863.14	5566.59	1697.77

Note. M and *SD* are used to represent Mean and Standard Deviation, respectively.

* Indicates the level of significance of age differences at $p < .05$, ** $p < .01$, *** $p < .001$.

Proportion Correct

The mean Proportion Correct (or accuracy) of the healthy young participants was significantly above chance on all Oddity categories (Scene: $t(75) = 39.78$, $p < .001$, Cohen's d = 4.56; Face: $t(74) = 23.82$, $p < .001$, Cohen's d = 2.75; Object: $t(61) = 19.61$, $p < .001$, Cohen's d = 2.49; Emotion: $t(75) = 36.65$, $p < .001$, Cohen's d = 4.20; and Size: $t(74) = 32.18$, $p < .001$, Cohen's d = 3.72). The mean accuracy of older participants was also significantly above chance across categories in the Indian sample (Scene: $t(70) = 43.54$, $p < .001$, Cohen's d = 5.17; Face: $t(70) = 21.46$, $p < .001$, Cohen's d = 2.55; Object: $t(54) = 14.36$, $p < .001$, Cohen's d = 1.94; Emotion: $t(71) = 22.04$, $p < .001$, Cohen's d = 2.60; and Size: $t(71) = 36.11$, $p < .001$, Cohen's d = 4.26). Between categories, the young participants demonstrated the highest performance on the Scene Oddity, and this was significantly higher than the accuracy of older participants ($t(142.65) = -2.17$, $p = .034$, Cohen's d = -0.36). Conversely, on the Size Oddity, the older participants had higher accuracy than all other categories, and this was significantly higher than young participants ($t(144.85) = 3.05$, $p = .003$, Cohen's d = 0.50). Interestingly, performance on the Object Oddity was lowest in both groups, even after the outlier exclusion criteria applied at the cleaning stage ($n = 14$ participants excluded from young group, and $n = 17$ from the older group on this category). However, young participants still scored significantly higher than older adults on the Object Oddity ($t(111.26) = -2.23$, $p = .028$, Cohen's d = -0.41). Similarly, young participants also showed a significantly higher performance on the Face ($t(144.00) = -2.11$, $p = .037$, Cohen's d = -0.35) and Emotion ($t(137.86) = -5.77$, $p < .001$, Cohen's d = -0.95) categories. See *Figure 30* for box plots comparing Proportion Correct across categories and age groups.

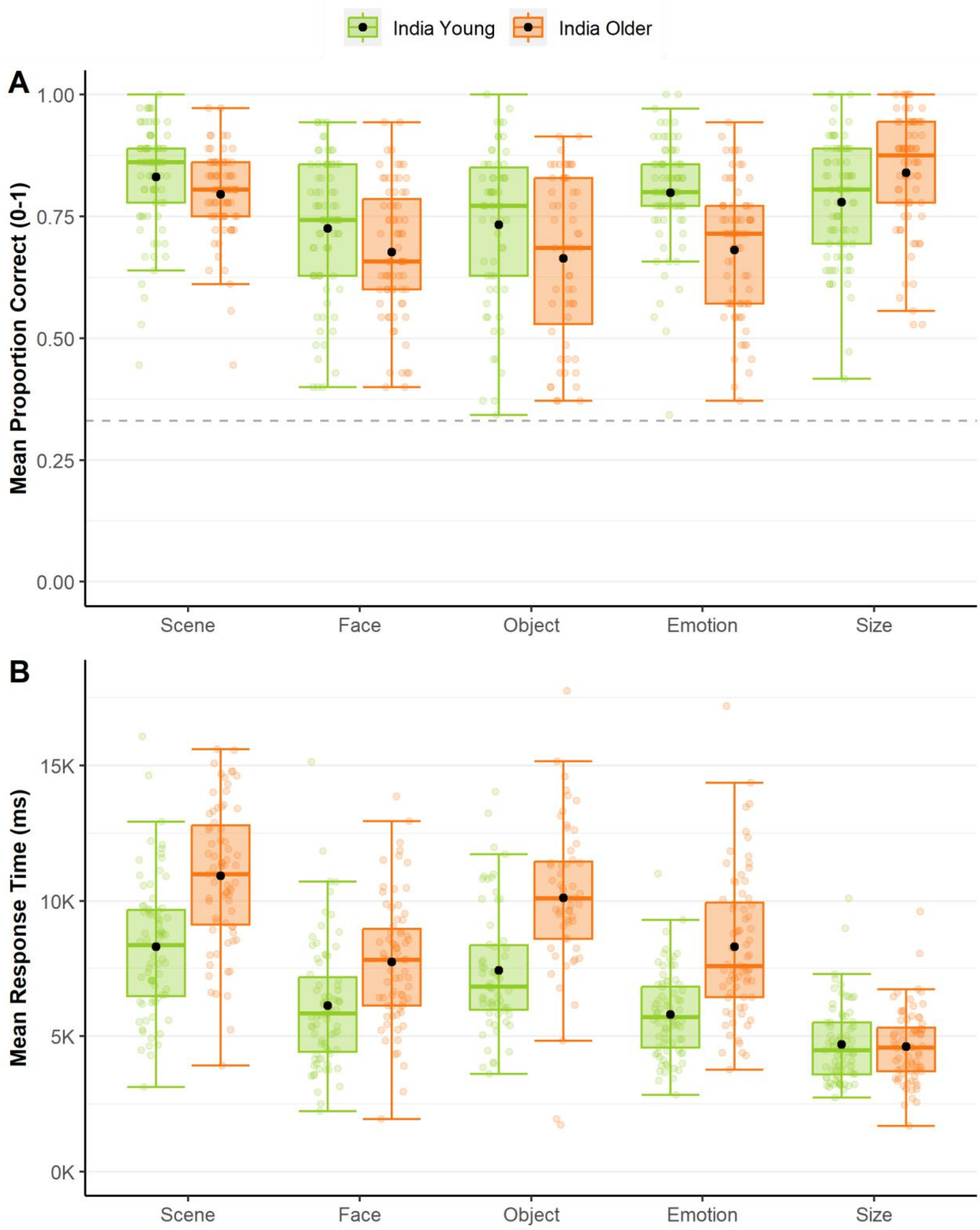
The linear mixed effects model built to predict Proportion Correct provided further insight into the performance reported above. The main effect of Category (F(4, 548.71) = 7.83, p < .001), Age group (F(1, 141.93) = 5.19, p = .024), and the Interaction between Category and Age (F(4, 549.15) = 12.78, p < .001) were found to be significant for this outcome measure. Further analysis with post-hoc tests showed that, while mean accuracy was the highest in the Scene category across age groups, there was no significant difference between the age trends of the Scene and Object (t(560) = -0.96, p = .873), Scene and Face categories (t(549) = -0.38, p = .996), and Scene and Emotion categories (t(548) = -3.15, p = .014) – the age trend of all these categories was characterised by a negative slope (i.e., decrease in Proportion Correct over age). Similarly, the slope of the Face category was not significantly different from the Object (t(559) = 0.61, p = .973), and Emotion categories (t(549) = -2.77, p = .046). Only on the Size category, there was a positive slope for the age trend (i.e., increase in Proportion Correct over age), and this was significantly different from the Scene (t(549) = -3.83, p = .001), Face (t(549) = -4.19, p < .001), Object (t(559) = -4.50, p < .001), and Emotion (t(549) = -6.99, p < .001) categories. Turning to the main effect of Digital Experience, this was also found to be a significant predictor of Accuracy (F(1, 140.25) = 5.68, p = .018).

Response Time

Young adults made significantly faster responses (measured for correct trials only) than older adults on the Scene (t(142.87) = 6.23, p < .001, Cohen's d = 1.03), Face (t(143.44) = 4.19, p < .001, Cohen's d = 0.69), Object (t(104.20) = 5.47, p < .001, Cohen's d = 1.02), and Emotion (t(112.90) = 6.98, p < .001, Cohen's d = 1.15) categories. However, the difference between age groups was not significant on the Size Oddity (t(144.97) = -0.30, p = .766, Cohen's d = -0.05), with the older group responding slightly quicker than the young group on average. Both groups displayed slowest average RTs on the Scene category, closely followed by the Object category, and fastest RTs on the Size category. The RT values are presented using box plots in *Figure 30.*

In the mixed effects model, Category (F(4, 550.62) = 9.64, p < .001), Age (F(1, 145.01) = 56.25, p < .001), and the interaction between Category and Age (F(4, 550.91) = 19.84, p < .001) were found to have a significant effect on Response Time. Results from post-hoc tests on the age trend showed that the increase in RT with age was not significantly different between Scene and Object (t(556) = 1.47, p = .582), Scene and Face (t(549) = -2.56, p = .079), and Scene and Emotion categories (t(548) = 0.21, p = .9996). However, the age trend observed for the Face Oddity was significantly different from the Object (t(556) = -3.83, p = .001) and Emotion categories (t(548) = 2.77, p = .046), as the Face category was characterised by a comparatively flatter slope. Finally, the Size (control) category showed the flattest age slope, and this was significantly different from all other categories (Size and Scene contrast: t(549) = 6.63, p < .001; Face: t(549) = 4.05, p < .001; Object: t(556) = 7.60, p < .001; and Emotion: t(548) = 6.85, p < .001). The effect of Digital Experience on RT also reached statistical significance (F(1, 143.77) = 3.91, p = .0498).

Figure 30: Box and whisker plots displaying (A) Mean Proportion Correct, and (B) Mean Response Time compared across Stimulus categories and Age groups in *Study B: India*



Note. Boxes represent the Interquartile Range (i.e., the middle 50% of values), with a horizontal line drawn within each box to mark the Median value. The whiskers, or the lines extending from either side of the

box, display the dispersion of data, with the error bars representing the 95% confidence interval. Raw data points have been added to the plots, with a small amount of jitter. The black dot on each box shows the Mean value. An intercept has been added to plot (A) to display performance at chance (0.33 or 33% accuracy).

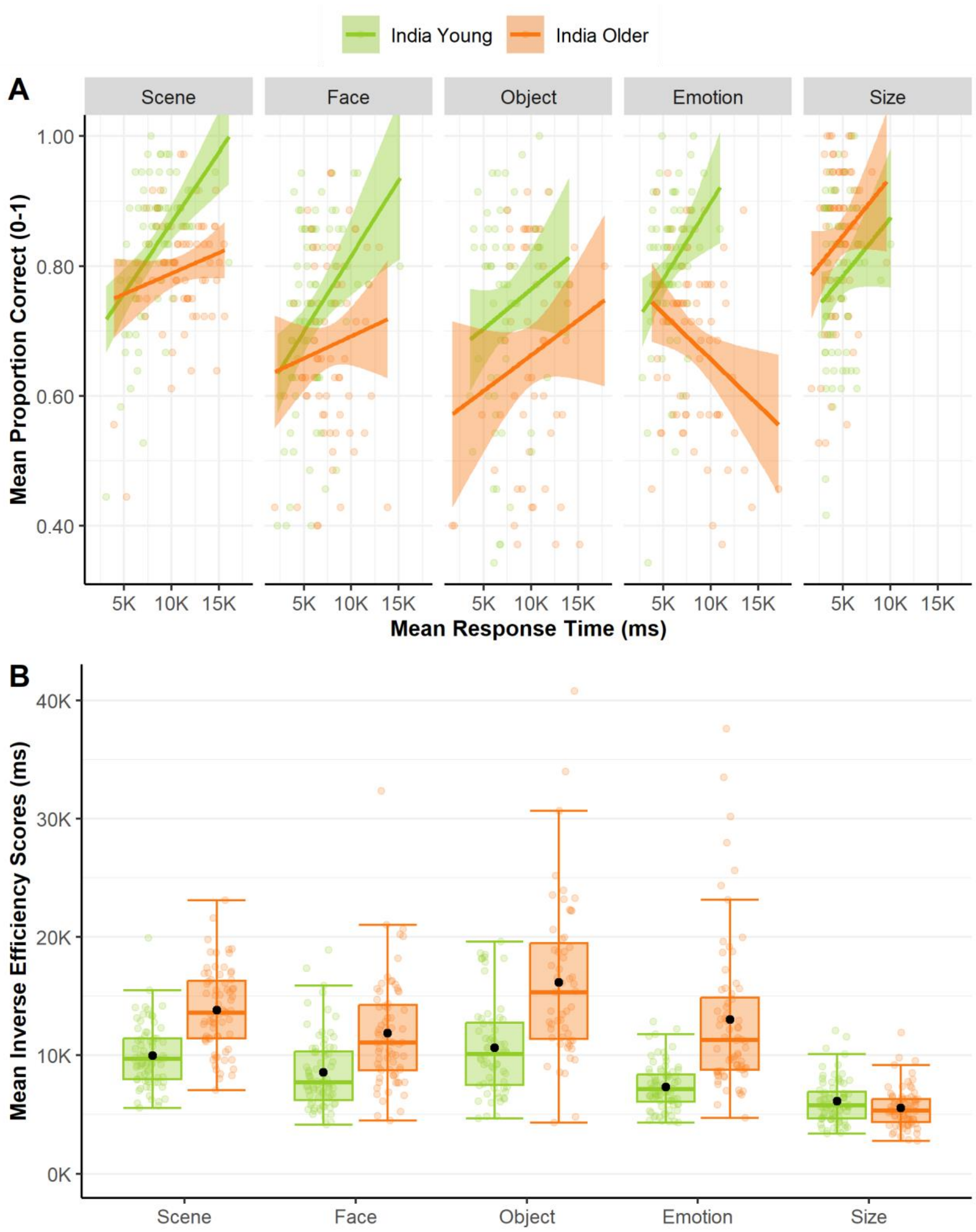
Inverse Efficiency Scores

Correlation tests were conducted to study the relationship between Proportion Correct and Response Time to determine whether there was a speed-accuracy trade-off which would influence the interpretation of results (correlation plots can be found in *Figure 31)*. It was found that the young group displayed significant medium correlations on the Scene ($r = 0.49$, $p < .001$), Face ($r = 0.38$, $p < .001$), and Emotion ($r = 0.33$, $p = .004$) categories, with RT and Proportion Correct increasing in the same direction i.e., higher response times were associated with higher accuracy. On the Size category, a small non-significant correlation was observed between both measures ($r = 0.21$, $p = .072$). There was also no evidence for a significant speed-accuracy trade-off on the Object category ($r = 0.18$, $p = .170$), where performance of the young adults (as well as older adults) was amongst the lowest. In the older group, there were no significant correlations between RT and accuracy on the Scene ($r = 0.18$, $p = .126$), Face ($r = 0.12$, $p = .332$), Object ($r = 0.18$, $p = .181$), or Size ($r = 0.20$, $p = .088$) categories. The emotion category was characterised by a small but significant negative correlation between both outcome measures ($r = -0.28$, $p = .019$), indicating that taking more time to respond was not associated with higher accuracy on this category – this is not suggestive of a speed-accuracy trade-off and could be attributed to other reasons such as fatigue or distraction. On the other hand, the results described for the young group point towards a speed-accuracy trade-off on most categories and, therefore, a combined outcome measure (i.e., IES scores) has been calculated and analysed further for both groups to account for varying response strategies when comparing group performance.

Young adults were found to have significantly lower IES (i.e., better performance) than older adults on the Scene (t(129.68) = 7.59, p < .001, Cohen's d = 1.26), Face (t(122.39) = 5.09, p < .001, Cohen's d = 0.85), Object (t(84.51) = 5.31, p < .001, Cohen's d = 1.00), and Emotion (t(83.15) = 7.20, p < .001, Cohen's d = 1.20) categories. On the contrary, on the Size category, the young group had a higher performance than the older group, but this difference did not reach statistical significance (t(144.61) = -1.84, p = .068, Cohen's d = -0.30). Furthermore, mean IES scores on the Size category were the lowest (i.e., most efficient performance) amongst all categories in both age groups, while the Object category had the highest IES scores (i.e., least efficient performance) in both groups. It was previously seen that the Object category was characterised by the lowest accuracy and relatively high RTs. See *Figure 31* for a box plot of the Inverse Efficiency Scores across categories and age groups in this study.

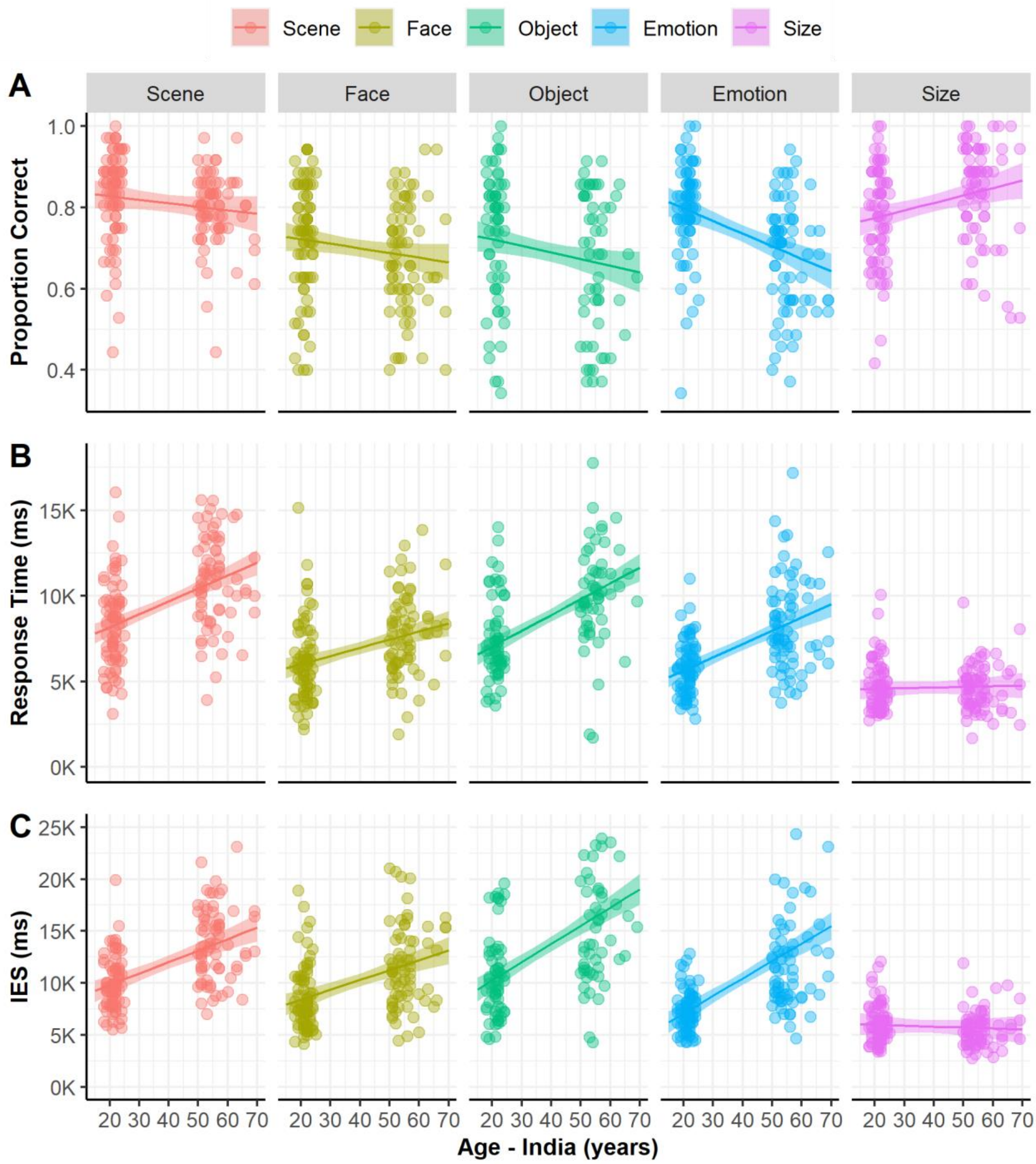
A significant main effect was found for Category (F(4, 552.69) = 4.78, p < .001), Age (F(1, 144.76) = 81.51, p < .001), and the interaction between Category and Age (F(4, 553.26) = 20.75, p < .001) in the mixed effects model predicting Inverse Efficiency Scores. Post-hoc comparisons which were used to explore the interactions between Category and Age showed that there was no significant difference between the age trend of the Scene and Face categories (t(549) = -0.71, p = .954). A contrast between the Scene and Object category was also non-significant (t(563) = 2.66, p = .062), even though the Object category was characterised by the steepest slope between categories (i.e., highest increase in IES with increasing age). The age trend for the Face category was relatively flatter and significantly different from the Object (t(562) = -3.31, p = .009) and Emotion categories (t(549) = 3.27, p = .010). The slope of the Size category was observed to be slightly negative and relatively flat - this age trend was significantly different from the Scene (t(549) = 5.34, p < .001), Face (t(549) = 4.61 p < .001), Object (t(562) = 7.61, p < .001), and Emotion (t(549) = 7.92, p < .001) categories. Finally, there was no significant main effect of Digital Experience (F(1, 142.63) = 0.47, p = .492) in this model. In a model which only included data for the scene and object categories, to facilitate a direct comparison, a significant difference was revealed between both categories (t(132) = 2.40, p = .018). Similar to results found in *Study A: UK,* the object category was characterised by a steeper slope which reflected poorer performance with increasing age. See *Figure 33* for a visualisation of the comparison of IES age trends for scene and object categories.

Figure 31: (A) Scatter plot visualising the relationship between Mean Response Time and Mean Proportion Correct, and (B) Box and whisker plot displaying Mean Inverse Efficiency Scores compared across Stimulus categories and Age groups in *Study B: India*



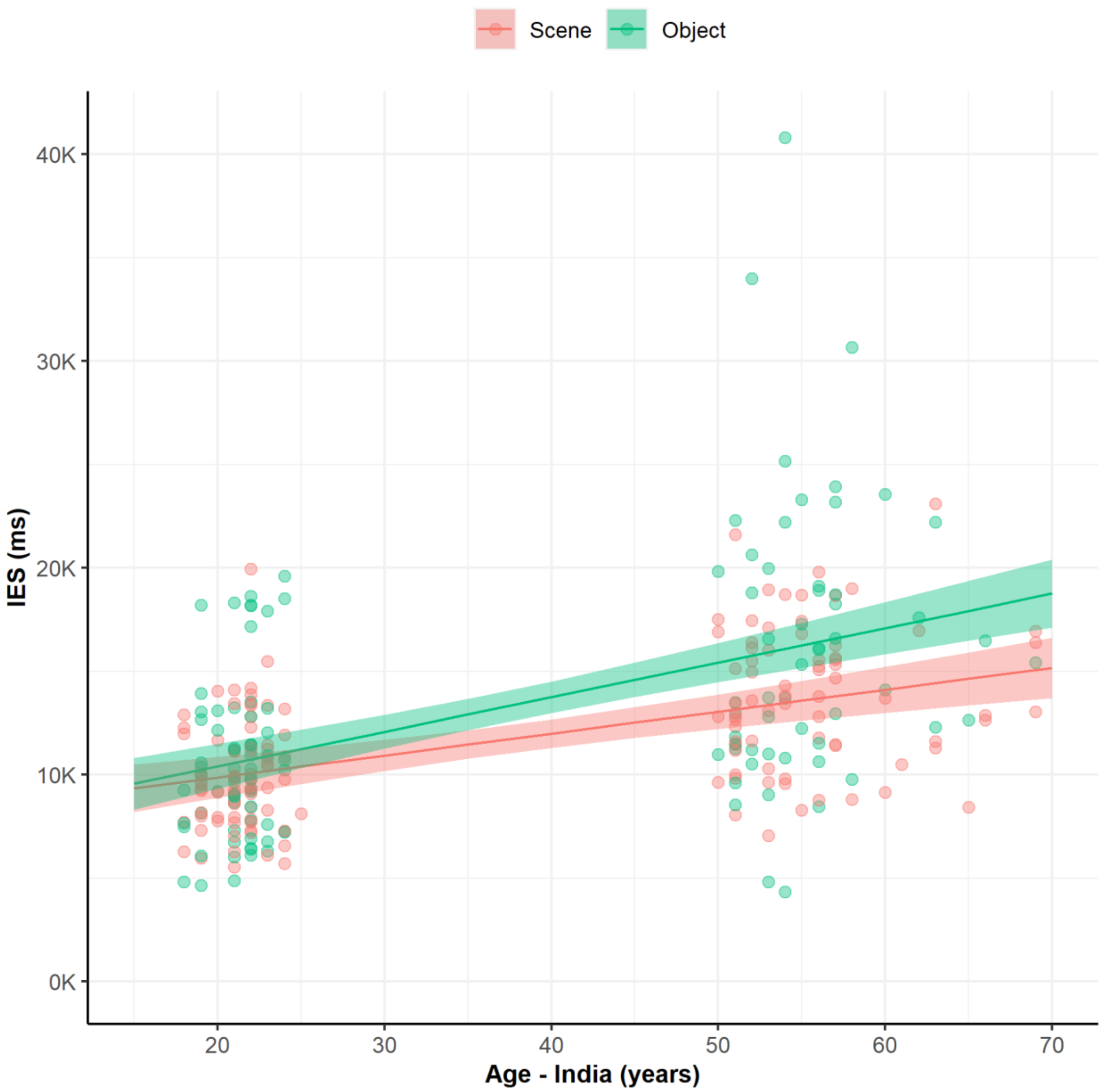
Note. The scatter plot in (A) displays the raw data points with regression lines (formula = y ~ x) drawn through them, and the bands represent the 95% confidence interval. In the box plot in (B), boxes represent the IQR, horizontal line within boxes = Median, Error bars = 95% confidence interval, coloured dots = jittered raw data points, black dots = Mean.

Figure 32: Line plots visualising the effect of Age on (A) Mean Proportion Correct, (B) Mean Response Time, and (C) Mean Inverse Efficiency Scores compared across Stimulus categories in *Study B: India*



Note. The line plots display the mixed effects model predictions of the marginal means (i.e., averaged over different levels of the fixed effects Age and Oddity category, and adjusted for Digital experience) for each of the outcome measures in (A), (B), and (C). The bands represent the 95% confidence intervals for the predicted values. These calculations were done using the 'ggemmeans' function in the R 'ggeffects' package. The raw data points have been added to each of the plots. As seen from the dispersion of the data points, the age range of the participants tested in the older group was wider than the young group; no jitter has been added to these points. Outliers displayed here were not removed as they did not change the model effects.

Figure 33: Focus Analysis for Scene and Object Oddity categories visualising the effect of Age on Mean Inverse Efficiency Scores in *Study B: India*



Note. The model effects visualised here focused on data for the Scene and Object Oddity categories. The line plots display the mixed effects model predictions of the marginal means (i.e., averaged over different levels of the fixed effects Age and Oddity category, and adjusted for Digital experience). The bands represent the 95% confidence intervals for the predicted values. These calculations were done using the ‘ggemmeans’ function in the R ‘ggeffects’ package. The raw data points have been added to each of the plots. No jitter has been added to these points. Outliers displayed here were not removed as they did not change the model effects.

4.4. Discussion

I applied the Oddity perceptual discrimination task (A. C. H. Lee, Buckley, et al., 2005) in this chapter to understand how cognitive ageing influences MTL-dependent complex perception across cultures. Task performance was measured in terms of accuracy, RT, and a combined speed-accuracy measure i.e., Inverse Efficiency Scores (IES). As speed-accuracy performance strategies (e.g., prioritising speed at the expense of accuracy or vice versa) varied between categories and age groups, for comparability, I focus on the combined speed-accuracy measure (IES) in the interpretation of results. In line with my hypotheses, my results have shown that cognitive performance significantly declines with age on Oddity perceptual discrimination categories requiring complex conjunctive processing (i.e., scenes, objects, faces, and emotions) compared to simple feature matching (i.e., size control task), and the Oddity task is sensitive to these changes even as early as midlife. These age effects were significant even after accounting for differences in education, digital experience, and participant-level individual variation between age groups. Notably, performance on object perceptual discrimination shows greater vulnerability to age-related decline than scene discrimination. Finally, I have found that the pattern of age effects observed with the British sample (*Study A: UK*) generalises to the Indian sample (*Study B: India*). I will reconcile these findings with previous research and theories of MTL function, discuss implications of category-specific vulnerabilities, and address considerations for cross-cultural application of this cognitive assessment.

These results add to a growing body of cross-species literature indicating that ageing has a detrimental impact on the perceptual discrimination of complex/ high-ambiguity stimuli (Burke et al., 2012; Gellersen et al., 2021; Ryan et al., 2012). This is in line with representational-hierarchical accounts of MTL function (Graham et al., 2010; Saksida & Bussey, 2010) which distinguish between the representational levels of visual information, with lower-levels such as size and shape features represented in early visual areas and higher-levels such as complex object or scene conjunctions represented in MTL sub-regions such as the PRC and HC respectively. In normal ageing, structural and functional changes associated with MTL sub-regions (Berron et al., 2018; Fjell et al., 2014; Leal & Yassa, 2015) are thought to impact the processing of high-ambiguity representations (Gellersen et al., 2021; Ryan et al., 2012) while leaving lower-level representations intact (Cowell et al., 2006). Evidence from mnemonic discrimination tasks have found that ageing impairs the formation of complex mnemonic representations across higher-level representational categories (Gusten et al., 2021; Holden et al., 2013; Leal et al., 2017; Reagh et al., 2016; Reagh & Yassa, 2014; Toner et al., 2009). In perceptual discrimination, ageing literature has largely focused on the vulnerability of the PRC and corresponding object representations (Burke et al., 2012; Newsome et al., 2012; Ryan et al., 2012), with a recent study also finding age-related impairments in scene representations (Gellersen et al., 2021). My work replicates the observation of age-related deficits in object and scene perception, and extends these findings to representations of high-ambiguity face and emotion perception.

Such age-related perceptual impairments across representational categories may underlie age impairments observed in mnemonic discrimination in earlier studies (Gusten et al., 2021; Holden et al., 2013; Reagh et al., 2016). Gellersen et al. (2021) propose that perceptual representations - understood as a measure of representational quality - which are poorer may result in mnemonic representations which are more susceptible to interference. These differences in representational quality could explain individual differences in mnemonic discrimination in healthy older adults (Gellersen et al., 2021) and early impairment observed in mnemonic discrimination in older adults at risk for MCI (Gellersen et al., 2023). On the other hand, Newsome et al. (2012) have shown that by reducing the degree of perceptual interference, it is possible to improve memory performance in older adults. Perceptual discrimination tasks, therefore, could serve as an effective means of evaluating the integrity of MTL functions.

Oddity task performance also differentiates between category-specific influences of age on MTL-based complex representations. Across cultures, the age-related performance decline was steepest on the object category, and this was observed to be greater for perceptual discrimination of objects compared to scenes. Comparable evidence has been found in a small number of mnemonic discrimination studies where category and age interactions are specifically tested (Gusten et al., 2021; Reagh et al., 2016). Using a similar analytic approach as Gusten et al. (2021), I replicate age trajectories which show a steeper decline for object perceptual processing compared to scenes. This greater vulnerability of object processing may be linked to tau accumulation patterns - the transentorhinal cortex, which consists of regions such as the anterior-lateral ERC and PRC and is involved in object processing, is known to be one of the earliest sites of tau accumulation (Braak & Braak, 1991). In normal ageing, Maass et al. (2019) found that a greater tau burden in these regions is associated with impairments in mnemonic discrimination of objects. My findings show that MTL-based complex object representations are more sensitive to ageing than scene representations even in perceptual discrimination, and this could be linked to differential vulnerabilities of wider object and scene processing networks (Maass et al., 2019; Ranganath & Ritchey, 2012). It is important to emphasize that these findings should not be interpreted as a lack of age effects on scene representations. On the contrary, several studies have shown that scene or spatial processing is vulnerable to age-related decline in humans (Newman & Kaszniak, 2000; Robin & Moscovitch, 2017; Rosenbaum et al., 2012) and rats (Gallagher et al., 1993; Gallagher & Rapp, 1997). Given the pattern of network-specific brain changes in normal ageing, it is possible that object processing simply shows earlier rather than greater sensitivity to age than scene processing. As the older adults tested in both *Study A: UK* and *Study B: India* were between 50-70 years - spanning middle to older age - task performance may have been more sensitive to early age-related brain changes discussed here.

One could argue that the differences observed here could be related to greater difficulty of the object stimuli compared to scenes. If this was the case, one would expect to see poorer performance on the object category across age groups. The MiND Scene Oddity and Object Oddity stimuli taken from Barense et al. (2010) were matched in terms of difficulty in the original study with young adults. In my results, IES scores reveal that performance on scene and object categories was closely matched for young adults in both *Study A: UK* and *Study B: India*, but a wide performance deficit was observed in the older group, suggesting that ageing rather than task difficulty contributed to the differences between both categories. Interestingly, in both studies, significant differences were not found between the age trajectories for scene and face perception, but object perception showed a significantly steeper decline compared to performance on the face Oddity task. Although both face and object perceptual discrimination are thought to rely on a similar level of representational processing in the PRC and associated regions (Hodgetts et al., 2015; A. C. H. Lee et al., 2008), there is limited understanding of how ageing impacts this perceptual category. Further research examining neural correlates of perceptual discrimination in ageing would be helpful to examine category-specific influences of age on perceptual discrimination of faces and emotions which have not yet been studied in this context.

Importantly, this is the first study to show that age-related impairments in perceptual discrimination of different representational categories generalise across cultures studied here. This finding supports the idea that neurobiological changes in ageing, such as loss of integrity in MTL regions or early pathological changes, may be similar across cultures, resulting in comparable trajectories of age-related decline (D. C. Park & Gutchess, 2006). Age-related changes in MTL regions such as the hippocampus are found to be similar across diverse groups (Chee et al., 2011; Fletcher et al., 2018). Furthermore, results from cross-cultural autopsy studies have revealed that neuropathological changes such as the age of onset, quantity, and qualitative characteristics of NFTs (i.e., abnormal accumulations of tau protein) in non-clinical cases generalise between cultures (Dani et al., 1997; S. K. Mohanty et al., 2004; Ogeng'o et al., 1996; Purohit et al., 2011; Yasha et al., 1997). This may explain why object processing is more vulnerable to age even in the Indian sample.

While the trajectories of ageing are similar between the UK and Indian samples, it should be acknowledged that the performance of Indian young and older adults is observably lower than their British counterparts on all outcome measures. Across representational categories, Indian young and older adults consistently show lower accuracy, longer RTs, and less efficient performance than the UK groups. These differences could be attributed to two sources of bias common in cross-cultural studies: method bias such as the test administration on a tablet device; and item bias such as the Oddity task stimuli (van de Vijver & Tanzer, 2004). Both Indian young and older adults self-reported lower digital experience than their UK counterparts, and digital experience was found to significantly influence accuracy and RT in the Indian sample but not for UK adults. Older adults, particularly, report lower technological self-efficacy (Vaportzis et al., 2017), and this may contribute to anxiety on digital assessments as well as chances of lower performance. A limitation of this study is that task stimuli were not validated in the Indian population to match for difficulty or semantic associations between representational categories and between cultures. On the object condition which used novel "greeble" stimuli (Gauthier & Tarr, 1997), for instance, Indian adults demonstrated lowest performance across categories and compared to the UK groups, even after excluding data from a large number of young and older participants due to at/ below chance level accuracy on this category. The possibility that the device and stimulus level effects discussed here inflated age effects on the object Oddity task in the Indian sample cannot be ruled out. Future cross-cultural studies should aim to recruit well-matched and well-characterised cross-cultural samples as well as address issues in assessment bias to draw direct comparisons of cognitive performance.

Another limitation of this study is that participants were not administered a memory screening test to rule out the possibility of MCI or other memory deficits, particularly in the older samples. Petersen's (2018) updated guidelines for MCI diagnosis estimates prevalence for adults between 60 - 64 years to be at 6.7%, and 65 - 69 years at 8.4%. In this study, the older adults included in the British sample had a mean age of 60.74 years, and in the Indian sample it was 55.57 years. However, the participation criteria included older adults between ages 50 - 70 years and excluded individuals who self-reported any known memory or cognitive impairments. Furthermore, performance outlier methods were implemented to exclude any suspected cases where performance fell below chance. Future studies could use cognitive impairment risk measures such as MMSE or ACE-III for which cross-culturally validated versions exist (for India, see Ganguli et al., 1995; Paplikar et al., 2020), family history of AD (Huang et al., 2004), or a well-established genetic risk allele for AD i.e., APOE-e4 (Yu et al., 2014) as exclusion criteria.

Nonetheless, this study is amongst the first to show that perceptual discrimination is sensitive to age-related cognitive decline across representational categories and across cultures. Results support the idea that object processing is more susceptible to ageing (potentially reflecting tau pathology) than scene processing (Berron et al., 2020). These findings contribute towards a broader understanding of cognitive ageing of MTL functions cross-culturally and demonstrate the utility of the Oddity task for the assessment of MTL functions and vulnerabilities in healthy ageing. Future directions could include applying this tool with large-scale cross-cultural cohorts to investigate how individual differences (such as genetic risk) and demographic factors interact with cognitive ageing across the lifespan; and clinically validating this tool for the differential diagnosis of dementia sub-types such as AD, SD, and bvFTD.

Chapter 5: General Discussion

5.1. Summary of Key Findings

In this thesis, I aimed to identify markers of age-related cognitive decline in Medial Temporal Lobe (MTL) functions and to assess how age-related vulnerabilities generalise cross-culturally. To achieve this, I have applied a novel digital neuropsychological tool - the Memory in Neurological Disorders (MiND) tablet-based application (introduced in *Chapter 1*) - with healthy young and older adults in two cultural populations i.e., UK (*Study A*) and India (*Study B*). Specifically, I have investigated how MTL-dependent pattern separation (*Chapter 2*), scene construction (*Chapter 3*), and complex perception (*Chapter 4*) vary across ages and cultures. Here, I summarise and integrate key findings from each of the chapters.

It has long been understood that the hippocampal sub-region of the MTL is critical for episodic memory (Eichenbaum & Cohen, 2004; Squire & Zola-Morgan, 1991; Tulving & Markowitsch, 1998). This function is thought to rely on the underlying operation of pattern separation (PS) within the hippocampus (Yassa & Stark, 2011). In *Chapter 2*, I applied the human Trial Unique Non-match to Location (hTUNL) task: a novel translational assessment of spatial PS based on paradigms implemented in rodent literature (see Oomen et al., 2015; Talpos et al., 2010). The task is designed to manipulate spatial separation distance between stimuli at retrieval across three categories (small, medium, and large), with the small separation distance hypothesized to place greatest demand upon hippocampal fine pattern separation (Oomen et al., 2015). In both *Study A: UK* and *Study B: India*, I found that task performance was sensitive to increases in demand placed on spatial PS, but the effect of age varied between cultures: ageing impaired PS performance in the Indian sample but not in the UK. I found that education could be a protective factor for PS in the UK; and I discuss other health and lifestyle risk factors which could influence PS in the Indian population.

Beyond memory, the hippocampus is acknowledged to play an important role in the construction of mental representations of scenes, which support diverse functions such as episodic memory, spatial navigation, and future thinking (Hassabis & Maguire, 2007; Maguire & Mullally, 2013). One way to assess scene construction is by testing the boundary extension (BE) phenomenon: BE is a cognitive phenomenon where in individuals tend to mentally represent and recall scenes beyond the boundary of what is viewed (Intraub & Richardson, 1989). Although conceptualised as a memory error, BE relies on healthy scene construction ability in the hippocampus (Mullally et al., 2012). I utilise the Rapid Serial Visual Presentation (RSVP) task (Mullally et al., 2012) to measure BE in *Chapter 3*. My results showed that the BE error is demonstrated across age and cultural groups - lending support to the proposal that BE is a universal phenomenon (Seamon et al., 2002; Spanò et al., 2017). In the context of ageing, results from both *Study A: UK* and *Study B: India* show that the BE error increases with age. However, my results reveal that the BE effect is less frequent in healthy adults than indicated by previous literature (De Luca et al., 2018; Mullally et al., 2012), and it varies as a function of stimulus characteristics (also see Bainbridge & Baker, 2020; Gandolfo et al., 2023). I discuss broader implications of these findings for our understanding of the BE phenomenon and cognitive tasks used to measure it.

The specialisation of the hippocampus for scene representations is also observed in visual perception (Graham et al., 2010; A. C. H. Lee et al., 2012). Taking a broader perspective of the MTL, emerging representational models posit that sub-regions of this brain area are involved in both memory and perception, and they are specialised for different levels of representation - namely, scenes in the hippocampus and objects in the perirhinal cortex - which contribute to diverse cognitive functions (Cowell et al., 2010; Graham et al., 2010; Saksida & Bussey, 2010). *Chapter 4* presents a task which is sensitive to the role of the MTL in complex perception i.e., the Oddity perceptual discrimination task (A. C. H. Lee, Buckley, et al., 2005) - I adapt this task to assess how age influences complex/ higher-level representations of scene, face, novel object, and emotion content categories, and lower-level size representations. Strikingly, in both *Study A: UK* and *Study B: India*, I find that complex perceptual processing is sensitive to ageing across representational categories, while lower-level perceptual processing remains intact. Interestingly, my results reveal that object processing is more vulnerable to age than scene processing across cultures - I discuss how this impairment in normal ageing may be linked to early tau pathology in the ERC (Maass et al., 2018). However, it must be noted that participants in *Study B: India* were observably more impaired on object processing than in *Study A: UK*. This could be related to the abstract computer-generated “greebles” (Gauthier & Tarr, 1997) used on this task as lesser digital experience was linked with lower accuracy and RT in *Study B: India.* I discuss these findings in the context of general and specific influences of age on MTL function, as well as wider application of perceptual discrimination paradigms.

Taken together, my thesis makes theoretical contributions towards our understanding of the role of the MTL and its susceptibility to ageing. I have found evidence for both general and specific effects of age on MTL specialisations, as well as universality and variability of cognitive ageing. These findings hold implications for the early detection of MTL cognitive decline, the development of cross-culturally generalisable cognitive paradigms, and the application of digital assessments such as the MiND app in cognitive ageing research. In the present chapter, I will expand upon these theoretical and practical implications, and propose ways in which future research can build upon this work.

5.2. Theoretical Contributions

My findings add to a growing body of literature in favour of representational views of MTL function (Graham et al., 2010; Kent et al., 2016; Saksida & Bussey, 2010).

Notably, I have found evidence for category specificity within the MTL for age-related cognitive decline. In *Chapter 4*, I have shown that object perceptual discrimination, which is localised to the object processing network in the MTL, is significantly more susceptible to age-related cognitive decline than scene perception, which is localised to the scene processing network (Graham et al., 2010; Hodgetts et al., 2015; Murray et al., 2017). Furthermore, this category specificity of age effects may explain why I did not find an effect of age on spatial pattern separation in *Chapter 2* - a previous study using an object PS paradigm has shown sensitivity to ageing (S. M. Stark et al., 2013). My results in *Chapter 3* can also be interpreted through this perspective as I have found that the boundary extension effect varies across stimuli. Work by Bainbridge & Baker (2020) has shown that object-oriented images consistently elicit a BE effect, while scene-oriented images are equally likely to cause a boundary extension or contraction effect. This pattern of results suggests that MTL dissociations observed for scene and object perceptual processing tasks in earlier studies (Barense et al., 2009; Hodgetts et al., 2015; A. C. H. Lee, Bussey, et al., 2005; A. C. H. Lee et al., 2006) also extend to vulnerabilities in age-related cognitive decline. In the next section, I will discuss practical and clinical implications of these results.

5.3. Practical Implications

I have found that the Oddity object perceptual discrimination is particularly sensitive to effects of age, compared to scene perception. This finding is supported by results from studies using mnemonic discrimination paradigms (Gusten et al., 2021; Reagh et al., 2016), and holds important implications for the early detection of age-related cognitive decline and age-related neurodegenerative diseases. As I have discussed in this thesis, the vulnerability of object representations to age may be linked to the accumulation of tau in object processing brain regions (Maass et al., 2019). Regions such as the anterior-lateral ERC and PRC, implicated in the representation of objects, are the earliest sites of tau accumulation in the brain (Braak & Braak, 1991). The Oddity perceptual discrimination task may be sensitive to these early brain changes. However, whether these early vulnerabilities mark a transition from normal to pathological ageing is still an unanswered question. Separating "normal" and "pathological" ageing is extremely difficult - even in the absence of clinical deficits, various forms of neuropathology are found in the ageing brain (Jagust, 2018). Recently, Primary age-related Tauopathy (PART) - which refers to neurofibrillary tangles in the brain without evidence of amyloid – has been reported to be a common observation in the ageing brain and is associated with normal ageing and mild cognitive impairment (Crary et al., 2014). Cross-cultural autopsy studies have also confirmed the near universal presence of this pathology in older non-demented individuals (S. K. Mohanty et al., 2004; Ogeng'o et al., 1996; Purohit et al., 2011). A clearer understanding of the implications of this pathology for age-related cognitive decline is yet to emerge, and cognitive tasks which are sensitive to these pathologies in the ageing brain may aid in providing a better picture.

When developing and applying such assessments across diverse populations, it is important to consider culture-specific factors which may directly or indirectly influence cognitive task performance. The processing of scene and object representations, for example, may be shaped by the visual environment of participants. Miyamoto et al. (2006) proposed that differences in physical environments modulate attentional patterns when viewing scenes. Their research showed that participants who are continuously exposed to Japanese scenes - which are judged to be more visually complex than American scenes due to greater object overlap and more ambiguous object borders - performed better at recognising changes in contextual or more "holistic" information. One explanation of these culture-specific styles of attention is that eye movement patterns, such as the distribution of fixations, adapt to the physical environment (Ueda & Komiya, 2012). This process is dynamic as, irrespective of cultural background, participants can be primed to perceive information in a specific pattern in accordance with the physical environment they are exposed to (Miyamoto et al., 2006; Ueda & Komiya, 2012). Furthermore, biological structures may also be shaped by environmental factors. The landmark study by Maguire et al. (2000) highlighted the neuroplasticity of MTL structures in response to spatial learning demands. Their findings revealed structural changes in the hippocampi of London taxi drivers with prolonged navigation experience i.e., hippocampal volume correlated with duration of driving experience. In the context of the present thesis, it is important to consider that the physical environments of populations sampled may have influenced perceptual performance. In contrast to the typical urban layout in UK cities, which features organised road networks, less-densely packed and spacious streets, Indian cities are characterised by more intricate road networks, tightly clustered structures, and crowded spaces. Accordingly, it could be hypothesised that individuals exposed to the (arguably) more complex visual environment in India are conferred with an advantage at discriminating between perceptually similar representations under conditions of high ambiguity. If this were true, one would expect Indian participants to demonstrate a generally higher performance than UK participants across Oddity representational categories, particularly for scenes. On the other hand, it is also possible that a greater tendency to attend to more "holistic" information in visually complex environments (Ueda & Komiya, 2012) may make perceptual discrimination of individual objects on Oddity tasks more difficult. While this thesis does not make direct statistical comparisons between cultural groups, it can be observed that the level of performance of Indian participants is generally lower across Oddity categories, providing support for the second hypothesis. However, further research is needed to uncover the mechanisms driving cultural differences. Other cultural or contextual influences may also contribute to variability in performance.

Several studies have shown that education, a proxy measure of cognitive reserve, acts as a protective factor against the clinical manifestation of Alzheimer's disease (Farfel et al., 2013; Roe et al., 2007; Sharp & Gatz, 2011; Stern, 1994; Stern et al., 1992). In the

Indian context, however, the picture is less clear: Iyer et al. (2014) found that variables such as bilingualism, rural dwelling, and occupational complexity modify the relationship between education and dementia. In their study, illiterate participants who engaged in skilled occupations such as crafts had a later age of dementia onset than illiterate participants who engaged in unskilled labour. As craft skills are often acquired early in life and practiced daily, similar to the acquisition and application of literacy skills obtained through schooling, they may facilitate the development of cognitive reserve even in the absence of formal education. On the other hand, rural dwelling is also shown to play a different role in the East and West. A study with the UK Biobank cohort highlighted higher residential density and urbanicity as factors linked with higher risk of dementia and AD (Lai et al., 2023), while Cadar et al. (2023) found that rural dwelling was associated with better memory in an English population but worse performance in a Chinese population (potentially moderated by SES). In the present thesis, it was not possible to directly examine the interplay between such factors as the samples were biased in favour of higher education and urbanicity, but it is important for cross-cultural research to consider that such factors may play different roles across populations. Given the difficulty in identifying and accounting for such variables, I argue that a cross-cultural generalisation approach (as applied in this thesis) rather than a comparative approach is more appropriate. "Culture" is a multidimensional and dynamic construct which can be difficult to operationalise and measure (A. B. Cohen, 2009). Moving forward, there is a need for the field of cross-cultural research to develop a more theoretically guided framework for quantifying and analysing culture. In line with this, Majid (2023) proposes a "culturally informed, theoretically motivated sampling" approach, which involves systematically sampling groups based on characteristics relevant to the topic of study (e.g., differences in spatial environments which may relate to scene perception abilities) as well as considering other modifying variables in the populations studied.

In this thesis, the investigation of MTL-based vulnerabilities in ageing across diverse contexts is a notable contribution. The 10/66 Dementia Research Group highlighted the fact that less than 10% of population-based dementia research was carried out in developing countries even though nearly two-thirds of affected individuals were estimated to live in these regions (Prince et al., 2004). While there has been a subsequent rise in research from these regions over the past two decades (Prina et al., 2019), there persists a systematic under-representation of LMIC populations in clinical trials and brain ageing research (Llibre-Guerra et al., 2023; Wig et al., 2024). The lack of cross-culturally generalisable cognitive assessments remains a significant barrier to LMIC inclusion in such efforts. This thesis tackles these challenges by effectively implementing novel translational cognitive tasks with British (HIC) and Indian (LMIC) populations, demonstrating potential for future integration into global clinical trials.

Finally, an important implication of these findings is the promising prospect of applying digital neuropsychological tools in cognitive ageing research. In this thesis, I demonstrated the feasibility of applying the MiND tablet-based application across age and cultural groups. Interestingly, despite significant differences in self-reported digital experience between age groups (i.e., older adults had lower digital experience), this variable was only found to influence performance on the Oddity task in *Study B: India*, which I argue could be attributed to stimulus appropriateness. The Oddity task uses computer-generated images of stimuli such as 3D scenes and abstract objects which, although designed to be culture-free, may be less familiar to participants in certain cultures and could carry different cultural associations. Research has found that novelty influences response selection and inhibition (Zinchenko et al., 2016), which may vary cross-culturally. Reassuringly, on all other tasks, there was no impact of digital experience on performance across age and cultural groups. This is confirmed by other studies which have also found support for the usability and validity of computerised cognitive testing in elderly populations (Scanlon et al., 2016; for a review, see Tsoy et al., 2021). Furthermore, translational paradigms which have gained cross-species validity

- such as the Oddity Perceptual Discrimination task (A. C. H. Lee, Buckley, et al., 2005) and the hTUNL task (Oomen et al., 2015; Talpos et al., 2010) applied in this thesis - show promise for application in co-clinical trials (Palmer et al., 2021). Combining these digital measures with plasma biomarkers could potentially increase sensitivity and specificity for detecting early cognitive decline in age-related neurodegenerative diseases (see Hampel et al., 2018; Tsoy et al., 2021).

5.4. Limitations and Future Directions

A notable limitation of this thesis is the absence of biomarker data. As the older groups I tested encompassed individuals between 50 and 70 years of age, it is not possible to rule out early pathological changes which may be linked with neurodegenerative diseases such as AD (Keller et al., 2016; Vickers et al., 2016). Additionally, I did not include a standardised memory assessment in my protocol - previous studies without biomarker data have administered such tests to identify at-risk individuals or categorize performance into age-impaired and age-unimpaired groups (e.g., Gallagher et al., 2006; Holden et al., 2012; Reagh et al., 2016; Stark et al., 2013). Although older adults in the present sample were largely recruited from a working population and demonstrated performance well above chance across tasks, it is important to consider this limitation when interpreting age-related changes.

The cross-sectional design applied in both studies is another limitation to discuss. Cross-sectional designs applied in ageing research are unable to capture individual trajectories of change over time, since they assess different age groups at a single time-point, making it difficult to infer actual age-related changes. Work by Tucker-Drob (2011) has shown that individual differences in variables which contribute to developmental processes account for 39% of variance, on average. Furthermore, in the context of cross-cultural psychology, Chu (2019) points out that the field of cross-cultural psychology is dominated by cross-sectional studies, which could conflate the effects of culture, age, and generation. Nonetheless, Salthouse (2012) contends that despite the proliferation of cross-sectional designs in cognitive ageing literature, the evidence for age-related cognitive decline is robust, showing similar rates of decline over generations.

It should also be acknowledged that the samples tested in both studies had high education and digital literacy levels - this is a common limitation of psychology studies which draw from University populations (for a discussion, see Hanel & Vione, 2016). Although this may reduce the generalisability of these results to wider contexts, the present study takes a crucial first step towards implementing a novel digital cognitive assessment across age and cultural groups, and further applications should validate the tool with nationally representative samples.

Nonetheless, in this thesis, I have identified cognitive tasks which are sensitive to detecting early age-related decline in MTL functions. An important future direction would be to investigate what point in the lifespan these changes begin to appear and how other factors, such as education or genetic risk, contribute to individual differences in cognitive ageing trajectories. One way to achieve this would be to apply the MiND app with large-scale longitudinal cohorts, such as the Avon Longitudinal Study of Parents and Children (ALSPAC; Fraser et al., 2013) in the UK or the Longitudinal Ageing Study in India (LASI; Perianayagam et al., 2022), to gain further insight into the dynamics of cognitive ageing across cultures.

5.5. Conclusions of Thesis

This thesis has adopted a fine-grained approach by examining the operational and representational components proposed to underlie broader cognitive functions such as memory and perception in the human medial temporal lobe (Cowell et al., 2019; Graham et al., 2010). In doing so, my findings have shown that vulnerability to age-related cognitive decline differs depending on task demands and representational content, and is influenced by factors such as education. The hippocampal operation of pattern separation may be sensitive to age later in life; conversely, MTL-based representations supporting scene construction and complex perception across content categories are sensitive to age-related changes as early as midlife. Object perceptual discrimination, in particular, shows greater sensitivity to age than scene perception, suggesting that this may be a useful candidate for assessing MTL integrity in ageing. The trajectories of age-related cognitive decline are strikingly similar across two cultures previously not compared in this context i.e., UK and India. This lends support to the idea that the cognitive ageing process is largely culture-invariant, possibly driven by age-related neurobiological changes which outweigh the influence of culture (D. C. Park et al., 1999). My work contributes towards the advancement of translational digital neuropsychological tools - such as the MiND app - in the assessment of cognitive ageing across cultures.

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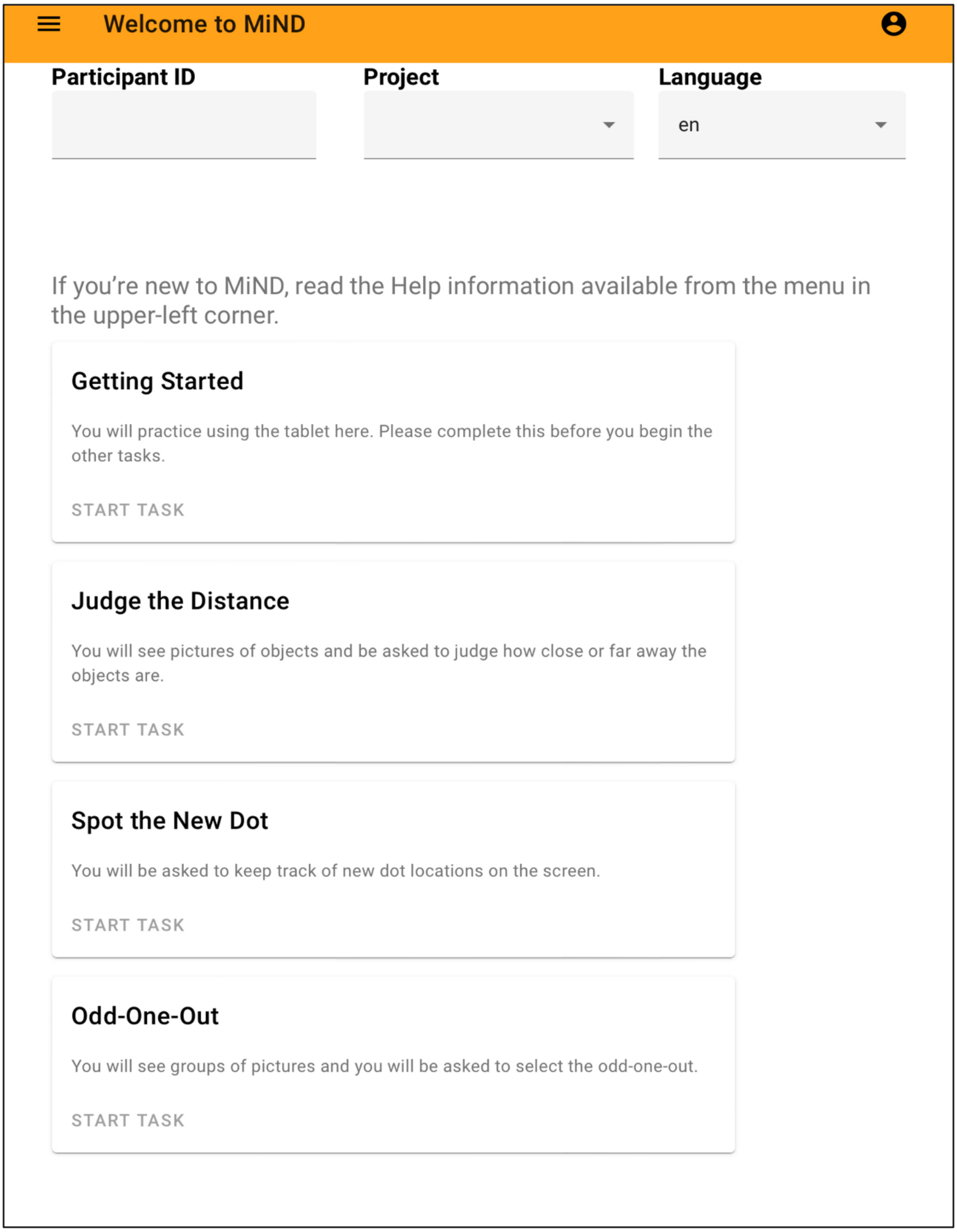
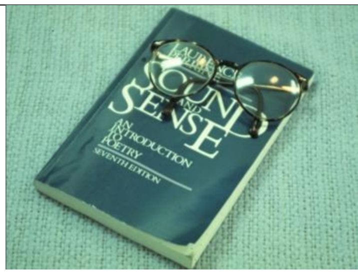
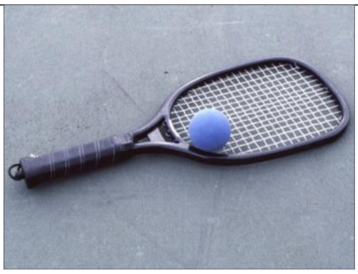
Appendices

Appendix A: MiND (v1) Tablet-based App Home Screen with Task Menu

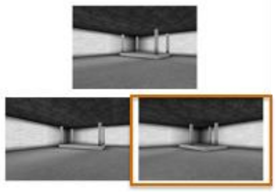
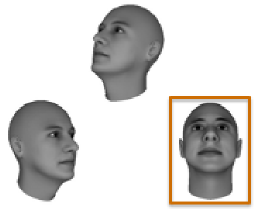
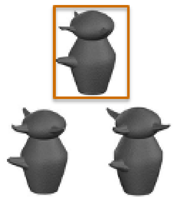
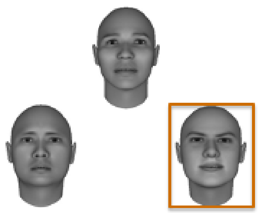


Appendix B: MiND Rapid Serial Visual Presentation Task (RSVP) Stimuli (taken from Mullally et al., 2012)

	Cat		Birdhouse
	Backpack		Blender
	Dog		Book
	Bulb		Beach chair
	Car		Traffic cone
	Crayons		Toy Dinosaur

	**Hairdryer**		**Dustpan**
	**Gift bag**		**Parrot**
	**Knife**		**Lawn chair**
	**M&M's**		**Man**
	**Oranges**		**Panda**
	**Racquet**		**Thread**

Appendix C: MiND Oddity Task Instructions and Examples for each Stimulus Category (*correct responses in orange)

Stimulus Condition	Block Instructions	Example Trial*
(i) Scene Oddity	“Two pictures will be the same room from different viewpoints, and one picture will be a different, but similar looking, room. Your task is to identify and then touch the **different room**.”	
(ii) Face Oddity	“Two pictures will be the same person from different viewpoints, and one picture will be a different, but similar looking, person. Your task is to identify and then touch the **different person**.”	
(iii)Object Oddity	“Two pictures will be the same object from different viewpoints, and one picture will be a different, but similar looking, object. Your task is to identify and then touch the **different object**.”	
(iv)Emotion Oddity	“Two pictures will be different people displaying the same emotion, and one picture will be a different person displaying a different emotion. Your task is to identify and then touch the **different emotion**.”	
(v) Size Oddity (Control)	“Two pictures will be the same sized square, and one picture will be a square of a slightly different size. Your task is to identify and then touch the **different sized square**.”