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Exploring cognitive and neural substrates of search and foraging behaviour across the lifespan: from younger to older adults

by

Sarah K. Salo

A thesis submitted to the University of Plymouth
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At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee. Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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Exploring cognitive and neural substrates of search and foraging behaviour across the lifespan: from younger to older adults

Sarah K. Salo

Abstract

Research suggests that search and foraging behaviours serve as valuable markers for pathological ageing. However, existing tasks have been limited to two-dimensional settings, neglecting additional cues and reference frames. To address this gap, a comprehensive plan of research was developed to establish a new three-dimensional paradigm, drawing from and integrating search traditions with foraging principles. This paradigm was then tested with older adults alongside neuropsychological profiling. Across seven experiments, this thesis investigates whether the neural and cognitive foundations of search and foraging behaviour can be predicted using a large-scale immersive virtual reality (VR) task, exploring the essential roles of executive and cognitive control mechanisms in achieving success. Chapter 3 introduces the novel VR task, which manipulates template provision and target distribution. The results suggest that fully motile three-dimensional search is guided by visual cues in a manner similar to two-dimensional visual search, challenging previous notions that large-scale search relies less on visual cues. Additionally, measures of cognition indicate that executive control supports performance in challenging tasks, whilst episodic memory aids lighter cognitive load conditions. In Chapter 4, the VR paradigm is implemented with both older and younger adults, accompanied by structural MRI and cognitive assessments. The findings reveal non-significant differences in search or foraging performance between age groups. However, older adults with atypical cognitive ageing profiles exhibit less efficiency compared to typical counterparts, particularly in cued inspections and target collection, with higher white matter connectivity predicting success. Chapter 5 delves into the explicit role of executive function and cognitive control through a task inspired by set-shifting paradigms, demonstrating greater shifting success when guided by greater executive control. Chapter 6 explores unexpected results from the cognitive screening procedure in greater depth. The final chapter contextualises the findings within existing literature and evaluates the paradigm's place amongst other attempts to integrate insights from search and foraging traditions.

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Chapter 1. General introduction

Within the UK, nearly 12 million people are over 65 years of age, and by 2030 will account for one in five people (Age UK, 2019). Ageing carries great economic and social impact (ONS, 2023), fundamentally associated with the effects of cognitive decline (Deary et al., 2009). There has been a call for ageing to be investigated in greater detail over the past couple decades (e.g. Li & King, 2019), as age is associated with neurological change. This is a natural process that occurs as humans age, however, the degree of degradation has greater implications, where steeper rates of decline indicate more severe and rapid consequences. Understanding the implications of ageing and cognitive decline, including against neurodegenerative processes such as Mild Cognitive Impairment (MCI), Alzheimer's disease (AD) and other forms of dementia, are essential for preventative measures. A strategic aim is, therefore, to develop sensitive and informative markers of cognitive decline. This will not only help to identify individuals early that may require additional support in the future but will also provide pathways to the development of remedial interventions or cognitive protection. It has been suggested that spatial ability degrades earlier in preclinical and prodromal dementia-type processes than the current diagnostic criterion of episodic memory degradation (Coughlan et al., 2018). Therefore, one way to quantify such changes is the measurement of search, navigation, and orientation of oneself within one’s environment.

Environmental search is a fundamental survival mechanism for many species and everyday human function depends upon frequent explorations of one’s surroundings, whether when seeking visually distinguishable targets (such as a familiar face in a crowd) or items elusive to the visual systems (such as a lost set of housekeys). Psychological assays of these behaviours have largely drawn a distinction between visually guided search, which is primarily studied in small-scale two-dimensional contexts, and large-scale foraging, which unfolds in three dimensions and is more likely to be directed by economic decisions (for a recent review see: Smith & DeLillo, 2022). This likely represents the dichotomy between scientific fields where advancements have been made: *search* mechanisms have been primarily examined by cognitive psychologists with an interest in attentional processes (e.g. Treisman & Gelade, 1980), and *foraging* mechanisms have been characterised by economists (e.g. Stabentheiner & Kovac, 2016), ethologists (e.g. Kramer, 2001), and anthropologists (e.g. game theory; Brown, Laundre, & Gurung, 1999), with an aim to model the sampling of environmental information. It can be argued that a comprehensive account of human exploratory behaviour requires a framework that can integrate these domain-specific insights so that they can inform the more general behaviours that rely on both attention to visual cues and economic decisions, and which operate in a three-dimensional world, especially as one ages. It has been suggested that reductions in white matter volume and a loss of projection fibres from frontal areas are thought to be essential in foraging behaviours (Garcia-Alvarez et al., 2019; Stuss & Levine, 2002), allowing for the identification of markers for cognitive decline, such as regional volume loss, microstructural connectivity, and decrease in tract fibre coherence. Such difficulties become particularly acute in neurodegenerative disorders such AD or MCI, which are characterised by (amongst other things) deficits in attentional and visuospatial processing (Mata et al., 2013; McKhann et al., 2011; Ramzaoui et al., 2018). These mechanisms will allow for greater discrimination of relationships between behavioural performance and underlying neural substrates and risk factors, allowing for the exploration of additional cognitive factors that might affect behaviour by testing whether visually guided foraging-like search is informed by individual differences in memory and cognitive control.

In order, therefore, to draw a clearer paradigmatic link between contexts, this thesis will examine whether large-scale search is modulated by the visual features of target and distractor items in a manner that is comparable to visual search findings. In addition, the potential cognitive underpinnings of search efficiency will be explored by relating performance to standardised measures of cognitive ability and economic decision-making. Not only has it been suggested that human cognitive control processes have their roots in foraging behaviour (Hills et al., 2010), but foraging efficiency has also been identified as a marker for age-related cognitive decline (Mata et al., 2009). By studying the relationship between visual search, foraging, and cognitive ability, the cognitive underpinnings of efficient exploratory behaviours can be elucidated, where the integration of these methods allows investigations in the relationship between neurodegenerative signatures and individual differences in foraging-like search. This ultimately builds a comprehensive picture of individual differences in age-related cognitive control deficits. Therefore, *Chapter 1* will address the theoretical underpinnings of visual search and foraging behaviours, highlighting the currently dichotomous nature, and discussing conceptual integration. Cognitive control will be discussed in terms of individual differences underlying search and foraging behaviours. Then, ageing will be considered in the context of foraging-like search, both in healthy ageing older adults and the implications when there are underlying neurodegenerative processes. Cognitive control, or the lack thereof, as one ages, will be considered. By summarising the current literature, *Chapter 1* will present an argument for the integration of visual search and foraging throughout the lifespan.

1.1 Visual search

Experimental examinations of human search have their conceptual and methodological origins in the visual search paradigm, where participants are required to detect the presence (or absence) of a target within an array of distractor items (for comprehensive reviews see: Eckstein, 2011; Smith & De Lillo, 2022). The target is usually distinguished from the distractors on the basis of one or more featural cues, and the modulatory effects of these cues on the efficiency of search formed the basis of Treisman and Gelade's (1980) Feature Integration Theory of visual attention. The theory drew a distinction between a target defined by a single feature (e.g. colour, brightness, orientation; Figure 1.1a), which can be automatically detected through parallel processing across the visual field, and a target defined by a conjunction of features (e.g. colour and form; Figure 1.1b) that requires focussed serial inspection of locations until it can be identified. The relationship between the features distinguishing the target and search efficiency was revealed through effects of the size of the array, where a single feature search is defined by a rapid 'pop out' of the target that is independent of the number of distractors, whilst response times for a conjunction search are proportionate to the number of distractors (Wolfe, 2018). Accordingly, it is generally understood that searching for a target defined by a conjunction of features requires greater demand on attentional processing than search for a single feature (Kristjánsson & Egeth, 2020; Trick & Enns, 1998), and this distinction between simple and effortful search also typifies theoretical accounts that offer alternative proposals to Feature Integration Theory (e.g., Bundesen et al., 2005; Duncan & Humphreys, 1989; Wolfe, 2007).

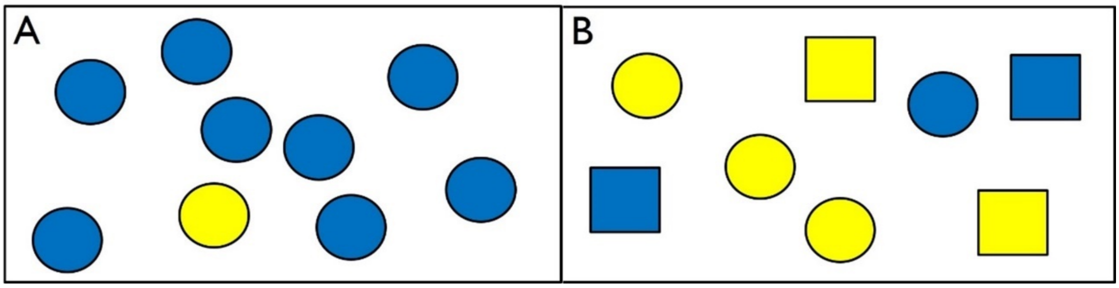

Figure 1.1. A pictorial example of the Feature Integration Theory of attention. A) Find the yellow circle. Targets defined by single features 'pop-out'. B) Find the blue circle. Targets defined by a conjunction of features requires greater attentional demands to search for the target.

Treisman and Gelade (1980) suggested that the mechanisms underpinning Feature Integration Theory are a two-stage theory, whereby one can interpret the scene through preattentive processing (a rapid and automatic analysis of one's visual field with attention only to basic, individual features) followed by attentive, or focussed, processing (the deployment of feature and object integration into a coherent representation) as a time- and effort-consuming process. Treisman (1986) then discussed the concept of 'binding', required when there were multiple features present to attend to. Each feature present required early vision encoding to create a 'feature map'. It was suggested that to pay attention to a conjunction (multiple) of visual features, these feature maps required binding together. For example (see Figure 1.1b), in an array of yellow and blue coloured circles and squares, one must bind 'blue' with 'circle' to attend to the blue circle effectively and successfully amongst the distractor array of yellow squares, yellow circles, and blue squares. Treisman (1986) suggested that binding ability was due to specialisation within the visual cortex. Data are processed in different areas of the visual cortex that specialise in specific aspects of visual processing. One such area of specialisation includes attending to orientation, specifically to lines and edges, as well as colour and movement. It was suggested these specialisations provide different but simultaneous functions and therefore, to successfully search, one must utilise the various specialised functions together to find the target. Horowitz and Wolfe (1998) furthered Treisman's model of binding by suggesting models of 'serial' and 'parallel' processing. Here the individual searcher selects one model, and the search response is dispensed when either the target has been discovered or it has been determined that all items present are distractors. Serial processing specifies singular attention to one item at a time, and parallel processing allows one to identify target identity in parallel, therefore allowing gradual certainty over time. Wolfe, Cave, and Franzel (1989) then proposed the theory of Guided Search as an alternative to the Feature Integration Theory. They suggested that the visual system uses guidance based on both bottom-up (salience of features) and top-down (prior knowledge) factors, and attention is guided to potential target locations through a combination of feature-based and spatial attention. It was stated that Treisman's model did not account for parallel processing in arrays when a target was not present; the Feature Integration model described parallel processing to identify targets based on a single feature, however if a target was not present, then previously gained information from serial processing may be dismissed, even if useful. Wolfe et al. (1989) however argued that information from parallel processing, such as colour, could be used to restrict serial searches even in a multicoloured array. For example, searching for a blue circle amongst yellow circles and blue squares presents a conjunction of feature array, where the target is defined by a conjunction, unable to be located by parallel processing. But as parallel processing can differentiate yellow and blue, and because no yellow item can be a blue circle, then parallel processing can inform serial processing of locations of yellow items so serial processing is not wasted on examining such items. Although there has been the suggestion that reducing visual processing to any two-stage process is restricting and many research studies have refuted the accuracy of the two-stage paradigm (Kristjánsson, Jóhannesson, & Thornton, 2014), where Duchowski (2017) critically suggests that Feature Integration Theory is over-simplified, there is still a large body of evidence which follow the basic principles of the two-stage theory and at best provides a basic guidance of visual search (Kristjánsson, 2015).

Following the proposed two-stage theories of visual search, additional models providing greater insight into attention and visual processing have been proposed, such as Wolfe's (2021) updated model of Guided Search. Here, in light of the restrictions suggested within two-stage models, Wolfe proposed a model integrating preattentive features, guidance, serial verses parallel processing, search termination, the contribution and role of non-selective processing (e.g. gist), functional visual fields, and search templates with regard to the relationship to memory. This updated model was suggested to provide a more comprehensive combination of factors that guide attention. One aspect of Wolfe’s (2021) model is that of search templates. Originally introduced by Treisman, a search template, or a memory-held representation of the target, is a top-down process that selectively locates targets by prioritising task-relevant information to serve as a mould to determine targets amongst distractors (Geng & Witkowski, 2019). Search templates have been suggested to provide more efficient target detection by specifying the relevant features one must attend to when searching, done by guiding attention and therefore reducing the need for exhaustive visual field processing. This increases search efficiency and aids in successful search (Crowe et al., 2021), but on a spectrum, where the more specific and recent the search template, the greater and more efficient search success is (Malcolm & Henderson, 2009; Vickery, King, & Jiang, 2005). However, this does not indicate that the template need be an exact replication of the target object, such as a friend’s face in a crowd without knowing what clothes they are wearing that day (Geng & Witkowski, 2019). It has been shown that search templates are activated proactively, approximately one second before a search event begins (Grubert & Eimer, 2018), thus allowing for quick and efficient identification of targets, as well as increasing one’s adaptability to search demands and decreasing cognitive load, and therefore providing effective solutions to target detection.

Trick and Enns (1998) considered that within a laboratory-based visual search task, one is directed to collect as many targets as quickly as possible amongst distractors and classically a response time slope quantifies success. When the features are discriminable (i.e. within a single feature search), this slope of response time over display size is generally shallow, whereas within a conjunction of feature search, the slope steepens as the task is more effortful and difficult. The intercept can then be used as a measurement of non-searching time, such as the time it takes to make a response (Wolfe, 2018). Wolfe (2018) furthers Trick and Enns suggestions of a slope-quantified search by positing that an infinite-capacity search will produce a flat slope whereas, per Treisman (1982), a serial, self-terminating search will produce a fully linear search with a two-to-one ratio of absent to present targets. Whilst search slopes are a valuable metric for understanding search success, there are limitations that need to be addressed. Wolfe (2018) provides the caveat that the pattern of fully linear search results does not prove a theoretical account of search, where a search slope assumes a linear relationship between search time and the number of items within the search display. However, visual search processes, especially outside of a constrained laboratory context, do not always follow a linear pattern, which oversimplifies the search process and therefore reduces the definitive nature of the classic search slope (Kristjánsson, 2015; Wolfe & Horwitz, 2004). Thus, following measures with constrained dichotomy come with cautions, as two-stage models cannot explain all visual search findings (such as negative slope trajectories; Kristjánsson, 2015). Concepts such as perceptual organisation play a role in visual search, where aspects such as object representation and texture segmentation account for guiding spatial vision, as Wang et al. (2005) contend that organisation may be easier with increased set size, providing one explanation for varying search slopes.

The other side to constrained visual search is the measurement and understanding of eye movements and how that supports or facilitates visual search behaviour. Whilst reaction time, as a primary measure of visual search, does indeed provide precise assessment of visual search operations (e.g. end-of-trial reaction time: the overall time taken to process the array and identify the target/s), it is limited in measuring change over time (Hollingworth & Bahle, 2020). Although one might click on the targets relatively quickly, they could be looking at, and therefore attending to, the same targets repeatedly (indicating revisits) without notice of distractors, or of a relatively equal proportion of new targets and distractors (indicative of ‘traditional’ search behaviour). Especially should one want to ‘scale up’ or provide greater context to search outside of a simulated and controlled environment, additional measures are required to fully understand the underpinnings of search (Crowe et al., 2021). Hollingworth and Bahle (2020) provide an example in their study measuring gaze in lieu of reaction time, where participants were observed at greater than chance levels to fixate on the cued colours (considered ‘capture’) however after time this pattern was reversed, and participants were less likely than chance to fixate (considered ‘successful avoidance’). It was concluded that reaction time would not be able to discern such nuance. Gaze tracking provides an essential addition to Treisman and Gelade’s (1980) ‘pop out’ theory where search is terminated after finding the target. The target ‘pops out’ effortlessly to the searcher due to a unique feature, and because reaction time was able to measure the time taken to find the singular target, a search slope using reaction time provided sufficient detail. However, when arrays include larger set sizes or conjunction of feature searches, eye tracking visual search paradigms can further elucidate not only attentional allocations, but also provide greater understanding about the search strategies employed (i.e. do participants look at the same targets repeatedly to confirm previous searches?) and information processed. This can allow for greater information on the temporal and spatial aspects of visual search behaviour from the searcher (Hollingworth & Bahle, 2020). Eye tracking is also suggested to provide greater sensitivity in understanding aspects of visual search. When adding context to a search scene, eye tracking has been suggested to elucidate connection from an inherent behaviour to “real world” applicability. Neider and Zelinsky (2006) described a task showing two-dimensional targets either on the ground or in the air, and eye tracking revealed that participants made initial eye movements toward the sky when looking for a helicopter target, suggesting context guides search, and eye tracking supports such insights into behaviour. By providing context, searchers reveal greater efficiency and shorter search times (Wolfe, 2020), with evidence that human observers visually search a scene differently, or use different strategies, depending on the context (and anticipation) of the scene (Neider & Zelinsky, 2006). However, as one searches for their missing keys around their flat, eye gaze is not enough. “Real world” searching employs full body movements to search within one’s space successfully and efficiently. Although eye tracking provides insight into real world processes (Malcolm & Henderson, 2009), idiothetic movement may indeed contribute to our understanding in greater detail.

1.2 Foraging

The mechanisms underlying human search have been established in two dimensions, with participants typically being sat before a computer monitor. In contrast, large-scale search in three dimensions has primarily been studied in the context of foraging (Schöberl et al., 2020; Wiegand et al., 2019), which can be considered as the laborious act of searching for resources (Mata et al., 2009), but can also be defined more broadly in terms of seeking and using environmental information to obtain reward (e.g. Pirolli & Card, 1999; Rosati, 2017). Foraging is a fundamental survival behaviour for most species, and it is driven by adaptive fitness (Hayden & Walton, 2014). To capture this heterogeneity, accounts of foraging focus on the reward-guided properties of behaviour, specifically where the individual must decide between continued allocation of effort to the current activity or patch of environment (exploitation), or to move to an alternative activity or patch (exploration; Ianni et al., 2016). As such, the concept of foraging can be equally applied to explorations of the external environment for subsistence (Calhoun & Hayden, 2015), internal search for information stored in mind (Todd & Hills, 2020), and simple decision making between one of two probabilistically defined options (Ellerby & Tunney, 2019).

1.2.1 Marginal Value Theorem

The decisions underlying efficient foraging were originally characterised by Charnov (1976), who developed the Marginal Value Theorem (MVT) to measure the optimality of the rate of return. Application of the MVT returns a statistical output to measure the point at which the rate of choosing to exploit or explore becomes optimal in terms of the rate of energy expenditure and preservation, with the prediction that the optimal forager will exploit a patch until its rate of return falls below that of the average across the foraging space. The calculation can, therefore, be applied to foraging behaviour to model when the searcher is likely to explore or exploit. Simply, when a bird searches for berries on bushes, time (and energy) is spent travelling between patches (depleting energy), or time is spent within the patch searching for the berries (depleting berries), and therefore both resources diminish over time. Thus, the benefit of staying in the same patch reduces over time. Charnov's (1976) MVT equation has blossomed into popularity and has been applied to a wide array of research including botany (e.g. McNickle & Calhill, 2009) and archaeology (e.g. James et al., 2022). The MVT is a prominent framework as Wolfe (2013) suggests that there can be endless variations of foraging within MVT where differences vary around length of travel time, patch density, and competition, and that it can be applied to a huge variety of contexts, from humans to insects (Fougnie et al., 2015; Louâpre, van Alphen, & Pierre, 2010). However, it has been argued that the relative simplicity of the MVT fails to capture human environmental search (Fougnie et al., 2015) – foragers may not possess an understanding of optimal profitability, particularly within unequally distributed patches, and limitations in the ability to calculate an optimal decision may lead to reliance on heuristics (Chin et al., 2015). Four heuristics have been considered to comprise the exploitation-exploration trade-off decision (Payne, Duggan, & Neth, 2007; Stephens & Krebs, 1986). These include the time one spends in patch; the number of prey, or competition, that are encountered; the giving-up time, where the forager must leave the patch when too much time has passed since the last foraged item; and the rate of items that have been encountered overall. Payne et al. (2007) furthered that two rules are more complex (i.e. giving-up time and rate of encounter) than the others and therefore should a forager follow such inherent rules, this will lead to greater exploitation than exploration. There have been mixed findings over the usefulness of each of the heuristics, where some are unable to fully explain individual variance in the decision to explore a new patch (Chin et al., 2015), but with support that some of the heuristics, such as giving-up time, can be reliable measures for exploratory behaviour (Mata et al., 2013).

Despite a relatively straightforward presentation to conceptualise foraging behaviours in both humans and animals, Charnov's (1976) MVT has been critiqued, finding that when variables become more complicated (e.g. greater variation in quality or values of targets, hidden targets) then foraging behaviour deviates from MVT optimality (Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020). It was then suggested that the MVT constrained one's understanding of foraging behaviour, where added factors such as motivation (the forager's desire and therefore speed contribution to resource collection and patch switching; e.g. Chetverikov et al., 2020), handling (collecting, processing, and consuming resources after they have been located; e.g. Bettinger & Grote, 2016), or rate of reward (amount of benefit or gain obtained during foraging time; e.g. Kane et al., 2022) impacted a forager's behaviour and revealed deficits in the equation's ability to quantify foraging behaviour across varying contexts. There have been multiple works (see, for example, Bartumeus & Catalan, 2009) that have subdivided resource foraging into clusters such as handling and eating costs within the context of search and predator pursuit, basic cost of foraging, or a plethora of factors encompassed in one (i.e. identification of prey, pursuit of predator, consumption, handling, digestion, and search costs). Bartumeus and Catalan (2009) suggested that overall, optimal foraging models oversimplify searching within a large-scale environment, and recommend that one must segment, or isolate, variables to understand the optimal human forager. Fougnie and colleagues (2015) describe that the aforementioned optimal foraging models are beneficial approximations of behaviour, but only when considered as starting points. In their experiment, it was assessed whether participants followed the MVT, but with the inclusion of seasons, which affects the temporal structure of foraging behaviour. Resource distribution was manipulated to change over time in accordance with the seasons, either with rising resources (scarce distribution to plenty) or falling distribution (plenty to sparse). It was found that the seasons (considered temporal context) affected foraging behaviour and exploitation judgements where the MVT principles were followed however only when distribution was rising. Fougnie et al. (2015) suggested this to mean that participants use previous experience (temporal context) to infer results and guide foraging behaviour. Thus, although the MVT provides a simple solution to foraging behaviour, as one only needs two pieces of information (i.e. the rate of target acquisition within the current patch and across all patches) in order to successfully search, it may also be too constricting and ignore essential aspects to successful foraging. Many factors influence successful human foraging, with memory playing a crucial role (Wolfe, Cain, & Aizenman, 2019). This complicates the application of the MVT principles, making foraging success more complex than a simple rate-of-return equation. Kosovicheva et al. (2020) proposed that one must plan to adequately forage, requiring executive functioning, which is not accounted for in the MVT nor across the breadth of literature supporting the ability of animals to efficiently forage. Bartumeus and Catalan (2009) even extend to suggest that the definition of ‘patch’ is subjective, and therefore how one measures a patch size might be different to another. It is at this juncture that alternative forms of quantifying foraging are essential, as clearly the MVT overly simplifies the exploration-exploitation trade-off.

1.2.2 Exploration-exploitation trade-off

To understand some of the underlying behaviours essential to foraging requires applying principles such as executive functioning or decision-making abilities, and this is where the MVT lacks such nuance. A core aspect of foraging success is the trade-off between exploration and exploitation, which requires economic decision-making ability, as well as an understanding, subconscious or otherwise, of exploration benefits over the cost of moving and uncertainty. It has been supposed that the exploration-exploitation trade-off is complicated, whereby the disparate breadth of literature leads to divergent operationalisations, and separate research suggest the exploration-exploitation trade-off is defined by either behaviour, uncertainty and choice, or outcomes (Mehlhorn et al., 2015). Mehlhorn et al. (2015) instead suggested the trade-off between exploration and exploitation as a representation of a continuum of behaviours rather than a binary choice, and goal setting can become a predominant factor in the forager's behaviours, over and above optimality, potentially combining all three definitions. In a laboratory context, for example, the forager's goal may change when faced with boredom of pressing the same keyboard key, overriding, and irrespective of, optimality. As such, Cohen et al. (2007) proposed a spectrum of underlying mechanisms associated with the exploration-exploitation trade-off, implying not necessarily mutually exclusive but potentially mutually enabling theories (Mehlhorn et al., 2015). Song, Bnaya, and Ma (2019), to address the disagreed exploration-exploitation mechanistic underpinnings throughout the literature, suggested that a minimalist paradigm would better represent such trade-offs. As such, participants were required to select whether they would rather, as a tourist in a foreign city, visit a new restaurant or return to the best restaurant thus far. Despite a reasonably adopted strategy, participants performed suboptimally by switching between exploitation and exploration more than necessary.

The decision to explore or exploit is also defined by the level of uncertainty a forager is exposed to. Effective decision-making requires one to find the appropriate balance between exploration and exploitation (Blanco et al., 2016). Choices become more random the greater the uncertainty, and therefore more exploratory, as participants have been found to sample more frequently between low- and high- value options (Gershman, 2019). It is suggested that ideal exploratory choices are directed when uncertainty is greater, and more information can be gained (Blanco et al., 2016). If one were to consider, for example, how to select a restaurant for dinner whilst in a new city, it would be more beneficial to sample many options when faced with the uncertainty of the taste or quality of the restaurants. Factors like the volatility of the environment, and past decisions and experiences contribute to the level of uncertainly one may face (Knox et al., 2013). Thus, should one find out that this city is known for its pizza, exploratory behaviour may reduce in favour of exploiting the pizza restaurants. Uncertainty bonuses are strategies that encourage exploration in situations characterised by high uncertainty or ambiguity, promoting the selection of actions or options with uncertain outcomes, allowing individuals to gather more information about their environment, without altering choice stochasticity (Gershman, 2019). To some degree, one must expect the world around them to change over time, and to learn from the environment to best adapt to change. Yet, decision-makers have been shown to not fully utilise their environment by not planning based on information gathered, but rather utilise myopic beliefs to inform exploration-exploitation choice (Knox et al., 2013). Therefore, whilst research supports an information gathering, exploration behaviour when faced with uncertainty, there is evidence for suboptimality in human foraging behaviours. This was suggested by Riefer et al. (2017), who did not find support for an uncertainty bonus in exploration. By examining supermarket shopping habits over a period of several years, greater exploitative behaviour was observed to persist. Factors such as individual difference or cognitive load were suggested to contribute to such differences. It has also been shown that over the lifespan, one's preference, or selected strategy, to exploit or explore one's environment changes (Blanco et al., 2016). To some degree, this dilutes the distinction drawn between optimal performance and suboptimality, as the continuum as proposed by Mehlhorn et al. (2015) suggests varying degrees of uncertainty residing along a spectrum of exploration and exploitation. Taken together, the trade-off between exploration and exploitation requires the forager to determine the optimal balance of switching depending on the context, the uncertainty of the environment, and the potential gains from exploration or exploitation. Adaptive decision-making in humans is seemingly suboptimal, and the trade-off between exploiting or exploring one's environment requires greater cognitive flexibility and resource than a singular decision. Optimal decision-making requires building an environmental representation, supported by effective planning, and therefore an additional component of successful foraging is that of one's organisation and planning.

1.2.3 Organisation and systematicity

An additional aspect critical to foraging behaviour is that of organisation. Organisation facilitates greater success when foraging, across both animal and human literatures, due to systematicity required to efficiently move about one's space (Smith & De Lillo, 2022). Kosovicheva et al. (2020) highlighted that executive functioning abilities are essential to successful foraging, where processes such as working memory preventing revisits, spatial attention guiding conjunction of feature searching, and motor planning and inhibition supporting goal-directed behaviours are required for successful foraging (Woods et al., 2013). However, it has also been noted that because individuals have the freedom to organise their foraging in various ways, relationships can only be inferred through correlation. This means the underlying cognitive mechanisms cannot be definitively identified (Smith & De Lillo, 2022). Nonetheless, research by Woods et al. (2013) has introduced a method called best-*r* for measuring organisation, which has been applied in both two- and three-dimensional contexts. Woods et al. (2013) suggested that highly organised and most successful foraging behaviours, in multi-target arrays, required participants to systematically search in a top-to-bottom or left-to-right fashion, or moving systematically horizontally or vertically in the search for targets; this has been suggested as analogous to the Cancellation Task (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2021). Traditionally a two-dimensional paper-and-pencil task, the Cancellation Task allows for systematic measurement of target selection order and starting point. Not only in the second dimension however, Kristjánsson et al. (2022) found that participants tended to forage horizontally, irrespective of the fact that the stimulus presentation was in the third dimension, and greater organisation was identified in single feature forging than conjunction, following similar principles found in two-dimensional search organisation tasks, like the Cancellation Task (e.g. Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2019; Woods et al., 2013).

It is clear that foragers benefit from organisation when foraging (e.g. De Lillo & James, 2012). The decision-making process underpinning quitting rules has been considered an inherent cognitive process, and therefore the cognitive processes underlying organisation and patch leaving behaviour may represent aspects of foraging behaviour that represent underlying decision-making. Harhen and Bornstein (2023) evaluated overharvesting in foraging paradigms, or staying longer in a patch than would be suggested by rate-of-return models (e.g. MVT). They suggested that systematically, humans overharvest, which may emerge as a by-product of a dynamic learning process; participants seemed to learn a representation of the environment through individual patch experience, which informed search strategy and therefore adjusted exploitative ('staying') behaviour as well as exploratory ('leaving') behaviour. Understanding the intricacies of organisation in foraging provides a valuable foundation for delving into foraging behaviour. Thus, exploration into how individuals structure their search patterns, allocate resources, and optimise their strategies within a given environment provides insights into the dynamic interplay between cognitive processes and resource acquisition.

1.2.4 Foraging behaviour

Multiple processes underpin efficient foraging behaviour which can provide clarity into finer-grained individual contributions as human foragers rely on an array of information to support efficient foraging. Predominantly, and until recently, simple feature and conjunction of feature search has resided within the two-dimensional realm, where following the classical example, one must search for the letter T amongst distractor L's (Eckstein, 2011). However, as has been discussed, the integration of both fields may allow for greater behavioural and cognitive nuance. The measurement of searching within a three-dimensional space, and therefore the integration of foraging behaviour, allows for greater ecological validity to understand what can perhaps be defined as large-scale foraging-like search. Therefore, Harhen and Bornstein (2023) suggested this to indicate that to observe optimal foraging behaviour, accounts of how the forager acquires accurate and complete information of the environment, and how it adjusts their strategy, needs to be obtained. And yet, one does not search for their missing keys or their friend in a crowd within the second dimension. Search and foraging are not necessarily dissimilar in human participants, nor necessarily dissociable. Relatively few studies have considered search where participants are required to physically explore a large three-dimensional space in search of a target, which in some respects, could be more akin to the behaviours required in real-world foraging-like search. Visual search has been claimed as a simple model of foraging behaviour (e.g. Gilchrist et al., 2001) and whilst some theories have attempted to investigate this integration (e.g. Baxter & Smith, 2022; Jiang et al., 2014; Pellicano et al., 2011; Smith et al., 2010), greater nuance into the underpinning of behaviour is necessary to understand what is required to undertake search, or foraging, or perhaps an indiscriminatory version of the two.

1.3 Foraging-like large-scale search (the combination of two concepts)

Although two-dimensional visual search tasks have long been considered as simple and controlled models of naturalistic three-dimensional foraging behaviour (e.g., Klein & MacInnes, 1999; Wolfe, 1994), it is only relatively recently that psychologists have attempted to explicitly explore the relationship between search and foraging processes within the same paradigms. Hills et al. (2015) posits that human visual search inherently involves integrating exploration and exploitation. This integration has been assigned a variety of terms such as hybrid search (Wolfe, 2012), hybrid foraging (Wolfe et al., 2016), or visual foraging (Kristjánsson, Jóhannesson, & Thornton, 2014). As will be discussed, irrespective of the term assigned, there is considerable overlap between terms, but still begin to address such integration of visual search and foraging behaviours.

1.3.1 Hybrid search

An extension, or variation, of the classic visual search paradigm is termed ‘hybrid search’ (Wolfe, Cain, & Aizenman, 2019) where one must search for a singular instance from multiple possible targets (e.g. all items from a shopping list, held in memory) in a distractor-filled display. This is differentiated from the aforementioned classic search of one target, where search is terminated following identification of a single target (or the overt determination that no target is present). Further, Wolfe (2012, 2018) posits that the integration of search and memory defines a hybrid search, with the suggestion that one must search for a singular instance of a target from multiple possible target options, and therefore requiring the use of memory as one must hold multiple templates in mind. A radiologist who must search an x-ray for signs of cancer amongst a distractor-filled display represents a hybrid search. In this example, the radiologist looks for specific signs of cancer, but these span multiple dimensions across abnormalities in shape, size, or density with distractor items on the x-ray that vary in shape, size and density. This also requires the radiologist to distinguish between overlapping tissues and structures that accompany x-ray scans using additional cognitive resources (such as memory) and prior knowledge. Thus, hybrid search is suggested to address the issue of 'real world' search, for when the need to search for multiple items presents itself, one must adapt one's search strategy utilising cognitive control processes. In real-world search scenarios, memory plays a crucial role in guiding attention or recognising previously searched for objects (Wolfe, 2018). As one might expect, the increase of targets means that, in comparison to traditional visual search tasks, reaction times increase in hybrid search, whilst error rates increase but efficiency decrease (Wolfe, 2012). In fact, as the number of items increased that were required to be stored in memory, reaction time increased logarithmically in response (Cunningham & Wolfe, 2014; Wolfe, 2012).

If hybrid search is the hybrid between memory and visual search, the implication is that in comparison to traditional search per Treisman and Gelade (1980), memory is not utilised. Horowitz and Wolfe (1998) found in their study examining memory that participants produced equal search slopes between a static and dynamically changing display. They concluded therefore that search does not require memory, as the slope should differ between conditions. Woodman, Vogel and Luck (2001) furthered the study by looking at visual working memory capacity, suggesting that if the capacity is reached and search is still efficient then memory is not required to successfully search. It was determined that indeed, search was efficient despite an attained visual working memory capacity, and therefore concluded similar results with Horowitz and Wolfe. Conversely, Peterson et al. (2001) suggested that Horowitz and Wolfe did not consider the intercepts of their search slopes, and found that visual search did indeed require memory, whereby participants returned to targets not for lack of recall but for inadequate initial processing. This was explored further, with a stringent visual search paradigm where participants were unaware of a memory component following a visual search task (Williams, Henderson, & Zacks, 2005). Participants performed better than chance, despite the unknown manipulation, therefore suggesting the conclusion that memory is required for visual search. Wolfe (2018) described that in an array with multiple targets, one's memory is required in order to successfully remember all target types as well as to avoid previously visited locations. Klein and MacInnes (1999) suggested that memory is inherent to visual search, measured by previous fixation and saccades, as participants tended to fixate away from a previously inspected item than move towards, suggesting memory was protecting from revisits. Thus, as the distribution of participants revisiting previously inspected targets did not match the prediction for memoryless search, it was suggested that these revisits were due to inadequate processing rather than a lack of memory or forgetting. Võ and Wolfe (2015) proposed that memory acts to inhibit perseveration in simple feature search: one must remember the properties of the target that they are searching for in order to disregard distractors and successfully search. It was concluded that memory was indeed essential, however with the caution that not all aspects of memory contribute to search success. Complex cognitive interactions make it difficult to parse apart the essential aspects of memory directly contributing to search success, where Li et al. (2018) warned that two-dimensional models may not require memory as would a three-dimensional model, evidencing that participants employed visual search strategies reliant on spatial memory.

1.3.2 Hybrid foraging

In a clear distinction from hybrid search, Wolfe (2018) introduced the concept of 'hybrid foraging', wherein the concepts of foraging and visual search are combined. Hybrid foraging integrates the need to search within a patch as well as within a display, where one must search for multiple instances of multiple target types which are held in memory (Wiegand, Seidel, & Wolfe, 2019; Wolfe, Cain, & Aizenman, 2019). Kosovicheva, Alaoui-Soce and Wolfe (2020) describe that multi-target visual search demonstrates patch leaving decisions akin to foraging. Yet, there is the caveat that despite multi-target searching exemplifying real-world search, comparatively less is known about the underlying visual search processes that guide one to search and forage their environment. Gil-Gómez de Liaño and Wolfe (2022) suggest a description of the relationship between visual search, foraging and hybrid foraging where foraging extends classic visual search paradigms by integrating decision-making requirements essential for when one stops searching a patch, even if targets are still present. Hybrid foraging then builds upon the relationship by adding multiple target instances for one to select between, involving the incorporation of memory, and thus providing the ability to assess how executive function processes govern organisational and decision-making strategies. If one considers a radiologist searching for signs of cancer, as well as incidental findings on an X-ray, the radiologist is said to hybrid forage. The requirement to search and forage for multiple targets (e.g. cancer and incidental findings) within a search space requires the integration of memory and executive functioning. It has been suggested that factors including cognitive demands and individual difference play a greater role in hybrid search and foraging behaviour. Measures such as exhaustive foraging facilitates investigations into search strategy and attentional control (Gil-Gómez de Liaño et al., 2022), where quantifying when one decides on the patch ‘quitting time’, or patch leaving behaviour, is suggested to allow for greater understanding of executive function abilities and specifically decision-making strategies (Gil-Gómez de Liaño et al., 2022). Quitting time was suggested to reflect basic aspects of human cognition; more complex tasks, such as task-switching, provides greater insight into underlying cognitive functions such as executive function (Gil-Gómez de Liaño & Wolfe, 2022). This can allow for greater understanding into cognitive control and individual behaviours in hybrid foraging.

It has been noted that some foragers, particularly young adults, tend to collect items in 'runs' rather than randomly (Wiegand, Seidel, & Wolfe, 2019). This consists of collecting all similar target items that are represented within a patch before collecting all of the next target item (e.g. within a hypothetical patch of blueberries, raspberries, and strawberries, all blueberries are collected first before moving on to the raspberries, and so on). Target selection is predominantly based on the previously collected target and not of random selection, forming a run of target acquisition (Wiegand & Wolfe, 2021). Kristjánsson and colleagues (2014) found, when the target item, or object being foraged for, is highly salient, the runs are relatively short and therefore there is a high frequency of switching. However, the more difficult the target is to find, the longer the run will be. One of the difficulties with utilising run statistics as a measurement of efficient foraging is the variability of search paradigms. Clarke, Hunt and Hughes (2022) highlight that within an environment, the relative proximity of targets and the number of distractors influences target switching. This can prove difficult when comparing runs across studies with any variation of target distribution and category. Most importantly however, utilising run statistics to measure efficient foraging does not characterise the underlying cognitive processes to guide foraging behaviour and it has been suggested that the intrinsic spatial aspects inherent to foraging are bypassed (Clarke, Hunt, & Hughes, 2022). For example, in a three-dimensional paradigm (explained in greater detail in the next section), Kristjánsson et al. (2022) found that run length between the single feature and conjunction tasks were smaller than has previously been reported in two-dimensional studies. They suggested this to imply that differences emerge in run patterns when applied to 'real world' tasks, however participants were stationary throughout the task.

1.3.3 Visual foraging

As has been discussed thus far, visual search literature (e.g. Treisman & Gelade, 1980) proposes that one detects the target via ‘pop-out’ which immediately terminates the search task. Hybrid search and foraging have widened the definition by considering multiple distractor-types, or multiple types of targets. What visual foraging is proposed to measure is the search for multiples of the same target type amongst an array of distractors (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2019). To facilitate such a search, visual foraging can incorporate patchy environments, providing multiples of the same target, and distractors, per patch. Visual foraging is suggested to enable investigations into aspects of visual search and foraging behaviour including orientating oneself within the environment, attentional load, and therefore template creation, maintenance, and provision (Kristjánsson, Thornton, & Kristjánsson, 2018; Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2019). Suggested to provide real-world applications as humans do not search for one unique target (Tagu & Kristjánsson, 2022), visual foraging is able to further investigate the domain general contributions of search and foraging behaviour. Specifically, visual foraging has been suggested to quantify visual attention (Kristjánsson et al., 2020) and executive function (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2020), both processes shown to be essential for visual search and foraging success.

Bella-Fernández and colleagues (2023) assessed visual foraging which encompassed, within an adjustable environment, searching for an undetermined number of targets amongst distractors. Real world large-scale search, like a rugby player searching the pitch for the ball, teammate position, and opposition players, without knowing how many of each will be there at any one time, consists of a great number of variables. Therefore, to obtain and employ strategy, a greater number of external (e.g. targets and distractors) and internal (e.g. working memory, executive function) components are required. For example, to quantify visual foraging in the second dimension (e.g. participants had to collect points by tapping targets on a touchscreen, and participants were able to switch between patches freely in search of targets), Bella-Fernández et al. (2023) found that young adults were more organised in single feature than conjunction conditions, and that greater organisation led to more effective search. However, it was also noted that as the set size increased, organisation decreased, and as time increased, within-patch search organisation decreased. Within a trial (lasting until the participant had collected 200 points, between 20-40 minutes), foraging was found to become less organised. Therefore, it was suggested that organisation measures could predict quitting rules, or the patch leaving criteria, within visual foraging.

Uncertainty in visual foraging environments has shown that although participants are able to adjust their search strategy, their search and foraging behaviour deviates from optimal behaviour (Kobayashi, Matsui, & Ogawa, 2024). Clarke, Hunt, and Hughes (2022), in their review of visual foraging within the development of a new Bayesian foraging model, included a discussion of a 'superforager', or an individual who shows no statistical difference in strategy between single feature foraging and conjunction of feature foraging in two-dimensional foraging tasks. It was proposed, as the name suggests, that there are some individuals who optimally forage, irrespective of task difficulty, as they can hold multiple templates simultaneously. Conversely, superforaging participants may show more errors than 'normal' foragers and show a suboptimality in efficient foraging when responding to task demands. To further understand the mediating factors underpinning the relationship between visual search and foraging, as research such as Kristjánsson et al.'s (e.g. 2022) lab has begun to investigate, large-scale integration is required to include physical factors. Although such attempts are currently stationary and two-dimensional, recent research has examined how search unfold in three dimensions (e.g. Kristjánsson et al., 2022; Wolfe, Cain, & Aizenmann,

2019) suggested to implement ‘real world’ paradigms on a broader spatial scope, which begins to invoke some of the more fundamental concepts of foraging.

1.3.4 Large-scale search in virtual reality

It has been suggested (e.g. Olk et al., 2018) that in order to translate search ability, one must be tested in everyday situations. This is a problem for classic search literature, whereby the translation of search for letter T’s amongst all the L’s is not comparable when moving from two-dimensional computer screens to real life search ability. Hybrid search, hybrid foraging, and visual foraging are suggested to address the issue of ‘real world’ search as one must adapt their search strategy to include memory (and multiple target considerations), unlike classic visual search tasks (Wolfe, 2013). However, hybrid searchers (Wiegand & Wolfe, 2020) and hybrid foragers (Wiegand & Wolfe, 2021) are still searching and foraging, respectively, in two-dimensional displays. Thus, to address this disconnect between ‘real world’ implementation, recent studies (e.g. Botch et al., 2023; Kristjánsson et al., 2022; Olk et al., 2018) have begun to utilise immersive three-dimensional settings. Such studies (Botch et al., 2023; Kristjánsson et al., 2022; Olk et al., 2018) have all utilised immersive virtual reality-based experimentation for participants to undertake variations of search tasks, however participants were stationary in each study and a button press would identify target selection. There have been relatively few studies of whether some of the phenomena characterised in visual search paradigms transpose to large-scale space, where participants are required to physically explore a three-dimensional space in search of a target. Indeed, some studies have experimentally addressed large-scale search (e.g. Gilchrist et al., 2001; Jiang et al., 2014; Smith et al., 2008, 2010) and have reported equivocal findings. However, it is essential to note that a more systematic examination of the potential influence of visual cues utilised in visual search might inform large-scale equivalents, following some exceptions discussed in the literature (e.g. Smith et al., 2008). True foraging also incorporates idiothetic, or full body movements, in order to explore one's environment, as well as shifts of perspective as the forager is able to rotate their viewpoint. These differences between monitor-based and three-dimensional foraging may impact upon the relationship between visual information and foraging efficiency (see, for example: Ruddle & Lessels, 2006).

Research has started to examine whether visual search effects do indeed represent domain-general properties of human search behaviour, or whether the different requirements of large-scale search (e.g. body movements, effort, viewpoint changes) invoke the contribution of more domain-specific functions (Smith et al., 2010). For example, Kristjánsson et al. (2022) report a paradigm that used immersive VR, requiring participants to stand before a simple array distributed before them in three dimensions, and to use a 'laser pointer' to select target items (also see: Olk et al., 2018; Sisk et al., 2021). However, relatively few studies have assessed search where participants are required to physically explore a large 3D space in search of a target – in some respects, this might be considered to be closer to the behaviours required in real-world foraging-like search. This was first addressed in a study by Gilchrist et al. (2001), who required participants to walk within an array of identical locations (35mm film cannisters) in search of a hidden target (a marble) that could be detected by shaking. Although this paradigm revealed some similarities with visual search (i.e. the relationship between search time and array size differed between target-present and target-absent trials) there were also fewer revisits to previously-inspected locations than would be expected in visual search, and this was attributed to the greater costs associated with physical exploration. Critically, targets were not distinguished by visual cues, and subsequent examinations of spatial cueing by probability in large-scaler search (e.g. Baxter & Smith, 2022; Jiang et al., 2014; Pellicano et al., 2011; Smith et al., 2010) have also been conducted without a systematic manipulation of the visual properties of the array. Baxter and Smith (2022) suggest a lack of evidence for the translation from two-dimensional to three-dimensional space, implying that not all large-scale visual search paradigms provide support for domain generality, however the range within individual performance suggested alternatively that different search measures may produce varying insights based on the underlying components of individual difference.

In this context, perhaps the only study that has examined fully motile large-scale search for a single target defined by visual cues is that of Smith et al. (2008). Participants were situated within an automated apparatus, which presented a search array defined by lights that were embedded in the laboratory floor. Simple search was examined in a feature-present condition, where the distractors were green lights and the target was green and red, and effortful search was examined in a feature-absent condition, where distractors were red and green whilst the target was green. There was always a target present, and participants were required to walk to the target location and activate an adjacent switch. Visually guided searches were compared to a 'foraging' condition, where all search locations were green, and participants were required to activate each one until they revealed the hidden target (i.e. the location where the red light illuminated when the switch was pressed). Visual search conditions recapitulated effects from traditional two-dimensional monitor-based tasks, where search times were equivalent for all array sizes in the simple condition but rose in proportion to array size in the effortful condition. In contrast, the forging condition revealed a much steeper relationship between search times and the size of the array, reflecting the necessity to individually activate each potential target location. In sum, these findings extended visual search mechanisms to large-scale space, showing that environmental search can be simple or complex, depending on the perceptual features that guide exploration. However, whilst participants made their responses by moving to a location, the execution of a search was not dependent upon physical exploration of space. In contrast, the foraging condition required each location to be visited in the absence of visual guidance towards the target. Moreover, the paradigm did not address the factors that may have guided foraging behaviour, especially considering the mechanisms that have been discussed in preceding parts of this Chapter. In their attempt to harmonise insights into search and foraging processes, Kosovicheva et al. (2020) state that there is still comparatively little knowledge of the underlying visual search mechanisms that guide our ability to search and forage the environment around us.

1.4 Cognitive control

Processes supporting efficient search behaviour includes cognitive control, the suggested link between all external explorations. Cognitive control, or the system of processes that moderate information, connects conventionally disparate cognitive domains, providing a domain-general underpinning for all forms of exploratory behaviour (Mata & von Helversen, 2015). Miller (2000) defines the considered system as one that elevates humans to "intelligent beings", whereby complex behaviours and decision-making towards far-removed goals, orchestrated by intention, mediates and controls lower-level processes. The key function is therefore to extract goal-driven learnt experiences—as all intended behaviours are driven by learnt experiences—to use for future situations. Yet, there has long been a debate about how to fully operationalise cognitive control. One field of view, as discussed by Braver (2012), is that cognitive control is a dual mechanism framework, defined by two distinct operating modes of proactive and reactive control. Proactive control is suggested to maintain goal-relevant information before a cognitively demanding event occurs in order to optimally focus attention and perception, whereby reactive control utilises attention when needed after a high interference event is identified. However, there are multiple definitions for what encompasses cognitive control. An alternative suggestion refers to the core mechanisms of cognitive control as conflict-driven and suggests that the detection of conflict initiates automatic cognitive control mechanisms (Kan et al., 2013). Further, there is also question whether cognitive control is indeed a dual process system, or domain general. Kan and colleagues (2013) summarised that the argument for a dual mechanism framework, within a conflict-resolution standpoint, suggests multiple but independent systems that support conflict processing. Akçay and Hazeltine (2011) proposed that when one encounters one type of conflict, a feedback loop, or the attentional system that attenuates inputs, is formed. They then queried whether control is global or local when conflict occurs, and therefore whether all ongoing processes will be recruited, or only a subset of relevant processes are affected. It was found that task conflict, independent of feature repetition (e.g. stimuli related to task conflict), was local within two differing conflict types (Simon and flanker tasks). The authors suggested this indicated that cognitive control is local within specific domains and therefore provided evidence against a single, unitary control process and modulated control confined to individual stimulus features (Akçay & Hazeltine, 2011). Yet, other (e.g. Kan et al., 2013) support domain general control. As cognitive control is the ability to regulate thoughts, emotions, and actions to achieve goals or adapt to changing situations, domain generality may be supported due to common brain regions and mechanisms are involved across different tasks, showing flexibility and transfer effects between domains.

1.4.1 Domain generality

There is an argument that conflict resolution is domain general, and therefore systems operate similarly and in parallel across all conflict types, across all domains. Reingold and Glaholt (2014) specify that rapid fixation sequences throughout a visual search environment are bound by the underlying processes which influence stimulus fixation duration. They determined that factors such as saccade selectivity within a search task and time differences between high similarity and low similarity distractors indicated a domain general process of cognitive control. Further, across a series of experiments, Kan et al. (2013) supported a shared system of processing, where participants were tasked with detecting conflict after experiencing ambiguity, and they were able to successfully exhibit conflict adaption, suggested to indicate sustained cognitive control engagement. Gratton and colleagues (2018), in their review of the theoretical and experimental basis of cognitive control, concluded that a multitude of processes are dynamically required for selecting, implementing, or suppressing goals in changing contexts, evidenced by neuroimaging, neurobiological, and neuropsychological research. Executive functioning task demands (e.g. inhibition and switching) were found to be modulated by domain general processes whilst event-related potentials were measured in young adults where multiple regions in the frontoparietal system was activated to achieve task demands (Barceló & Cooper, 2018).

The primacy of cognitive control in the formation of optimal search decisions lies in the theory that its' evolutionary origins are in the planning and control of subsistence foraging behaviours in the ancestral environment. Hills et al. (2010) argued for its generality by showing that foraging strategies could be primed across domains, such that explore-exploit strategies in a visuospatial search task influenced subsequent behaviour in a lexical search task, and *vice versa*. Hills et al. (2012) also reported that optimal search strategies (as defined by MVT) could be applied to the search for items in memory. For example, when participants are required to name as many animals as possible, it was found that they would switch to different categories (i.e. explore) when their exemplars within a category began to be depleted, suggesting that cognitive control mediates memory search (Hills et al., 2013). The necessity for dynamic switching during search and foraging accounts for decisions moving from one memory region to another (e.g. working memory to episodic; Hills et al., 2015). This suggests that the core of visual search and foraging abilities would have therefore developed over time, leading to the argument that such domain general processes are across multiple contexts. Not only memory, but executive functioning has been found to contribute to foraging-like behaviours, representing fundamental support to domain general arguments (Hills et al., 2015). These factors predict large-scale search behaviour (or, laboratory-based visual search behaviour) and it has been argued that they lie at the very basis of human cognitive operations, as exemplified by the theory that central executive processes can be characterised as domain general foraging strategies (for a recent review see Smith & De Lillo, 2022). Ultimately, Hills (2011) summarises that domain generality provides a baseline for cognitive control processes.

1.4.2 Top-down/bottom-up processing

A key aspect to cognitive control is the distinction between bottom-up and top-down processing, where depending on the context, the presented stimulus can be interpreted based on their feedforward or feedback mechanisms (Gratton et al., 2018). The interplay between feedforward and feedback mechanisms enables the brain to efficiently process and make sense of incoming sensory information, facilitating cognitive control processes such as attention, perception, and decision-making. Executive functioning is essential to cognitive control, including selective attention, as one must attend to the visual stimuli required to draw one's attention toward the target, and allow for discrimination away from the distractor. An example of this is the Stroop Task, where cognitive control is inferred from the attentional bias toward the ink colour and away from the predominant tendency to read the presented word (Gratton et al., 2018). The more salient the target is, the higher the priority the attentional stimuli will hold (Han & Kim, 2009). Individual differences in cognitive control have also been shown to predict switching behaviour in search, where poorer cognitive abilities are associated with a reduction in explore decisions (Chin et al., 2015; Mata & von Helversen, 2015). Chin and colleagues (2015) suggested that executive control was a moderator for patch leaving decisions, and theorised that executive control may contribute to information updating mechanisms or memory span over time.

Han and Kim (2009) further discuss the relationship between visual search and attentional stimuli, suggesting that it is influenced by working memory, both for what information is stored in working memory but also what is attended to within a visual scene. Gratton and colleagues (2018) proposed an integration of concepts within cognitive control whereby although decision-making is integral, one must also update and maintain information held in working memory, as enhanced top-down control has been shown to lead to signal modulations at the frontal gyrus, a region mainly associated with working memory (Weidner et al., 2009). Engle (2010) provides further support to working memory-specific aspects of cognitive control, where within a domain general working memory capacity, attentional control provides visuospatial processing benefits, particularly beneficial to visual search and foraging success. Hills et al. (2010) posits that such mediation between exploration and exploitation suggest an integration, or domain generality, of processes. Hills et al. (2012) proposed that the explore-exploit decision is not just physical but mental, and suggested when asked to search amongst semantic patches, that participants do not select a singular patch and exploit it (e.g. selecting pets and then naming all the pets they can think of) but searched for a near term to the current one (e.g. cat-dog-wolf). This was thought to represent a domain generality in human foraging, especially in the exploration-exploitation trade-off, where the processes required to modulate foraging trade-off controls both internal and external search (Hills et al., 2010). Clarke, Hunt, and Hughes (2022) proceeded to deliberate whether greater working memory ability is required as working memory performance is not a good indicator of individual difference, and in fact flexible strategies (or the lack therefore) may contribute more prominently to success. Children execute single feature foraging tasks similarly to adults, but perform significantly worse at conjunction foraging (Ólafsdóttir, Gestsdóttir, Kristjánsson, 2021). This potentially highlights the essential role of executive functioning in successful foraging, and not necessarily working memory, as children's prefrontal cortices, which include executive functioning abilities, are not fully developed (Ólafsdóttir, Gestsdóttir, Kristjánsson, 2021).

Clearly, it can be suggested that sufficient evidence is provided for the essential role of memory. However, the relationship is nuanced and multifaceted, with indications that visual working memory, amongst others, plays a crucial role in guiding attention and facilitating efficient target detection, particularly in tasks involving feature conjunctions. If multiple cognitive domains are needed to conduct successful and efficient search, there might be more underlying components required to search beyond foveal or physical search. True foraging-like search also incorporates full body movements to explore one's environment, as well as shifts of perspective as they rotate their viewpoint. These differences may impact upon the relationship between visual information and search efficiency (e.g. Ruddle & Lessels, 2006) whereby planning search movements around a large-scale space and deciding to switch from one patch of items to another likely require a great degree of cognitive control. Therefore, the integration of visual search, foraging, and cognitive control may highlight the intricate interplay between perceptual processes, goal-oriented exploration, and higher-order functions. Visual search and foraging strategies emerge as dynamic components shaped by cognitive control mechanisms, where understanding how these cognitive processes collaboratively inform environmental interactions can provide a holistic perspective on flexibility and adaptation. Not only has it been suggested that human cognitive control processes have their roots in foraging behaviour (Hills et al., 2010), but foraging efficiency has also been identified as a marker for age-related cognitive decline (Mata, 2009). The relationship between ageing, visual search and foraging success, and cognitive control, is complex and involves both decline and compensatory mechanisms.

1.5 Typical and pathological ageing

As individuals age, changes in cognitive control processes, such as attentional allocation and working memory, can significantly impact both visual search and foraging behaviours. Age-related declines in cognitive control may lead to difficulties in efficiently filtering relevant information during visual search tasks and in making optimal decisions during foraging, affecting the overall effectiveness of these cognitive processes (Mata & von Helversen, 2015). Recognising the complex relationship between ageing, visual search, foraging, and cognitive control is essential for developing strategies to support older individuals in maintaining adaptive behaviours and decision-making abilities in various environments.

1.5.1 Ageing and visual search

Exploring the intricate relationship between ageing and visual search provides valuable insights into the impact of age-related factors on the speed, accuracy, and strategies employed during visual search tasks. Across the literature, there have been a number of suggestions that older adults are less efficient than younger adults at visual search tasks (see Zanto & Gazzaley, 2014 for a review) as ageing induces a vulnerability to distractor items as well as slowed processing speed (determined by reaction time) and steeper search slopes (revealing inefficient search; Hahn & Buttaccio, 2018). Research (e.g. Porter et al., 2010) suggests that older adults display deficiencies in conjunction search, disproportionately to that of younger adults, where factors such as longer eye gaze fixations and increased saccades were noted. Although younger adults were found to perform worse on conjunction of feature trials than single feature, older adults still performed worse overall. Further, Potter et al. (2012) found that older adults searched more exhaustively (exploitatively) in a task requiring participants to search through a real-life display for pasta jars. Seated opposite shelves, participants would hold down a button, and then lift their hand to point at the jar once they found the target. There were both target present and target absent trials, and exhaustive search was determined through the ratio of success in single feature trials (searching for yellow straws amongst an array of multi-coloured straws) and conjunction of feature trials (double conjunction: searching for multi-coloured straws amongst either jars identified by coloured twists and multi-straw colour; triple conjunction: jars identified by coloured twists, yellow straws, or half-full jars of multi-coloured straws). Potter et al. (2012) therefore suggested their findings were reflective of a cautious and potentially compensatory search strategy in ageing. There has also been a difference between groups of older adults found in the visual search literature, where Potter et al. (2012) found that participants in their 70s and 80s performed significantly worse than their younger, older adult counterparts. They suggested this was due to memory failures in binding multiple features and increasing susceptibility to distraction.

However, recent findings suggest that when cognitive measures such as slowed processing and visuomotor speed are accounted for, younger and older adults perform similarly in terms of search performance success (Aziz et al., 2020) as the qualitative search patterns are similar across the lifespan (Yabuki & Goodhew, 2021). Wiegand et al. (2019) identified that younger and older adults conducted similar "run" patterns in their search task that required identifying multiple targets after a memorisation phase. The runs were determined to follow featural properties (e.g. identifying multiple instances of the same feature before switching to another feature), and it was therefore surmised that top-down attentional contributions (i.e. paying strategic attention in the pursuit of success at task-relevant goals; Awh et al., 2012) were preserved across ageing. Even when presented with a conjunction visual search task (participants were required to identify either a singular target present or absent within an array defined by colour and orientation), older adults performed just as efficiently in searching for the targets, albeit slower, than the younger cohort (Agnew, Phillips, & Pilz, 2020). The authors theorised this may indicate a difference in search strategy, but not search ability, to compensate for reduced response speed (Agnew, Phillips, & Pilz, 2020). The differences that were noted by Wiegand et al. (2019) were also that of a strategic nature, where older adults appeared to adopt a more conservative, and thus more exploitative, strategy. This led Wiegand et al. (2019) to suggest that older adults followed their own meta-cognitive strategic bias to exhaustive search, and query whether increasing attentional or memory load, or time limits, would elicit a more exploratory strategy, but with an overall conclusion that older adults differed in strategy rather than ability. Therefore, across the ageing literature, there is inconsistency about whether older adults are truly disadvantaged in visual search tasks as compared to younger adults. There is agreement that older adults are slower (e.g. Hahn & Buttaccio, 2018; Yabuki & Goodhew, 2021) however the extent to which older adults are less efficient at visual search tasks, and to what degree, is still debated.

1.5.2 Pathological ageing and visual search

Due to characterisations of visuospatial and attentional processing deficits that are commonly identified with neurodegenerative disorders such as MCI and AD (Ramzaoui et al., 2018) visual search tasks have been suggested as potentially diagnostic for underlying neurodegenerative processes. Individuals suffering from early to moderate impairment (as identified by the Mini-Mental State Exam; MMSE) have displayed slowed response times and increased distractor sensitivity in visual search tasks (Ramzaoui et al., 2018), proposing that alternative responses (i.e. distractor items) are important to consider in neurodegenerative disease progression (Baddeley et al., 2001). More, and longer, fixations during visual search have also been identified in AD patients (Ramzaoui et al., 2022). This was suggested to represent a deficit of the attentional system, attributed to disengagement, and therefore may benefit impairment identification. Tales et al. (2011) investigated whether there was a difference in visual search performance between typically and atypically ageing older adults, specifically with amnestic MCI participants. A two-dimensional visual search task was employed where participants were required to find a left- or right- facing arrow within an array of up- and down- pointing distractor arrows. Visual search performance (measured by quantifying the reaction time to all stimuli subtracted from the reaction time just to the target) was significantly poorer in a subset of amnestic MCI participants, with the other subset revealing unexplained similarities to the control group's performance. After a longitudinal follow-up, Tales et al. (2011) found that whilst some diagnoses of amnestic MCI remained stable (71%), others converted to a variety of dementias (29%); the participants that did convert to a dementia diagnosis showed a degradation in visual search performance at both baseline and follow-up periods (follow-up 2.5 years post initial assessment), and so whilst not suggesting a marker for early dementia, Tales and colleagues proposed that visual search could be utilised as an identifier of underlying pathologies likely to convert to dementia. Further, in a review by Ramzaoui and colleagues (2018), single feature search was suggested to be preserved within AD patients, whereas conjunction search was found to be disproportionately impaired. It was posited that these deficits arose due to feature-binding difficulties that emerge in neurodegeneration. A similar pattern, although less severe, was present amongst patients with an amnestic MCI diagnosis. In comparison to typically ageing older adults, patients with AD have also been suggested to show slower searching in conjunction trials, which Ramzaoui et al. (2022) surmised to indicate an impact with top-down sequential guidance for target identification. However, in single feature search, when bottom-up detection is required, AD patients show preserved performance, as did their time to initiate search. This may be due to a domain general pool of cognitive resources (Porter et al., 2010), where greater resources are able to be drawn upon, however more effortful tasks require a larger number of resources. Porter et al. (2010) found that pupil dilation (revealing effort expenditure moment-by-moment during tasks) was weaker in conjunction tasks for AD patients, suggesting more effortful discriminations are required in visual search tasks which disproportionately affect those suffering from AD, as the finding was not replicated in typically ageing older adults. Therefore, AD participants may be susceptible to deficits in visual search mechanisms, particularly conjunction, or more effortful search, than are typically ageing older adults.

1.5.3 Ageing and foraging

As has been described thus far, visual search abilities change as one ages. However, research also suggests that foraging decisions are particularly affected by ageing, where prefrontal areas of the brain associated with exploration-exploitation decision-making are particularly affected in the ageing process (Mata et al., 2013). It has been suggested that due to limited, or reduced, cognitive abilities, older adults' default to simpler (and therefore less efficient or successful) decision-making strategies, even when more complex strategies provide greater reward (Mata, Schooler, & Rieskamp, 2007) or when provided with the optimal strategy (Mata, Wilke, & Czienskowski, 2009). Mata and colleagues (2009) posit that age-related deficits are due to the adaptive selection and efficient application of strategies, where older adults are less strategic. In a series of experiments evaluating exploration and exploitation behaviours comparing older and younger adults, Mata et al. (2009) measured the time spent in two-dimensional fishing ponds, applying MVT properties to understand the optimal point for one to leave the pond and fish in the next. The first experiment manipulated travel time so moving between ponds incurred a time cost, either taking a shorter travel time (15 seconds) or longer (35 seconds) in a 40-minute task, and participants could select to move between ponds as desired. They found that older adults missed more fish and caught fewer fish than younger adults, as well as waited to find fish in a patch significantly longer. The second experiment assessed strategy, where participants were told to employ an incremental strategy (i.e. to initiate a patch entry with a predetermined finite waiting time and increase it incrementally each time a single item is discovered), and adjust the strategy based on shorter or longer travel time. Here, even though older adults were given the optimal strategy, they still performed significantly worse than their younger counterparts by collecting fewer fish, however, the older adults stayed in patch similarly to that of the younger adults. This suggested that although both age groups were able to adjust their strategy, older adults preferred a suboptimal exploitative strategy whereas younger adults followed MVT properties more closely. However, it was also suggested that additional factors such as motor or attentional errors in the older adult cohort may have accounted for some of the difference, or at least that the differences found may have additional contributing factors.

Two hypotheses have been proposed to explain the underlying nature of exploratory behaviours as one ages. Mata, Wilke, and Czienskowski (2013) describe these two hypotheses as functional adaptivity and mechanistic cognitive decline. Functional adaptivity suggests that as one ages, the need to explore (e.g. to gain knowledge of the environment leading to successful later exploitation) reduces as one's knowledge increases, therefore making an exploitative strategy adaptive. This has also been considered a 'cooling off' process (Lloyd et al., 2023) where the naïve learner explores a new environment in a stochastic manner to gain knowledge, and over time the learner explores less (and therefore exploits more), utilising the knowledge learned from previous explorations. On the contrary, mechanistic cognitive decline does not imply adaptation, and instead suggests deleterious effects on the cognitive processes that control exploration ability throughout the ageing process. Both hypotheses, as summarised by Mata et al. (2013), predict an increase in exploitation and decrease in exploration through the ageing process, although one suggests adaptivity whilst the other suggests a deleterious and unavoidable mechanistic inevitability.

Mata and colleagues (2013) therefore employed a series of experiments to investigate the neural and cognitive mechanisms underlying ageing processes in foraging to elucidate whether adaptivity or mechanistic cognition underpin foraging behaviour. Like Mata et al. (2009), a fishing task was employed where participants were required to fish in ponds and in one experiment no strategy was given, but an incremental strategy was provided to the participants in the second experiment. However, Mata et al. (2013) also utilised word puzzles in the third and fourth experiments to investigate similar foraging behaviours within memory. The intention behind the experiments was to test the hypothetical underpinnings of adaptation or cognitive decline, and therefore measures such as giving-up time, motivation factors, risk taking, and fluid cognition were used to determine underlying exploratory tendencies. Findings suggested that ageing was indeed associated with reductions in both internal and external exploratory behaviours, however results were inconclusive as to the mechanisms underlying exploitation behaviour in ageing. Weak evidence suggested a deleterious mechanism of cognitive decline as exploration significantly correlated with cognitive ability, but for only one cohort of four, and therefore Mata et al. (2013) suggested more research was required. Similarly, findings in the visual foraging literature suggest that older adults are less likely to seek rewards or inhibit their behaviour to avoid negative consequences (Wiegand & Wolfe, 2021). This led to lower levels of foraging efficiency.

Conversely, there has been evidence to support no difference between younger and older adults in hybrid foraging tasks. Wiegand, Seidel, and Wolfe (2019) found that across measures such as false alarms, memory effects on set size based on the number of missed targets, average rate of collected targets, and transformed reaction time (i.e. mean reaction time was subtracted from each mouse click's reaction time and then divided by the standard deviation, allowing for comparison of relative condition differences between participants, independent of mean reaction time and therefore age-related slowing), older adults performed similarly to that of their younger counterparts when general age-related slowing was accounted for. Even when placed under higher memory load (up to 64 objects), Wiegand, Seidel, and Wolfe (2019) did not find evidence for age-specific impairment in memory or slope. There were also similar switching performances: older and younger adults both suffered high cost in their switching between target types (runs) within a patch. The only differences identified by Wiegand, Seidel, and Wolfe (2019) between younger and older adults was strategy, where older adults showed higher exploitation preferences both qualitatively (participants were explicitly asked about their strategy: older adults described moving onto the next patch after they had found all the targets whereas younger adults identified moving when they felt they were slowing down or when they could not easily identify a target) and quantitatively (older adults stayed in patch until their rate of collection fell significantly below average whereas younger adults followed MVT properties). Wiegand and Wolfe (2021) supported these findings in a task that required participants to search for representations of real-world objects (i.e. picture of a butterfly, violin, etc) in a moving display. The value of the representation differed, making some representations more valuable to collect than others. Participants were able to freely move between patches by switching to a new screen of item representations. Older adults showed exploitative preferences which was suggested to be due to differences in strategy rather than a reduction in attentional or memory ability as older adults were more conservative and expressed desire not to "waste" targets.

1.5.4 Pathological ageing and foraging

What has not been discussed in the literature thus far, to the knowledge of this author, is how idiothetic, or fully motile, foraging behaviour manifests in neurodegenerative conditions. As has been highlighted in earlier sections, executive functions decline as one ages, particularly in neurodegenerative processes. This can be extended to decrements in foraging behaviours, as success has been shown to rely on executive function (e.g. Gil-Gómez de Liaño & Wolfe, 2022). One might assume, based on the findings across the typical and pathological ageing and visual search and foraging literatures, that due to deficits in attentional systems, effortful searches, and executive function (e.g. planning, organisation), those suffering from Alzheimer's disease may indeed show even greater exploitation behaviours in foraging tasks than that of their typically ageing counterparts. Some research has shown that, in an internal forage, both MCI and AD individuals had less coherent clusters of semantic categories as well as fewer switches (Johns et al., 2013). Given that AD differentially affects switching and clustering behaviours (Abbott, Austerweil, & Griffiths, 2015), and per Hills et al. (2012) suggestion that foraging occurs not only externally but internally, measures such as category fluency, which are typically used diagnostically for AD and MCI patients, can provide some evidence for deficits in foraging behaviour in MCI and AD. It has been recently proposed that computerised foraging tasks may effectively act as a diagnostic battery for assessing neurodegeneration, where cognitive skills such as executive function and attentional flexibility can be assessed (Mukaetova-Ladinska et al., 2022). As Mata and von Helversen (2015) suggested, domain generality underpins all forms of exploratory behaviour, and therefore the reduction of cognitive resources would imply a reduction of exploration in new environments in not only typically, but also pathologically, ageing older adults.

1.5.5 Ageing and cognitive control

Differences in search performance, suggested to be due to evolutionary adaptations, are exemplified in classical deficits in ageing (i.e. slowed metabolism, muscle degradation; Reser, 2009). Typical ageing is associated with degradations in working memory, affecting visual, verbal, and spatial performance, with evidence from resting state brain activity that working memory, and specifically spatial working memory, differentially separated the abilities between younger and older adults (Jabès et al., 2021). Research into ageing reveals deficits with suggestions that exploration in internal and external situations both follow similar systems within cognitive control (Mata & von Helversen, 2015). For example, the prefrontal cortices that subserve executive function are affected by both typical and atypical ageing, impacting decision making in foraging-like contexts (Mata et al., 2013) and Wiegand, Seidel, and Wolfe (2019) summarise that attentional control from top-down selection may contribute to foraging deficits, as well as reduced episodic memory abilities, or lessened cognitive load capacities within a domain general process. Borges, Fernandes, and Coco (2019) suggest that, beyond generalised slowing of processing speed, cognitive control mechanisms explain the difficulties experienced by older adults. Especially in visual search, cognitive control processes are required, but costly. Thus, older adults can show impaired operations when necessitated to attend to the target whilst inhibiting attention to the distractor efficiently. Within a foraging context, ageing is found to follow a pattern of reduced exploration (and therefore increased exploitation), discussed increasingly throughout the literature (i.e. Louâpre et al., 2010; Mata et al., 2009; Smith & De Lillo, 2022). This is suggested to indicate that cognitive control can be necessary to disengage or initiate patch searching behaviours, as one's ability to maintain or switch optimally within a task decreases with age (Mata & von Helversen, 2015). This is especially true in comparison to younger adults, as older adults displayed a lower level of success growth when gaining information from several word search puzzles; participants were able to switch between puzzles (patches) as desired, leading to an overall reduction in switching frequency (Chin et al., 2015), thus suggesting an exploitative preference to find all of the words in the puzzle before moving on to the next puzzle.

Research suggests that age-related deterioration has implications for areas of cognition such as exploratory behaviours (Mata et al., 2013) where specifically the medial temporal lobe and hippocampus play key roles in spatial and episodic memory, which are integral to search and foraging, and are also sensitive to ageing (Li & King, 2019). Furthermore, areas involved with executive functioning properties such as decision-making and planning reveal neural correlates for spatial search abilities (Li & King, 2019). The ability to shift between tasks and inhibit prepotent or conflicting responses has been shown to provide essential contribution to cognitive control, especially in age-related performance (e.g. between younger and older adults; Schnitzspahn et al., 2013). Conversely, it has been argued that executive functioning is overly omnibus, and that lower-level functions (e.g. divided attention) explain decrements in visual search and foraging behaviour rather than aspects of executive functioning suggested through measures such as the Stroop, Inhibition of Return, or Flanker (Verhaeghen, 2011). Yabuki and Goodhew (2021) support this theory in their study of two-dimensional search for varying orientations of green or blue T's or L's where participants had to respond by identifying which row the target was located in (out of either a stimulus set of three or nine letters). It was found that despite a relatively demanding search task, searched for targets remained constant and were not disproportionately affected by age.

As age is associated with reductions in white matter volume and a loss of projection fibres from frontal areas (Bennett & Madden, 2014), then such features allow the identification of markers for cognitive decline, such as regional volume loss, microstructural connectivity, and decreases in tract fibre coherence. Executive function and working memory are thought to originate in the prefrontal cortex (Funahashi & Andreau, 2013), and age-related changes have been found to be associated with top-down attentional guidance in frontoparietal activation (Madden, 2007). The current primary diagnostic criterion of AD is episodic memory degradation (Apostolova, 2016), however, navigational and search deficits might occur before episodic memory impairments are noted (Coughlan et al., 2018). Cognitive control mediates foraging and visual search (Hills et al., 2013; Wyatt et al., 2024), and although the precise structural and behavioural mechanisms are yet to be determined, there are strong implications for the underlying structure of cognitive control and how that modulates foraging and visual search behaviour. Therefore, measuring differences in foraging decisions, along with their cognitive underpinnings (especially in terms of executive function and episodic memory), may assist in identifying change. Considering concerns in the translation from typical to atypical ageing, spatial deficits are noted in neurodegenerative conditions such as MCI and AD before significant clinical impairment, with links to atrophy and neuronal loss in the medial temporal lobe (Li & King, 2019), with suggestions that one's spatial abilities may be predictive and discriminatory in amnestic variants of MCI (Laczó et al., 2011). Therefore, elucidating the neural substrates will provide greater insight into the processes underpinning search and foraging behaviour.

1.6 Neural underpinnings

Ageing is associated with neurological changes in the brain, including reductions in white matter volume and a loss of projection fibres. It has been found that typically ageing-related decline is associated with global microstructural and tract-specific macrostructural changes in the brain (Schilling et al., 2022), with widespread reductions in white matter integrity in older adults as compared to younger adults (Yang et al., 2016). White matter tracts with higher integrity support the rapid relay of information, whereas decrements in integrity are associated with typical and pathological ageing. These losses suggest demyelination, or the deterioration of the myelin sheath, in the brain (Davis et al., 2009). This can be characterised through assessments such as magnetic resonance imaging (MRI), which measures radio frequency signals emitted from hydrogen atoms in the brain by applying electromagnetic waves to localise the signal using spatial magnetic gradients (Lerch et al., 2017).

Whilst several methods can be used to interpret brain imaging details, two methods are highlighted as approaches to analyse brain volume and structure. T_1-weighted scans capture the differences in how hydrogen nuclei in various tissues return to their equilibrium state after being disturbed by radio frequency pulses. The T_1 time represents the time constant for this relaxation process and the contrast in the image is determined by various factors such as molecule concentration, myelin shortening, and water content (Lerch et al., 2017). T_1-weighted imaging describes the brain structure, and outputs such as volume, cortical thickness, and voxel-based morphometry can be derived for analysis (Goto et al., 2022). The other technique is Diffusion Weighted Imaging (DWI), which is one of the predominant methods for inferring microstructure (Lerch et al., 2017). Baliyan et al. (2016) explain that DWI is a method of generating signal contrast based on thermal agitation, or Brownian motion, of water molecules. Unconstrained by brain tissue, the movement of water molecules is isotropic (i.e. of equal probability of diffusion in all directions). The human brain contains intra- and extra-cellular water molecules. Anisotropy of their movement results from their relative freedom of movement along the axon, compared to movement across axonal walls (Alba-Ferrara & de Erausquin, 2013). Diffusion Tensor Imaging (DTI) can measure this displacement of water molecules across brain tissue and provide *in vivo* information about the microstructure of cerebral white matter (Madden et al., 2004). DTI has been used to probe age-related decline in the integrity of white matter tracts that connect frontal and parietal regions of the brain, detecting forms of dementia such as AD (Bennett et al., 2012; Madden et al., 2012).

Two specific measures that can be derived from DTI are fractional anisotropy (FA) and mean diffusivity (MD). FA is a representation of a fraction of the tensor (i.e. a part of a vector in space) that can be understood by anisotropic (or, directional) diffusion (Madden et al., 2012). FA has values from 0 to 1, where the higher number indicates increased directionality of diffusion. For example, FA values are typically higher (around 0.7) in the centre of white-matter tracts such as the corpus callosum than in brain tissue of less directional coherence (Kochunov et al., 2012). Degeneration, such as an ageing brain, has been associated with lower FA values, particularly in frontal white matter, because water molecules are less constrained within axons that make up white matter tracts (due to demyelination). MD indexes the mean diffusion irrespective of directionality (i.e. in each of the three orthogonal directions; Bennett & Madden, 2014), and is calculated as the mean of the three eigenvalues of the tensor. Higher MD values can represent increased water content and relatively less resistance, ultimately reflecting a reduction in membrane constraint, and therefore higher diffusion rates. MD is a nonspecific, but sensitive, measure of 'barrier' integrity (Clark et al., 2011). Several candidate mechanisms contribute to alterations in MD's non-specificity. These include demyelination, where damage to the myelin sheath disrupts normal diffusion patterns; axon loss, which can lead to changes in tissue microstructure and diffusion properties; and fluid changes, such as increases in extracellular fluid due to inflammation, which can affect the diffusion of water molecules and consequently impact MD values (Sepehrband et al., 2019). FA has been found to be negatively associated with age (e.g. lower FA equates to greater degradation), whereas MD is positively associated across white matter pathways (e.g. higher MD equates to greater degradation), and both values have been shown as sensitive measures of microstructural changes related to the ageing process (Schilling et al., 2022). Whilst there are additional measures to investigate brain structure, neuronal activity is modulated through structural connections, and therefore DTI is ideally used to quantify the structural identity of white matter (Yang et al., 2016).

1.6.1 Neural correlates of visual search

Top-down and bottom-up processing is key to understanding visual search behaviour across the lifespan. Older adults are less likely to fully utilise target templates (Ramzaoui et al., 2021) and prior knowledge (Whiting et al., 2005) highlighting a decrement of working memory in visual search as one ages. Older adults' attention has also been discovered to be captured by distractors more (Ramzaoui et al., 2022; Whiting et al., 2005). Kalkstein et al. (2011) proposed that changes in top-down modulation played a mediating role in the age-related deficits observed in visual imagery processes. Functional imaging studies have shown that the superior frontal and dorsal parietal regions are essential for top-down processing whereas the ventral frontoparietal network (e.g. middle and inferior frontal gyrus, temporoparietal junction) is fundamental to bottom-up engagement (Bennett et al., 2012). Bennett et al. (2012) describes two frontoparietal tracts that have been implicated in visual search behaviour - the superior (top-down information) and inferior (bottom-up guidance) longitudinal fasciculi. The superior longitudinal fasciculus runs between the dorsal frontoparietal attention network and the inferior longitudinal fasciculus traverses the frontotemporal and occipitoparietal regions. Connectivity in these tracts were found to correlate to visual search performance including conjunction search accuracy and search speed, but without differential predictions of performance, indicating that both top-down and bottom-up processing contributed to search behaviour.

The interplay between top-down and bottom-up processing in visual search is modulated by the locus coeruleus (LC), a brainstem nucleus that releases norepinephrine (NE) and plays a pivotal role in regulating attention and optimising the balance between goal-directed expectations and salient environmental stimuli during visual exploration. It has been suggested that nearly all of NE released in the neocortex originates from the LC, and in terms of visual search behaviour, the LC has been associated with a burst of activity in response to target stimuli, but not to distractors (Cohen, McClure, & Yu, 2007). As a system, the LC and NE regulate a variety of processes, including executive functions such as attention and working memory (Poe et al., 2020), which are key mechanisms in visual search. Poe and colleagues (2020) discuss that the LC also engages in behaviours requiring cognitive flexibility, such as shifts in attention or strategy, as well as decision-making. Further, Wyatt and colleagues (2024) predict that alterations in NE signalling leads to disruptions in flexible coupling amongst large scale brain networks, mediated by the salience network. These NE signalling alterations were proposed to be related to early tau accumulation in the LC, strongly implicating NE neurotransmitters as essential to attentional shifting. Given that successful binding mediates efficient conjunction search in visual search tasks, a reduction in NE signalling—coupled with early tau accumulation, which is associated with the onset of AD—suggests that NE signalling related to early tau accumulation in the LC may play a key role in impaired conjunction search in disorders like AD.

An additional region shown to be integral to visual search is that of the ventromedial prefrontal cortex (vmPFC), which has also been shown to structurally connect with the object-sensitive lateral occipital cortex (LOC; a region highly specialised for visual objects). It was suggested that bidirectional projections, quantified by probabilistic tractography, from the vmPFC to the visual cortex may mediate expectancy and stimulus-specific attentional processes during visual search and related discriminations underlying fronto-occipital functional interactions (Pantazatos et al., 2012). These connections were proposed to align with the theory of bottom-up and top-down processing in visual search. Here, sensory information gathered from a search task (bottom-up) is matched and processed simultaneously with expectations and anticipations of the visual search targets (top-down). This occurs due to the mutual and positive functional and effective connectivity between the vmPFC and LOC during the search task, where existing white matter tracts are present

(Pantazatos et al., 2012). Further, the prefrontal cortex is associated with top-down control (Cohen, McClure, & Yu, 2007). Therefore, research has supported the integration of both top-down and bottom-up processing required for successful visual search, as evidenced by neuroimaging studies (e.g. Cohen et al., 2007; Poe et al., 2020; Wyatt et al., 2024) utilising tractography methods to show connections between previously disparate regions. As it has been discussed thus far, a loss of projection fibres from frontal areas are not only connected with visual search mechanisms, but these markers of ageing are also thought to be central to age-related change to foraging behaviours.

1.6.2 Neural correlates of foraging

Wyatt et al. (2024) conducted an extensive review assessing the neural correlates associated with the exploration-exploitation trade-off. Overall, they posited that exploration-based decisions engaged regions associated with cognitive control, and specifically goal-directed attention, whereas exploitation-based decisions relied on the default mode network brain regions (i.e. medial prefrontal cortex, lateral and medial temporal lobes, posterior inferior parietal lobule, and posterior cingulate cortex; Spreng et al., 2010) implicated in reward processing. The default mode network (DMN) has been associated in estimating value of unknown options (i.e. leapfrog task, exploitation; Lloyd et al., 2023), key in foraging and exploration-exploitation trade-off success. Wyatt et al. (2024) found that the salience network mediated switching within the default and frontoparietal networks to guide appropriate responses to relevant stimuli, and thus supported switching between exploration and exploitation as the salience of rewards shifted. Spreng and Turner (2021) discussed that one way to conceptualise exploitation specifically is as a system of reward and attention neural circuits. They proposed that three processes (i.e. motivational, affective, integrative) shape exploration-exploitation decision-making and are affected by the ageing process. These three processes that shape foraging decision-making (Spreng & Turner, 2021) are implicated in a model detailing the putative brain systems that are implicated in exploitative tendencies. This model describes that within the DMN, the medial prefrontal cortex integrates prior knowledge with dopaminergic rewards signals from the nucleus accumbens (NA). This provides positive signalling into the two core nodes of the salience network; the anterior cingulate cortex (ACC) and LC integrate NE attentional signals, which promotes attentional focus. These two networks, the DMN and salience network, are combined in the adaptive gain model (Spreng & Turner, 2021) which modulates attention. The increased dopaminergic positive reward signalling feeds into the salience network and provides phasic attention which then leads to successful exploitation, whereas negative reward signalling promoting tonic attention leads to exploration. It has been suggested that the LC is the origination site of tau pathology, integral to AD degradation, the point where the adaptive gain model is disrupted in degenerative processes (Spreng & Turner, 2021; Wyatt et al., 2024).

Activity in the ACC has been found to positively correlate with estimating the background (or unknown) reward rate, but negatively correlate with the value of the current patch (Lloyd et al., 2023). Thus, less flexible shifting can occur between the signalling processes, increasing dwell time in exploitative search. Based on research by Clark et al. (2011) on clinical psychiatric cohorts, disruptions to the dopaminergic pathways were found to be associated with reduced exploration, suggesting a necessity for dopamine to promote efficient exploration and exploitation behaviour. It was argued that, in conjunction with reductions in attention, dopaminergic disruption may result in a different threshold for the exploration-exploitation trade-off, and provide some explanation for the variations in strategy, or the preference for exploitative behaviours, as one ages. Cohen, McClure, and Yu (2007) describe a model of neural networks attenuating the reward and cost for adaptive switching between exploration and exploitation, integrated in the LC. As cost is calculated by the ACC whilst reward is calculated by the vmPFC and orbitofrontal cortex, the information converges on the ventral tegmental areas and LC. This allows the LC to provide a response (e.g. phasic, or exploitation; or tonic, or explorative), and therefore modulates NE gain and release in the decision network, regulating exploration and exploitation. However, it has also been noted that the LC is difficult to reliably image due to its size and deep brain location (Wyatt et al., 2024).

1.6.3 Neurological evidence for cognitive control

Gratton, Sun, and Petersen (2018) identified specific brain networks that contribute to distinct mechanisms of cognitive control. As one might expect, the frontal and parietal cortices are essential, considering their known contribution to executive functioning abilities. Further networks, the cinguloopercular network (CON) and frontoparietal network (FPN), as well as suggestions for the salience, dorsal, and ventral attention networks, are implicated in cognitive control. Although shown to be distinct pathways, there is a clear integration of information between the networks, specifically in contribution to working memory and adaptive control. Gratton et al. (2018) further highlighted areas of the brain found to contribute to cognitive control. The dorsolateral prefrontal cortex and the ACC were suggested to be hierarchically organised to impose top-down biases of stimulus and response section, and therefore promote task-relevant and -irrelevant representations. As both the dorsolateral prefrontal cortex and ACC are involved in the FPN and CON networks, respectively, cognitive control processes such as attentional control and information integration provide flexible engagement in tasks.

The cognitive control hypothesis is an additional way to explain a change in behaviour in ageing, which Spreng and Turner (2021) also link to the increase in exploitative tendencies. The cognitive control hypothesis (e.g. Hills et al., 2013; Mata & von Helversen, 2015) proposes that effective foraging behaviours are influenced by higher-order cognitive control processes. According to this hypothesis, cognitive control functions, such as attentional control, working memory, and inhibitory control, play a crucial role in shaping how individuals gather, process, and utilise information during foraging tasks. The hypothesis suggests that cognitive control mechanisms contribute to adaptive decision-making, goal-directed behaviour, and the ability to flexibly adjust foraging strategies based on changing environmental conditions. Cognitive control is dependent on prior knowledge, and therefore exploiting known information can be an adaptive strategy when cognitive resources are diminished. Spreng and Turner (2021) also suggest that greater cognitive control is required for exploration, and thus under greater demand, exploitative behaviours increase, especially if one considers that the control processes decline with age. Age-related changes in the prefrontal cortex, known for its role in executive functions and cognitive control, may influence decision-making strategies during foraging tasks (Wyatt et al., 2024). Additionally, alterations in white matter tracts, such as the integrity of the fornix or the cingulum bundle (Madden et al., 2007), can impact the communication between brain regions critical for cognitive control, contributing to the complex interplay between neural structures, ageing, and adaptive behaviours in foraging scenarios.

1.6.4 Implications of pathological ageing

Alzheimer's disease, as a progressive and selective neurodegenerative disease, displays degradation most prominently in the DMN (Hahn et al., 2013). Altered connectivity has been observed in neurodegenerative disorders such as AD (Alves et al., 2019), implicating deficits across networks and affecting multiple systems of processing. Lower white matter integrity underpins visuomotor deficits which have been suggested as a behavioural target for detecting dementia risk. Rogojin et al. (2023) found that visuomotor deficits, measured by participants sliding their finger on a touchscreen from a central starting point to a target on varying planes and directionality, were predictive of early-stage AD development, and therefore suggested that such measures allow for objective identification of

AD. The DMN, previously identified to significantly degrade in the ageing processes, has also been identified for impaired connectivity in AD patients (Ibrahim et al., 2021). This is especially true between the posterior cerebral cortex and the ACC and vmPFC. It has been suggested that lack of activity in the DMN may be a specific biomarker for identifying AD (Sachdev, 2022), where research has reported that network disruptions to the DMN precede structural changes (Hampton et al., 2020), and individuals with high AD biomarkers (i.e. amyloid proteins) experience longitudinal degradation of the default mode and salience networks (Schultz et al., 2020). However, there has also been variability noted in the DMN between individuals suffering from not only AD, but MCI and typically ageing adults (Hampton et al., 2020; Sachdev, 2022).

In summary, research attempts to understand the underlying biological mechanisms in ageing and AD pathology by assessing the visual search and foraging correlates to successful and efficient performance. Ongoing research endeavours to comprehensively unravel the mechanisms that underlie typical and pathological ageing, including visual search behaviours modulated by top-down and bottom-up processing, and executive functions mediating foraging, facilitated by cognitive control. The key aspects of research posit that the crucial difference between younger and older adults is the balance of exploitation verses exploration behaviour, where the argument has been made that this reflected changes in brain networks including the vmPFC, ACC, and the subcortical nuclei of the ventral-tegmental area, specifically the NA (dopamine reward/affect circuit) and LC (noradrenergic attention/salience circuit). These networks are also associated with visual search, and specifically in the integration of top-down and bottom-up processing, which feed into the cognitive control hypothesis of reliance on prior knowledge and allocation of resources. Thus, neurocognitive substrates of visual search and foraging overlap, supported by regions required in cognitive control processes, which therefore describe an integrated system required for large-scale search behaviour.

1.7 Overview of thesis research

This thesis endeavours to elucidate whether large-scale search (as the integration of visual search and foraging behaviours) can act as an early predictor of neurodegenerative processes. Over a series of experiments, the creation, validation, and implementation of a novel, immersive VR search task aims to provide insight into younger and older adult search behaviour in correlation with individual differences of cognition and the natural structure of the brain. *Chapter 3* presents Experiments 1-5, detailing the development and implementation of the large-scale search paradigm in immersive VR on a large cohort of young adults. This is paired with a battery of neuropsychological tests to investigate individual difference. These experimental manipulations help to clarify the cognitive underpinnings of efficient search and exploratory behaviours. *Chapter 4* describes the application of the VR paradigm and cognitive battery, with the addition of structural brain imaging, to elucidate search behaviour in conjunction with neural brain structures on two cohorts: younger adult controls and an older adult cohort. The integration of these methods allows for investigations in the relationship between neurodegenerative signatures and individual differences in foraging-like search across the adult lifespan. *Chapter 5* details a rule shift paradigm following the form of preceding VR manipulations to further investigate the underlying properties of rule shifting, target template creation in a shifting environment, and the subsequent executive control mechanisms that may underpin success. *Chapter 6* describes an exploratory investigation into the Montreal Cognitive Assessment, describing younger and older success (or lack thereof) in the context of visuospatial and executive properties. Finally, *Chapter 7* presents a general discussion of visual search and foraging findings in the context of the literature, experimental methodology, and persistent gaps in knowledge. This thesis ultimately builds a comprehensive image of individual differences in age-related cognitive control in the context of visual search and foraging, with the potential to inform healthcare practice for ageing populations and inspire further scientific and theoretical exploration.

Chapter 2. General Methodology

The University of Plymouth's Faculty of Health ethical review board approved all following research procedures. All participants gave written consent. All the experiments followed the same core protocol and procedure: participants were first asked to describe basic demographics including age, birth date, and level of completed education, and were asked to designate their handedness preferences following the ten-item questionnaire: Edinburgh Handedness Inventory (EHI). Following, participants were then administered the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), completed a search task in immersive VR, followed by a battery of standardised cognitive assessments. Described in the General Methodology are some of the measures applied, beginning with a general description of the behavioural task – manipulations that were specific to each experiment are separately described in their respective chapters. Experiments 1-4 (*Chapter 3*) were preregistered before data collection (Exp 1: https://osf.io/d4prm/ ; Exp 2: https://osf.io/v6jxc/ ; Exp 3: https://osf.io/qgdxn/ ; Exp 4: https://osf.io/jkq9a/).

2.1 Large-scale search task

2.1.1 Apparatus

The large-scale search task was conducted in a large clear laboratory space measuring 5.4m x 6.5m. Participants wore an HTC Vive Pro Eye VR head mounted display (HMD), with a wireless adaptor, to view the environment, and their location was recorded using a Vive tracker worn on a belt around their waist. An HTC Vive Pro controller was used to interact with the environment, and participants held this in their dominant hand. A researcher was present in the room throughout the experimental session, and participant safety was ensured through the chaperone system that presented a boundary grid to participants, within the virtual environment, to warn them if they were within 50cm of the laboratory wall. Unity Professional Software (Version 2021.3.6; Unity Software, 2021) was used to build and design the behavioural task, run through Unity Professional Editor, with the utilisation of SteamVR plugins (Valve Software, 2021). Interactable objects (i.e. cylinders and rectangular prisms; sized in Unity metres: $x = 0.08$, $y = 0.16$, $z = 0.08$) were presented for participants to search (see Figure 2.1). Smooth textures were used on the interactable objects, with Unity in-built shapes and colours utilised; either dark blue (RGB: 10-16-241) or yellow (RGB: 250-217-0). The target was a sphere (size in Unity metres: $x = 0.062$, $y = 0.062$, $z = 0.062$), designed to be undetectable without moving the interactable encompassing it. Upon its first exposure, the target changed from red (RGB: 219-6-0) to grey (RGB: 95-95-95), after which it would remain grey for the remainder of the trial. The patches (sized in Unity metres: $x = 0.6$, $y = 0.55$, $z = 0.6$) were large, raised cylinders (akin to tables), each with an array of interactable objects placed on top. The floor featured a pebble texture that was coloured a lighter grey (RBG: 159-152-152), and the patches were formed of a granite material, located in consistent positions (placed equidistant from the starting point, other patches, and the chaperone wall) throughout the space between participant and trials. Starting location was consistent across all participants and conditions, indicated by a bright green disc (RGB: 0-190-5; sized in Unity metres: $x = 0.5$, $y = 0.01$, $z = 0.5$) that would appear on the floor in the centre of the environment, and participants were required to stand on this in order to progress between and within trials and conditions.

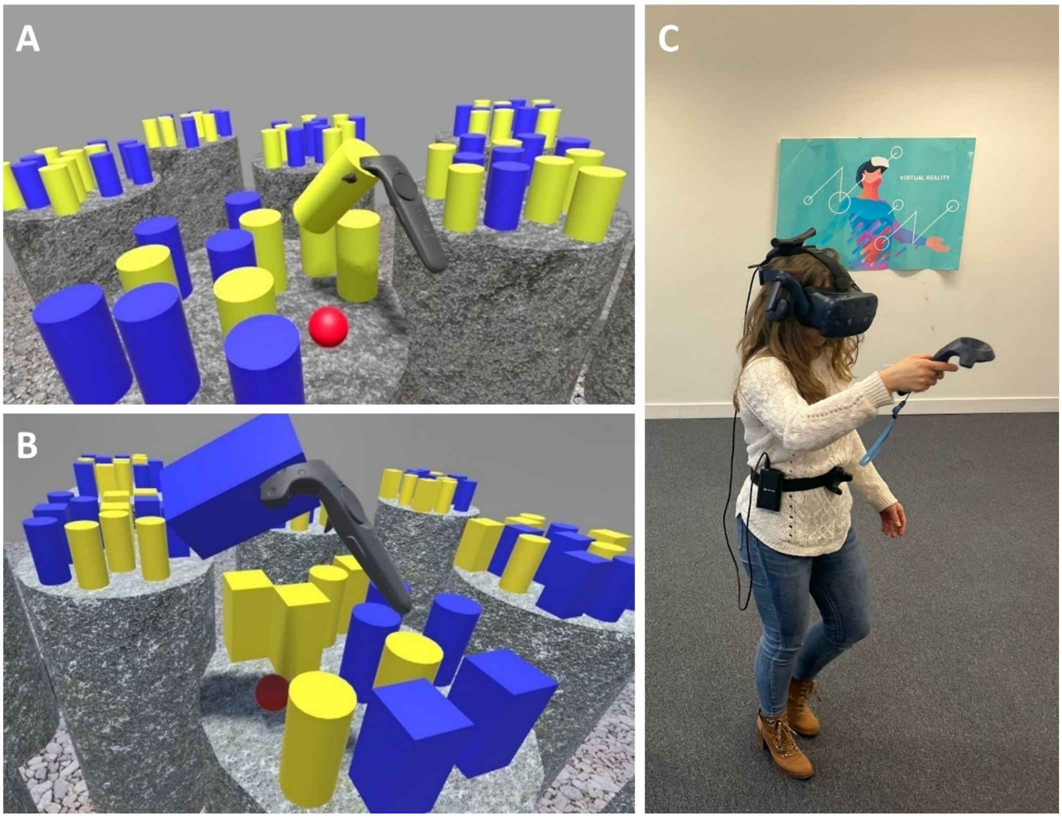

Figure 2.1. Example views of the virtual search environment through the HMD: A) the single feature condition in Experiments 1-4, where cylindrical containers were either yellow or blue; B) conjunction of feature condition in all experimental manipulations (i.e. 1-5) where cylinders and rectangular prisms were defined by either yellow or blue. C) View of experiment location and VR apparatus.

2.1.2 Design

The task itself was a simple three-dimensional analogue of established ‘visual search’ and ‘foraging’ tasks (Hills et al., 2010; Kristjánsson et al., 2022; Louâpre et al., 2010), where participants were required to inspect beneath virtual cylinders and prisms (e.g., “cups” and “boxes”, respectively) in search of targets (e.g., red coloured balls). Participants interacted with the containers by using the controller to lift them – if a container were concealing a target, then the ball would be revealed upon lifting the object. The target would turn from red to grey after 0.9 seconds when discovered – this provided a cue that it had been counted (thus contributing to their total) and served to indicate that a target had already been acquired if participants made a revisit to the same location. Each participant was presented with two conditions, a single feature search and a conjunction of feature search (with the exception of Experiment 7, see *Chapter 5*). In each condition, 24 patches (e.g., "tables"; see Figure 2.2) each displayed 12 interactable objects (12 cups, or 6 cups and 6 boxes) on the top at approximately midriff height (see Figure 2.1).

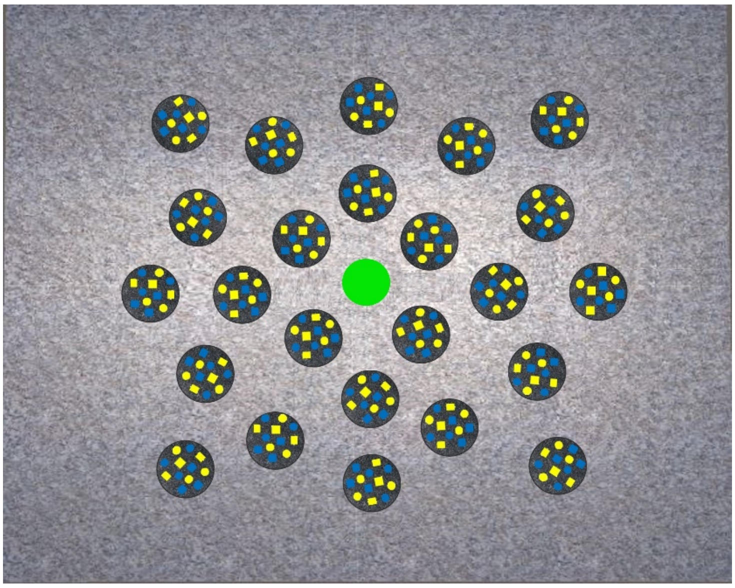

Figure 2.2. Top-down schematic illustrating the layout of patches within the search arena, as well as the search array distributed across patches. This image shows a conjunction array, where target locations were defined according to both colour and form (e.g. blue cups and yellow boxes). The start position for each trial was in the centre of the array, indicated by the green circle.

2.1.3 Procedure

Participants first completed the MoCA with a certified administrator. They were then set-up for the search paradigm (see Figure 2.1c), being guided through belting the tracker onto their waist, securing the battery pack, adjusting the HMD, and using the controller (exclusively with their dominant hand). Once the participant was comfortable in the VR apparatus, the chaperone system was explained and demonstrated. Controller interactions were then verbally explained. Accordingly, participants were instructed to inset the top of the controller into one of the objects, press and hold a trigger on the underside of the controller with their index finger and lift the object to inspect, and release the trigger to return the object to its original location. Objects were set to automatically return to the exact starting location and did not require the participant to place the object after inspection. Instructions to all conditions and trials were provided on the "wall" of the array, where the participant was verbally directed to read the instructions, and written instructions directed the participant to stand on the green disc and press the trigger when they were ready to start the practice; participants had full control when to move onto the practice trial, allowing for variability such as reading speed or comprehension. All participants completed a practice trial before the start of the experiment, this was designed to illustrate the basic search mechanism. Specifically, upon standing on the green disc and pressing the trigger, two tables appeared with 12 interactable objects—the same aforementioned single feature stimuli. Participants were free to test out the interaction and experience walking around in a virtual environment. The practice trial ended automatically where all tables and objects disappeared (timings discussed in their respective experiments). If participants felt uncertain with the interactions, they were offered an additional attempt at the practice trial. If the participant indicated they felt comfortable to continue, they were verbally guided to read the experimental instructions that had appeared on the "wall".

Once the participants were ready, they were instructed to stand on a bright green circle that appeared in the centre of the environment to begin the experimental trials. In the single feature condition, the array was formed of an equal number of yellow and blue cylinders, referred to as 'cups'. Each patch contained six yellow and six blue cups, which were randomly allocated to 12 fixed positions per patch (see Figure 2.1a). Target and distractor colours were counterbalanced between participants. In the conjunction condition the array was formed of both cups and boxes (rectangular prisms), with an equal number of both forms being coloured yellow or blue. Each interactable therefore represented a conjunction of colour and form (i.e., blue cups, yellow cups, blue boxes, and yellow boxes; Figure 2.1b), and they were distributed in the same way as items in the single feature condition. Here, the targets were located under two dichotomous features (i.e., only the yellow cups and blue boxes), which were counterbalanced amongst participants (for similar designs in visual search see: Kristjánsson et al., 2020; Ólafsdóttir et al., 2019).

Each search trial provided participants with 60 seconds to discover as many targets as possible. There was no explicit signal for time or progress during a trial, and when 60s had elapsed the search display (i.e. containers and targets) were extinguished, leaving an empty array of tables. The green disc then appeared in the centre of the array and participants were required to stand on it. They then pressed the trigger to begin the subsequent trial, whereupon the search display reappeared upon the tables. Containers were randomly allocated to table co-ordinates on each trial, whilst maintaining the equal distribution of features on each table. The combination of limited time, the number of hidden targets, and their distribution across the search array meant that it was not physically possible for participants to collect all targets in a trial, thus avoiding ceiling effects in analysis of target acquisition. There were ten search trials per condition, and single feature and conjunction searches were blocked by condition, with order counterbalanced across participants. Participants were made aware that they could take a break at any point between trials, and between conditions, if required.

Upon completion of the virtual task, participants were administered a series of standardised tests on the Cambridge Neuropsychological Test Automated Battery (CANTAB; Fray, Robbins, & Sahakian, 1996), administered via an Apple iPad. The iPad was placed on a tabletop at a 45⁰ angle, and participants used their index finger to interact with the screen. Standardised instructions were administered via the CANTAB application. All participants completed the CANTAB battery in the same order.

2.2 Cognitive tasks

A few tasks from the CANTAB (Fray, Robbins, & Sahakian, 1996) battery were selected on the basis of the cognitive ability they measure, and the hypothesised relationship between those abilities and the efficiency of search and foraging behaviours. The MoCA was selected on the basis of exclusionary criteria (*nb* criteria was deemed inappropriate following preregistration, see section *2.3 Analysis*) and anticipated older adult participation, as an informative measure of cognitive status.

2.2.1 Montreal Cognitive Assessment (MoCA)

The MoCA (version 8.1; Nasreddine et al., 2005) is a widely used screening tool for assessing various cognitive domains, consisting of tasks and questions that evaluate cognitive abilities such as short-term memory, visuospatial skills, executive function, attention, concentration, working memory, verbal fluency and language, and orientation. The MoCA is a singular, one-sided sheet of A4 paper containing all stimuli, where participant cognition is evaluated based on written or drawn responses to stimuli such as clock drawing, cube copying, and alternating trail making. Verbal tasks include picture naming, serial number repetition, verbal fluency, serial subtraction, a vigilance task, sentence repetition, time-place orientation, and list learning short-term and long-term recall. Seated at a table, the participant is required to mark on the MoCA administration sheet for the visuospatial elements (e.g. clock drawing, cube copying), and then the examiner administers the rest of the assessment verbally out of the participant's view. The assessment typically takes around 10 to 15 minutes to administer and provides a total score out of 30. Scoring criteria determines that a total score of 25 or less indicates an abnormal result. Lower education can be accounted for if one has been educated for less than 12 years. This would result in an additional point being added to the total score, still out of 30. The MoCA is further discussed in *Chapter 6.*

2.2.2 Reaction Time (RTI)

The CANTAB RTI measured reaction time and movement time. Participants were presented with five circles in a semi-circle on the top half of the tablet screen, and a singular circle at the bottom. Participants were instructed to hold the bottom button until one of the top circles flashed a yellow colour. Participants, upon seeing the yellow, were required to lift their index finger from the bottom button, tap the circle that flashed yellow, and then return their finger to the original bottom circle. Participants are instructed to react as fast as possible, and outcomes were measured by reaction time and movement time (see Table 2.1).

2.2.3 Intra-Extra Dimensional Set Shift (IED)

This CANTAB task is a measure of executive function, testing rule acquisition and reversal, including set formation, maintenance and shifting. Two artificial dimensions (pink shapes and white lines) were presented on the iPad screen in two of four boxes. Initially, the task utilises simple stimuli (two pink shapes that differ in form) and then as the task progresses, compound stimuli are used (pink shapes overlaid with white lines). Participants had to select between one of two options presented in two of the four boxes (each option contained one or both artificial dimensions, depending on the present difficulty) by tapping on the box that conformed to the unknown rule. Audio feedback was provided to indicate a correct or incorrect response (i.e. a “ding” would play for a correct response, a negatively valanced noise would indicate an incorrect response), and participants were required to work out the rule that determines which stimulus was correct utilising previously correct or incorrect responses. Following six correct responses, the stimuli or rule would change. The rules would either be based on intra- (i.e. pink shapes are the relevant dimension) or extra-dimensionality (i.e. the relevant dimension shifts from the pink shapes to become the white lines), and scores would indicate number of errors made, total trials completed, and latency (see Table 2.1).

2.2.4 Paired Associates Learning (PAL)

CANTAB PAL sensitively measures episodic memory with visual memory and learning contributions. A circle of six boxes containing differing patterns is opened one-by-one in a randomised order on the screen. Once all boxes had been opened, a target pattern was presented in the centre of the screen and participants had to select the correct location of the prompted pattern. One or more boxes would contain a pattern at a time, with increasing difficulty, and if a box was incorrectly selected, all the boxes would be opened in sequence again. This required participants to learn the location of the target(s) in the circle. Success was measured by errors made, the number of trials required to correctly locate the abstract geometric design, memory scores, and the total number of stages completed (see Table 2.1).

2.2.5 Spatial Working Memory (SWM)

The CANTAB SWM task required retention and manipulation of visuospatial information with notable executive demands. Beginning by presenting coloured boxes on the screen, participants were required to search for hidden tokens by tapping each box to either reveal a token or an empty space. Each potential hiding place (e.g. the coloured box) only contained one token and tokens would only be hidden in each place once, requiring participants not to search in the same place twice. There would only be one token to find at a time. The number of hiding places increased over time from four places to search up to twelve, and box location and colour was changed every trial to discourage stereotyped search strategy. Success was measured through errors and strategy (see Table 2.1).

2.2.6 Verbal Paired Associates (VPA)

This CANTAB task is a verbal assessment of associative and episodic memory that requires memorisation of word pairs. Eight word-pairs were auditory presented by the test with differing concrete (e.g. “cat-dog”) and abstract (e.g. “picture-timing”) pairing, and participants were asked to verbally recite which target word was paired with the prompt word. The entire list would be presented up to three times, therefore giving participants up to three attempts to provide the correct response. If all the word pairs were accurately recalled before three attempts, the task would terminate. This also included a short delay recall trial where participants had to respond with the target word following the prompt, without hearing the word-pair list read out again. The DGS (see below) was used as the filler task between the immediate and delay recall, lasting 1-3 minutes depending on performance. This was the suggested filler task as recommended by the CANTAB documentation. Here, VPA errors and number of attempts are considered, as well as a total score that accounted for the difficulty level missed or learnt (see Table 2.1).

2.2.7 Digit Span (DGS)

CANTAB DGS was primarily selected to serve as a filler task between immediate and delay trials of the VPA. But also, it has been suggested that relationships between visual search and attention are mediated by working memory (Soto & Humphreys, 2007) and therefore DGS was used to measure verbal working memory with a forward digit span. Via an audio file of spoken words, a sequence of digits was presented, and the participant would immediately be prompted to recall the digits aloud in the same sequential order as presented. The test presented increasingly longer sequences until the participant responded incorrectly on three occasions at that span length. Therefore, the longest sequence passed represents the participant’s score (see Table 2.1).

Table 2.1. Description of CANTAB tasks and selected measures.

CANTAB task	Measure name	Measure description
RTI	RTIFES	RTI Total Error Score: The total number of trials where the subject made any form of response error.
	RTIFMMT	RTI Mean Movement Time: The mean time taken for a subject to release the response button and select the target stimulus after it flashed yellow on screen.
	RTIFMRT	RTI Mean Reaction Time: The mean duration it took for a subject to release the response button after the presentation of a target stimulus.
IED	IEDEEDS	IED EDS Errors: The number of times that the subject failed to select the stimulus compatible with the current rule on the stage where the extra-dimensional shift occurs. Lower is better. This is a measure of the subject's ability to shift attentional set.
	IEDYERTA	IED Total Errors (Adjusted): The total number of times that the subject chose a wrong stimulus (i.e. one incompatible with the current rule, adjustment for every stage that was not reached.) Lower is better. This measures of the subject's efficiency in attempting the test. Subjects failing at any stage of the test will have had less opportunity to make errors. The adjustment is carried out to compensate for this missing data and provide a more comparable error score to subjects completing all stages of the test.
	IEDTL	IED Total Latency: The sum of the subject's response times (in milliseconds) over all trials excluding the first two trials of Stage 1. The response time for a single trial is measured from the appearance of the stimuli, up to the time where the subject made their final choice for that trial.
	IEDTT	IED Total Trials: The number of trials completed on all attempted stages. Lower is better.
	IEDTTA	IED Total Trials (Adjusted): The number of trials completed on all attempted stages with an adjustment for any stages not reached. Lower is better. Subjects failing at any stage of the test will have had less opportunity to make choices (correct and erroneous). The adjustment is carried out to compensate for this missing data and provide a more comparable error score to subjects completing all stages of the test.
PAL	PALFAMS	PAL First Attempt Memory Score: The number of times a subject chose the correct box on their first attempt when recalling the pattern locations. Calculated across assessed trials.
	PALNPR	PAL Number of Patterns Reached: The number of patterns presented to the subject on the last problem they reached.
	PALTE	PAL Total Errors: The total number of times a subject selected an incorrect box when attempting to recall a pattern location. Calculated across all assessed trials.
	PALTEA	PAL Total Errors (Adjusted): The number of times the subject chose the incorrect box for a stimulus on assessment problems (PALTE), plus an adjustment for the estimated number of errors they would have made on any problems, attempts, and recalls they did not reach. This measure allows one to compare performance on errors made across all subjects regardless of those who terminated early versus those completing the final stage of the task.
SWM	SWMBE	SWM Between Errors: The number of times the subject incorrectly revisits a box in which a token has previously been found. Calculated across all assessed four, six and eight token trials.
	SWMDE	SWM Double Errors: The number of times a subject commits an error that is both a within error and a between error. Calculated across all assessed four, six and eight token trials.

	SWMS	SWM Strategy (6-8 boxes): The number of times a subject begins a new search pattern from the same box they started with previously. If they always begin a search from the same starting point, we infer that the subject is employing a planned strategy for finding the tokens. Therefore, a low score indicates high strategy use (1 = they always begin the search from the same box), a high score indicates that they are beginning their searches from many different boxes. Calculated across assessed trials with 6 tokens or 8 tokens.
	SWMTE	SWM Total Errors: The total number of times a box is selected that is certain not to contain a token and therefore should not have been visited by the subject, i.e. between errors + within errors - double errors. Calculated across all assessed four, six and eight token trials.
	SWMWE	SWM Within Errors: The number of times a subject revisits a box already shown to be empty during the same search. Calculated across all assessed four, six and eight token trials.
VPA	VPAERSDR	VPA Delayed Recall Total Errors: The total number of errors made by a subject when recalling word pairs during the delayed recall phase.
	VPAMWDSD	VPA Delayed Recall Total Model Weighted Difficulty Score: The sum of difficulty values of the trials presented and scored as correct during the delayed recall phase.
	VPAERTOT	VPA Total Errors: The total number of errors made when recalling the word pairs across all attempts made by the subject.
	VPAMWDST	VPA Total Model Weighted Difficulty Score: The sum of difficulty values of the trials presented and scored as correct across all attempts made by the subject.
DGS	DGSFMAXP	DGS Maximum Span Passed Forwards: The longest sequence problem successfully reached and passed by the subject.

2.2.8 Edinburgh Handedness Inventory (EHI)

Participants were administered the EHI (Oldfield, 1971) as a finer-grained quantification of handedness preference, as laterality has been previously associated with search efficiency (Smith et al., 2005). The EHI describes a series of ten questions probing the hand preference of ten everyday tasks (e.g. “writing”, “scissors”, “upper hand of broom”, etc). The Laterality Quotient (Schachter, 2000) quantifies handedness preference for each item based on responses ranging from “always left hand” to “always right hand”. Responses are coded as such: “always left hand” is scored -10, “usually left hand” scores -5, no preference receives a score of 0, “usually right hand” is scored at +5, and “always right hand” scores +10. This allows for a value to be created ranging from -100 to +100 by summing the participant’s selection across the ten responses, thereby creating a quotient of handedness rather than a dichotomous selection. This is suggested to be sensitive to the degree and direction of handedness (Schachter, 2000).

2.3 Analysis

Search performance was analysed on the basis of participant success (number of targets acquired), total inspections (total number of objects searched, cued and uncued), the percentage of cued objects inspected (percentage of objects searched that contained a target; referred to henceforth as percentage cued), and the number of tables visited (patch visits), with each variable being separately calculated across single feature and conjunction trials. Foraging-like properties of search were analysed in terms of organisation and patch-leaving (i.e. exploration) behaviours. In addition to pre-registered analyses, search organisation was measured using the best-*r* method, and this was calculated for both within-patch (the sequence in which each object was inspected within each patch) and between-patch (the order in which patches were inspected). Woods et al. (2013) suggested that highly organised foraging behaviours, in multi-target arrays, find that healthy adults systematically search by columns or row with generally horizontal or radial movement. Therefore, Woods and colleagues (2013) suggested that an additional way to measure organised—or systematic—foraging was to calculate best-*r*. Within a two-dimensional paradigm, Pearson's correlation coefficient *r* can be derived from a linear regression by calculating the *r*-value for x- and y-values independently (representing horizontal or vertical foraging). All the x-values of inspected locations, relative to the order they were inspected, creates the x-value Pearson's correlation—the same can be done for the y-axis values. From the two *r* calculations (linear regression for both x- and y- coordinates), a selection is made for the highest, or 'best', *r*-value to represent the search. Since search locations in the present study occupied the same height along the y-axis (lifting the cups to inspect), best-*r* was measured along the x- and z-coordinates (participant left-right, forward-back movement). Research using best-*r* (e.g. Kristjánsson et al., 2022; Woods et al., 2013) has predominantly been focussed in two-dimensional environments. Consequently, factors such as the addition of physical movement in three-dimensional spaces may influence best-*r* results; idiothetic search and foraging behaviours in three dimensions are inherently more complex than in two dimensions. There could be concern that best-*r* may not adequately reflect poor organisation in these scenarios, as it assumes a linear path, which is not always the case in three-dimensional searches, especially in patchy environments. For example, as illustrated in Figure 2.2, the starting location in Experiments 1-6 was centred within the array, potentially limiting the sensitivity of the best-*r* measure to detect organised movement. Participants may not exhibit unorganised movement, but they also may not follow a systematic pattern (e.g. starting from the top-left and moving horizontally or vertically, row by row). Factors such as these may obscure the nuances of search strategy. However, best-*r* has been shown as a good measure of search organisation, and in three dimensions, best-*r* provides a metric of systematicity and organisation that can accommodate equal and unequal target distribution whilst distinguishing between within- and between- patch behaviour.

Further measures to quantify foraging behaviour included a derived measure termed ‘exploitation’, aimed to quantify the complexity underpinning exploratory behaviour whilst assuming foragers do not understand optimal profitability, which measures such as the MVT lack (Chin et al., 2015; Fougnie et al., 2015). Exploitation assessed cued inspections before a switch was made to search a different patch, which was quantified to assess exploitation or exploration tendency across manipulations. Specifically, a value was derived by finding the total number of cued inspections per patch divided by the number of patches inspected, divided by six (the number of total possible cued objects) and multiplied by 100 to convert into a percentage of exploitation. For example, if a participant exploited 50% of the patch, they would have inspected three of six cued cups/boxes before moving onto the next patch. Finally, revisits to previously inspected objects and patches were also quantified. Revisits were determined by counting the number of times a participant revisits either a previously inspected item or patch, divided by the total number of inspections, and multiplied by 100 to get a percentage of revisits. Each of the above variables are reported in each experiment by trial success, where reported means would indicate the mean number of targets collected per trial, for example.

Pre-processing of data was undertaken using R-Studio version 4.2.1 (2022), and analyses were conducted using IBM SPSS Statistics (Version 28). Within subjects t-tests were conducted on performance-related dependent variables, Pearson's correlations were used to identify significant relationships between behavioural variables from the large-scale search task and cognitive performance, and best-*r* assessed the organisation of search behaviours, both within- and between- patches. ANOVAs were conducted to assess significance across manipulation and between participant groups. Specific analyses undertaken are detailed in each chapter.

Chapter 3. Experiments 1-5

3.1 Introduction

Treisman and Gelade’s (1980) Feature Integration Theory of visual attention distinguishes between targets defined by a single feature, which are automatically detected through parallel processing, and those defined by a conjunction of features, requiring focussed serial inspection. This distinction between simple and effortful search typifies theoretical accounts challenging Feature Integration Theory (e.g. Bundesen et al., 2005; Duncan & Humphreys, 1989; Wolfe, 2007). Accordingly, it is generally understood that searching for a target defined by a conjunction of features requires greater demand on attentional processing than search for a single feature (Kristjánsson & Egeth, 2020; Trick & Enns, 1998). The mechanisms underlying human search have, therefore, been established in two dimensions, with participants typically being sat before a computer monitor. In contrast, large-scale search in three dimensions has primarily been studied in the context of foraging (Schöberl et al., 2020; Wiegand et al., 2019), can also be defined more broadly in terms of seeking and using environmental information to obtain reward (e.g. Pirolli & Card, 1999; Rosati, 2017), where psychologists have recently begun exploring this relationship more explicitly. ‘Hybrid' paradigms attempt to capture real-world search factors but are mainly limited to two-dimensional displays. Few studies have required participants to physically explore large three-dimensional spaces in search tasks, and findings regarding the similarity of search phenomena in large-scale tasks remain equivocal (e.g. Baxter & Smith, 2022; Jiang et al., 2014; Pellicano et al., 2011; Smith et al., 2010), although greater variability between participants in large-scale search tasks has been noted (Baxter & Smith, 2022), suggesting behaviour is moderated by individual difference. Smith et al. (2008) extended visual search mechanisms to large-scale space, revealing that environmental search complexity depends on guiding perceptual features. But, the paradigm did not address the factors that may have guided foraging behaviour.

Kosovicheva et al. (2020) summarise efforts to integrate understanding of search and foraging processes, noting a relative lack of knowledge about the visual search processes guiding one's ability to explore and forage their environment. The present chapter details a novel immersive VR paradigm that was devised to address this question by requiring participants to physically forage a three-dimensional environment for targets that were defined by a single feature or a conjunction of features. There were multiple targets in each trial, and participants were tasked with collecting as many of them as they could within a limited time frame, thus incorporating a decision-making component related to resource allocation to the task. The potential for visual features to modulate search strategy, as well as search success, was examined by constructing multiple patches that each contained a number of different search locations. By this token, it was possible to not only examine how participants optimised their search by prioritising search locations according to their visual features, but also assess the rate at which participants chose to exploit the patch that they were currently searching within and when they chose to explore in favour of an alternative patch.

In addition to the behavioural assessment of search and foraging decisions, the contribution of cognitive processes to search performance was also examined. The role of cognitive control was particularly focussed on, which is thought to connect conventionally disparate cognitive domains, providing a domain-general underpinning for all forms of exploratory behaviour (Mata & von Helversen, 2015). Individual differences in cognitive control have also been shown to predict switching behaviour in search, where poorer cognitive abilities are associated with a reduction in explore decisions (Chin et al., 2015;

Mata & von Helversen, 2015). As such, the variability in cognitive control processes was examined, possibly explaining differences in search behaviour, which one would predict should be evident in both sensitivity to visually-guided components of search as well as the rate of switching between patches of search locations (e.g. Han & Kim, 2009; Hills et al., 2013; Ruddle & Lessels, 2006). Measures of learning and memory were also administered to participants as working memory capacity has previously been associated with performance in effortful search (Gratton et al., 2018).

In a series of experiments, participants engaged in a visually guided foraging task, interacting with virtual containers with an aim to acquire as many hidden target items as possible. Each experiment manipulated the visual features that participants could use to guide their search – in one condition target locations (i.e., the containers) were defined by a single feature (colour) and in another they were defined by a conjunction of features (colour and shape). The core prediction was that search defined by a single feature would be more successful (i.e., participants would acquire more targets within a time-limited trial) than conjunction search. Across experiments, information made available to participants was manipulated to assess how they learned about the environment through their exploration. In traditional visual search tasks, participants are provided with a search 'template' (Treisman & Gelade, 1980) by the experimenter, in the form of instructions that specify the features of the target that they are required to detect (which is then thought to be maintained in memory). In Experiments 1 and 2, participants were provided with a search template at the beginning of each condition, but instructions were not provided in Experiments 3 and 4. On the basis of the additional cognitive resources required to undertake conjunction searches (Eckstein, 2011; Smith & De Lillo, 2022) it was predicted that the presence of a search template would interact with the nature of the visual cues available, such that single feature searches would be performed similarly, irrespective of instruction, whereas conjunction searches would be performed less efficiently when participants were required to learn this information themselves. To further incorporate features of search that are closer to foraging for resources, the density of hidden targets was manipulated – in Experiments 1 and 3, each cued location (i.e. the locations that possessed the visual features that were predictive of targets) contained a target, whilst in Experiments 2 and 4, a smaller proportion of containers revealed a target upon interaction. Search was expected to be more efficient in the equally distributed experiments than in the unequal experiments, irrespective of the number of targets acquired, and explore decisions (i.e. switches to a new patch of containers) were expected to be more frequent in the unequal experiments. A final control experiment (Experiment 5) was included to equate the perceptual information presented to participants in single feature and conjunction conditions.

Therefore, the explicit (i.e. search template) and statistical (i.e. target density) information available to participants was manipulated – on the basis of classic visual search paradigms, performance was expected to be affected by such information, and yet theories that discuss the additional forms of information available to foragers, as well as one's ability to learn about environmental economics through exploration, suggest that visual information may not necessarily play an important role. As real space navigation of the environment relies on simultaneous processing across multiple signals including visual, motor, vestibular and kinaesthetic (Scholberl et al., 2020), and if strategy is also informed by idiothetic information (e.g. Gilchrist et al., 2001; Ruddle & Lessels, 2006) then additional cues to successful search and foraging may be derived from one physically moving and interacting within the space. Across all the presented experiments, search performance was expected to be positively related to participant cognitive profiles. Specifically, it was predicted that individuals with greater cognitive control abilities would adopt more optimal search strategies (i.e. targets collected, number of inspections, cued inspections, patches visited), in line with the prediction that executive control processes have their roots in domain general foraging-like decisions.

3.2 General Methods

3.2.1 Participants

The first three iterations (Experiments 1-3) of this chapter were initially devised as a series. An initial power analysis using G*Power (version 3.1.9.5) and based on a 95% chance of detecting a medium effect size (F test: Repeated measures, within-between interaction) specified 57 participants across the three experiments with two conditions (i.e. single feature, conjunction of feature). Therefore, to create equal number of participants between the three experimental conditions, the total number of participants was increased to N = 60 (N = 20 per experimental condition). However, following successful completion of Experiments 1-3, Experiments 4 and 5 were included as extensions. Follow-up experiments reported here followed the same sample size (N = 20). It is important to note that this study was designed and powered to examine the primary search and foraging behavioural measures. Consequently, any analyses related to individual differences were underpowered yet exploratory in nature, as the study was not specifically powered to detect effects in these secondary measures. Participants were compensated for their time and either paid at the rate of £10 per hour or given participation points (a form of course credit administered at a rate of two points per hour).

As introduced in *section 2.2*, the pre-registered reports stated that exclusionary criteria were based on the Montreal Cognitive Screen (MoCA) and Reaction Time task (RTI; CANTAB) results, as these would indicate lower attention or effort to the task. However, it was later realised that these were inappropriate exclusionary criteria, and therefore participants who did not perform as expected were still included. Firstly, the MoCA results, in the present chapter, identified that 31.3% of participants failed the examination (scoring 25 points or below, with total possible score of 30; Nasreddine et al., 2005), despite being current undergraduate students. However, it was reflected upon that following the standardised normative cut-off to decide eligibility would inaccurately represent failure to attend as the MoCA is not normalised for adults outside the age range of 55-85 (Nasreddine et al., 2005). Further, considering the attentional measures included in the MoCA (five digits forward, three digits backward; tapping on letter 'A'; serial 7's), no participant failed the section, indicating an appropriate level of attention given to the task. Secondly, as misunderstood at the time of preregistration, the CANTAB does not provide normative results for the RTI task, and therefore it was impossible to identify a level of effort or success, or a cut-off point, based on individualised performance. As such, no participants were excluded and any participant that did not complete all detailed tasks and assessments was replaced.

3.2.2 Design and procedure

Sessions lasted approximately 90 minutes. As described in *Chapter 2. General Methodology*, participants were administered demographics, EHI, MoCA, the VR paradigm, and CANTAB battery. The VR task was as described; the large-scale task required participants to inspect beneath cups and boxes in search of targets. Each participant was presented with the single feature and conjunction search, where the featural cues are described in the respective manipulation below. Experiments were manipulated by target distribution and whether a template was provided. All participants completed a 30-second practice trial before the start of the experiment, this was designed to illustrate the basic search mechanism. After 30s, the practice trial ended automatically where all tables and objects disappeared. If participants felt uncertain with the interactions, they were offered an additional attempt at the practice trial. Most participants did not require a second presentation, although some did take advantage of the opportunity. Each search trial provided participants with 60s to discover as many targets as possible. Participants could take a break at any point between trials, and between conditions, if required. However, all participants chose to run through the experiment with few pauses, the longest lasting less than 10s. Then, all participants underwent the CANTAB assessment, as outlined in the *General Methods* section. The battery was consistent for all participants, and the tasks were administered in the same sequence as described.

3.2.3 Analysis

Behavioural variables are described in *Chapter 2. General Methodology.* Search performance was analysed based on the number of targets collected acquired), total inspections (cued and uncued), the percentage of cued objects inspected, and the number of patches visited, with each variable having results for single feature and conjunction trials. Foraging variables were analysed in terms of within-patch and between-patch search organisation, quantified by best-*r*. Exploitation measured cued inspections before a switch, quantified to assess exploitation or exploration behaviour across manipulations. Revisits to previously inspected objects and patches were also measured. It was determined that the percentage of revisits to previously inspected objects across all trials were very low (single feature: M = 2.8%, SD = 2%; conjunction: M = 3.3%, SD = 2.6%) and therefore were not indicative of foraging behaviour success, however revisits to patches across all trials were much higher (single feature: M = 23.6%, SD = 20.4%; conjunction: M = 29.3%, SD = 28.7%), and therefore were analysed and interpreted.

Within subjects t-tests were conducted on performance-related dependent variables, Pearson's correlations were used to identify significant relationships between behavioural variables from the large-scale search task and cognitive performance, and best-*r* assessed the organisation of search behaviours, both within- and between- patches. Additional analyses are detailed in their respective experiments.

External variables

To verify that an effect was not present due to participant demographics or counterbalancing, tests of between-subjects effects (obtained from between-subjects, one-way ANOVA) were conducted to compare counterbalancing conditions, age, gender, handedness, and level of education. One dependent variable, the number of targets found, was selected to compare for effects, run for both the single feature and conjunction of feature conditions. For the single feature, and conjunction of feature conditions, respectively, for each independent variable, no effects were found for counterbalancing ($p = .839$; $p = .221$), age ($p = .985$; $p = .964$), gender ($p = .18$; $p = .291$), level of education ($p = .397$; $p = .405$), or handedness (EHI; $p = .44$; $p = .825$).

3.3 Experiment 1

Two-dimensional visual search tasks are considered as simple and controlled models of naturalistic three-dimensional foraging behaviour (e.g., Klein & MacInnes, 1999; Wolfe, 1994), but this has yet to be explicitly explored. Existing hybrid search and stationary three-dimensional paradigms have been helpful in beginning to understand the relationship between such behaviours, however fully motile VR provides greater information underpinning the relationship between search and foraging behaviours (Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020). Experiment 1 provided a large-scale space for participants to physically explore. This aimed to first examine visual search properties by manipulating the cueing of one or more visual features in a single feature verses conjunction of feature search. This was anticipated to illuminate the effects of single or multiple features in search success on target acquisition. The second aspect was to integrate foraging behaviours such as the exploration-exploitation trade-off and movement throughout a patchy environment, allowing investigations into how foraging decisions impact visual guidance. Thus, akin to a classic visual search task, targets were hidden under objects either defined by a single feature or a conjunction of features. With equal distribution, targets would always be present under the cued objects, and participants were explicitly told where to search. It was anticipated that participants would be more successful in the easier (single feature) search (i.e. more targets collected, greater cued inspections). Foraging behaviour was expected to reflect a balance between exploration and exploitation, with greater search organisation and fewer revisits in the single feature condition.

3.3.1 Methods

Participants

Twenty participants were collected (female: N = 14, male: N = 6; age 18-34 years, M = 21.15, SD = 3.7) through the University of Plymouth's participant recruitment system, and they received either course credits or money (at a standard rate of £10/hour) for taking part.

Design

In an immersive VR environment, participants interacted with an array of containers in search of multiple targets (red balls). In the single feature condition, containers were either yellow or blue cylinders (referred to as cups; see *Chapter 2, Figure 2.1a*), and targets were hidden beneath all containers of the cued colour. In the conjunction conditions, interactables comprised of cylinders and square prisms (cups and boxes), of which there were yellow and blue of each form. Targets were hidden beneath two different conjunctions of these items (e.g. blue boxes and yellow cups; see *Chapter 2, Figure 2.1b*). In both conditions, participants were instructed that the targets were only hidden beneath the cued items.

Procedure

Sessions followed the procedure specified in *Chapter 2. General Methodology*. Prior to the practice trials, the instructions read "*Welcome! Please find all of the hidden red balls by searching under cups. You can search by placing the controller in the cup, holding down the trigger, and lifting the controller up. Once you find a red ball, it will change colour to Grey. If you find a grey ball, it means you have already searched under that particular cup. Try not to search in the same place twice. Please search as efficiently as you can. This Practice will end automatically. When you are ready to begin the Practice, please stand on the Green disc and press the trigger*." At the end of the practice trial, the experimenter verbally verified whether the participant felt comfortable with the interactions. Upon confirmation, the participant was verbally directed to read the next set of instructions and once ready, they were free to proceed with the task. The task instructions read (with alternatives in square brackets): "*Well done, you have completed the Practice Trial. You will now complete a series of trials. Each time, your task is to find as many hidden Red balls as possible. The Red balls will only be hidden under the Yellow cups* [blue cups]*, and never the Blue cups* [yellow cups]. *The balls change colour when found, so if you find a grey ball you have already searched there. You will have 60 seconds to complete each trial. Please ensure you keep the controller in the hand you started the task with. There is a break between each trial. When you are ready to begin every new trial, please stand on the Green disc and press the trigger. Remember to search as efficiently as you can. To begin the experiment, please stand on the Green disc and press the trigger.*" In the conjunction condition, the instructions were identical with the exception of the location of the target, which specified: "*The Red ball will only be hidden under the Yellow cups and Blue boxes* [blue cups and yellow boxes]*, and never the Blue cups and Yellow boxes* [yellow cups and blue boxes]*.".*

3.3.2 Results

Search behaviour

On average, participants successfully collected more targets in the single feature (M = 60.77, SD = 23.57) compared to the conjunction condition (M = 34.79, SD = 16.59; *t*(19) = 5.68, *p* < .001, *d* = 1.27). A greater percentage of total inspections was directed to the cued objects in the single feature condition (M = 97.81%, SD = 2.37%) than in the conjunction condition (M = 88.54%, SD = 14.24%; *t*(19) = 2.7, *p* = .014, *d* = .61; see Figure 3.1a). The percentage of cued inspections may be subject to ceiling effects, where a significant number of participants achieved scores near 100% success rate. This can distort the results of t-tests by reducing variability and potentially masking true differences between groups. To check for ceiling effects, a Shapiro-Wilk Test of Normality was conducted, revealing deviation from normal distribution across both conditions (single feature: *p* < .001; conjunction: *p* < .001), and therefore Wilcoxon Signed-Ranks Test was used as it compares two related groups without assuming normality. This revealed that participants made significantly more cued inspections in the single feature condition (Z = -3.85, *p* < .001) than conjunction condition. Participants made a greater average number of total inspections in the single feature condition (M = 63.5, SD = 23.81) compared to the conjunction condition (M = 40.10, SD = 16.49; *t*(19) = 5.58, *p* < .001, *d* = 1.25). Participants also visited significantly more patches in the single feature condition (M = 10.58, SD = 3.65) than in the conjunction condition (M = 7.86, SD = 2.40; *t*(19) = 3.28, *p* = .004, *d* = .73).

Foraging strategy

The best-*r* measure indicated that there was greater between-patch search organisation in the conjunction foraging condition (M = .65, SD = .07), compared to single feature search (M = .53, SD = .11; *t*(19) = -4.45, *p* < .001, *d*= -.99), although within-patch organisation did not differ between conditions (single feature: M = .37, SD = .12; conjunction: M = .39, SD =

.12; *t*(19) = -.41, *p* = .68, *d* = -.09). Participants were significantly more exploitative in single feature search (M = 79.28%, SD = 15.94%) than conjunction (M = 58.74%, SD = 16.66%; *t*(19) = 6.61, *p* < .001, *d* = 1.48; see Figure 3.1b). Participants did not differ in percentage of patch revisits between the two conditions (singe feature: M = 2.59%, SD = 2.48%; conjunction: M = 2.98%, SD = 2.94%; *t*(19) = -.60, *p* = .56, *d* = -.13).

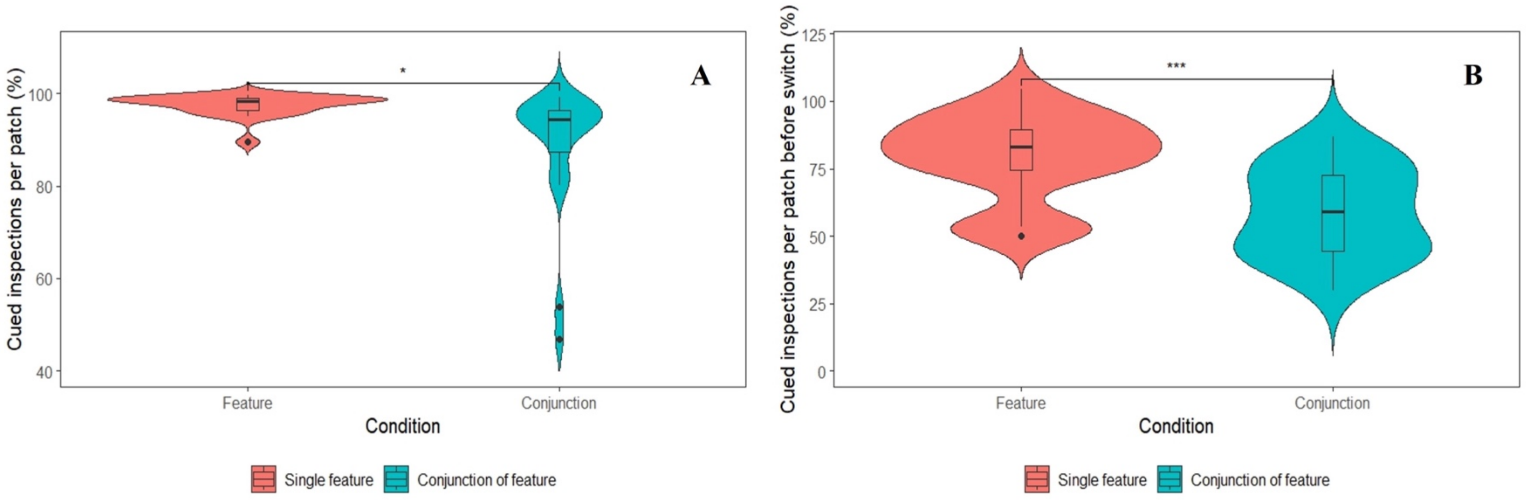

Figure 3.1. Violin plots describing the A) percentage of cued inspections per patch (search variable) and B) before a switch (exploitation; foraging variable) between single feature and conjunction conditions. Note: the scaling in A has been adjusted to better illustrate the clustered responses. Boxplots are included to summarise the data; the lower box represents first quartile of responses and upper box represents third quartile. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by ***.

Individual differences

Pearson’s correlations (see Appendix A: Tables A1, A2, A3) revealed that in the single feature condition, only foraging variables were predicted by individual difference. Participants with a spatial working memory strategy that varied in start location (SWMS) were more likely to show exploitative preferences although were less likely to revisit previously inspected patches. In the conjunction condition, participants with greater within-patch search organisation were more likely to show spatial working memory revisit errors, and spatial working memory errors were associated with lower exploitative behaviours. The percentage of cued inspections was associated with multiple areas of cognition: episodic memory, verbal and working memory including verbal memory delay, and spatial working memory, where overall more cued inspections were associated with greater cognitive ability across a several domains.

3.3.3 Discussion

Experiment 1 revealed that when participants searched for hidden targets, they were more successful when the target was defined by a single feature search than by conjunction of features. It has long been suggested that single feature search is easier, or requires less effort, than conjunction search (Smith & De Lillo, 2022). These findings are consistent with existing theories of visually guided search (e.g. Smith & De Lillo, 2022; Treisman & Gelade, 1980), indicating that search is guided by visual features, and differences between single feature (simple) and conjunction of feature (effortful) search were observed. Large-scale search seems to be influenced by visual search manipulations in a manner consistent with two-dimensional visual search, indicating broad domain-general functioning of visual guidance. This is despite the fact that not all findings from traditional visual search tasks translate directly to fully motile searches, and that previous work suggests less emphasis on visual cues in large-scale environments (e.g. Ruddle & Lessels, 2006).

Measures of foraging-like behaviour revealed that participants were more organised when searching between patches in the conjunction condition than single feature, however participants did not differ in within-patch organisation. As participants were told explicitly where the target was located, this would reduce the need to organise within-patch due to strategy provision instead of a self-derived strategy. Eckstein (2011) suggested that search performance can be mediated by provided information and the utilisation of such information therefore represents an optimised search strategy. By explicitly providing the target location, this reduced the need for participants to organise within-patch but would still require participants to organise their between-patch search, as was found, but with greater conjunction organisation than single feature. Greater organisation in the conjunction condition does not follow the literature, where previous results have shown that participants were less organised in inter-item conjunction searching (e.g. Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2021), however Ólafsdóttir et al.'s (2021) stimuli was not organised in patches and resided two-dimensionally for participants to select targets on an iPad screen. There is a possibility that findings reflect, due to the complexity of the conjunction array, a requirement for participants to implement greater strategy to their movements around the space as they organise their between-patch search in order to collect as many targets as possible. Thornton, Nguyen, and Kristjánsson (2022) identified greater switching behaviours between features when conjunction searching, which would allow participants to prioritise spatial efficiency over minimising time as a strategy.

Additionally, participants were significantly more exploitative in the single feature search. The difference in strategy was directly informed by exploitative behaviour because participants were more likely to leave a patch before finding all targets in the conjunction condition. As one might recall, exploitation represents the average number of cued inspections in one patch before moving onto the next. Exploitation was the ideal strategy, which clearly has interacted with effort. When presented with the target location, or when collection rate matches expectations, optimality would be suggested to be fully exploitative within a patch to gain the most targets with the least amount of movement and energy expenditure (Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020). If search is more difficult (i.e.

conjunction of feature conditions) then perhaps one is more likely to move on, even though the optimal strategy to exploit remains the same. Attention is split across features and targets differently, and that seems to drive a different form of organisation. However, what is less understood is how the contribution of foraging decisions may become more important when the distribution is unequal in a large-scale environment where targets are not always reliably associated with their cues.

Participants showed very little individual difference in the single feature condition, only aspects of spatial working memory were indicative of search success. Spatial working memory, alongside working memory, verbal memory, and episodic memory were all additional predictors of success in the conjunction condition, where cognitive underpinnings are clearly relied upon to support conjunction of feature search in a way that is not required for single feature (or less effortful search). The relationship between visual search and working memory is well established visual search tasks (e.g. Smith & De Lillo, 2022) where working memory abilities have been suggested to explain variations in search ability, especially when one is required to detect and learn new environments. Group differences have been identified in conjunction conditions exclusively when comparing spatial working memory performance between single and conjunction of feature conditions (Takahashi & Hatakeyama, 2011), signifying that spatial working memory contributes to conjunction-specific visual search success. Presently, spatial working memory contributed to more cued inspections, greater organisation, and more exploratory behaviour with additional measures of cognition supporting cued inspections. Therefore, conjunction searching requires greater cognitive contributions and reliable variations point to additional abilities that may underpin performance.

The two-dimensional foraging literature has evaluated factors such as the value of reward and target distribution (Wolfe, Cain, & Alaoui-Soce, 2018), where reward drives exploration supported by individual difference: some foragers were motivated by reward to guide search, but others were guided by proximity and priming. As target distribution influences search patterns (Smith & De Lillo, 2022), trade-offs between search efficiency and patch diversity guide behaviour, mediated by individually derived benefits from memory capacity (Nauta, Khaluf, & Simoens, 2020). But how such decisions are made, when faced with unequal distribution in a large-scale environment, has yet to be explored. Experiment 2 therefore aimed to investigate the underpinned mechanisms of unequally distributed arrays when visual search properties remained constant. The implemented search task was similar to Experiment 1 where clear instructions defined target location, but within an unequally distributed array, anticipated to provide further information about the contribution of foraging-like decision-making.

3.4 Experiment 2

Foraging literature suggests that the distribution of targets affects how one searches (e.g. Cain et al., 2012) but the decision-making processes underpinning such behaviours when guided by visual cues are presently underexplored. Therefore, Experiment 2 followed a similar paradigm to that of Experiment 1, where participants were explicitly told where to search in single feature and conjunction of feature displays, however there were not always targets present under the cued objects (unequal distribution). It was expected that properties of visual search would be similarly represented to that of Experiment 1, whereby measures such as targets collected, and inspections will be greater in single feature than conjunction of feature searches. It was also anticipated the distribution would affect foraging measures and decision-making such that exploratory behaviours would increase, and participants would show greater organisation within- and between- patches in conjunction conditions.

3.4.1 Methods

Participants

Twenty participants (female: N = 13, male: N = 7; age 19-29, M = 20.95, SD = 2.63) were recruited through the participant recruitment system for course credit or equivalent monetary payment as described in the *General Methods*.

Design and procedure

In Experiment 1 each cued item concealed a target. However, in Experiment 2 the number of targets within each patch, and the location of the item beneath which they were concealed, were randomly determined. Randomisation was constrained so that no patch could contain zero targets, but patches could otherwise contain between 1 and 6 targets. To create relative equivalence between participants, the number of targets in the first patch was selected from a range of numbers between 1 and 6 (e.g. 3 targets in patch one). Therefore, patch two could only contain 1, 2, 4, 5, or 6 targets. This continued until all numbers in the range had been utilised, and then the range restarted, until all 24 patches had been allocated. Thus, not all participants would receive the same number of targets, however the distribution was relatively stable across participants. In the single feature condition, on average and across all participants, participants received 4.34 targets per table (SD = .22; range = 4.34 – 5.27 targets). Similarly, in the conjunction condition, on average and across all participants, participants had 4.86 targets per table (SD = .33; range = 4.19 – 5.43 targets). All other aspects of the design and procedure were identical to Experiment 1 – as such, the instructions for the search task stated only that the targets would always be found beneath cued items and never uncued items, with no mention that not all cued items concealed a target (exactly as in Experiment 1).

3.4.2 Results

Search behaviour

Participants collected significantly more targets on average in the single feature condition (M = 30.11, SD = 11.09) than in the conjunction condition (M = 15.47, SD = 6.67; *t*(19) = 5.88, *p* < .001, *d* = 1.32), and they also directed a greater percentage of their overall inspections to cued objects in the single feature condition (M = 98.47%, SD = .97%) compared to conjunction search (M = 91.42%, SD = 13.35%; *t*(19) = 2.38, *p* = .028, *d* = .53; see Figure 3.2a). Similar to Experiment 1, a significant number of participants inspected cued items near 100% success which may be subject to ceiling effects. A Shapiro-Wilk Test of Normality was conducted, displaying deviation from normal distribution across both conditions (single feature: *p* = .02; conjunction: *p* < .001). A Wilcoxon Signed-Ranks Test revealed that participants made significantly more cued inspections in the single feature condition (Z = -3.47, *p* < .001) than conjunction condition. Participants on average inspected more objects in total in the single feature condition (M = 62.74, SD = 22.14), compared to the conjunction condition (M = 34.30, SD = 12.40; *t*(19) = 6.03, *p* < .001, *d* = 1.35), and they visited more patches on average in single feature search (M = 10.73, SD = 2.97) than in conjunction search (M = 7.82, SD = 1.76; *t*(19) = 4.00, *p* < .001, *d* = .90).

Foraging strategy

Best-*r* indicated that within-patch organisation was greater in the single feature condition (M = .43, SD = .12) than in the conjunction condition (M = .36, SD = .11; *t*(19) = 2.27, *p* = .035, *d* = .51), although between-patch organisation did not differ between conditions (single feature: M = .59, SD = .09; conjunction: M = .63, SD = .08; *t*(19) = -1.18, *p* = .25, *d* = -.27). Participants were also significantly more exploitative in the single feature condition (M = 79.54%, SD = 13.47%) than conjunction (M = 53.34%, SD = 15.96%; *t*(19) = 7.18, *p* < .001, *d* = 1.61; see Figure 3.2b). There was no difference identified in the percentage of revisits made between conditions (single feature: M = 1.86%, SD = 1.13%; conjunction: M = 2.85%, SD = 3.94%; *t*(19) = -1.10, *p* = .28, *d* = -.25).

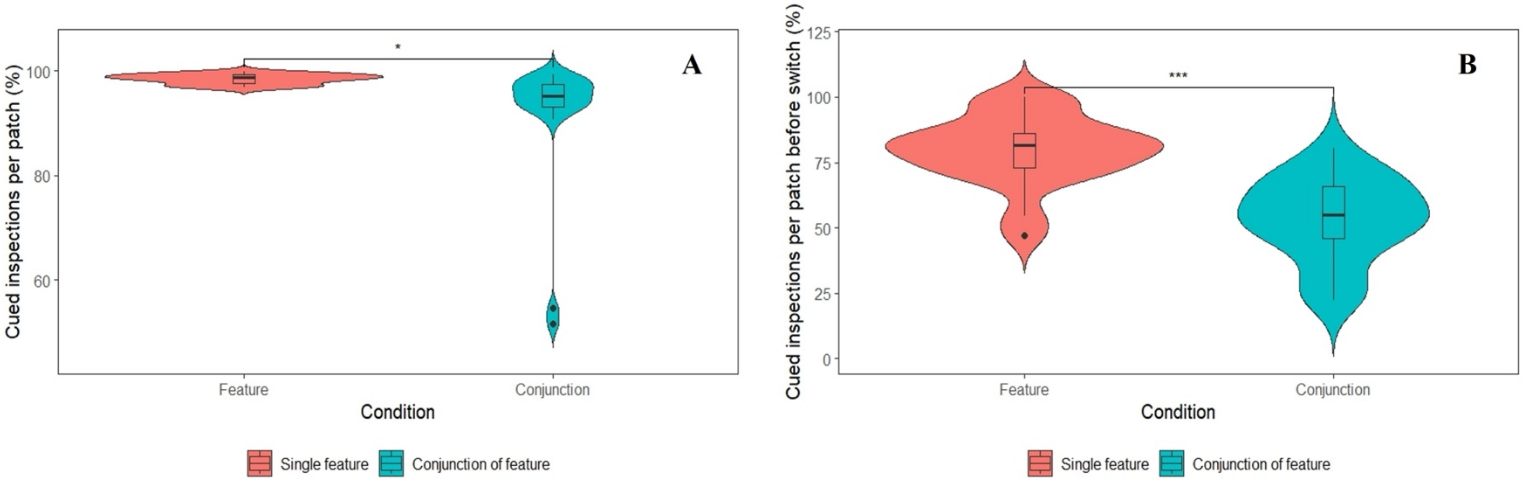

Figure 3.2. Violin plots describing the A) percentage of cued inspections per patch (search variable) and B) before a switch (exploitation; foraging variable) between single feature and conjunction conditions. Note: the scaling in A has been adjusted to better illustrate the clustered responses. Boxplots are included to summarise the data; the lower box represents first quartile of responses and upper box represents third quartile. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by ***.

Individual difference

Pearson's correlations (see Appendix A: Tables A4, A5, A6) identified that several aspects of cognition were related to search and foraging success. Within the single feature condition, participants with higher total number of inspections made fewer verbal memory errors and participants who visited more patches showed greater working memory span abilities. Foraging variables indicated participants who were more organised between-patch showed a spatial memory strategy that always began in the same location. In the conjunction condition, participants who were more organised between-patch were more likely to have higher delayed verbal memory recall. Finally, fewer spatial working memory errors revealed a relationship with a higher percentage of cued inspections.

3.4.3 Discussion

Similar to Experiment 1, participants were more successful in single feature than conjunction search: collecting more targets, inspecting a greater number of containers and patches, and directing a greater proportion of their inspections to cued targets. However, manipulation of target density within the array revealed that between-patch search organisation did not differ between conditions, although within-patch search was more organised in single feature search. Between-patch search was more organised in the conjunction condition in Experiment 1 – since participant instructions were identical in Experiment 2, this difference suggests that target distribution affected the search strategies adopted by participants. Although this was expected to be more apparent in the conjunction condition, this general pattern is in line with previous demonstrations in three-dimensional but stationary, inter-item search space, where single feature search was more organised than conjunction search (e.g. Kristjánsson et al., 2020). Previous research (Cain et al., 2012) reflected similar findings; in a two-dimensional simple array, target distribution was manipulated by target-present and target-absent trials, with unequal distribution between target-present trials. It was noted that participants were able to optimise their search strategy by terminating their search more quickly when finding further targets was unlikely. This may account for the similarities identified in between-patch organisation, explaining that perhaps the reduced organisation in the conjunction condition possibly reflects the increased, effortful nature of multiple features. Finally, exploitation was found to be greater in the single feature than conjunction condition. Exploitative strategies in single feature conditions may represent optimality, especially when participants are aware of target location (Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020), as greater success by gaining all targets in one patch with less required effort of physically exploring additional patches would indeed represent a successful strategy.

Akin to Experiment 1, variations in single feature performance were related to individual differences in areas such as working memory, spatial memory, and verbal memory. Participants with greater working memory span visited more patches, and those who made more item inspections had fewer verbal delay errors. Visual search processes have been shown to utilise multiple forms of working memory, especially in more effortful arrays (Anderson et al., 2010). Presently, it was identified that those who were more organised within the array were more likely to show a constrained spatial memory strategy. It can be supposed that these two variables are disconnected due to the nature of explicit instructions and the effect of distribution. Ólafsdóttir, Gestsdóttir, and Kristjánsson (2021) found that within a two-dimension conjunction condition, participants collected all of one target type (such as all of the red discs) before moving onto the second (such as all of the green squares), reducing the conjunction task (i.e. searching for all the red discs and green squares) into two, highly organised single feature tasks. In the present experiment, participants were explicitly told where the targets were, so if they exhaustively searched each patch, irrespective of target presence or not, greater organisation between-patch could be present despite the lack of explicit strategy.

Greater verbal memory ability was found in participants with more organised within-patch searching in the conjunction condition. It has recently been proposed that both visual and verbal representations lie within working memory, where attentional guidance was suggested to be modulated when holding either visual or verbal representations in working memory (Kawashima & Matsumoto, 2017). This was anticipated to represent top-down deployment of visual attention. And so, one consideration is that in the present study, a strategic use of verbal memory representations can be used to guide attention. Further, participants who had greater spatial memory ability made more cued inspections within the array. Attentional selection mediates not only visual working memory but spatial location on the basis of featural cues (Heuer & Schubö, 2016). By that, it was found that for both colour and shape featural cues, it was just as advantageous to attend to features as it was spatial location. Therefore, in the present experiment, when locations have been committed to memory, greater spatial working memory can facilitate greater search success alongside attentional contributions to feature-based search.

Experiment 2 showed that properties of visual search were unaffected by target distribution as single feature search was more successful than conjunction of feature search, whereas within-patch foraging organisation was affected by distribution. With explicit instructions, participants were able to rely on the provided heuristics of the search paradigm, using top-down processes derived from *a priori* knowledge. A search template, or a working memory-held representation of the target, is a top-down process that selectively locates targets by prioritising task-relevant information to serve as a mould to determine targets amongst distractors (Geng & Witkowski, 2019). This increases search efficiency and aids in successful search (Crowe et al., 2021), as well as increasing one’s adaptability to search demands and decreasing cognitive load, and therefore providing effective solutions to target detection. On the other hand, the further search templates are from the target, the slower one is to find the target; the best templates for success are identical to the target (Vickery, King, & Jiang, 2005). Thus, the absence of explicit instructions would mean that as participants search for hidden targets within the space, they will also need to be more strategic in their search in order to learn what cues predict target location, and thus building representational templates to guide search success. This is anticipated to introduce greater executive and working memory demands. This may modulate the effects reported in Experiments 1 and 2.

3.5 Experiment 3

A search template has been suggested to increase search efficiency and aid in successful search (Crowe et al., 2021), allowing for quick and efficient identification of targets as well as increasing one's adaptability to search demands and decreasing cognitive load. Thornton, Nguyen, and Kristjánsson (2022) suggest that the creation and switching between templates, especially in conjunction conditions, put greater cognitive demands on memory systems. Berggren and Eimer (2018) proposed that attention is guided by a single template at a time, therefore requiring the participant, when in a conjunction of feature condition, to switch between two templates to search, or to search utilising one template and then to apply the second. This requires multiple target templates to search a conjunction array, and therefore more working memory resources would be required to effectively search and switch between two target templates. It is known that templates to guide search are crucial (Lancry-Dayan, Gamer, & Pertzov, 2021) however there is a difference between being provided with a template and having to generate one's own template. This difference is mediated by cognitive load and top-down and bottom-up processing, requiring the creation of successful internal representations to successfully search. Internal representations also allow for greater insight into individual difference and cognitive processes underpinning search. By manipulating the lack of template provision, visual search task performance is expected to decrease with the increase of cognitive requirements. Thus, Experiment 3 followed a similar structure to Experiment 1 where participants were presented with equal distribution (all targets were present under the cued objects), but without a provided template. It was expected that, without an *a priori* template, participants will be required to sample information in order to learn target location, resulting in greater exploratory behaviours. This may reflect smaller differences than have been identified previously in Experiments 1 and 2 between single feature and conjunction conditions. It has been suggested that top-down guidance is heavily relied upon for successful search behaviour and in the absence of such information, search is guided by proximity (Chen & Zelinsky, 2006), and thus foraging success was also anticipated to be defined by greater disorganisation. These behaviours will lead to greater associative strength than preceding experiments in aspects of working memory, spatial abilities, and executive functioning as participants will require and rely more heavily on cognitive resources than previous experiments.

3.5.1 Methods

Participants

Twenty participants (female: N = 10, male: N = 10; age 18-32 years, M = 22.1, SD = 4.28) were recruited, and participants were compensated for their time with either course credit or a monetary equivalent as explained in the *General Methods*.

Design and procedure

The search task was identical to the one presented in Experiment 1 – participants searched for hidden targets whose locations were cued by the featural properties of the containers that concealed them, and there was a target beneath every cued container. Whilst the practice instructions were the same as described in the *General Methods*, there was a difference in the experimental instructions, where participants were not provided with the features that cued the location of the hidden targets in either search condition. Instead, instructions were as follows: *"You will now complete a series of trials. Each time, your task is to find as many hidden Red balls as possible. The balls change colour when found, so if you find a grey ball you have already searched there. You will have 60 seconds to complete each trial. Remember to search as efficiently as you can."*

3.5.2 Results

Search behaviour

On average, participants found significantly more targets in the single feature condition (M = 49.49, SD = 22.20) than in the conjunction condition (M = 34.45, SD = 18.43; *t*(19) = 3.12, *p* = .006, *d* = .70), and a greater percentage of inspections were made under the cued objects in the single feature condition (M = 79.35%, SD = 17.9%) than in the conjunction condition (M = 68.73%, SD = 20.07%; *t*(19) = 3.2, *p* = .005, *d* = .71; see Figure 3.3a). Participants made on average more total inspections in the single feature (M = 66.62, SD = 33.56) than conjunction (M = 52.90, *SD* = 26.28; *t*(19) = 2.67, *p* = .015, *d* = .60) conditions. However, participants did not differ significantly between the average number of patches searched (single feature: M = 8.85, SD = 3.53; conjunction: M = 8.23, SD = 3.66; *t*(19) = .86, *p* = .40, *d* = .19).

Foraging strategy

Analysis of best-*r* data revealed that there was no effect of condition on the organisation of either between-patch (single feature: M = .57, SD = .13; conjunction: M = .63, SD = .16; *t*(19) = -2.0, *p* = .065, *d* = -.44) or within-patch search (single feature: M = .34, SD = .08; conjunction: M = .34, SD = .09; *t* (19) = .28, *p* = .78, *d* = .06). Participants were significantly more exploitative in the single feature condition (M = 79.23%, SD = 17.09%), compared to the conjunction condition (M = 55.75%, SD = 17.26%; *t*(19) = 5.74, *p* < .001, *d* = 1.28; see Figure 3.3b), and they revisited a greater percentage of patches in the conjunction (M = 3.14%, SD = 1.98%) than single feature (M = 2.31%, SD = 1.58%; *t*(19) = -2.32, *p* = .032, *d* = -.52) condition.

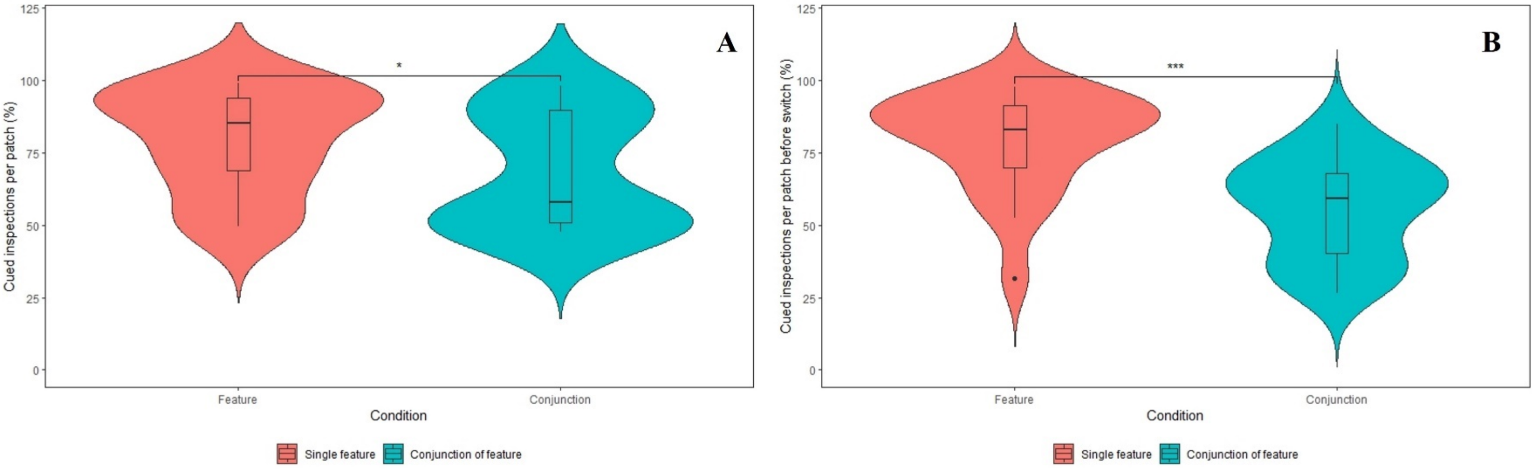

Figure 3.3. Violin plots describing the A) percentage of cued inspections per patch (search variable) and B) before a switch (exploitation; foraging variable) between single feature and conjunction conditions. Boxplots are included to summarise the data; the lower box represents first quartile of responses and upper box represents third quartile. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by ***.

Individual difference

Pearson's correlations identified relationships between the search and foraging behavioural measures and individual differences. In the single feature condition, participants with fewer delayed verbal memory errors were more organised within-patch. Between-patch organisation was associated with several measures of immediate and delayed verbal memory where fewer errors, but greater trial difficulty success revealed greater between-patch organisation. Exploitation rates were related to measures of working memory and spatial memory errors, where higher exploitation was correlated with fewer spatial memory errors but greater working memory. Participants who selected the correct stimulus per rule (IEDEEDS) were more likely to make fewer inspections in total, but greater cued inspections.

Significant relationships between cognitive tests and search performance in the conjunction condition were only observed in two of the behavioural variables. A fewer number of total inspections made were correlated with selecting the correct stimulus per rule and greater verbal working memory ability. Additionally, the number of tables searched were associated with working memory ability where more tables were searched when working memory was poorer.

3.5.3 Discussion

Search results indicated that single feature arrays yielded a greater number of targets collected, more total inspections, and more cued inspections than conjunction arrays. In contrast, the number of patches inspected was equivalent across conditions. This indicates that without explicit instruction, or a top-down template, participants were still more successful in single feature conditions, showing that guidance of search remains equivalent. As one must create one's own stopping rule based on the template they have created (e.g. when does one stop searching one patch and move onto the next; Cain et al., 2012), if the template that has been created is incomplete or lacking in the complexity required for conjunction search (i.e. searching under *both* the yellow cups *and* blue boxes) then inspections may be similar across conditions. Thornton, Nguyen, and Kristjánsson (2022) propose that when utilising a template, switching can be a selected search strategy in the decision whether to employ target templates in parallel or sequentially. This was supported by the lack of significant difference between number of tables inspected, indicating that visual search strategy within a patch was similar across single feature and conjunction conditions, and thus affected by the requirement to create a search template.

Measures of foraging found similar results: participants were no more organised, neither within-patch nor between-patch, in either condition. It has been shown that factors such as time in patch reveal reduced organisation in foraging (Bella-Fernández, Suero Suñé,

& Gil-Gómez de Liaño, 2023). Huynh Cong and Kerzel (2021) propose that if a template is required in order to detect a target's presence, then the amount of cognitive resource will be similar between single feature and conjunction search. Presently, without a provided template, participants seem to sample various strategies in order to derive the rule. This was reflected in the nonsignificant difference between conditions for patch inspections and search organisation. Results also revealed that participants were significantly more exploitative in single feature than conjunction conditions. Given the similar number of patch inspections between the two conditions, this suggests that participants may have developed more inefficient templates in the conjunction conditions. Berggren and Eimer (2018) suggest that conjunction templates can be created, however attention is still guided by a single template at a time. For example, in a conjunction array, one might hold two templates: one for the yellow cups and one for blue boxes. Therefore, a more successful template in the single feature condition would lead to more exploitative behaviours as participants know where the targets are hidden, but the lack of a created template might then lead to more exploratory behaviour. Finally, participants revisited more patches in the conjunction conditions. Kibbe and Kowler (2011) too found that revisits increased as the complexity of search increased, and this likely reflects a poorly organised search, indeed supported by present findings.

Individual differences associated with search and foraging success (i.e. verbal immediate and delayed memory, spatial memory, working memory, and executive functioning) revealed success across several measures. Greater verbal memory, including greater success on immediate verbal trials and fewer errors, predicted more organised search, where research suggests underlying verbal processes are required in visual search (Jackson, Shaw, & Helton, 2023). Greater working memory and fewer spatial memory errors predicted more exploitative behaviours and reduced patch inspections. Working memory has been evidenced to guide attention across spatial reference frames during active exploration, and spatial memory was shown to be integral to improved search performance (Botch et al., 2023), requiring updating and maintenance of visuospatial information for a successful search strategy. Without a template, one is required to sample more information (therefore making a greater number of inspections) to understand the underlying rule. Thus, to facilitate rule learning through search efficiency, working memory and spatial memory abilities support success. Further, greater executive functioning abilities revealed more cued, but fewer overall, inspections. Efficiently searching and foraging one's space demands a successful template, heightening cognitive resource demands, likely requiring executive control as well as working memory. A connectivity study using fMRI revealed increased activity in prefrontal regions linked to executive functions like planning and task control, and the precentral gyrus revealed associations with verbal memory, underscoring critical regions for visual search success (Remington et al., 2021). Templates to guide search are crucial (Lancry-Dayan, Gamer, & Pertzov, 2021) and present findings implicate that greater cognitive abilities facilitate overall success.

Overall, results indicated that requiring participants to create their own template (thus increasing cognitive load) within an equally distributed array of targets revealed behavioural and cognitive profiles key to facilitating search guidance and sampling of information. Research suggests that incomplete templates hinder decision-making abilities and attentional guidance, slowing search (Hout & Goldinger, 2015), and that in the absence of top-down information only then is bottom-up salience utilised, relying on proximity instead (Chen & Zelinsky, 2006). Thus, it is predicted that it is harder yet to create and maintain a search template when targets are less evenly spread. Humans have been shown to be responsive to environmental conditions (Constantino & Daw, 2015), and so, if the distribution of targets is unequal, it is anticipated that foraging-like decisions will not be maintained, since this represents the least predictable combination of factors. Specifically, information sampling would increase and therefore so would disorganisation and exploration, but with visual search properties still guiding similarly across conditions.

3.6 Experiment 4

The penultimate manipulation was implemented to investigate whether unequal target distribution affects economic decision-making and template creation. Research suggests that bottom-up search relies on proximity (Chen & Zelinsky, 2006), and that inaccurate templates lead to a degradation of attentional guidance and decision-making (Hout & Goldinger, 2015). Further, when faced with uncertainty, exploration has been suggested increase as an information sampling and gathering exercise (e.g. Cohen, McClure, & Yu, 2007; Walker et al., 2022) which suggests that in the absence of an *a priori* template, participants will be less organised (as they are guided by sampling and the object immediately adjacent) and more exploratory (as they inspect each patch by randomly sampling rather than top-down guidance). Previous manipulations identified that participants were more exploitative in single feature conditions when provided with *a priori* information or target reinforcement. Thus, it was expected that participants would still follow visual search behaviours, exhibiting greater success in single feature than conjunction of feature, however, in terms of foraging behaviours, it was predicted that overall performance would be less organised, with greater exploration, and greater revisits in the conjunction of feature (more effortful) conditions. It was also anticipated that cognitive control measures, including executive function, working memory, episodic memory, and spatial working memory, would have a stronger association with search and foraging success.

3.6.1 Methods

Participants

As discussed in the *General Methods*, following the example of Experiments 1-3 where G*Power identified 20 participants were required for each experiment, twenty participants (female: N = 14, male: N = 6; age 19-33 years, M = 22.95, SD = 4.02) were collected, and participant time was compensated with either monetary reimbursement or course credit as per the *General Methods*.

Design and procedure

Experiment 4 followed the same general design as described in Experiment 3 (i.e. participants searched for hidden targets, guided by the distinguishing features of the containers that concealed them) except in the distribution of targets, which followed the same principles applied in Experiment 2 – i.e. the number of targets at each patch, and the spatial location of the item beneath which they were concealed, were randomly determined, with relative equivalence between participants. In the single feature condition, on average and across all participants, there were 4.81 targets per table (SD = .39; range = 4.09 – 5.67 targets). Similarly, in the conjunction condition, on average and across all participants, there were 4.88 targets per table (SD = .26; range = 4.44 – 5.42 targets). The procedure was identical to that of Experiment 3, where no explicit instructions were provided for target location, requiring participants to learn the target location by inspecting cued containers.

3.6.2 Results

Search behaviour

Participants found significantly more targets on average in the single feature condition (M = 24.31, SD = 11.48) than in the conjunction condition (M = 17.20, SD = 7.70; $t(19)$ = 3.07, p = .006, d = .69), and a higher percentage of inspections were made to cued objects in single feature search (M = 67.74%, SD = 17.7%), compared to conjunction search (M =

59.88%, SD = 16.78%; *t*(19) = 2.29, *p* = .009, *d* = .51; see Figure 3.4a). Participants made on average a greater number of total inspections in the single feature condition (M = 76.43, SD = 31.68) than in the conjunction condition (M = 60.40, SD = 30.43; *t*(19) = 2.90, *p* = .009, *d* = .65), although there was no effect of condition upon the average number of tables searched (single feature: M = 8.58, SD = 3.28; conjunction: M = 7.75, SD = 2.96; *t*(19) = 1.09, *p* = .29, *d* = .24).

Foraging strategy

Best-*r* measures revealed that there was no effect of condition upon either the within-patch (single feature: M = .34, SD = .09; conjunction: M = .31, SD = .07; *t*(19) = 1.19, *p* = .25, *d* = .27) or between-patch (single feature: M = .56, SD = .11; conjunction: M = .63, SD = .14; *t*(19) = -2.06, *p* = .054, *d* = -.46) organisation of search. Percentage of revisits also did not significantly differ between conditions (single: M = 1.86%, SD = 1.13%; conjunction: M = 2.25%, SD = 1.68%; *t*(19) = -1.53, *p* = .14, *d* = -.34). It was found however that participants were significantly more exploitative (see Figure 3.4b) in the single feature condition (M = 81.2%, SD = 13.5%) than in the conjunction condition (M = 61.24%, SD = 16.33%; *t*(19) = 7.52, *p* < .001, *d* = 1.68).

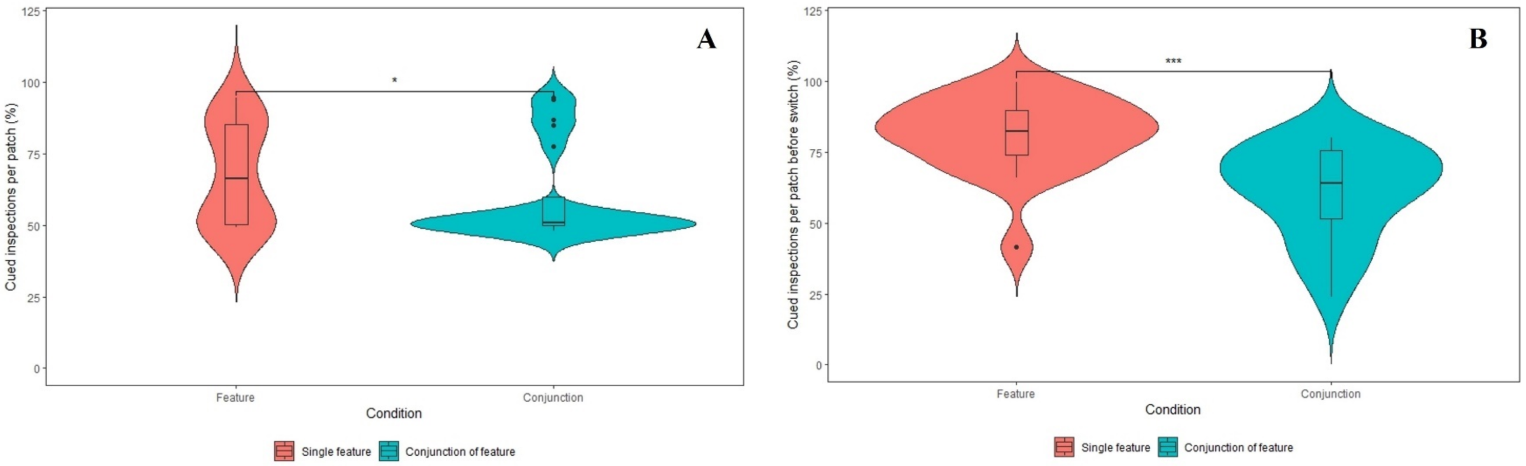

Figure 3.4. Violin plots describing the A) percentage of cued inspections per patch (search variable) and B) before a switch (exploitation; foraging variable) between single feature and conjunction conditions. Boxplots are included to summarise the data; the lower box represents first quartile of responses and upper box represents third quartile. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by ***.

Individual difference

Pearson's correlation revealed (see Appendix A: Tables A10, A11, A12) that the only dependent measure in the single feature condition that related to the cognitive tasks was patch revisit behaviour, which showed a negative correlation with a failure to select the compatible stimulus, where fewer failures (errors) were associated with greater revisits. In the conjunction condition, the number of targets acquired was associated with greater episodic memory. Between-patch organisation was associated with spatial working memory, where participants with higher spatial working memory errors displayed greater organisation. Patch revisits were associated with executive functioning errors revealing that participants with more executive functioning errors made fewer revisits. Participants exhibiting greater exploitative behaviours were more likely to have greater episodic memory.

3.6.3 Discussion

In terms of search success, results revealed that even under greater uncertainty that previous manipulations, search appeared to the be reliably guided by visual features, where more effortful search was associated with less efficient performance. Thus, irrespective of target distribution or template provision, visual search properties described in the two-dimension literature persist to three-dimensional search.

Foraging behaviour, akin to Experiment 3, identified that participants did not differ in how they organised their between- and within- patch search between single feature and conjunction search. Bettinger and Grote (2016) suggest that as patch resources diminish, and especially when one is required to handle resources (e.g. in this case, lift each object to inspect), patches have higher handling times, and within-patch foraging increases. Thus, the lack of significance identified between foraging organisation in single feature and conjunction conditions could be due to target distribution. As information sampling is required in order to generate rule predictions, and this was similar across both conditions. Further, as suggested above that proximity guides search in the absence of top-down information (Chen & Zelinsky, 2006), organisation would reduce if participants were guided by gaining information rather than by templates. Information gain by sampling would also lead to greater exploration, as supported presently. Nauta, Khaluf, and Simoens (2020) note that in sparse environments, search efficiency decreases as target detection is inherently more difficult. Therefore, in difficult and uncertain conditions, and especially in the most difficult conjunction condition, participants sampled to gain information, only inspecting slightly more than three out of six cued items before moving onto the next patch. However, in the single feature condition (i.e. slightly easier), exploitation increased slightly. Informed movement (or possibly, an effective target template?) increases success, guided by organisation alongside exploration, however the greater the unequal distribution, the more effort required to increase success. Thus, overall, it can be suggested that an unequally distributed environment decreases foraging behaviours, especially when top-down information in the form of an *a priori* target template is not provided.

Individual differences identified that episodic memory, spatial working memory, and executive functioning were related to search and foraging success. In the present experiment, greater episodic memory indicated a greater likelihood of collecting more targets and high exploitation. Episodic memory has been found to guide attention automatically, where previous research has suggested that learnt colours and shapes biased saccades, even when the learnt colours and shapes represented a current distractor (Kerzel & Andres, 2020). As such, it is suggested that when required to create a template for search and foraging success, episodic memory plays a significant role in template creation for colour-shape associations to guide one's search (Kerzel & Andres, 2020). If the associations between colour and shape are applied correctly, search will be more efficient. This will increase the number of targets collected, and guide search to exploit patches for the known target location, whereas if the association is incomplete then the template will also be incomplete, and search will be less efficient. Executive functioning errors, explicitly assessed by attentional shifts, were associated with revisits to previously inspected patches. It has been posited that the attentional system plays a supervisory role over executive functioning processes when search is complex (Smith & De Lillo, 2022) with suggestions that revisits were due to premature shifts, or slips, in attention rather than deficits in memory ability (Longstaffe, Hood, & Gilchrist, 2014). Greater spatial working memory abilities revealed greater organisation between patches. De Lillo and James (2012) found across two experiments in stationary VR that organisational principles were inherent to spatial working memory abilities. Specifically, in a large-scale environment, they identified that participants benefited from the spatial structure of the task and used such information to organise their search facilitated by spatial working memory. Indeed, presently, the associations between greater spatial working memory abilities and greater organisational success indicated that participants were able to create more successful strategies, showing greater organisation.

Across a series of experiments, search behaviours revealed a clear distinction between single feature and conjunction of feature conditions. However, the differences found may not be a result of the attentional demands placed by the tasks, but instead of the varying complexities between the two conditions. In Experiments 1-4, the single feature condition contained only one dimension, whereas the conjunction of feature condition contained two. Thus, Experiment 5 was designed to address potential discrepancies in the visual complexities of the single feature condition, verifying that only the attentional relevance of features was being manipulated.

3.7 Experiment 5

It has been suggested that conjunction of feature search requires serial processing where one feature is attended to first, followed by the second feature (Berggren & Eimer, 2018), and conjunction of feature processing takes longer (Smith & De Lillo, 2022). However, there has also been research suggesting that perception and memory demands are similar between single and conjunction of feature searching, where it was proposed that conjunction of features do not demand more attentional resources to integrate multiple features than single feature arrays (Fournier, Herbert, & Farris, 2004). Thus, in this final iteration, the complexity of the array was equated across conditions, manipulating the search demands such that participants were required to attend to two features to successfully search. Experiment 5 replicated Experiment 3 with the exception of the appearance of the single feature array. Two features demarcated the objects, but cues were still defined by a single feature. Hidden targets were equally distributed across the array and participants were not provided with a template. This was anticipated to investigate the attentional demands necessary to determine feature complexity.

3.7.1 Methods

Participants

Following suit of the previous four iterations, twenty participants (female: N = 17, male: N = 2, non-binary: N = 1; age 18-22 years, M = 19.25, SD = 1.16) were recruited to participate for either course credit or monetary compensation as discussed in the *General Methods*.

Design and procedure

Experiment 5 paradigm replicated Experiment 3, aside from the single feature search display. The target was associated a single feature *search* (targets were hidden under one feature, i.e. colour) but participants were presented with a conjunction of feature *display* (i.e. objects defined by both colour and shape). This consisted of both prisms and ovals coloured magenta and cyan (cyan = RGB: 3-243-214; magenta = RGB: 231-12-250), to give two features per object, however the target was always present under a single feature (i.e. ovals; see Figure 3.5). Following the design of Experiment 3, participants were required to search under a single feature (i.e., magenta, cyan, oval, or triangular prism) in the single feature condition. The conjunction of feature condition was as described in Experiment 3, with yellow and blue cups and boxes, the target locations were defined by a conjunction of features (e.g. yellow cups and blue boxes). In both conditions of Experiment 5, participants were not provided with instructions however there was equal distribution of targets (i.e. all targets were present under all cued objects). Participants were given identical instructions to those specified in Experiment 3, where they were asked to search as efficiently as possible, but received no instructions on which items were concealing the targets.

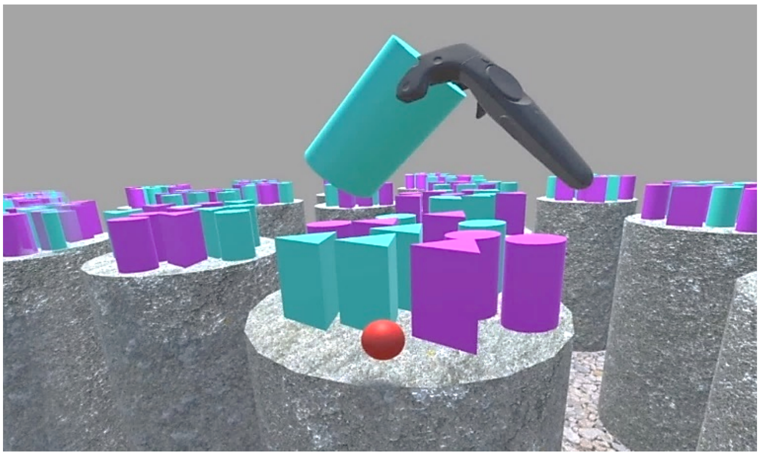

Figure 3.5. View of single feature condition of Experiment 5 from the HMD (participant's view).

3.7.2 Results

Search behaviour

Search behaviour measures revealed that participants collected more targets on average in the single feature condition (M = 46.99, SD = 22.38) than in the conjunction condition (M = 39.07, SD = 20.36; *t*(19) = 2.48, *p* = .023, *d* = .55), and that a greater percentage of inspections were made to cued items in single feature search (M = 80.48%, SD = 19.43%) compared to conjunction search (M = 66.66%, SD = 21.25%; *t*(19) = 3.14, *p* = .005, *d* = .70). However, there was no effect of condition on either the total number on average of inspections made (single feature: M = 64.63, SD = 35.46; conjunction: M = 64.80, SD = 38.63; *t*(19) = -.03, *p* = .98, *d* = -.01), or the average number of tables visited (single feature: M = 8.00, SD = 3.38; conjunction: M = 7.66, SD = 3.02; *t*(19) = .64, *p* = .53, *d* = .14).

Foraging strategy

Foraging measures identified that participants were significantly more exploitative in single feature (M = 77.88%, SD = 20.49%) than conjunction of feature (M = 65.42%, SD =

22.16%; $t(19) = 4.79, p < .001, d = .51$) conditions. However, there was no difference between conditions for best-*r* measures of between-patch (single feature: M = .59, SD = .08; conjunction: M = .60, SD = .13; $t(19) = -.46, p = .65, d = -.10$) or within-patch organisation (single feature: M = .35, SD = .07; conjunction: M = .33, SD = .09; $t(19) = .74, p = .47, d = .16$). In addition, there was no effect of condition on percentage of patch revisits (single feature: M = 3.18%, SD = 3.02%; conjunction: M = 3.46%, SD = 3.34%; $t(19) = -.64, p = .53, d = -.14$).

Individual difference

Correlational analysis of the relationships between search behaviour and performance on cognitive tasks (see Appendix A: Tables A13, A14, A15) only revealed reliable associations for measures of foraging strategy. In the single feature condition, participants with greater within-patch organisation showed greater verbal recall on the delay trial, and participants with greater between-patch organisation exhibited higher working memory span abilities. In the conjunction condition, participants with greater between-patch organisation were more likely to have greater episodic memory, as did participants with greater within-patch organisation. Finally, the higher patch revisits a participant made showed a higher lower likelihood of executive functioning errors.

Verifying control experiment

A series of independent sample t-tests were conducted to ascertain whether performance was equivalent between Experiments 3 and 5 (see Table 3.1). Non-significant results would suggest that attending to single features in both single feature and conjunction feature arrays relies on similar attentional mechanisms. In contrast, significant differences would imply that the complexity of the task influenced success. Indeed, no significant differences were identified between the two experimental manipulations, indicating that one feature or two does not affect attention allocation to targets and findings from Experiments 1-4 do indicate differences in search ability between conditions.

Table 3.1. *t*-values resulting from independent sample t-test for visual search and foraging measures comparing performance between Experiment 3 and 5.

	Single feature				**Conjunction of feature**			
	t	Exp 3 M (SD)	Exp 5 M (SD)	*d*	*t*	Exp 3 M (SD)	Exp 5 M (SD)	*d*
Targets collected	.355	49.49 (22.2)	46.99 (22.38)	.11	-.752	34.45 (18.43)	39.07 (20.36)	-.24
Percentage of cued inspections	-.192	79.35% (17.9%)	80.48% (19.43%)	-.06	.318	68.73% (20.07%)	66.66% (21.25%)	.1
Total inspections	.183	66.62 (33.56)	64.63 (35.46)	.06	-1.139	52.9 (26.28)	64.80 (38.63)	-.36
Number of patch visits	.778	8.85 (3.52)	8.00 (3.83)	.25	.538	8.23 (3.66)	7.66 (3.02)	.17
Within-patch best-*r*	-.275	.34 (.08)	.35 (.07)	-.09	.224	.34 (.09)	.33 (.09)	.07
Between-patch best-*r*	-.481	.57 (.13)	.59 (.08)	-.15	.7	.63 (.16)	.60 (.13)	.22
Exploitation	.227	79.23% (17.09%)	77.88% (20.49%)	.07	-1.54	55.75% (17.26%)	65.42% (22.16%)	-.49
Total number of patches revisited	-1.137	2.31% (1.27%)	3.18% (3.02%)	-.36	-.358	3.14% (1.98%)	3.46% (3.34%)	-.11

NB. No significance was identified.

3.7.3 Discussion

The purpose of this experiment was to equate array complexity to measure perceptual and cognitive mechanisms. As simple search usually has only one feature, whereas effortful search has more than one, to ascertain whether effects were due to the effort of the attentional demands, rather than the complexity of the array, this experiment equated a similar number of features in the array, but single feature search only required participants to attend to one of them. Results indeed established that the preceding findings are not solely due to the perceptual simplicity of the single feature arrays; despite the single feature array now being defined two features, it did not change search and foraging performance. Therefore, the differences in search behaviour measured across Experiments 1-4 are not necessarily due to the perceptual complexity of the display but the attentional demands of the search cues.

3.8 Comparison of Experiments

To compare performance across the core experimental manipulations detailed here (i.e Experiments 1 – 4) a series of 2 (Template instructions: present, absent) x 2 (Distribution: equal, unequal) x 2 (Condition: Single feature, conjunction of feature) mixed design ANOVAs were conducted across the four experimental conditions. Experiment 5 was not included in analyses as it was administered as a control. The *F* statistics are described in Table 3.2. To elucidate significant interactions, where appropriate, post-hoc analyses with Bonferroni correction were conducted. Note that there were no significant three-way interactions.

3.8.1 Results

Table 3.2. *F*-ratios results from ANOVA analyses of effects between experimental manipulations.

	Condition	**Template**	**Distribution**	**Condition x Template**	**Condition x Distribution**	**Template x Distribution**	**Condition x Template x Distribution**
Score (total number of targets found)	70.70**	1.68	46.86**	6.12*	6.67*	.39	.21
Percentage of cued inspections	27.88**	78.54**	2.19	.16	.49	4.56*	.02
Total inspections	68.75**	7.29*	.27	5.04*	.56	1.34	.08
Number of separate patches inspected	21.68**	2.42	.08	7.59*	.07	.14	.00
Within-patch best-*r*	2.77	8.30*	.001	.33	3.92	.40	1.60
Between-patch best-*r*	21.05**	.003	.09	.14	1.35	.29	1.75
Exploitation	173.95**	.28	.04	.24	.08	1.03	1.81
Total number of patches revisited	4.73*	.19	1.75	.02	.02	.09	.75

NB. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **

The number of targets collected in the single feature conditions (M = 41.17, SD = 2.02) were significantly greater than conjunction conditions (M = 25.48, SD = 1.80, $p < .001$) and participants found more targets with equal (M = 44.87, SD = 2.14) than unequal distribution (M = 21.77, SD = 2.14, $p = .038$) as shown in Figure 3.6. There was, however, no effect of template provision on the participant's score. There was no interaction between template provision and target distribution, however both factors significantly interacted with condition: in the single feature condition, participants collected significantly more targets with a template provided than without (M = 8.54, SD = 4.04, $p = .038$), but without a difference in template provision in the conjunction of feature condition ($p = .81$). When provided with a template, participants performed significantly better in the single feature condition (M = 20.31, SD = 2.64, $p < .001$); similarly, without a template, participants still collected more targets in the single feature condition (M = 11.07, SD = 2.64, $p < .001$) than conjunction. A further interaction between condition and distribution revealed that in both the single feature (M = 27.92, SD = 4.04; $p < .001$) and conjunction conditions (M = 18.28, SD = 3.00, $p < .001$), participants collected more targets when there was an equal distribution of targets than unequal. It was similarly shown that in both equally (M = 20.51, SD = 2.64, $p < .001$) and unequally (M = 10.87, SD = 2.64, $p < .001$) distributed environments, participants collected more targets in single feature than conjunction conditions. No interactions were identified between template provision and distribution.

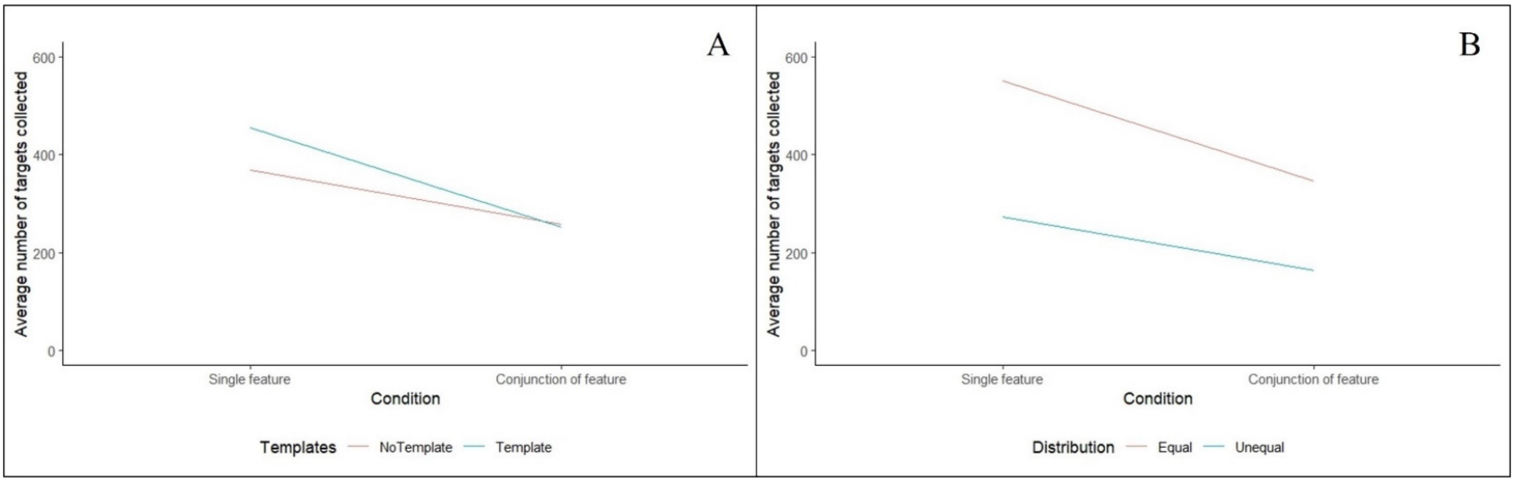

Figure 3.6. The average number of targets collected between single feature and conjunction conditions when provided with: A) a template or without, B) in the equally or unequally distributed condition.

Similarly, it was found that single feature conditions produced a higher percentage of cued inspections (M = 85.77%, SD = 1.41%) than conjunction (M = 77.17%, SD = 1.83%, $p < .001$), more total inspections (M = 67.32, SD = 3.16) than conjunction (M = 46.92, SD = 2.53, $p < .001$), more patch inspections (M = 9.68, SD = .38) than conjunction (M = 7.92, SD = .31, $p < .001$), and more exploitative behaviours (M = 79.81%, SD = 1.69%) than in conjunction (M = 57.27%, SD = 1.85%, *p* < .001). Conversely, higher between-patch search organisation was found in conjunction conditions (M = .63, SD = .013) than single feature (M = .56, SD = .012, *p* < .001), as well as a greater percentage of revisits in the conjunction of feature (M = 2.81%, SD = .31%) than single feature (M = 2.16%, SD = .19%, *p* = .033) conditions. Within-patch best-*r* did not significantly differ between single feature and conjunction conditions.

When participants were provided with a template, they made a higher percentage of cued inspections (M = 94.01%, SD = 2.00%) than when template formation was required (M = 68.93%, SD = 2.00%, *p* < .001), and there was greater within-patch organisation when provided with a template (M = .39, SD = .013) than without (M = .33, SD = .013, *p* = .005). Participants made, on average, a greater number of total inspections where they were required to create their own template (M = 64.09, SD = 3.65) than when provided with one (M = 50.16, SD = 3.65, *p* = .009). Template provision did not affect the participant's score, number of tables inspected, between-patch organisation, exploitative behaviours, or revisits to previously inspected patches.

There was an interaction found between the experimental condition and template provision for two further measures of search. In the conjunction of feature condition, participants made a significantly greater total number of inspections when they had to create their own template (M = 19.45, SD = 5.05, *p* < .001) than when provided with one. However, template provision did not affect single feature inspections (*p* = .19). When provided with a template, participants made, on average, significantly more inspections in single feature conditions (M = 25.92, SD = 3.48, *p* < .001) than conjunction, and when participants were required to create their own template, they similarly made a greater number of inspections in single feature (M = 14.87, SD = 3.48, *p* < .001) than conjunction arrays. Likewise, in the single feature condition, participant made a greater number of patch inspections when a template was provided (M = 1.94, SD = .75, *p* = .012) than when required to create their own, however there was no benefits of template provision in the conjunction condition (*p* = .81). When participants were provided with template, they made significantly more patch inspections in the single feature condition (M = 28.15, SD = 5.37, *p* < .001) than conjunction, however when they were required to create their own, patch inspections did not differ (*p* = .18)

There was also an interaction between template provision and the target distribution for the percentage of cued inspections participants made. When there was an equal distribution of targets, participants made more cued inspections when provided with a template (M = 19.04%, SD = 4.00%, *p* < .001) than when they had to create their own, and when presented with an unequal distribution, participants significantly benefited from a template (M = 31.13%, SD = 4.00%, *p* < .001) than without. When participants were required to create their own template, they made significantly more cued inspections with an equally distributed display (M = 10.23%, SD = 4.00%, *p* = .013) than unequal, however when provided with a template, distribution did not affect cued inspections (*p* = .64).

3.8.2 Discussion

The omnibus analyses made within-subjects comparisons between search conditions (i.e. single feature and conjunction), and between-subjects comparison between template provision and the distribution of targets. The effects of condition revealed that across most of the search and foraging measures (with the exception of within-patch organisation), participants were more successful or efficient on single feature trials than conjunction of feature. This is an established finding across the visual search literature (e.g. Smith & De Lillo, 2022; Treisman & Gelade, 1980), that simple (single feature) search is easier than the effortful conjunction of feature search. Therefore, large-scale search seems to be influenced by visual search manipulations in a manner consistent with two-dimensional visual search.

Results also showed, across several measures (i.e. cued and total inspections, within-patch organisation), that irrespective of target distribution, participants benefited more from being provided with a template, with several measures (i.e. score, total inspections, patch inspections) identifying that the interaction between condition and template led to greater success. This therefore illuminates the relative ease of search when a template is provided instead of creating one's own target representation. Bottom-up processing is immediate and contributes the salience of the scene, but slower and more effortful top-down processing is required to create a search template (Theeuwes, 2010). A search template is crucial to successful search, and the easier the target is discriminated, the quicker it can be found (Lancry-Dayan, Gamer, & Pertzov, 2021). Thus, information sampling is required to ascertain featural properties of the space, but when a template is provided, this facilitates more successful search.

Target distribution, however, did not seem to significantly impact any measures aside from overall number of targets collected, with an interaction between the participant receiving a template and equal distribution rising to significance for cued inspections only. Measures of foraging including between- and within- patch organisation, exploitation, and revisits were unaffected by distribution across the four experimental manipulations. Previous research (Cain et al., 2012) has proposed that irrespective of distribution, participants are able to vary their search strategy. Furthermore, it has been found that participants adjust their search in response to differing target distributions, but suboptimally (Kalff, Hills, & Wiener, 2010). Louâpre et al. (2010) too suggested that participants seemed unable to adjust foraging responses to spatial distribution, as it was found that despite varying resource distributions, a similar mechanism was used throughout. Therefore, perhaps across the four manipulations presently discussed, strategy adjustment between experimental iterations was present, but suboptimal, masking effects across the experiments, or similar strategies were employed irrespective of distribution. An interaction between template provision and target distribution was also revealed for the percentage of cued inspections where participants were most successful in the equally distributed array when provided with a search template. Previous research (Paeye, Schutz, & Gegenfurtner, 2016) has shown that reinforcement, or the reward one gets when successfully discovering a target, when searching is integral to learning the target location. Thus, reinforcement, alongside template provision, would provide great support in learning target location, and therefore making more cued inspections. Overall, it was clear that across search and foraging measures, greater success was determined by the condition with template provision providing some search support, but target distribution affecting very little.

3.9 General Discussion

The present Chapter describes a novel paradigm of experimental manipulations designed to test the underpinnings of visual search and foraging behaviour in a novel three-dimensional environment. Factors such as template provision and target distribution were manipulated to assess the effects on visual search and foraging performance, where cognitive measures including decision-making, attentional, working memory, and spatial memory requirements identified of potential sources of variation. Results implicated cognitive substrates of search and foraging efficiency: data suggests that visual and attentional guidance operates similarly between two- dimensions and three-, whereas foraging behaviour produced less consistent results as it was more greatly affected by experimental manipulation. Measures of cognition contributed to success, highlighting the overall benefits of memory and executive functioning in foraging-like, large-scale search.

Search success (e.g. targets collected, cued and total item inspections, patches visited) was greater in single feature conditions that conjunction of feature conditions. Following traditional visual search properties, visual search mechanisms guide search similarly, irrespective of two-dimensional computer screens or three-dimensional immersion. This is also irrespective of a single feature search in a single or conjunction of feature array. Search success measured across Experiments 1-4 was not necessarily due to the perceptual complexity of the display but attentional demands. Further, it was expected that search efficiency would be lower in the experimental manipulations where participants were not informed of the association between featural cues and targets, requiring learning of these associations. Indeed, template provision did provide search benefits. Representations of the targets, known as attentional templates, necessitate a visual depiction of the target integrated within working memory to guide attention (Nako, Smith, & Eimer, 2015). With the provision of a search template, participants were able to organise themselves better than without a presented template, especially when target distributions were unequal. Results showed that participants who identified or followed the guiding properties were significantly more successful in single feature than conjunction of feature conditions. Therefore, overall, participants were more successful when search was guided by a single featural cue, despite the requirement for serial inspection, and the differences in the presentation of search template instructions meant that participants adopted different strategies for searching.

Target distribution was expected to support search efficiency, with greater performance anticipated in equally distributed arrays as compared to unequal, irrespective of the number of targets acquired. It is important to note here that effects of distribution were not purely due to participants collecting all the targets when distribution was unequal. No participant managed to collect all targets, irrespective of manipulation. The distribution of targets was found to affect the number of targets collected, where equal distributions produced greater number of targets collected than the unequally distributed experiments, and especially in the single feature conditions as compared to conjunction conditions. It was also found that the percentage of cued inspections was affected by target distribution where trials that contained complete distributions with template provision allowed for greater cued inspections. Wolfe (2013) discovered that across six studies, participants changed their foraging strategy in response to the experimental demands, including nonuniformed distribution of resources. Therefore, target distribution did indeed support search efficiency in some respects. However, target distribution did not influence further measures of search efficiency (i.e. total number of inspections, patch visits) or any aspects of foraging behaviour (i.e. between- or within- patch organisation, exploitative behaviour, patch revisits). Various studies have suggested that effects of target distribution have led to suboptimal foraging performance where participants were found to be unable to adjust their strategy (e.g. Kalff, Hills, & Wiener, 2010; Louâpre et al., 2010). As such, the effects of target distribution appear to support search behaviour (to a small degree) but not foraging in a large-scale environment.

Within- and between-patch search organisation, measured by best-*r* (Woods et al., 2013), varied across all four experiments. Results indicated that condition impacted between-patch organisation, and greater within-patch organisation was supported by template provision. However, when participants were not provided with a template (i.e. Experiments 3 and 4), neither organisation measure significantly differed between conditions. This could reflect of several points. First, Woods et al.'s (2013) measure of organisation was based on a paper-and-pencil cancellation task, where following rows and columns (indicating more organised search) might have been less effortful and thus facilitating identified success. Kristjánsson et al. (2022) utilised best-*r* in a three-dimensional task, where targets could be located on the x-, y-, or z- axis, and best-*r* was found as a good measure for organisation. However, neither aforementioned task required motility when organising one's search, and therefore perhaps additional idiothetic cues supersede organisation, or variations in large-scale strategy masks individual and group effects. It could also be considered that best-*r* is not the best measure for motile organisation, and perhaps other measures may elucidate organisational behaviours in greater detail such as inter-target latency (Kristjánsson et al., 2022), mean inter-target difference or path intersection (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2021). Statistical modelling approaches, such as Clarke, Hunt, and Hughes' (2022) Bayesian approach, have been used to facilitate direct comparison between foraging tendency and visually directed target collection, and this may provide greater insight into foraging organisation. Or, the creation of a large-scale, clearly organised search array that limits decision-making requirements could further quantify. A final consideration to understand participant organisation was identified in the exploitation measure—participants selected cued items irrespective of organisation. Thornton, Nguyen, and Kristjánsson (2022) found that fully exploitative behaviours was reflective of an exhaustive strategy selection to prioritise speed. Therefore, as some conditions revealed that participants were no more or less organised, this could indicate a speed-accuracy trade-off, suggesting participants were more concerned with target acquisition. Participants might then quickly, fully exploit a patch, leading to searching within patches in an unorganised fashion.

Exploitation, the percentage of cued items inspected per patch before switching to a new patch, revealed that across all conditions, participants were more exploitative in single feature conditions. It was predicted that explore decisions (i.e. switching to a new patch before all the targets are found) would be more frequent in the unequally distributed experiments as participants would have higher uncertainty about target location and therefore sample for information. Participants were more exploitative in single feature conditions, and therefore more exploratory in conjunction conditions, however this was not affected by template or distribution manipulation. This does indicate that participants tended to sample for information when faced with greater uncertainty. When in the easier condition (single feature), research suggests that it would be most advantageous to fully exploit a patch for greatest target acquisition before exploring to a new patch (Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020). If uncertainty increases, it is then suggested that search strategy should be revised to gain greater information of the environment, and exploration then becomes optimal (Cohen, McClure, & Yu, 2007; Walker et al., 2022). Exploitation was greater in lower uncertainty manipulations therefore indicating that information sampling increased as uncertainty increased. It was anticipated that exploitation would differ between experiments based on the template and distribution manipulations, however this was not found. This suggests the deployment of a similar strategy, driven by the complexity of the array, across experimental manipulation. It is unclear whether this relationship arises due to the large-scale implementation or experimental manipulation. A suggestion to investigate the explicit relationship between exploration and exploitation would be to employ a *N*-armed bandit task (Calhoun & Hayden, 2015) in addition to a large-scale task. This may provide an isolatable decision-making context when individuals are faced with numerous options to elucidate the trade-off between the desire to exploit a known reward against potentially beneficial information without including the necessity for idiothetic movement.

The final prediction proposed that individuals with greater cognitive control abilities would adopt more successful search strategies, in line with the idea that executive control processes have their roots in domain general foraging-like decision-making. As Clarke and colleagues (2022) point out, individual difference plays an important, but complicated, role in visual search and foraging where averaging participant performance without considering individual difference could potentially miss variations in success. Presently, some cognitive abilities were found to predict performance across experimental manipulations. Executive function abilities predicted the likelihood of search and foraging success in Experiments 3 and 4, but not Experiments 1 or 2. This indicates that the creation of one's own template placed greater demands on executive functioning abilities than when templates were provided. Executive functioning is known to control goal- and action- oriented behaviours (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2021). It has been suggested that the prefrontal cortex, the region known to key in executive function performance, moderates top-down information (Funahashi & Andreau, 2013). As template creation is facilitated by top-down processing, the lack of a provided template does indeed place greater demand on attention, an important component of executive function and especially in search and foraging tasks (Gil-Gómez de Liaño & Wolfe, 2022). Therefore, template creation requires greater executive functioning, including attention, where greater abilities lead to overall search and foraging success as one can create a more accurate target representation. Further, it was found that those with better executive functioning, or who made less errors, had fewer revisits to previously inspected locations, fewer overall inspections, but greater cued inspections. Those with better executive function have been previously shown to better identify targets against distractors (Todd & Hills, 2020), thus with better goal-directed abilities and accurate target representations, participants would indeed make less revisits and inspections, but more cued inspections.

Working memory was associated with success for cued inspections in Experiment 1, the number of patches inspected in Experiment 2 and 3, with higher exploitation associations in Experiment 3. Supporting the ability to manipulate, update and maintain information (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2021), working memory is considered necessary for the creation and maintenance of templates. In the present study, Experiment 3 revealed that when a template was not provided, working memory was associated with higher exploitation and patch inspections, however, Experiment 4 did not show any associations with working memory. This suggests that working memory supports search behaviour when conditions are easier but as the task becomes harder or uncertainty increases, other areas of cognition are relied upon (specifically executive functioning, as discussed above). Recent work has suggested that working memory is less efficient when feature binding is required (Kong & Fougnie, 2019), that no link has been found between working memory and foraging performance (Jóhannesson, Kristjánsson, & Thornton, 2017), and in a study assessing hybrid foraging ability between children and adults, similarities arose in single feature hybrid foraging but not conjunction of feature, which led the authors to suggest that executive function is essential to success, but not working memory (Ólafsdóttir, Gestsdóttir, Kristjánsson, 2021). As such, although working memory contributed to a few measures of success in the less effortful versions of the tasks, perhaps executive function contributes more greatly to search and foraging success, especially when greater cognitive control is required.

Spatial working memory revealed search and foraging success across all four experimental manipulations. Measures such as between- and within- patch organisation, exploitative tendencies, cued inspections, and lower revisits were all correlated with higher spatial working memory abilities. It has been noted across the literature the interdependent nature of spatial working memory and visual search (e.g. Kim, Kim & Chun, 2010; Takahashi & Hatakeyama, 2011), where environment exploration relies heavily on spatial working memory (Van der Stigchel & Hollingworth, 2018). Previous research has supported that in stationary VR tasks, successful organisation was dependent on spatial working memory (De Lillo, Kirby, & James, 2014). Further, in the present series of experiments, cued inspections, irrespective of template and distribution, were guided by spatial working memory abilities, where it has been shown that spatial working memory is required in order to discriminate targets from distractors (required for cued search; Anderson et al., 2010). Clearly, the present results follow the literature that spatial working memory is essential for search and foraging success.

The present series of experiments found support for reliance on episodic memory for two contrary experiments: Experiment 1 was defined by template provision and equal distribution whereas Experiment 4 did not provide a template and targets were unequally distributed. Wolfe (2021) suggested that episodic memory contributes to guiding search. It has also been proposed that target exemplars associated with search arrays, especially with real-world context, improves search, as guided by episodic memory (Võ & Wolfe, 2013). Based on the dissimilarities of the properties defining Experiments 1 and 4, it might be suggested that episodic memory is required for search distinguished by both template and distribution, or neither, but not one or the other. It has been posited that forms of search guidance including episodic memory, semantic memory, and templates can be in competition with each other, rather than work in conjunction, and that the area of cognitive strength with the strongest single signal dominates, hiding the contributions of the other regions (Võ & Wolfe, 2013). Therefore, perhaps when one is provided with a strong template (suggesting that the template load facilitated by working memory is lessened and the search process becomes more automated; i.e. Olivers et al., 2011) and continuous target reinforcement (e.g. the target is always present when expected) then episodic memory guides with greater signalling. Similarly, when no template has been created, with lack of reinforcement, episodic memory again predominantly guides. It has been proposed that episodic memory contributes to guiding successful search but only when there is a lack of other cues (Võ & Wolfe, 2015). The suggestion is that other forms of search guidance only support success when either a template is provided, or an equal distribution is ensured. It is clear further research is required to parse apart where the guiding principles underpinning episodic memory are in large-scale search success.

Interestingly, a slight relationship between verbal memory and search and foraging measures was found: participants in Experiment 4 were not shown to utilise verbal memory, however associations were found across Experiments 1-3. Specifically, when a template was provided (Experiments 1 and 2), participants employed immediate verbal memory, but only in the conjunction of feature conditions, whereas across Experiments 1-3, delayed memory was associated with success. Successful recall of delayed memory requires consolidation, which could also indicate a version of template consolidation in order to successfully search. Previous research has suggested that the process of consolidation includes forming working memory representations (Rideaux & Edwards, 2016), such as a template, and therefore better consolidation of the cued items may facilitate greater search. Verbal memory was associated with performance, suggesting that this ability may support in the formation of verbal representations of task instructions or verbal representations of target items. Alternatively, the CANTAB VPA is not a specific measure of verbal ability, where associative and episodic memory also contribute to task success. Perhaps the significant findings are identifying episodic contributions rather than verbal. Further research into verbal underpinnings of visual search and foraging is required to quantify the underlying mechanisms behind search, foraging, and verbal ability.

3.10 Conclusion

As has been shown, large-scale visually guided search reflects similar distinctions between single feature and conjunction of feature as two-dimensional visual search. It also reflects aspects of foraging such as idiothetic cues (etc.), which were shown not to diminish the utility of visually guided cues. Inspection of cued items was consistently greater for single feature than conjunction search, even when instructions or templates were not specified, suggesting that attentional systems drive search efficiency. Foraging behaviours (e.g. exploitation, within- and between-patch organisation, revisits) were associated with several different areas of cognition, such as spatial working memory, executive function, and working memory. It is noted that some previous visual search research has found a lack of evidence for the translation from two-dimensional to three-dimensional space (i.e. Baxter & Smith, 2022) implying that not all large-scale visual search paradigms provide support for the translation from two- dimensions to three-dimensions. Baxter and Smith (2022) did remark however that individual difference played a large role in search performance, and that results may differ depending on the search indices employed. As such, further research is clearly required to delve into what properties of search do indeed transfer into a large-scale space, as well as further investigation into what components are domain general. Understanding what mechanisms of visual search are (and are not) domain general will allow for a finer-grained understanding of visual search and foraging properties, as well as what aspects are key for success in fully motile, three-dimensional environments.

Chapter 4. Experiment 6

4.1 Introduction

Ageing carries great economic and social impact (ONS, 2019), fundamentally associated with the effects of cognitive decline (Deary et al., 2009). As discussed in *section 1.5,* research has identified age-related decrements in both visual search and foraging behaviour. Older adults have been shown to be less efficient (Zanto & Gazzaley, 2014), especially in conjunction tasks (Porter et al., 2010), often employing compensatory strategies that are still inefficient (Potter et al., 2012). Potter et al. (2012) used search times as a measure of search success in target present or absent trials, observing that all participants had a search time ratio of 2:1 target absent to present. However, further effects of age were noted: absent to present search time ratios increased with age from 1.74:1 for participants in their 20s to 2.14:1 for 80-year-olds. This was suggested to reflect a more cautious and compensatory search strategy unrelated to movement speed. These findings extend to the pathological ageing literature; for instance, Tales et al. (2011) found that visual search times were longer in patients diagnosed with amnestic MCI who later converted to a dementia diagnosis than the healthy controls or amnestic MCI who did not convert to dementia. Ramzaoui et al. (2018; 2022) noted that conjunction searching was disproportionately impaired in those diagnosed with AD, and Ramzaoui et al. (2018) posited that the attentional load associated with conjunction searching does not explain the disproportionate decrement between healthy adults and AD as single feature searching is preserved, but instead deficits were suggested to be due to binding difficulties.

Conversely, when accounting for slowed processing speed rather than compensatory mechanisms, others have suggested that older adults perform similarly to that of their younger counterparts (e.g. Agnew, Phillips, & Pilz, 2020; Aziz et al., 2021; Wiegand et al., 2019). Wiegand, Seidel, and Wolfe (2019) found that across measures such as false alarms, memory effects on set size based on the number of missed targets, average rate of collected targets, and transformed reaction time, there were few differences in behaviour apart from strategy (as discussed in *section 1.5.1)*. Further, in a search task where participants were required to find a naturalistic target (e.g. an earring) based on a primed target template in a two-dimensional task, Aziz et al. (2021) noted that younger adults had quicker reaction times in the search task than older adults, however both displayed similar patterns of search performance across both the single feature and conjunction conditions, suggested to reveal that search mechanisms were similarly guided between young and older adults. Therefore, although there is agreement across the literature that older adults are slower than younger adults affecting visual search speed, this does not extend to strategy, and although there may be differing underlying strategies in search between younger and older adults, this has been suggested to not reduce overall success.

Previous evidence from two-dimensional visual search tasks have revealed that younger adults conform to the optimality heuristic (Wolfe, 2013), whereby foraging efficiency (e.g. searching under correct verses incorrect locations) operates at an optimal level (Mata et al., 2009), with minimal revisits, and low inter-target latencies (i.e. Kristjansson et al., 2020). Changes in foraging behaviour have been associated with decreases in connectivity (especially in the frontal regions), alterations in microstructural connectivity, and regional volume loss of the white matter, and these have also been identified as neural markers of age-related impairment in other cognitive domains (Garcia-Alvarez et al., 2019; Stuss & Levine, 2002). Both typical and atypical ageing processes impact the prefrontal cortices responsible for executive function, influencing decision-making in foraging-like situations (Mata et al., 2013). Neurodegenerative disorders like AD or MCI, which are characterised by (amongst other things) deficits in attentional and visuospatial processing (Mata et al., 2013; McKhann et al., 2011; Ramzaoui et al., 2018), show that navigational and search deficits might precede episodic memory impairments (Coughlan et al., 2018). The foraging literature has supported claims that older adults use suboptimal compensatory strategies (e.g. Mata, Schooler, & Rieskamp, 2007; Mata, Wilke, & Czienskowski, 2009), where decrements in decision-making abilities defined poorer foraging performance. For example, Mata et al. (2009) employed a fishing task, finding that older adults (as compared to younger adults) were more conservative when deciding to switch from one patch to the next, leading to longer staying times in patches and therefore poorer performance, and Mata et al. (2007) suggested that older adults are adaptive to task manipulations but instead choose inappropriate strategies leading to poorer performance.

It is suggested that idiothetic cues (e.g. information derived from motor efference, proprioceptors, and vestibular signals; Hill et al., 2024) provide additional contributions, which older adults may be able to rely upon. Albeit in a spatial navigation task, it has been found recently that ambulatory contributions reduce ageing effects. Hill et al. (2024) compared a spatial navigation task on a computer screen and in immersive VR, finding that the magnitude of differences between older and younger adults was attenuated in immersive settings. However, age-related differences were not entirely erased, and it was suggested that differences in spatial precision persist. Further, Gazova et al. (2013), in their large-scale, idiothetic Morris Water Maze task, identified allocentric (world-centred), but not egocentric (body-centred), differences between younger and older adults, which they suggested to support a compensatory shift from hippocampal to non-hippocampal dependent strategy. This was evidenced by both age groups showing learning over time, where Gazova and colleagues (2013) noted that early-stage AD patients were not able to spatially learn whereas their cognitively healthy older adults did, therefore suggesting a point of differentiation. As such, whilst some support is provided for the idiothetic contributions older adults can benefit from, it is clear there are still gaps in the literature for contributions to search and foraging behaviour, as especially whether this persists through atypical ageing processes. Therefore, assessing differences in search and foraging decisions within a large-scale environment, alongside their cognitive foundations (particularly executive function and episodic memory) and structural integrity, can help identify age-related changes and their typicality, particularly in earlier stages of degradation processes.

4.1.1 Neural implications of ageing

As discussed in *section 1.5*, search and foraging behaviours might show differences in atypical ageing earlier than traditional behavioural markers (e.g. episodic memory, reductions in daily living skills; Apostolova, 2016). Ageing is associated with neural degradation, particularly in pathological processes. LC degradation is age-related, noted to sustain significant neuronal and volume loss as AD progresses (Jacobs et al., 2021), where the adaptive gain model typifies attentional control centred on the LC, which produces nearly all the brain's NE (Spreng & Turner, 2021). Not only have the loss of NE concentrations been identified in AD (Matchett et al., 2021), AD is characterised by abnormalities in tau protein (Wyatt et al., 2024). Earliest tau pathology originates from the LC (Mather & Harley, 2016), and thus deficits in the exploration-exploitation trade-off (Cohen, McClure, & Yu, 2007) and attentional regulation (Poe et al., 2020) are associated with the LC-NE network. As discussed in *section 1.6.2,* the adaptive gain model predicts greater exploitation bias in older adults due to the positive reward signalling that facilitates phasic attention from LC signalling. This promotes focussed attention, but also sustained bias, leading to exploitation. As tau pathology originates from the LC, and as a decline in executive functioning marks MCI and AD diagnosis (Kirova, Bays, & Lagalwar, 2015), this can be extended to suggest that neurodegenerative processes increase exploitative tendency. Older adults tend to be more exploitative than younger adults in foraging tasks (e.g., Lloyd et al., 2023; Mata et al., 2013; Wiegand, Seidel, & Wolfe, 2019), likely due to compensatory strategy adjustments. As such, the underpinnings of foraging success may reside in networks known to degrade with pathological ageing. Further, Spreng and Turner (2021) predicted a series of integrated pathways proposed to be associated exploitation bias in ageing. Specifically, the vmPFC combines past experiences (through its links to other default network regions) and emotional value information (through dopamine signals from the NA). Positive signals from the vmPFC to the attention modulation circuit, which includes the ACC and LC within the salience network, influence noradrenergic functioning and enhance focused attention.

Zhang et al. (2020) found that AD showed reduced signal variability in blood oxygenation (specifically brain-oxygen-level-dependent; BOLD signalling), especially in the posterior DMN, linked with poorer cognition and predictive of a steeper disease decline trajectory. MCI also showed reciprocal variability in resting state BOLD signalling within the default mode and salience networks, as compared to both AD and typically ageing adults, associated with poorer global cognition and faster cognitive decline, and suggested to represent compensatory behaviour before the functional networks break down and clinical progression towards AD begins (Zhang et al., 2020). Therefore, whilst individual difference of degradation is noted in neurodegenerative disease progression, there are underlying negative processes (e.g. demyelination, degradation) in consistent networks associated with search and foraging behaviours. Behavioural indicators of early AD have been found in preclinical populations (e.g. when one has begun to notice slight cognitive changes but no detectable behavioural changes) through navigational research (Bayat et al., 2021). Participants were monitored as they drove their personal vehicle for a month (measures included smoothness of driving, speeding, night trips, gyration radius, and trips shorter than one mile), and findings suggested driving space and performance were predictive of preclinical AD biomarkers (Bayat et al., 2021). Thus, spatial cognition research may reveal interactions between behavioural and cognitive changes earlier than other domains.

As highlighted in *section 3.9*, exploitative behaviour did not differ between template or distribution manipulations as expected. It was queried whether additional idiothetic contributions greatly assisted with success and whether measures to isolate the decision-making process might elucidate greater insight into the exploration-exploitation trade-off. Therefore, in the present experiment, a simple measure of the exploration-exploitation trade-off was implemented, allowing investigations into the explicit relationship between exploration and exploitation (Calhoun & Hayden, 2015) without idiothetic contribution. The "Leapfrog" task (Knox et al., 2012) offers only two possible rewarding actions, where the option with the greater reward alternates and thus 'leapfrogging' over the other. The participant has partial knowledge of the higher reward option, and so selecting the best option (i.e. higher reward; exploiting) gives little information but (potentially) greater reward, but one then gains information by exploring between the two options with the opportunity to incur cost (i.e. selecting the lower reward). It was suggested that the Leapfrog is a simple task to understand strategies and underpinnings of exploratory decision-making (Blanco et al., 2016), where Knox and colleagues (2012) found that participants updated their knowledge throughout their Leapfrog task where the rate of exploratory choices increased with the number of previously selected consecutive exploitation option. Applied to older adults to investigate the decision-making process in relation to cognitive decline, Blanco et al. (2016) found, akin to previous reports of age-related differences (as discussed in *section 1.5.3*; e.g. Mata et al., 2013), that older and younger adults employed different strategies, which ultimately led to suboptimal performance in the older adult cohort. This was suggested to provide an isolatable decision-making context when individuals are faced with numerous options to elucidate the trade-off between the desire to exploit a known reward against potentially beneficial information without including the necessity for idiothetic movement.

Experiment 6 was designed to explore the neural and cognitive underpinnings of search and foraging behaviour in adults ages 65 years and older. Informed by the experiments reported in Experiments 1-5, the findings from the young, healthy adult cohort guided the creation of a concise battery measuring foraging-like large-scale search and cognitive ability, which was then applied to a cohort of older adults. The present experiment was identical to Experiment 5 (i.e. the single feature array held a conjunction of feature stimuli), which allowed measurement of predictive features whilst controlling for the visual complexity of the array across conditions. Younger and older adults participated in an immersive VR paradigm defined by single feature and conjunction of feature visual properties with equally distributed hidden targets in a patchy array. It was anticipated that younger adults would show greater success (i.e. more targets collected, more cued inspections) than older adults, and success would be greater in the single feature condition than the conjunction condition across both cohorts. Further, it was predicted that younger adults would perform more successfully than the older adult cohort in measures of foraging, such as greater exploration and organisation. A Leapfrog task was designed and implemented to investigate the trade-off between exploration and exploitation without visual search or idiothetic contributions, and it was anticipated that older adults would be more exploitative than younger adults. All participants also underwent structural MRI to quantify white matter integrity associated with measures of performance and cognitive control, which was anticipated to allow for a deeper understanding of the relationship between foraging-like large-scale search behaviour and degrees or areas of degradation. Following the proposed integrated system associated with exploitation bias in older adults as discussed above (Spreng & Turner, 2021), the vmPFC, NA, ACC, and LC were selected as the key brain regions to investigate the underlying connections in search and foraging behaviours.

Understanding the interplay between cognitive function and neural underpinnings is crucial for identifying early markers of neurodegeneration. This Chapter aimed to explore the relationship between behaviour in the VR task, brain structure using DWI, and cognitive function. The VR task was designed to assess search and foraging behaviours, which were hypothesised to correlate with performance on cognitive function tests, specifically executive function, working memory, episodic memory, and spatial working memory. These cognitive functions are critical for everyday decision-making and adaptive behaviour. Therefore, it was anticipated that individuals who performed better on these tasks would also show higher white matter connectivity as measured by DWI, specifically between the vmPFC, NA, ACC, and LC regions. Spatial deficits often precede significant clinical impairment in neurodegenerative conditions such as MCI and AD and are linked to atrophy and neuronal loss (Li & King, 2019). Given that spatial abilities have been suggested as predictive and discriminatory in neurodegenerative processes (Laczó et al., 2011), elucidating these neural substrates through search and foraging success could provide insights into early markers of neurodegeneration. It was expected that younger adults would show greater structural integrity compared to older adults. Within the older adult group, variability in brain connectivity and structure was anticipated to correlate with differences in cognitive performance, such as fewer errors and greater task completions. It was also expected that behaviours such as greater cued inspections, and higher exploratory and organised behaviours would correlate with cognitive functions, and that these would be associated with greater connectivity DWI findings, elucidating the neural underpinnings of cognitive functions and behaviours. Differences in decision-making and success metrics in search behaviour across age groups, particularly in executive control, would help identify age-related changes. Thus, understanding how search and foraging success reflects these cognitive functions could reveal underlying neural substrates indicative of neurodegeneration.

4.2 Methodology

4.2.1 Participants

Two sets of participants were recruited for comparison: younger and older adults. The younger adult controls (YA; N = 45) were recruited for either course credit and travel compensation (4 course credits and £5) or monetary renumeration only (£40 per session). YA were aged between 18-35 (M = 23.87, SD = 3.88; female: N = 29, male: N = 16). YA were recruited through the University of Plymouth's participation pool, word-of-mouth, community poster pool, and research participation databases of the Plymouth area. Level of education was collected through the CANTAB application (see Table 4.1 for level description and participant demographics), where participants reported the highest level of formal educational qualification achieved. Most participants described being more strongly right lateralised (N = 43; left lateralised: N = 2) based on the Edinburgh Handedness Inventory (EHI), utilising a scoring system as suggested by Schachter (2000), described in *Chapter 2: General Methods*, to produce greater sensitivity to degree and direction of handedness preference. Older adult participants were recruited from the community through the University of Plymouth's Older-Adult Participant Group, the University of the 3rd Age, word-of-mouth, and community poster boards. Older adults (OA; N = 53, N = 5 exclusions) participated in the study. Five participants were excluded from analyses: two participants requested to stop participation during the VR task due to nervous feelings with the system, two participants "got bored" and requested to withdraw, and one participant dropped out between the first and second session. Therefore, of the resulting 48 participants, age ranged from 65-93 (M = 74.4, SD = 6.01; female: N = 29, male = 19), and received monetary renumeration (£40) for their time. 46 participants described being more strongly right lateralised (left lateralised: N = 2). Education varied amongst participants (see Table 4.1). OA participants were also provided a space to disclose any diagnoses should they choose, however this was optional and most participants wrote they had nothing to disclose.

Table 4.1. Self-reported level of education demographics across participants.

Level of education labels	**Younger adult N (%)**	**Older adult N (%)**
Left formal education before age 16	0 (0%)	7 (14.6%)
Left formal education at age 16	0 (0%)	3 (6.3%)
Left formal education at age 17-18	17 (37.8%)	10 (20.8%)
Undergraduate degree or equivalent	15 (33.3%)	22 (45.8%)
Master’s degree or equivalent	12 (26.7%)	5 (10.4%)
PhD or equivalent	1 (2.2%)	1 (2.1%)

Sample sizes were determined based on acquired funding for MRI access. Specifically, 30 hours of scanning time was funded by the University of Plymouth and the Brain Research and Imaging Centre (BRIC). The selected MRI protocol was determined to take 15 minutes per participant, with an additional five minutes per participant for screening and scanning preparation, and therefore to optimise scanning time it was determined that three participants per hour could be collected. This totalled 90 participants overall: N = 45 YA and N = 45 OA. Following, to verify participant power, a power analysis using G*Power (version 3.1.9.5) was conducted. Based on a 95% chance of detecting a medium effect size (f = 0.2; F test) for a repeated measure, between-within interaction, total sample size specified 84 participants. Thus, it was determined that power was sufficient to detect effects.

Each participant completed the MoCA. Based on the cut-off score as determined by Nasreddine et al. (2005), indicators of cognitive impairment are determined by an obtained score of 25 points or less out of 30. It was found that 71.1% of younger adults passed the MoCA (M = 26.47, SD = 2.69; total score range: 16-30). In the OA cohort, 54.2% met or exceeded the cut-off score (M = 25.65, SD = 2.96; total score range: 16-30). For further discussion of the MoCA scores between and within cohorts, and the implications of younger adult failure, see *Chapter 6.*

All participants were screened prior to participation for MRI and VR compatibility. Previous research has shown that OA are able to manage immersive and motile VR (e.g. McAvan et al., 2021; Merhav & Wolbers, 2019), which was indeed supported presently. The OA had no difficulty participating in immersive, motile VR. Before the session was scheduled, participants were asked to fill out an MRI pre-screening questionnaire (see Appendix B) to verify suitability. Additional questions were also asked: *1) Do you have normal vision or vision that can be corrected to normal with glasses or contact lenses? 2) Are you able to walk without assistance in a 10x10 metre space?* Any positive answers from the pre-screening questionnaire were sent to the radiographers for MRI compatibility verification. Any participant that had irremovable metal implants, were claustrophobic, were pregnant, or were unable to walk unassisted were not invited to participate in the study.

4.2.2 Design and procedure

Sessions lasted around two hours per participant. Approximately half of the participants in each cohort completed the full experiment in one session, the other half had their participation split across two sessions. This was due to participant fatigue, inconsistent wireless connection with the VR equipment, or laboratory availability. The order of tasks was counterbalanced across participants, also to maximise limited laboratory space and time. As such, three participants arrived simultaneously, and were ‘rotated’ around three lab spaces for data collection; two research assistants aided, one running the VR task and the second administering the CANTAB. The lead experimenter, this PhD candidate, was MRI safety trained and therefore conducted the MRI scanning facilitated by qualified radiographers. Participants undertook a Leapfrog task and brain MRI alongside demographics, MoCA, CANTAB and behavioural tasks as used in previous experiments.

The VR task was as described in *Chapter 3.* Experiment 5. All participants searched for hidden targets, where the target location was cued by the featural properties of the concealing containers, and a target was present under every cued container, across both single feature and conjunction conditions. The single feature *condition* was defined by two features (i.e. cyan and magenta ovals and triangular prisms), but the featural *cue* was defined by a single feature (colour *or* form; e.g. cyan coloured objects). The conjunction of feature trials, akin to Experiments 1-5, was defined by yellow and blue cups and boxes, and target location was defined by colour and shape. Participants were not provided with the features that cued the location of the target. Instructions were identical to those in Experiment 3, 4, and 5, and were located on the wall of environment. These read: *"You will now complete a series of trials. Each time, your task is to find as many hidden Red balls as possible. The balls change colour when found, so if you find a grey ball you have already searched there. You will have 60 seconds to complete each trial. Remember to search as efficiently as you can."* All participants completed a 60-second practice trial which consisted of two patches and single feature stimuli as described in *Chapter 3*, Experiments 1-4 (i.e. yellow and blue cups). The practice time of 30s was extended from Experiments 1-5 due to OA requirements. The first few OA who partook in the experiment required a second attempt at the practice to feel comfortable with the interactions, and therefore the practice was extended to 60s, and then there were no second attempt requests. Additionally, all participants were also administered the CANTAB, as described in *Chapter 2*. The order of tasks was conducted in the same order as Experiments 1-5, and all participants received the same battery.

Whole brain MRI was conducted on each participant, and regions of interest (ROI) were later derived. The regions selected were based on previous findings of neural markers for search and foraging success (e.g. Cohen, McClure, & Yu, 2007; Spreng & Turner, 2021; see *section 1.6.2*). As previously discussed, the adaptive gain model (Spreng & Turner, 2021) describes a model of attentional control where the LC displays phasic activation during exploitation but tonic activation with exploration, and the putative system implicated in exploitation bias derive on the default mode and salience networks. Therefore, regions of interest selected were the ACC, vmPFC, NA, and LC. However, neither Cohen et al. (2007) nor Spreng and Turner (2021), in their respective models of neural underpinnings of exploratory and exploitative behaviour, describe a connection between the LC and NA. Thus, due to the lack of evidence for a direct connection between the LC and NA, connectivity between these two nodes was not quantified.

4.2.3 Leapfrog

To understand the underpinnings of reward-based exploitation-exploration trade-off in a simple, two option decision-making task, a Leapfrog task was designed (see Figure 4.1 for a representation of trial structure). Known to be associated with the DMN due to the requirement to estimate the value of unknown options (Lloyd et al., 2023), the Leapfrog task was implemented to investigate the explicit relationship between exploration and exploitation without idiothetic contribution. The Leapfrog task has been suggested to provide an isolatable decision-making context differentiated by age, specifically for to older and younger adults (Blanco et al., 2016), and therefore this task was used to assess the simple strategies behind the exploration-exploitation trade-off. The Leapfrog task was presented to participants on a Phillips monitor. Participants were sat approximately 50cm from the screen, sized 47.5cm by

27cm, with a refresh rate of 60Hz and 1920 x 1080 resolution. Two options were presented, denoted by coloured buttons represented by two keyboard keys (see Figure 4.1). To select the leftmost option, green, participants had to press the "Z" key and to select the rightmost option, red, participants had to press the "M" key on the keyboard. Participants were verbally instructed to sit in front of the monitor and read the instructions. The task instructions explained that one option was always more valuable than the other, and that it would change over time, alternating superiority. The participants were unaware of which option was more valuable, and when it would change, but participants were instructed to gather as many points as possible. Payoffs began at 10 and 20 points; the lowest option would 'leapfrog' over the present highest option to become the new highest option, and thus increasing that option total by 20 points (see Figure 4.2). Volatility was high, meaning that the chance the lowest option would leapfrog over the other would happen frequently, setting the probability of the option switching to 0.125 (Knox et al., 2012). Participants were given 2s to respond, and if the time before response exceed 2s, then large red text reading "Too Slow" would appear on the screen (see Figure 4.1) and the trial was repeated. The task instructions, following a similar structure to that of Otto et al. (2014), specified: *"Welcome! The aim of this task is to get as high of a score as possible by pressing the Z or M key. Option Z and M will both keep getting more valuable over time. Option Z and M will take turns being the better option. The only way to know which option is currently better is by sampling the options. The better option will always give you 10 more points than the worse option. When the worse option becomes the better option, it will jump in value by 20 points. There will be a text pop up saying 'Choose' to let you know when you can press a button. You have a limited amount of time to press a key before time runs out, which is indicated by 'Too slow' text appearing. Good luck!"*. The experimenter answered any questions the participants had, and then the participant was verbally instructed to begin the task. There were 250 trials in total, and the task lasted approximately 10 minutes. Two measures were derived from the Leapfrog task as suggested by Knox et al. (2012) and Blanco et al. (2016) and were calculated as such: the sum of times the participant selected the same button consecutively (henceforth referred to as Lexploit for ‘Leapfrog Exploit’ to differentiate between the exploitation measure associated with the foraging task) and divided by the total number of responses made, and multiplied by 100, to create a percentage. Average reaction time was measured by the time it took for participants to respond to each option.

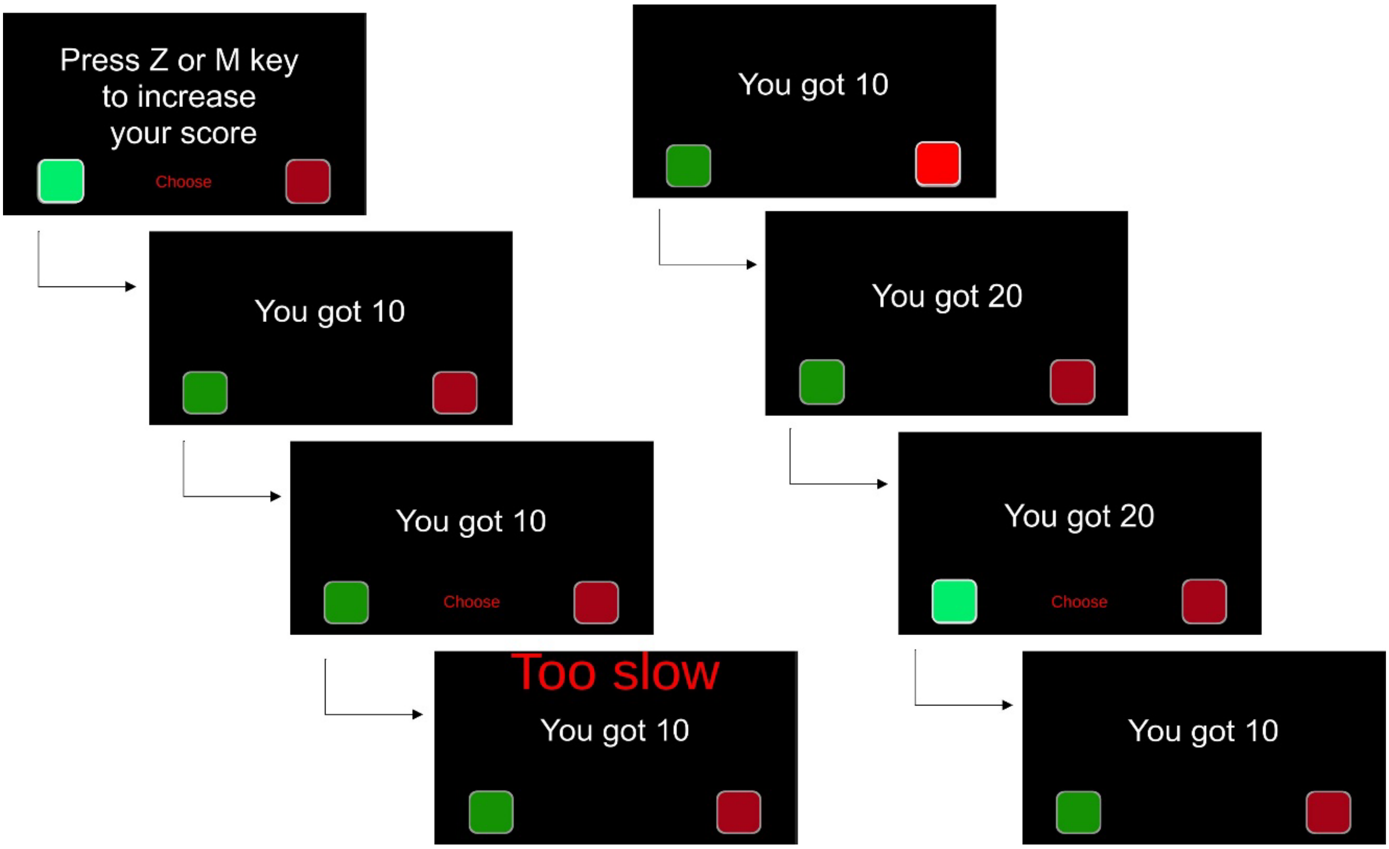

Figure 4.1. An example of the Leapfrog task; screens displayed in sequential order, left to right. Beginning by selecting one option (green; left), the lower reward of 10 points were gained. After being prompted by “Choose”, a non-response leads to a “Too Slow” warning. Selecting the alternate option (red; right) gained the higher reward of 20 points. Exploring again to left (green) option resulted in the lower reward.

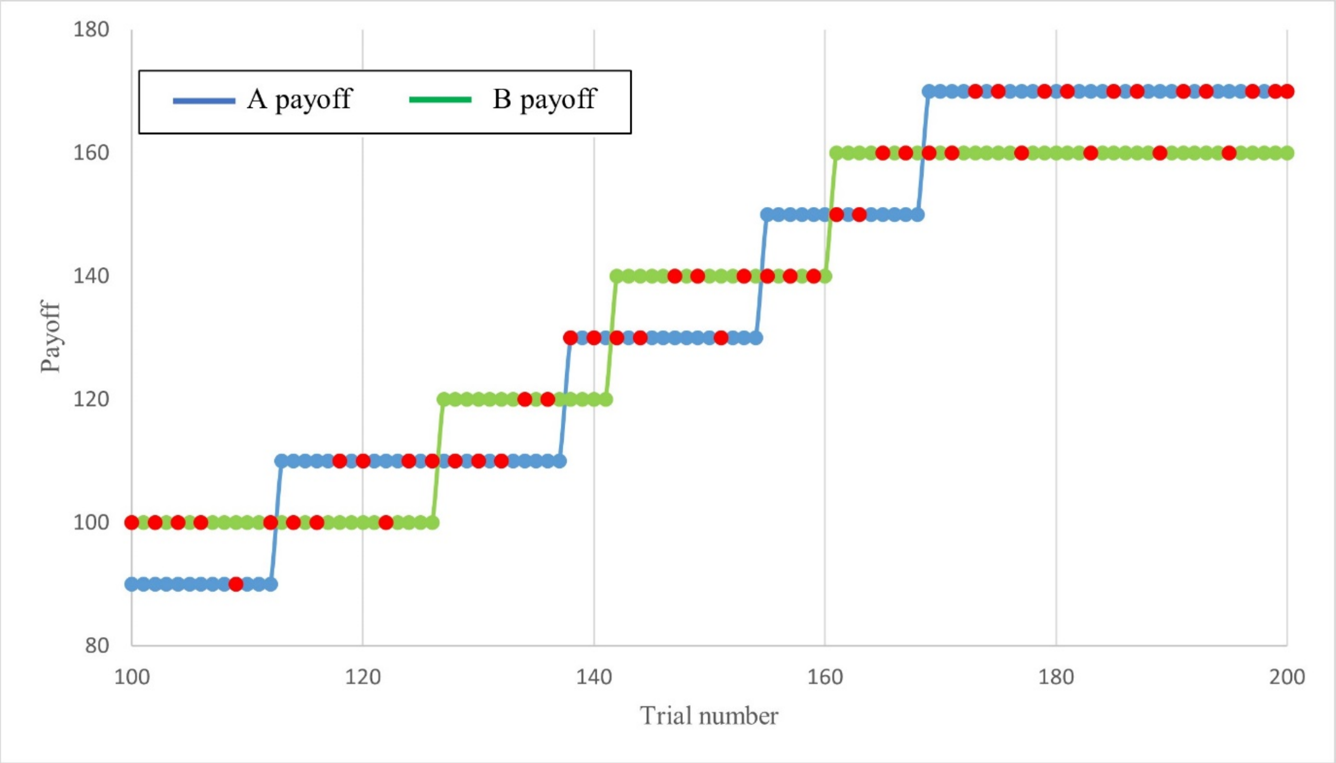

Figure 4.2. An example of one participant's responses over 100 trials. The blue and green lines denote the true payoffs for each option, and the red dots indicate the participant's responses.

4.2.4 Structural Magnetic Resonance Imaging (MRI)

Scanning protocol

Participants were scanned utilising a 3-Tesla Siemens Prisma (Magnetom Prisma, Siemens Healthineers) system at the BRIC. Participants were escorted into the MRI anteroom, where they were again screened by a qualified radiographer following the screening questionnaire (Appendix B). Three participants were excluded before data collection began due to undisclosed metal implants. If the participants passed the screen, the radiographer would then verify no metal remained on their person (i.e. keys, coins, jewellery, etc) and assist the participant into MRI scanner. Participants were laid in supine position, with a 32-element, head-only coil. Padding was placed to minimise movement, maximise comfort, and between two points of bare skin to prevent thermal burns (e.g. body-absorbed radio wave energy dispersed onto nearby fatty tissue resulting in a burn). Participants underwent T_1-weighted and Diffusion-weighted imaging (DWI); scan time lasted approximately 15 minutes. The radiologist visually inspected all scans immediately post-imaging to ensure no gross movement or image distortion were evident.

High-resolution structural T_1-weighted images were obtained using an MPRAGE sequence with the following contrast parameters: TR = 2100ms, TE = 2.26ms, TI = 900ms, voxel size = 1mm isotropic. The field of view was 256 x 256mm, the matrix was 256 x 256mm, and the thickness of the slices was 1.0mm, with 176 slices per slab, and scan time was 3.46min. Two sets of DWI scans were obtained. The first sequence ran an acquisition DWI scan with high spatial and angular resolution (TR = 3000ms, TE = 71.40ms, voxel size = 3mm isotropic, b = 1000 s/mm^2, 205 diffusion gradient directions). The second sequence acquired two unweighted volumes with reversed phase-encoding direction ("-PA") with near identical parameters (TR = 3000ms, TE = 71.40ms, voxel size = 3mm isotropic, b = 0 s/mm^2), to enable susceptibility and distortion correction.

Preprocessing

Each participant's diffusion-weighted data was first analysed separately using the University of Oxford's Centre for Functional Magnetic Resonance Imaging of the Brain (FMRIB) Software Library (FSL) release 6.0 (www.fmrib.ox.ac.uk/fsl; Smith et al., 2004). A binary brain mask was generated using the first non-gradient volume (i.e. b = 0) using the Brain Extraction Tool (BET). Data was corrected for head movement and eddy current distortions using Eddycorrect, aligning all volumes. DTIfit then was used to individually fit diffusion tensors per voxel, where the brain mask would limit fitting the tensors to brain space. DTIfit produced an FA voxelwise map (i.e. voxel-specific eigenvalues λ1, λ2, λ3 for each diffusion direction) per participant.

Probabilistic tractography

One way to post-process DTI data is probabilistic tractography, which has been suggested as a sensitive measure to simple and complex tract integrity (Behrens et al., 2007). Probabilistic tractography (PT) parameterises structural connectivity from a seed region, or between seed and target regions, by repeated iterations of a tracing algorithm which moves from voxel to voxel depending on the directional information contained within each voxel and the termination conditions (Hernandez-Fernandez et al., 2019). This results in a distribution of streamlines, enabling estimates of the likelihood of connections between two brain regions. This quantifies the confidence in regional connectivity (Kim et al., 2023). It has been suggested (Zhan et al., 2015) that PT, whilst being more computationally intensive, can be more robust to partial volume and uncertain fibre directions (which are both inevitable, to some degree) than other forms of tractography, for both imaging noise and pathological ageing. PT quantifies connectivity, and previous research has suggested that studies utilising diffusion imaging with PT are promising for detecting structural pathology changes early (as described by Kim et al., 2023). Tract-based analyses provide reproducible and generalisable biomarkers for AD identification, where other measures may be more susceptible to variation in individual fibre shape (Qu et al., 2023). Zhan et al. (2015) compared nine different tractography methods, finding that PT best identified changes in white matter integrity between MCI and controls. Therefore, probabilistic tractography was used for the present study to quantify connectivity between key nodes in a network of cortical regions and subcortical nuclei implicated in a leading model of the neural systems governing exploratory and exploitative behaviour (Spreng & Turner, 2021) in ageing adults.

PT was analysed separately, for each participant, using FMRIB's Diffusion Toolbox (FDT; Behrens et al., 2003) to produce a ROI-by-ROI connectivity matrix. ROIs were generated from seed, waypoint, and exclusions traced in standard MNI space. NA, vmPFC, and ACC masks were constructed from the Harvard-Oxford atlases (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006), utilising the ‘cingulate gyrus, anterior division’, ‘frontal medial cortex’, and left and right combined ‘accumbens’ regions, respectively (see Figure 4.3). The LC region was not available in the atlas, and therefore the LC mask was derived from Tona et al. (2017) by combining the traced regions from their two raters. Voxel sizes were resampled to fit the present data (0.5x0.5x0.5 to 2x2x2). This was thresholded at 0.2 to encompass the same extent covered in the original data. Diffusion parameters were first estimated for each voxel using BEDPOSTX, which generated a probability diffusion function for the primary direction of diffusion. PROBTRACKX then estimated the distribution of connections between each ROI in the network analysis (see below for greater detail). To create the connectivity distribution, 5000 streamlined samples started from each voxel within the seeded regions, moving from voxel to voxel (steplength_0.5, curvature threshold_0.2) until conditions were satisfied for termination. Connectivity values were obtained for each target region that represented how many streamlined samples from a seed region terminated in that target region. Each region was seeded to measure connectivity in both directions (e.g. ACC to vmPFC, vmPFC to ACC). PT was quantified by the number of successful streamline completions averaged across directions (e.g. seed to target; ACC to NA averaged with NA to ACC). This provided a clear metric to compare YA and OA cohorts.

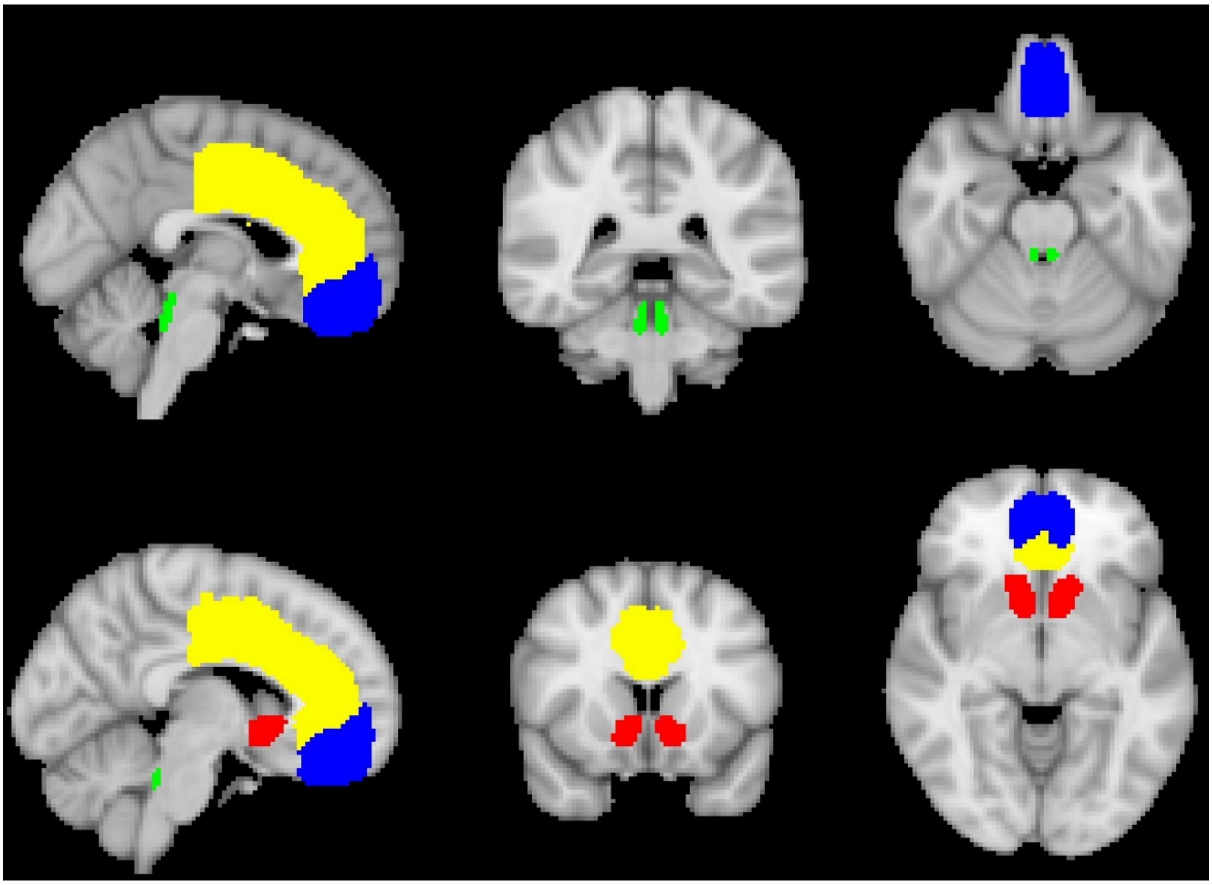

Figure 4.3. Masks used to define probabilistic tractography seed and waypoint regions. Yellow depicts anterior cingulate cortex (ACC); blue represents ventral medial prefrontal cortex (vmPFC); green represents locus coeruleus (LC); red depicts nucleus accumbens (NA).

A final measure of connectivity derived was quantifying FA and MD values throughout the PT distribution. FLIRT was used to register the individual FA and MD volumes to MNI152 space. The individual PT distributions were then thresholded at 15% of a robust range of nonzero voxels, leaving only voxels with a high likelihood of seed connectivity success (Bennett et al., 2012) and used to mask the FA and MD volumes, from which summary statistics were extracted.

Tract-based integrity measures

Mean and standard deviation FA values were calculated for the body, genu, and splenium tracts of the corpus callosum as previous research suggests these tracts are predictive of visual search performance in OA (Bennett et al., 2012). The corpus callosum connects brain regions involved in attentional function, essential for visual search success (Bennett et al., 2012), and OA have been shown to have reduced connectivity in such tracts, especially relative to other brain regions (Bennett et al., 2014). It has been noted that microstructural changes to areas of the corpus callosum are age-related and specific. For example, research suggests that white matter degradation progresses anterior to posterior as one ages (Sullivan & Pfefferbaum, 2006) and therefore such observations may provide a baseline for identifying abnormalities in the brain (Lebel, Caverhill-Godkewitsch, & Beaulieu, 2010). Voxelwise statistical analysis of the FA data was carried out using Tract-Based Spatial Statistics (TBSS; S. Smith et al., 2006), part of FSL (Smith et al., 2004), to sample from the centre of white-matter tracts and avoid other tissue or cerebrospinal fluid. FA images were first created by fitting a tensor model to the raw diffusion data using FDT, and then brain-extracted using BET (Smith, 2002). All participants' FA data were then aligned into a common space using the nonlinear registration tool FNIRT (Andersson et al., 2007a; 2007b), which uses a b-spline representation of the registration warp field (Rueckert et al., 1999). Then, the mean FA image was created and thinned to create a mean FA skeleton which represents the centres of all tracts common to the group. Each subject's aligned FA data was projected onto this skeleton and the resulting data fed into voxelwise cross-subject statistics.

Mean FA values were also calculated for all tracts, per participant. The binarised thresholded tracts were mapped per individual onto each FA map, which allowed for an averaging of FA values for tract-based voxels. From this, MD could also be derived by multiplying thresholded tracts by individual diffusion maps. This allowed for the mean and standard deviation, per participant, for both FA and MD values to be obtained, across all tracts.

4.2.5 Analysis

The behavioural variables are as described in the *section 2.4*: the search variables are defined by the participant's score, percentage of cued inspections, total inspections, and the number of patches visited. Foraging variables were quantified by within- and between- patch best-*r*, exploitation, and percentage of cup and patch revisits. Exploitation rates were calculated on the basis of cued objects searched before a switch to a new patch. Percentage of revisits is the percentage of erroneous visits to a previously visited item or patch per trial. It was determined in *Chapter 3* that item revisits did not require further investigation due to the low occurrence. However, in the present experiment, item revisits occurred at a greater frequency. Specifically, whilst the percentage of revisits across both cohorts was relatively low, the minimum and maximum percentage of patch and item revisits were high, and therefore determined to require further investigation. Across all trials, item revisits in the younger adult cohort revealed a higher percentage of revisits in the single feature (M = 5.15%, SD = 7.72%; min = .42%, max = 52.40%) and conjunction (M = 4.50%, SD = 3.33%; min = .66%, max = 14.51%) condition than identified in *Chapter 3*. Further, Smith et al. (2008) found that in their large-scale task, participants revisited locations only 1.4% of the time, less frequently than identified in previous two-dimensional search tasks. Thus, present revisits were subjected to further analysis. Similarly, across all trials, item revisits in the OA cohort revealed individuals with high percentages of revisits in the single feature (M = 4.55%, SD = 8.52%; min = 0%, max = 56.67%) and conjunction (M = 3.34%, SD = 2.66%; min = 0%, max = 14.06%) condition.

Mixed-design 2 (age: young, old) x 2 (condition: single feature, conjunction of feature) ANOVAs were employed to analyse significance difference between age groups and task conditions, as were linear regressions to understand success over the course of the task. Between-subject t-tests were employed to assess the differences between the two age groups on performance-related variables, learning over time, and neural substrates. As exploratory measures, Pearson's correlations were used to identify significant relationships between behavioural variables from the large-scale search task and cognitive performance, and ANCOVAs were utilised to assess processing speed contributions to OA results, where both reaction time and movement time were added as covariates to search and foraging measures to assess success alongside physical contributions.

4.2.6 External variables

To ensure that no effect was present due to counterbalancing or participant demographics, tests of between-subjects effects were run to compare counterbalancing conditions, gender, handedness, and level of education. One dependent variable, the number of targets found, was selected to compare for effects, run for both the single feature and conjunction of feature conditions. For the single feature, and conjunction of feature conditions, respectively, for each independent variable, no effects were found for counterbalancing (p = .083; p = .15), gender (p = .49; p = .56), level of education (p = .42; p = .25), or handedness (p = .63; p = .81).

4.3 Results

4.3.1 Behavioural data

To compare performance between the two cohorts, a series of 2 (Condition: Single feature, conjunction) x 2 (Age group: younger, older) mixed-design ANOVAs were conducted (see Table 4.2). To interpret significant interactions, where appropriate, post-hoc analyses with Bonferroni correction were conducted. Note that were no two-way interactions.

Table 4.2. *F*-ratio results from mixed-design ANOVA between younger and older adults.

	Condition	**Age Group**	**Condition x Age Group**
Score (total number of targets found)	3.79	33.17**	.64
Percentage of cued inspections	.63	1.74	.03
Total inspections	.01	28.97**	.04
Number of separate patches inspected	5.35*	27.33**	.26
Within-patch best-*r*	.10	.75	.01
Between-patch best-*r*	1.41	.78	.00
Exploitation	39.92**	.004	2.24
Percentage of cups revisited	1.74	.69	.16
Percentage of patches revisited	6.80*	1.70	1.60

NB. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **

The number of targets collected significantly differed between age groups where YA (M = 42.21, SD = 2.39) collected more targets than OA (M = 23.05, SD = 2.31, $p < .001$). There was no effect of condition on score. YA (M = 63.45, SD = 3.39) also made more total inspections than OA (M = 38.08, SD = 3.28, $p < .001$), with no effect of condition. More patches were inspected in the conjunction (M = 7.26, SD = .39) than the single feature (M = 6.39, SD = .36, $p = .023$) condition, and YA (M = 8.52, SD = .47) inspected more patches than OA (M = 5.12, SD = .45, $p < .001$). It was found that participants were more exploitative in the single feature (M = 90.25%, SD = 2.44%) condition than the conjunction (M = 74.75%, SD = 2.10%, $p < .001$) condition, however exploitative preferences did not differ between age groups. A greater percentage of revisits to previously inspected patches occurred conjunction of feature (M = 5.15%, SD = .78%) conditions over single feature (M = 3.60%, SD = .45%, *p* = .011), however again age group did not differ.

To disentangle whether the significant differences identified were due to reaction or movement time deficits as an aspect of ageing, ANCOVAs were run for each measure that was significant for age group using RTIFMMT (movement time) and RTIFMRT (reaction time) as covariates (see Table 4.3). Between-subjects effects revealed that all interactions were still significant for age group, where reaction or movement time did contribute to some factors, however as evidenced by the partial eta squared, very little variance was accounted for. This indicates that benefits or decrements in reaction time or movement time did not greatly contribute to differences identified between YA and OA.

Table 4.3. *F*-ratio and partial eta squared for between- and within- subjects effects of covariate contributions to the significant measures between younger and older adults.

	RTIFMRT		Condition		Condition x RTIFMRT		Condition x Age	
	F	η_p^2	*F*	η_p^2	*F*	η_p^2	*F*	η_p^2
Number of targets collected	2.19	.024	4.73*	.05	3.92	.042	.32	.003
Total number of cup inspections	.076	.001	3.41	.037	3.41	.036	1.62	.018
Total number of patch inspections	7.04*	.073	1.48	.016	2.15	.023	1.68	.018
	RTIFMMT		Condition		Condition x RTIFMMT		Condition x Age	
	F	η_p^2	*F*	η_p^2	*F*	η_p^2	*F*	η_p^2
Number of targets collected	5.27*	.055	1.38	.015	.57	.006	.054	.001
Total number of cup inspections	3.54	.038	.16	.002	.15	.002	.14	.002
Total number of patch inspections	4.99*	.053	.52	.006	1.63	.018	1.30	.014

NB. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **

4.3.2 Individual differences in younger and older adults

Pearson’s *r* correlations between the behavioural measures and measure of cognition for the younger adult cohort are displayed in Table 4.4 and Table 4.5. Note that none of the cognitive measures significantly correlated with either measure of within-patch best-*r* or between-patch best-*r* across both conditions. In the younger adult cohort, several cognitive measures including fewer reaction time errors, greater episodic memory, and greater executive functioning ability were associated with greater target collection in the single feature condition. The single feature condition also revealed a greater percentage of cued inspections and total inspections in association with fewer reaction time errors, greater episodic memory, greater executive functioning ability, and greater spatial working memory. Item revisits identified greater revisits correlating with greater episodic and spatial memory errors, as well as longer executive function latency. The total number of patches inspected were correlated with faster reaction times, greater episodic memory, and greater executive function but lower latency. Exploitation in the single feature condition revealed significant relationships with movement time, episodic memory errors, executive function latency, and verbal memory ability. Finally, higher patch revisits were associated with greater spatial memory errors. YA scores in the conjunction condition similarly showed that the greater number of targets collected was correlated with faster movement time, as did the number of total inspections. Greater item revisits were associated with lower episodic working memory ability. Greater total patch inspections correlated with faster movement time, and more patch revisits were associated with high movement times, greater spatial memory errors, and greater working memory.

Table 4.4. Pearson's *r* correlations between measures of memory (episodic, verbal, working, and spatial) and visual search and foraging variables in the young adult cohort.

	PALTEA SF/CoF	PALFAMS SF/CoF	PALTE SF/CoF	VPAER TOT SF/CoF	VPAMW DST SF/CoF	DGSFMAXP SF/CoF	SWMTE SF/CoF	SWMBE SF/CoF	SWMDE SF/CoF
Score	.32*/.19	.32*/.16	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Total Inspection	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Percentage Cued	.35*/.19	.35*/.13	*NS*	*NS*	*NS*	*NS*	-.40**/ -.17	.35*/.19	*NS*
Number of patches	.33*/.02	.33*/-.02	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Exploit	*NS*	*NS*	-.19/-.34*	-.16/ -.34*	.10/.31*	*NS*	*NS*	*NS*	*NS*
Cup Revisit	-.28/ -.42**	-.20/-.34*	.37*/ .43**	*NS*	*NS*	*NS*	.30*/.25	*NS*	*NS*
Patch Revisit	*NS*	*NS*	*NS*	*NS*	*NS*	.19/.32*	*NS*	*NS*	.33*/.34*

NB. SF = single feature condition; CoF = conjunction of feature condition; *NS* = non-significant correlation between single feature or conjunction condition. * indicates *p* < .05, ** indicates *p* < .001

Table 4.5. Pearson's *r* correlations between measures of executive function and attention, and visual search and foraging variables in the young adult cohort.

	RTIFMRT SF/CoF	RTIFMMT SF/CoF	IEDEEDS SF/CoF	IEDYERTA SF/CoF	IEDTT SF/CoF	IEDTL SF/CoF
Score	-.32*/-.11	-.50**/-.49**	.31*/.04	.31*/.26	*NS*	-.41**/-.16
Total Inspection	*NS*	-.45**/-.42**	*NS*	*NS*	*NS*	*NS*
Percentage Cued	-.39**/-.11	-.34*/-.13	*NS*	.32*/.17	-.31*/-.17	-.33*/-.1
Number of patches	-.32*/-.05	-.50**/-.40**	.31*/-.05	*NS*	*NS*	-.40**/-.07
Exploit	*NS*	-.28/-.31*	*NS*	*NS*	*NS*	.004/-.35*
Cup Revisit	*NS*	*NS*	*NS*	*NS*	*NS*	.46**/.15
Patch Revisit	*NS*	.24/.32*	*NS*	*NS*	*NS*	*NS*

NB. SF = single feature condition; CoF = conjunction of feature condition; *NS* = non-significant correlation between single feature or conjunction condition. * indicates $p < .05$, ** indicates $p < .001$

Pearson's *r* correlations between the behavioural measures and measure of cognition for the OA cohort are displayed in Table 4.6 and Table 4.7. The OA's score identified greater working memory in the single feature condition, as did the total number of items inspected. A greater percentage of cued inspections revealed associations with faster movement speed, higher pattern count in episodic memory, and greater executive function errors. The greater number of patches visited were associated with faster reaction speed and greater working memory. Age was also included as it has been shown that there are significant cognitive differences between 65-years-old and 93-years-old (Small, Dixon, & McArdle, 2011). Participant age was correlated with fewer number of targets collected, fewer patches visited across both conditions, and fewer total inspections, where greater age indicated decrements in success. Higher exploitation was associated with fewer episodic memory errors. Higher patch revisits were related to faster movement time. Similarly, a greater percentage of cued inspections in the conjunction condition revealed significant correlations with faster reaction time and higher episodic memory. The greater number of patches visited were associated with faster reaction speed and greater working memory. Greater between-patch organisation revealed that verbal working memory ability was associated with fewer errors but greater difficulty success. A higher percentage of cup revisits were correlated with less movement time but higher reaction time errors. Higher exploitation was associated with lower executive function latency. Finally, increased age was associated with decreased organisation.

Table 4.6. Pearson's *r* correlations between measures of memory (episodic, verbal, and working) and visual search and foraging variables in the older adult cohort.

	PALTEA SF/CoF	PALNPR SF/CoF	PALTE SF/CoF	VPAERTOT SF/CoF	VPAMWDST SF/CoF	VPAMWDSD SF/CoF	DGSFMAXP SF/CoF
Targets collected	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	.29*/.19
Total Inspection	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	.35*/.23
Percentage Cued	.25/.32*	.36*/.39**	*NS*	*NS*	*NS*	*NS*	*NS*
Number of patches	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	.37*/.30*
Within-patch best-*r*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Between-patch best-*r*	*NS*	*NS*	*NS*	-.10/-.29*	.13/.32*	.06/.34*	*NS*
Exploit	*NS*	*NS*	-.29*/-.21	*NS*	*NS*	*NS*	*NS*
Cup Revisit	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Patch Revisit	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*

NB. SF = single feature condition; CoF = conjunction of feature condition; *NS* = non-significant correlation between single feature or conjunction condition. * indicates $p < .05$, ** indicates $p < .001$

Table 4.7. Pearson's *r* correlations between measures of executive function and attention, and visual search and foraging variables in the older adult cohort.

	RTIFMRT SF/CoF	RTIFMMT SF/CoF	RTIFES SF/CoF	IEDEEDS SF/CoF	IEDTL SF/CoF	Age SF/CoF
Targets collected	*NS*	*NS*	*NS*	*NS*	*NS*	-.45**/-.29*
Total Inspection	*NS*	*NS*	*NS*	*NS*	*NS*	-.46**/-.24
Percentage Cued	-.40**/-.35*	*NS*	-.26/-.35*	.35*/.28	*NS*	*NS*
Number of patches	-.33*/-.31*	*NS*	*NS*	*NS*	*NS*	-.53**/-.43**
Within-patch best-*r*	*NS*	*NS*	*NS*	*NS*	*NS*	.01/-.38**
Between-patch best-*r*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Exploit	*NS*	*NS*	*NS*	*NS*	-.21/-.41*	*NS*
Cup Revisit	*NS*	-.21/-.32*	.15/.29*	*NS*	*NS*	*NS*
Patch Revisit	*NS*	-.36*/-.22	*NS*	*NS*	*NS*	*NS*

NB. SF= single feature condition; CoF = conjunction of feature condition; *NS* = no significant correlation between single feature or conjunction condition. * indicates $p < .05$, ** indicates $p < .001$

4.3.3 Learning slope

Traditional analyses of visual search behaviour conducted linear regression on performance over time (e.g. Wolfe, 2020). To understand trial-by-trial success, each dependent variable was subjected to a linear regression by trial number. Regression analyses were specifically selected to assess the individual trial-by-trial effects to elucidate the learning slope over the ten trials for each condition. This provides a comprehensive understanding of how search behaviour evolves over time, identifying trends or patterns. *F*-statistics for each behavioural measure are reported in Table 4.8. Then, between-subjects t-test were used to understand whether differences existed over a trial-by-trial basis between YA and OA. As such, each trial per behavioural measure was used as a separate observation, averaging each performance measure per participant, with Bonferroni corrections. This approach ensured respect of statistical assumptions of each test and avoided issues of multiple comparisons and dependent observations. Therefore, for the regressions that rose to significance (Table 4.8), between-subjects t-test were run to understand whether differences existed over a trial-by-trial basis between groups. Between-subjects t-test revealed that YA collected significantly more targets than OA over trials in both single feature (young: M = 44.57, SD = 28.02; old: M = 24.41, SD = 17.98; *t*(928) = 13.14, *p* < .001, *d* = .86) and conjunction (young: M = 40.04, SD = 21.88; old: M = 22.45, SD = 11.52; *t*(928) = 15.47, *p* < .001, *d* = 1.02) conditions. YA made significantly more item inspections over trials than OA in the single feature (young: M = 63.37, SD = 30.35; old: M = 38.31, SD = 21.14; *t*(928) = 14.69, *p* < .001, *d* = .96) and conjunction (young: M = 63.53, SD = 33.67; old: M = 38.41, SD = 20.58; *t*(928) = 13.82, *p* < .001, *d* = .91) condition. YA also made a greater percentage of cued inspections over trials than OA across both the single feature (young: M = 70.75%, SD = 23.77%; old: M = 64.32%, SD = 21.47%; *t*(928) = 4.33, *p* < .001, *d* = .29) and conjunction (young: M = 66.79%, SD = 23.00%; old: M = 62.90%, SD = 21.02%; *t*(928) = 2.70, *p* = .007, *d* = .18) conditions (see Figure 4.4). YA inspected significantly more patches over trials in single feature (young: M = 7.99, SD = 4.33; old: M = 4.79, SD = 3.56; *t*(928) = 12.36, *p* < .001, *d* = .81) and conjunction (young: M = 9.06, SD = 4.90; old: M = 5.46, SD = 2.87; *t*(928) = 13.73, *p* < .001, *d* = .90) searches. In terms of the foraging measures, within-patch organisation did not differ across trials. Between-patch organisation significantly differed over trials, but younger and OA did not differ in performance in either the single feature (young: M = .60, SD = .30; old: M = .63, SD = .33; *t*(928) = -1.34, *p* = .18, *d* = -.09) or conjunction (young: M = .62, SD = .29; old: M = .65, SD = .32; *t*(928) = -1.38, *p* = .17, *d* = -.09) condition. In the conjunction condition only, percentage of exploitation significantly differed over trials, however younger (M = 10.57%, SD = 8.77%) and OA (M = 11.31%, SD = 8.68%; *t*(928) = -1.29, *p* = .20, *d* = -.08) did not differ in performance. Finally, in the conjunction condition only, YA (M = 4.64%, SD = 6.22%) made significantly more item revisits over trials than OA (M = 3.55%, SD = 6.12%; *t*(928) = 2.68, *p* = .007, *d* = .18).

Table 4.8. Regression analyses reporting the *F* ratio and r^2 for each search and foraging measures for single feature and conjunction conditions, analysing the success of each variable over time on a trial-by-trial basis across whole cohort.

	Single feature		**Conjunction of feature**	
	F	r^2	*F*	r^2
Targets collected	40.83**	.042	26.14**	.027
Total Inspection	25.99**	.027	10.88**	.012
Percentage Cued	45.87**	.047	13.91**	.015
Number of patches	44.29**	.046	12.23**	.013
Within-patch best-*r*	.20	.00	2.91	.003
Between-patch best-*r*	4.93*	.005	4.16*	.004
Exploit	.00	.00	20.48**	.022
Cup Revisit	.051	.00	7.97*	.009
Patch Revisit	.412	.00	.06	.00

NB. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **

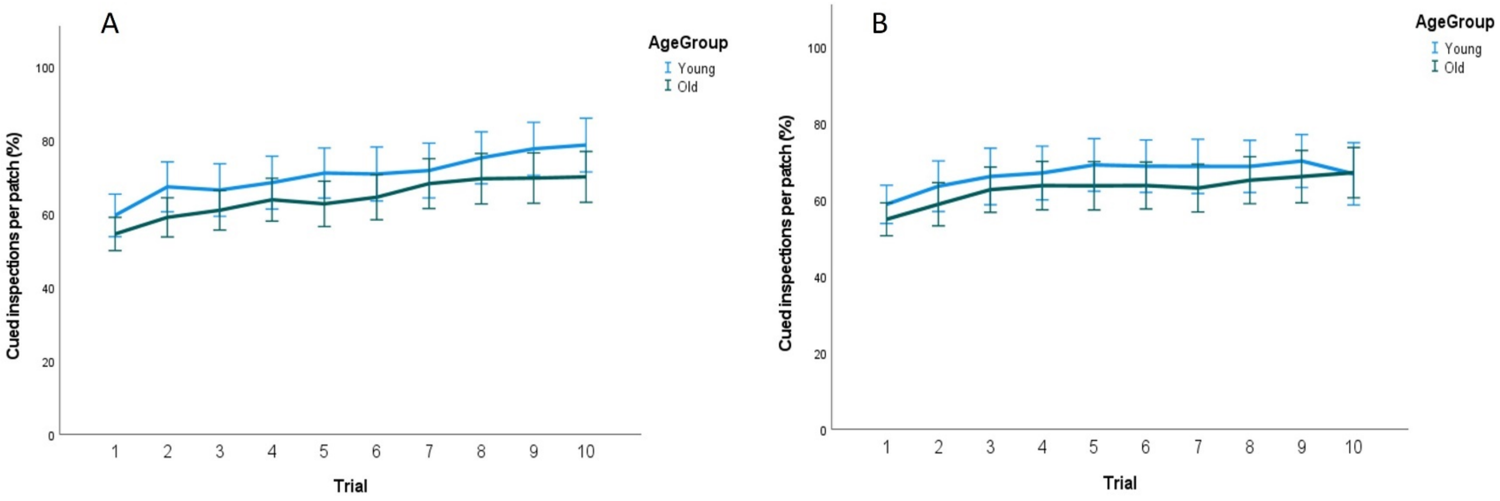

Figure 4.4. Percentage of cued inspections per patch across trials between younger (blue) and older (green) adults for: A) single feature condition; B) conjunction of feature condition. Errors bars are at 95% confidence interval.

To further assess how learning over time was affected by measures of cognition, the *r*-coefficient from each regression was subjected to bivariate correlations against the cognitive and connectivity measures (*nb* a higher *r*-value would indicate more rapid learning across the ten trials). This was to create a single variable of learning slope to correlate against cognitive measures. Correlations revealed several relationships between cognition, connectivity, and learning over time. Tables 4.9 and 4.10 display the correlations for YA, and Tables 4.11 and 4.12 show the OA correlation for significant dependent measures across cognitive and neural predictors.

Table 4.9. Pearson's *r* correlation matrix for younger adults indicating significant relationships between measures of learning slope across trials and cognitive measures of individual difference.

	Within patch CoF	Score SF	Score CoF	Cup Inspect SF	Cup Inspect CoF	Percent Cued SF	Percent Cued CoF	Patch visits CoF	Exploit SF	Exploit CoF	Cup Revisits CoF
Age	-0.01	0.16	0.04	0.12	0.04	.40**	0.03	-0.02	0.03	0.00	0.11
RTIFMRT	0.03	-.36*	-0.08	-0.28	0.18	0.20	-0.23	-0.12	0.18	-.40**	0.27
RTIFES	-0.21	-.476**	-0.11	-.382**	-0.18	0.07	-0.05	-.46**	-.29*	-.55**	0.02
PALTEA	0.02	0.17	-.351*	-0.03	-.31*	0.08	0.22	0.27	-0.10	0.12	0.05
PALFAMS	-0.02	0.20	-.352*	0.01	-.30*	0.06	0.20	0.26	-0.11	0.13	0.11
IEDEEDS	-.31*	0.21	0.23	0.19	0.04	-0.04	0.10	0.09	0.13	0.09	-0.12
IEDYERTA	-0.27	0.29	-0.03	.31*	-0.05	0.05	.31*	-0.03	0.11	0.28	-0.06
IEDTT	0.01	-.32*	-0.04	-0.26	0.02	-0.07	-0.16	-0.08	-0.05	-.31*	.31*
IEDTTA	0.23	-.30*	0.06	-.34*	0.05	-0.05	-0.28	0.03	-0.11	-0.28	0.06
VPAERTOT	-0.01	-.33*	0.05	-0.29	0.10	0.07	0.00	-0.11	0.02	-0.23	-0.13
VPAMWDST	0.00	.29*	-0.17	0.26	-0.24	-0.13	-0.04	0.24	-0.04	0.28	0.17
VPAMWDSD	0.12	0.23	-0.15	.29*	-0.22	-0.06	-0.08	0.24	0.04	0.08	0.16
SWMWE	0.02	0.15	-.32*	-0.17	-0.11	.40**	-0.19	0.13	-0.13	-0.07	-0.02
SWMDE	0.08	0.15	-.31*	-0.11	-0.04	.40**	-0.25	0.08	-0.17	-0.07	-0.03
SWMS	-.34*	0.16	-0.03	0.00	-0.11	0.11	0.12	0.26	-0.14	0.13	0.12

NB. * indicates $p < .05$, ** indicates $p < .001$. SF = single feature condition, CoF = conjunction of feature condition.

Table 4.10. Pearson's *r* correlation matrix for younger adults indicating significant relationships between measures of learning slope across trials and neural predictors.

	Within patch SF	Between patch CoF	Score CoF	Cup Revisits CoF
NA_ACC	-.38*	0.10	-0.25	0.07
NA_vmPFC	-.35*	-0.05	0.14	0.06
ACC_vmPFC	-.45**	0.07	0.20	-0.06
vmPFC_LC	-0.16	-.30*	0.04	0.26
mean FA	.37*	0.21	0.11	-0.16
mean MD	0.00	-0.09	-.38*	.32*

NB. * indicates $p < .05$, ** indicates $p < .001$. SF = single feature condition, CoF = conjunction of feature condition.

Table 4.11. Pearson's *r* correlation matrix for older adults indicating significant relationships between learning slope across trials and cognitive measures of individual difference.

	Within patch CoF	Between patch SF	Score SF	Score CoF	Cup Inspect SF	Cup Inspect CoF	Percent cued CoF	Patch visit SF	Patch visit CoF	Exploit CoF	Cup Revist SF
Age	-0.06	-0.01	-0.17	-0.13	-0.15	-0.01	-0.18	-.41**	-.41**	-0.11	-0.13
RTIFMRT	0.06	-0.15	-0.18	-0.04	-0.23	0.10	-.37**	-0.22	-0.22	0.19	-0.24
PALNPR	-0.15	0.01	0.21	0.17	0.10	0.04	.32*	.31*	.31*	0.23	0.16
IEDEEDS	-.39*	.42**	0.29	0.27	0.22	0.03	0.08	.31*	.31*	0.15	-0.10
IEDYERTA	-0.23	0.09	-0.06	.38**	-0.03	.29*	0.01	-0.04	-0.04	-0.02	-0.08
IEDTTA	0.2	-0.00	0.13	-.38**	0.14	-.29*	0.01	0.06	0.06	0.04	0.05
IEDTL	-0.02	-0.07	0.03	-.42*	-0.25	-0.13	-0.26	-0.03	-0.03	-0.25	-0.35
VPAERTOT	-0.08	0.12	-0.09	-.32*	-0.07	-0.17	-0.20	-0.20	-0.20	-0.19	-.39**
VPAMWDST	0.08	-0.17	0.05	.33*	0.07	0.26	0.05	0.15	0.15	0.21	0.24
DGSFMAXP	-0.10	0.25	0.28	.38**	0.19	0.17	.29*	.33*	.33*	0.25	0.16
VPAERSDR	-0.01	-0.03	-0.19	-.35*	-0.22	-0.23	-0.17	-0.20	-0.20	-.33*	-.37**
VPAMWDSD	0.02	0.04	0.05	.38**	0.14	.40**	0.01	0.19	0.19	.41**	0.23
SWMBE	-0.22	-0.03	-.29*	0.12	-.31*	0.05	0.10	-0.16	-0.16	-0.01	0.15

NB. * indicates $p < .05$, ** indicates $p < .001$. SF = single feature condition, CoF = conjunction of feature condition.

Table 4.12. Pearson's *r* correlation matrix for older adults indicating significant relationships between measures of learning slope across trials and neural predictors.

	Within patch SF	Exploit SF	Exploit CoF
mean Genu	0.05	$-.402^{**}$	0.01
mean Splenium	0.13	$-.361^{*}$	-0.08
NA_ACC	-0.05	-0.20	$.286^{*}$
ACC_LC	$.345^{*}$	0.06	0.11

NB. * indicates $p < .05$, ** indicates $p < .001$. SF = single feature condition, CoF = conjunction of feature condition.

4.3.4 Leapfrog

The Leapfrog was administered to assess the exploration-exploitation trade-off. Lexploit, or the percentage of exploitative selections in the Leapfrog task, was significantly higher for YA (M = 72.32%, SD = 12.45%) than OA (M = 62.10%, SD = 14.59%; $t(89) = 3.58$, $p < .001$, $d = .75$). Reaction time, in milliseconds, on the Leapfrog task identified that OA (M = 500, SD = 170) responded significantly slower than YA (M = 320, SD = 70; $t(89) = -6.67$, $p < .001$, $d = -1.4$).

4.3.5 White matter integrity

Independent sample t-tests were run to assess the difference in corpus callosum FA and connectivity between age groups. OA had significantly lower FA than YA in the body (young: M = .67, SD = .03; old: M = .63, SD = .04; $t(90) = 5.98$, $p < .001$, $d = 1.25$), genu (young: M = .69, SD = .03; old: M = .62, SD = .04; $t(90) = 9.53$, $p < .001$, $d = 2.0$), and splenium (young: M = .71, SD = .02; old: M = .66, SD = .04; $t(90) = 6.98$, $p < .001$, $d = 1.46$). However, although completed streamline tract connectivity was lower in OA than YA, connectivity did not statistically differ (Table 4.13). Mean FA and MD values derived from completed streamlines were also compared between groups: OA had significantly higher mean tract-based FA (M = .25, SD = .022) than YA (M = .28, SD = .02; *t*(90) = 6.15, *p* < .001, *d* = 1.28), but OA (M = 1.13 x 10^3, SD = 9.88 x 10^5) had significantly lower MD than YA (M = 9.21 x 10^4, SD = 5.92 x 10^5; *t*(90) = -12.1, *p* < .001, *d* = -2.53). Figure 4.5 depicts three participants' binarised PT connectivity in MNI space.

Table 4.13. Mean, standard deviation, *t*-statistic and Cohen's *d* comparing younger and older adult tract connectivity measured by the number of completions averaged bidirectionally.

	Younger adults		**Older adults**		***t*-test results**	
	M	SD	M	SD	*t*	*d*
NA - ACC	1.44 x10^6	4.7 x10^5	1.58 x10^6	7.69 x10^5	-1.04	-.22
NA - vmPFC	4.6 x10^5	3.87 x10^5	5.1 x10^5	4.49 x10^5	-.59	-.12
ACC - vmPFC	2.67 x10^6	1.24 x10^6	2.82 x10^6	1.3 x 10^6	-.56	-.12
ACC - LC	2.03 x10^3	2.98 x10^3	5.5 x10^3	1.65 x10^4	-1.38	-.29
vmPFC - LC	9.48 x10^2	3.0 x10^3	1.13 x10^3	3.04 x10^3	-.29	-.06

NB. No significant difference was observed between groups. NA = nucleus accumbens; ACC = anterior cingulate cortex; vmPFC = ventral medial prefrontal cortex; LC = locus coeruleus.

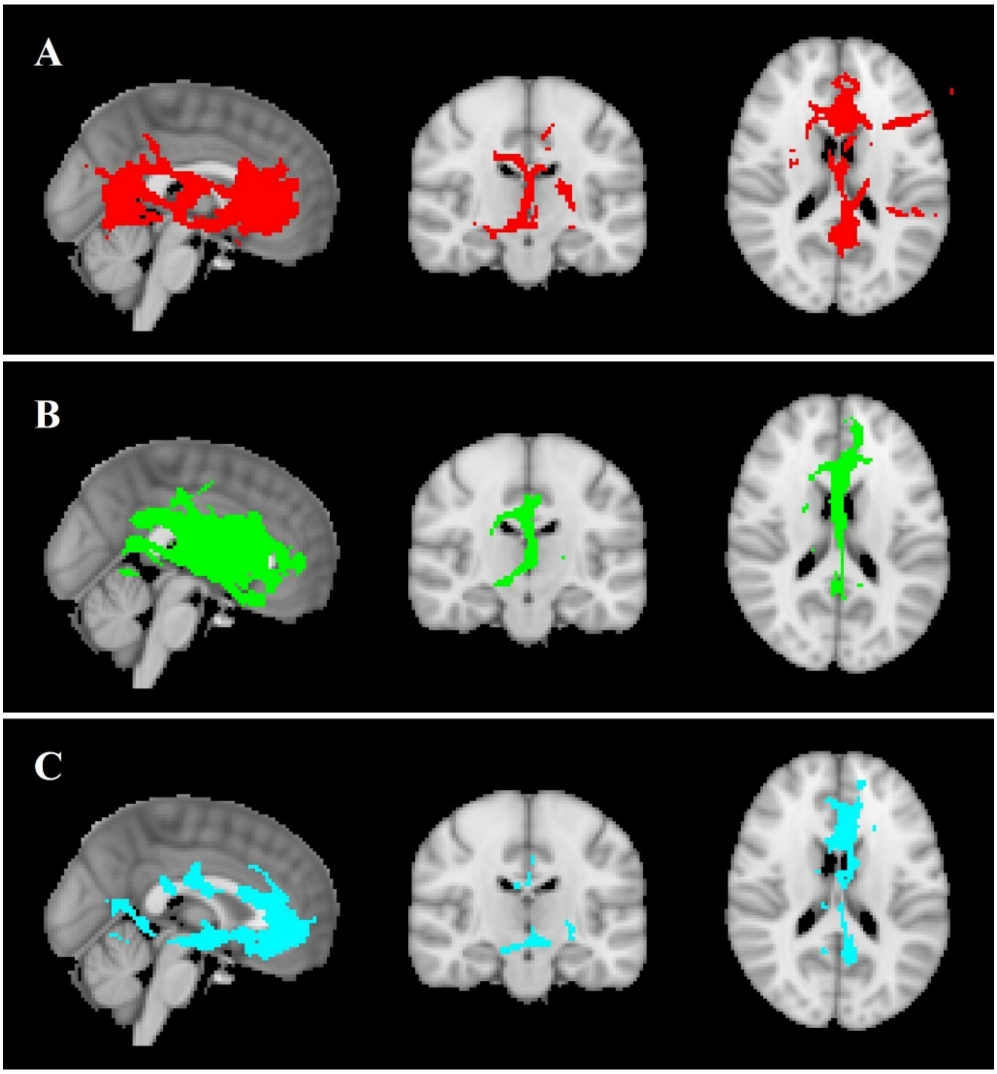

Figure 4.5. Three participants' MRI data illustrating the extraction of FA values from the streamlined distributions overlayed on an MNI brain: A) example of connectivity from a 21-year-old brain; B) example of connectivity from a 93-year-old brain; C) example of connectivity from a brain from a participant diagnosed with Alzheimer's disease.

4.3.6 Neural correlates

Pearson's correlations, to assess the relationships between PT tracts and behavioural measures, revealed that in the younger adult cohort, connectivity revealed little variance in behaviour. Fewer tract completions between NA and vmPFC were linked to greater patch visits conjunction ($r = -.30$, $p = .048$). Higher Lexploit preference in the Leapfrog task was related to fewer tract completions between the LC and ACC (*r* = -.49, *p* < .001), and vmPFC and LC (*r* = -.47, *p* = .002). Additionally, mean FA in the body of the corpus callosum predicted within-patch organisation and cup revisits, where higher organisation (conjunction: *r* = -.33, *p* = .031) and fewer cup revisits (conjunction: *r* = .31, *p* = .043) showed relationship with higher FA. Higher mean FA in the splenium of the corpus callosum related to fewer cup revisits (single feature: *r* = .35, *p* = .021; conjunction: *r* = .30, *p* = .048) across both conditions. Finally, lower FA of connective tracts revealed greater exploitative behaviour (*r* = -.40, *p* = .007) in the single feature condition for YA.

In the OA cohort, greater connectivity between the NA and ACC identified greater success on the MoCA (*r* = .29, *p* = .048), more targets collected in the conjunction condition (*r* = .31, *p* = .03), and more total inspections (*r* = .38, *p* = .008) in the conjunction condition. Target collection and total inspections in the conjunction condition were also associated with greater connectivity between the NA and vmPFC (score: *r* = .35, *p* = .015; inspections: *r* = .38, *p* = .007), and the ACC and vmPFC (score: *r* = .34, *p* = .02; inspections: *r* = .39, *p* = .007). Finally, higher connectivity between the ACC and LC and lower organisation within-patch showed a relationship in the conjunction condition (*r* = -.30, *p* = .039).

Age, using OA data only, was found to be correlated with FA in the body of the corpus callosum, with older age indicating lower FA (*r* = -.312, *p* = .031). Higher mean FA in the body of the corpus callosum was related to more organised within-patch search (*r* = .32, *p* = .026) in single feature conditions, as well as the total number of single feature patch inspections (*r* = .30, *p* = .041). Age was also associated with lower genu FA (*r* = -.292, *p* = .044). Greater mean FA in the genu of the corpus callosum revealed greater organisation in conjunction conditions, both for within-patch (*r* = .34, *p* = .02) and between-patch (*r* = .33, *p* = .024) organisation. Higher mean FA in the genu identified several other successful behaviours in the single feature condition, namely more targets collected (*r* = .34, *p* = .02), higher total inspections (*r* = .31, *p* = .034), higher cued inspections (*r* = .35, *p* = .014), and more total patch inspections (*r* = .31, *p* = .032). Higher cued inspections were also associated with the genu (*r* = .31, *p* = .032) in the conjunction condition. Higher mean FA in the splenium of the corpus callosum was linked to greater target collect in both single feature (*r* = .38, *p* = .007) and conjunction (*r* = .30, *p* = .038) conditions. Higher splenium FA further identified total patch inspections (*r* = .30, *p* = .036) in single feature conditions. Finally, higher mean FA of the connective tracts was correlated with greater success on measures of search including cued inspections (single feature: *r* = .40, *p* = .004; conjunction: *r* = .38, *p* = .008) and total number of patches inspected (single feature: *r* = .35, *p* = .014; conjunction: *r* = .32, *p* = .027). Lower mean MD revealed similar associative success across measures of search including total targets collected (single feature: *r* = -.32, *p* = .029), total cup inspections (single feature: *r* = -.32, *p* = .029), cued inspections (single feature: *r* = -.35, *p* = .015; conjunction: *r* = -.36, *p* = .015), and total patch inspections (single feature: *r* = -.40, *p* = .005; conjunction: *r* = -.30, *p* = .038). One measure of foraging, within-patch organisation in the conjunction condition, was also related to mean MD (*r* = -.33, *p* = .022) where lower MD indicated greater organisation.

4.3.7 Predictive factors

It was hypothesised that search and foraging success would elucidate neural substrates of difference as potential markers of neurodegeneration. To investigate the predictive factors underpinning search and foraging success in the OA cohort, cognitive measure results were used to create groups defined by ability to compare those with impaired performance against unimpaired. This was anticipated to further quantify pathological verses typical ageing. The OA participants were divided into two groups based on two cognitive measures anticipated to guide search and foraging behaviour. The PAL, which measures episodic memory, was considered as it has been shown as a sensitive and specific measure to differentiate pathological processes of AD from healthy controls (Hicks et al., 2021) and discriminatory capacity in healthy OA intragroup analysis (Jardim et al., 2024). Addressing predictive differences between groups in a visual search task using an episodic memory measure instead of the classically-assessed working memory may provide additional insights into how memory systems interact during complex tasks. While visual search primarily engages working memory (Woodman & Luck, 2004), episodic memory also plays a crucial role in tasks requiring the integration of past experiences to guide current behaviour (Hannula & Ranganath, 2009). Using episodic memory measures can reveal how participants drew upon previous encounters with the task environment (i.e. learning over trials), which might not be captured by working memory assessments alone and help identify subtle cognitive differences that impact performance. PALFAMS was selected to evaluate predictive factors as it quantified success on the first attempt on the task rather than errors, providing a direct measure of task performance and success, and the CANTAB produces normative PALFAMS results. Groups were split by normative z-scores on the PALFAMS measure; abnormal results were indicated by z-scores at -1.00 and below (<16th centile, $\leq$-1 SD). It has been suggested that to detect MCI with high sensitivity at low severity level, assessment scores at 1 SD and below should be applied (Busse et al., 2006). Therefore a "normal" group (N = 36) was created for normative PALFAMS scores at z = -0.99 or higher, whereas the "abnormal" group (N = 12) scored z = -1.00 and below.

It was found that two measures in the single feature condition showed a difference between the two groups defined by episodic memory: a higher percentage of cued inspections was revealed in the normal group (M = 67.10%, SD = 23.53%) when compared to the abnormal (M = 53.17%, SD = 17.75%; *t*(46) = 1.87, *p* = .034, *d* = .63) group, and more patch inspections were demonstrated in the normal (M = 5.29, SD = 3.52) than the abnormal (M = 3.28, SD = 1.74; *t*(46) = 1.89, *p* = .033, *d* = .63) group. Episodic memory also indicated exploitative (Lexploit) preference for the abnormal (M = .69, SD = 13) over normal (M = .60, SD = .15; *t*(45) = -1.98, *p* = .027, *d* = -.66) group. In terms of structural integrity, PALFAMS score revealed higher integrity in the NA and vmPFC pathway in normal (M = 5.98 x 10^5, SD = 4.68 x 10^5) as compared to abnormal (M = 2.45 x 10^5, SD = 2.50 x 10^5; *t*(46) = 2.47, *p* = .017, *d* = .83) group, and higher integrity in the ACC and vmPFC pathway in normal (M = 3.05 x 10^6, SD = 1.29 x 10^6) as compared to abnormal (M = 2.12 x 10^6, SD = 1.10 x 10^6; *t*(46) = 2.23, *p* = .031, *d* = .74) group. However, these groups did not differ in corpus callosum FA nor mean FA or MD values thresholded from the selected tracts.

An additional measure was considered to underpin success based on impairment: executive functioning (IED) was selected to quantify cognitive differences as visual search and foraging success are underpinned by executive functioning control (e.g. Gil-Gómez de Liaño & Wolfe, 2022), and are especially susceptible to age-related changes in the prefrontal cortex (Wyatt et al., 2024). The IEDYERTA adjusts the errors made by the trials the participant did not reach, and produces normative results, and therefore IEDYERTA was selected to represent executive functioning predictions between normal (N = 38; $z \geq -0.99$) and abnormal (N = 10; $z \leq -1.00$) groups. It was found that executive functioning errors revealed greater exploitation preference (Lexploit) in abnormal participants (M = .65, SD = .14) than normal (M = .52, SD = .14; *t*(45) = 2.45, *p* = .018, *d* = .91) participants. Further, IEDYERTA also demonstrated greater connectivity between the NA and ACC in normal (M = 1.45 x 10^6, SD = 6.24 x 10^5) as compared to abnormal (M = 2.06 x 10^6, SD = 1.08 x 10^6; *t*(46) = -2.34, *p* = .024, *d* = -.83) groupings, and between the NA and vmPFC in normal (M = 4.29 x 10^5, SD = 3.79 x 10^5) than abnormal (M = 8.17 x 10^5, SD = 5.73 x 10^5; *t*(46) = -2.57, *p* = .014, *d* = -.91) participants, but not within the corpus callosum. The groups did not differ in tract-based mean FA or MD values.

As above, learning slope across trials was also analysed between normal and abnormal OA groups. Linear regression analyses were conducted for each dependent variable, examining trial-by-trial effects to understand learning trajectories. *F*-statistics for each behavioural measure are reported in Table 4.14. Subsequently, for significant regressions, between-subjects t-tests were performed to investigate group differences across individual trials, each trial number representing a separate observation. Table 4.15 displays independent sample t-test results between the two OA groups for each cognitive measure. Results from the independent sample t-test revealed that when defining the OA groups by PALFAMS success, normally scoring OA collected more targets than OA in the abnormal group in the single feature (normal: M = 26.64, SD = 19.42; abnormal: M = 17.71, SD = 10.19) and conjunction (normal: M = 23.63, SD = 11.23; abnormal: M = 18.89, SD = 11.71) conditions. Normal OA made more total item inspections than the abnormal group across the single feature (normal: M = 40.54, SD = 22.44; abnormal: M = 31.61, SD = 14.82) and conjunction (normal: M = 40.51, SD = 21.70; abnormal: M = 32.09, SD = 15.19) conditions. Normal OA also made a greater percentage of cued inspections than abnormal OA in the single feature (normal: M = 66.20%, SD = 22.56%; abnormal: M = 58.67%, SD = 16.67%; see Figure 4.6a) and conjunction (normal: M = 64.07%, SD = 21.89%; abnormal: M = 59.39%, SD = 17.79%; see Figure 4.6b) conditions. Normal OA inspected more patches in the single feature (normal: M = 5.29, SD = 3.82; abnormal: M = 3.28, SD = 1.99) and conjunction (normal: M = 5.63, SD = 2.50; abnormal: M = 4.97, SD = 3.74) conditions than abnormally scoring OA. Finally, exploitative behaviour was significantly greater in the abnormally scoring OA cohort than the normal group in the single feature condition only (normal: M = 95.21%, SD = 36.55%; abnormal: M = 105.87%, SD = 36.12%;).

Table 4.14. Regression analyses reporting the *F*-ratio and r^2 for each search and foraging measures for single feature and conjunction conditions, analysing the success of each variable over time on a trial-by-trial basis across the older adult cohort.

	Single feature		**Conjunction of feature**	
	F	r^2	*F*	r^2
Targets collected	21.83**	.044	20.82**	.042
Total Inspection	16.01**	.032	6.84*	.014
Percentage Cued	24.56**	.049	9.81*	.02
Number of patches	16.28**	.033	11.40**	.023
Within-patch best-*r*	.08	.00	.36	.001
Between-patch best-*r*	1.89	.004	1.00	.002
Exploit	.00	.00	6.27*	.013
Cup Revisit	.05	.00	3.69	.008
Patch Revisit	.01	.00	.85	.002

NB. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **

Between-subjects analyses revealed that when assessing group differences using the IEDYERTA z-scores (see Table 4.15), normally scoring OA collected more targets than OA in the abnormal group in the single feature (normal: M = 25.92, SD = 18.62; abnormal: M = 18.64, SD = 13.96) condition. Normal OA made more total item inspections than the abnormal group across the single feature (normal: M = 39.95, SD = 19.13; abnormal: M = 32.07, SD = 26.68) conditions. Normal OA inspected more patches in the single feature (normal: M = 5.06, SD = 3.70; abnormal: M = 3.76, SD = 2.75) condition. Finally, exploitative behaviour was significantly greater in the abnormally scoring OA cohort than the normal group in the conjunction (normal: M = 108.22%, SD = 84.65%; abnormal: M = 134.34%, SD = 93.66%) condition. Figure 4.6c and 4.6d depict nonsignificant differences in cued inspection between groups defined by IEDYERTA scores.

Table 4.15. *t*-scores and Cohen's *d* between older adults grouped by normal and abnormal z-scores on episodic memory and executive functioning cognitive tests, respectively, on significant search and foraging behaviours over the course of the task.

	PALFAMS				**IEDYERTA**			
	Single feature		Conjunction of feature		Single feature		Conjunction of feature	
	t	*d*	*t*	*d*	*t*	*d*	*t*	*d*
Targets collected	4.82**	.51	3.96**	.42	3.65**	.41	-.41	-.05
Total Inspection	4.07**	.43	3.94**	.42	3.35**	.38	-1.33	-.15
Percentage Cued	3.36**	.35	2.12*	.22	.90	.10	-.94	-.11
Number of patches	5.49**	.58	2.8*	.23	3.27**	.37	.35	.04
Exploit	-2.73*	-.29	.06	.01	1.71	.19	-2.66*	-.30

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

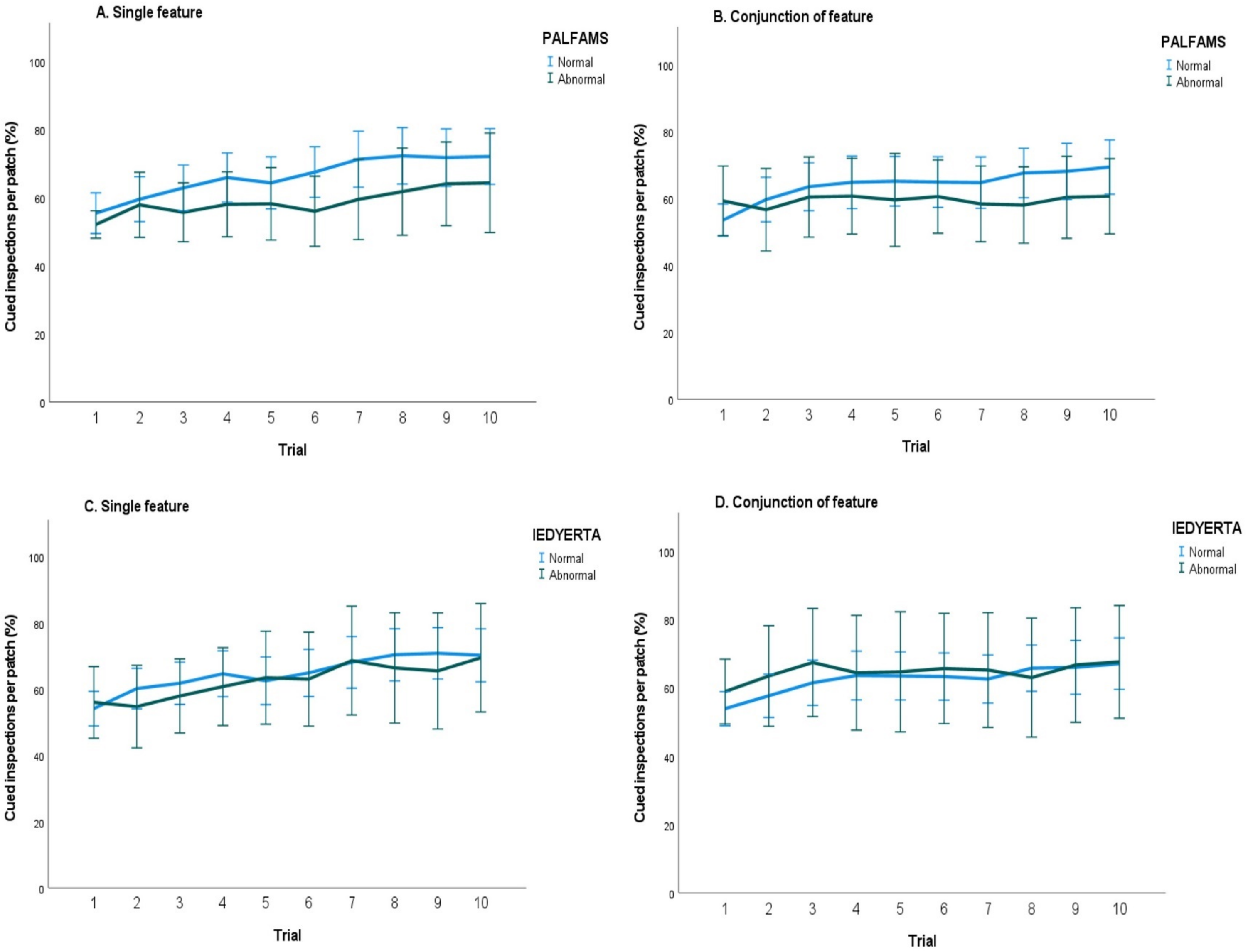

Figure 4.6. Percentage of cued inspections per patch across trials between older adults defined by abnormal cognitive z-scores (blue) and normal z-scores (green) for: A) single feature condition as grouped by episodic memory; B) conjunction of feature condition as grouped by episodic memory; C) single feature condition as grouped by executive function; D) conjunction of feature condition as grouped by executive function. Errors bars represent 95% confidence intervals.

In a brief exploration of the two abnormal groups defined by either episodic memory or executive function, the participants comprising of both groups were qualitatively compared. Of the PALFAMS abnormal group (N = 12) and IEDYERTA abnormal group (N = 10), only three participants' shared occupancy in both. One such participant had diagnosed Alzheimer's disease. However, the other two participants who were defined with abnormal performance in both groups did not disclose any diagnoses or underlying neurological problems. In a review of the diagnoses participants could optionally disclose, it was noted in the group defined by abnormal PALFAMS results that the oldest participant was included, as was one participant who disclosed a nondescript neurological problem. This was not reflected in the group defined by abnormal IEDYERTA scores.

4.4 Discussion

Experiment 6 was devised to investigate the cognitive and neural underpinnings of search and foraging behaviour in adults over the age of 65 years. Utilising an identical VR paradigm to Experiment 5—where participants were not provided with a template, but targets were equally distributed—48 older adults were compared to 45 younger adults in large-scale search performance, brain structure integrity, and measures of cognition. It was hypothesised that older adults would perform less successfully than younger adults across a variety of measures: collect less targets and make fewer cued inspections in measures of visual search, make less inspections overall, be more exploitative and less organised in measures of foraging and show decrements in cognition in areas such as episodic and spatial memory, and executive functioning. It was also predicted that older adults would have lower white matter tract integrity than younger adults. Predominantly, it was queried whether predictive factors (e.g. neural connectivity, cognitive performance) could predict behavioural success as early markers of pathological ageing.

4.4.1 Comparing younger and older adult performance

YA were compared to older adults across all measures of search and foraging behaviour. OA showed significantly reduced performance from YA in the number of targets found and the total number of item and patch inspections, but not cued inspections or any of the foraging measures. In an experiment where the value of the target was the primary manipulation, Wiegand and Wolfe (2021) did not find differences between YA and OA search ability or success, and Wiegand and Wolfe (2020) suggested that ageing did not impact visual search as there were no differences between YA and OA performance aside from generalised slowing. Perhaps the differences identified presently (i.e. targets collected, item and patch inspections) may be related to generalised slowing as participants were required to physically move about their space in order to inspect items. Analyses controlling for reaction time and movement time (CANTAB RTI) reveal that both reaction and movement time were significant contributors to target collection and patch inspection success but with very low effect size. This indicates that whilst differences between YA and OA performance cannot be fully explained by physical movement, they were contributing factors to VR-based search success. It should be considered that both RTI measures were administered on an iPad whilst the VR task required participants to move about their space and physically interact with the environment. Therefore, despite contributions of reaction and movement times, it may not indicate that the differences found were due to generalised slowing as suggested by Wiegand and Wolfe (2020). Differences in reaction time have been found in the translation from two-dimensional tasks to three-dimensions, as Barrett et al. (2022) observed that OA displayed slower reaction times in a three-dimensional task as compared to YA, but there were no differences in search accuracy. Further, in a study investigating YA and OA movement and reaction time through motor control of target-oriented arm movements, results indicated that OA had slower physical movements and slower initiation time, but with great variability intragroup (Yan, Thomas, & Stelmach, 1998). Therefore, to elucidate whether OA do truly show a deficit in target collection and overall inspections, explicit measures of movement speed in VR would provide evidence to generalised slowing contribution, as well as contributions of initiation time and physicality.

Literature recently has suggested that differences between OA and YA search is due to variations in strategy (e.g. Agnew et al., 2020; Wiegand et al., 2019). Therefore, regression analyses were conducted to quantify behaviours over the course of the task between the two age groups. This revealed that over task progression, YA were more successful across all measures of search including collecting more targets and inspecting more cued items, total items, and patches. Previous research has suggested that OA show larger search slopes as compared to YA (Hahn & Buttaccio, 2018), in contrary to Wiegand and Wolfe (2020; 2021). Cued inspection, a measure of search strategy and accuracy, was shown to significantly differ over the course of the task between YA and OA, despite not significantly differing when all trials were considered concurrently, suggesting that differences between age groups differed in trial-by-trial approaches, but this did not affect overall success. Agnew, Phillips, and Pilz (2020) observed that OA and YA were equally efficient searching for targets, suggesting that OA vary in their search strategy, but not search ability, as a compensatory mechanism for reduced response times. This was supported by Wiegand et al. (2019), who found that OA follow their own meta-cognitive strategy, and that top-down contributions to search success were preserved. Wiegand and Wolfe (2020) queried whether hybrid search aids visual search success in ageing by enabling compensatory strategies or using top-down knowledge to guide OA despite declines in other abilities. The present paradigm required participants to develop a representational target template to successfully, and efficiently, search. A lack of significant difference between YA and OA overall search success, but with differing learning slopes, indicated an equal creation of a target template to facilitate successful search overall, with the deployment of compensatory search strategy for OA to perhaps support deficits trial-by-trial in physical movement, and reaction and movement times.

Older and younger adults displayed similar foraging performances. Organisation, for example, did not differ between age groups. Even when performance was assessed on a trial-by-trial basis, between-group differences did not arise. It has been suggested that depending on the presented stimuli (such as colour and motion of targets), organisation performance may not reveal age-related differences whereas other stimuli, such as line orientation and flicker, show age-related effects (Kurylo, 2006). This indicates that age-related degradation in performance may be dependent on the presented stimuli rather than ability. The present experiment defined the targets by colour and shape, two features suggested to reside within a similar locale, which potentially contributed to age-related sensitivities in discriminating visual search stimuli. In a cluster analysis on search organisation (e.g. a cancellation task), Benjamins and colleagues (2019) found four clusters of organisation ability (i.e. omissions, revisits, bad search organisation, and good search organisation) in a large (N = 523) sample of healthy adults aged 19-84. It was qualified that the outcome measures were not affected by age, and that despite the four clusters, a large proportion of the cohort displayed relatively poor search organisation. Perhaps organisation may not be as clear of an outcome measure of search and foraging success as previously considered. The best-*r* measure utilised presently, whilst previously implemented in a three-dimensional space (Kristjánsson et al., 2022), has not yet been utilised with idiothetic contributions. Maybe attending to the additional information in a motile paradigm reduces organisation overall, especially in uncertain environments, seen to increase information sampling.

Additionally, foraging measures revealed that YA and OA were similarly exploitative in the search, even when compared over trials. Wiegand, Seidel and Wolfe (2019) found that OA foraged somewhat less efficiently than YA due to a more exploitative search strategy, however research has found that when investigating uncertainty (as one might face in an environment with hidden targets and no provided template) that OA and YA did not differ in their exploratory behaviour (Yagi et al., 2023). As the current paradigm presented uncertainty in the form of unknown target location and distribution, it is possible that uncertainty drove equal exploration between both groups. Bella-Fernández et al. (2022) suggested that exploitation may also be represented and interpreted differently depending on one's selected analysis scale (*nb* if the reader recalls, Mehlhorn et al., 2015 described the trade-off between exploration and exploitation as a spectrum rather than a binary definition). Bella-Fernández et al. (2022) posited that the definition of exploitation could either be described as foragers searching for targets in a display until the decision is made to leave one patch for a more profitable next patch, or to encompass a finer-grained analysis of item-by-item inspection to determine whether it is a target or distractor before moving to the next item. Mehlhorn et al. (2015) discussed that the behaviours in the exploration-exploitation trade-off are not necessarily qualitatively opposing, and do not necessarily act independently. In the present experiment, more patches were inspected in the conjunction condition, while higher exploitation occurred in single feature conditions, regardless of age group. In highly uncertain environments, both groups were less exploitative and were more exploitative in the single feature condition. Exploitation can become optimal under greater uncertainty (Cohen, McClure, & Yu, 2007; Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020; Walker et al., 2022). Therefore, less exploitation in the conjunction condition may lead to more patch sampling to understand the environment better (Lloyd et al., 2023), rather than simply seeking immediate rewards.

The Leapfrog task was administered to quantify the exploration-exploitation trade-off in a simple, two-button decision task, between the two age groups. It was found that YA were more exploitative (Lexploit) than OA, but OA was significantly slower in reaction time. In their study utilising a similar paradigm, Blanco and colleagues (2016) identified that across two experimental manipulations looking at the influence of strategy and prior knowledge, OA and YA explored similarly across trials, but OA had slower reaction time. Despite a lack of quantitative difference, Blanco et al. (2016) noted that there was variance in performance due to selected strategy: how participants approached the task statistically varied between OA and YA. These findings are contrary to previous two-dimensional foraging tasks. Mata et al. (2009; 2013) found that OA were more exploitative and tended to stay in patch longer than YA, irrespective of the concurrent decrease in efficiency. It was noted by Mata et al. (2009) that OA possibly did not want to make errors, therefore as a selective strategy, exploitation ensured targets were not missed. It is curious to find in the present task that YA were more exploitative. Perhaps YA did not use prior knowledge in the same way OA did. Blanco et al. (2016) suggested that tracking and using uncertainty requires greater control facilitated by acquiring and using information over time. Furthermore, Mata et al. (2009) stated that adaptive foraging strategies may be affected by long-term experience. Decrements in performance may reveal suboptimal decision-making, requiring the consideration of how one deviates from optimal strategy (Blanco et al., 2016). Choice reaction time tasks have also shown similar results to that of Blanco and colleagues—Vaportzis, Georgiou-Karistianis, and Stout (2013) identified that OA were slower than their younger counterparts, but just as accurate. Participants had to respond with either a left or right key to identify either a target or nontarget, respectively, where strategy was identified as the difference between the age groups. Similarly, differences observed in the present study and Mata et al.'s (2009) fishing task may also be the result of varying strategies suited for different resource distribution.

Although strategy was not explicitly analysed in the present experiment, perhaps the exploitative behaviour noted in the YA cohort are related to strategy or knowledge rather than a simple exploration-exploitation discrimination.

The older adult cohort was also divided by attained z-score on two cognitive tasks, with episodic memory and executive functioning success creating ‘normally’ and ‘abnormally’ scoring groups. Between-subjects comparisons revealed greater cued inspections and patch inspections in the normal group. Comparing performance over the course of the task between the two groups (utilising episodic memory scores) revealed further results: not only did groups differ between cued and total patch inspections as previously identified, but trial-by-trial analysis also revealed significant differences in both conditions between the number of targets collected, total item inspections, patch revisits, and exploitation in the single feature condition. Similar results were noted when groups were defined by executive function: across the single feature condition, OA groups significantly differed on the number of targets collected, total item and patch inspections, whilst in the conjunction condition groups differed in exploitation. Groups defined by abnormal scores on executive functioning revealed similar findings in the single feature condition, but not in the conjunction condition. Research has suggested that despite associations between age-related decline and executive function, top-down context is maintained though neural compensatory mechanisms (Madden et al., 2017). Barceló and Cooper (2018) further that executive functioning ability is underpinned by domain general processes, and therefore perhaps multiple processes contribute to executively driven success, leading to fewer indicators of search and foraging success. This reveals that OA with greater executive functioning impairment, but especially episodic memory deficits, create a less efficient strategy over trials than OA who show more preserved cognition. Previous research has supported OA ability to create and maintain representational templates by successfully utilising cues to guide visual search (Hahn & Buttaccio, 2017), which requires greater episodic memory contributions (Võ & Wolfe, 2013). Presently, the OA with abnormal scores were significantly less efficient and less successful across all measures of search performance (e.g. targets collected, and total, cued, and patch inspections) across both conditions, indicating that search performance may be predictive of episodic memory decline. Research has suggested that episodic memory may be differentially sensitive to age-related decline (Korkki et al., 2020). Therefore, findings may support that measures derived from a large-scale search task can predict early degradation.

Measures of foraging revealed that the two OA groups did not differ in their organisation of the space. There are suggestions that older adults choose to do "enough" rather than "more than enough" due to the cognitive effort required (De Bruin, 2017). Thus, should one be required to organise movement efficiently when also creating a target representation, it could be suggested that OA may selectively distribute cognitive resources to some aspects of the task (i.e. template creation) and not others (i.e. organisation). Further, in terms of decision-making, OA have been shown to display preserved decision-making performance when attempting to maximise gains, whereas performance declines when minimising costs (Cooper, Blanco, & Maddox, 2017). If applied to the present task, success in maximising gain could considered as one successfully collecting targets, however this may result in greater exploitative behaviour in lieu of organised search, leading to performance-related costs. It could also be considered that visual search properties are more susceptible to ageing in comparison to foraging behaviours, and therefore the lack of difference in performance between both older adult groups (as well as between YA and OA) is reflective of relative preservation in aspects of foraging. As has been discussed previously, research suggests that perhaps ageing is reflective of compensatory mechanisms underpinning search and foraging behaviour (Mata et al., 2009; Potter et al., 2012; Wiegand & Wolfe, 2020) and therefore whilst organisation strategies differ, results (e.g. targets, cued inspections, etc) do not. Further research into the strategy younger, older, and abnormally scoring older adults use would provide further granularity into the underpinnings of foraging behaviour.

With the slight exception of exploitation (identified in the Leapfrog task only), the OA groups did not differ between foraging measures. It has been suggested that exploration requires greater cognitive control than exploitation (Spreng & Turner, 2021). Following the idea that OA create compensatory strategies to preserve performance (Wiegand & Wolfe, 2020), it may be that a compensatory strategy would result in exploitation, irrespective of optimality, to gain the minimum of *some* information and *some* targets when faced with greater cognitive demand and uncertainty. Specifically, perhaps a strategy, in lieu of inspecting all targets or sampling explicitly for information gain, may be to use a combination of both. Analyses of learning over trials revealed that abnormally scoring OA were more exploitative than the normal group in the VR task. Chin et al. (2015) found that OA patch-leaving behaviour was attenuated by executive control: OA with greater control exhibited greater flexibility in patch-leaving decisions. Executive function score defining OA groups did identify greater exploitation in abnormal groups in the conjunction condition. It has generally been suggested that OA are more exploitative in foraging tasks (Spreng & Turner, 2021), with suggestions that OA tend to over-pick patches (Wiegand & Wolfe, 2021). As such, this may sometimes be true, where gradual exploitative tendency occurs in ageing, and is predictive of underlying degenerative processes but revealed more slowly than other underlying processes, with the facilitation of compensatory mechanism to mask difficulties. It is suggested that both literatures—that OA are more exploitative (Potter et al., 2012) and that OA lack optimality but adjust their foraging behaviours (Mata et al., 2009)—are supported. Various processes contribute to success, in support of domain generality, and deficits are only identified when these compensatory processes fail to offset cognitive decline.

Intra-older adult performance revealed that abnormal groups were more exploitative in the Leapfrog task than the normal groups and YA were more exploitative than OA. As has been discussed thus far, the literature suggests that OA are more exploitative. Perhaps this is not the case, and akin to Yan, Thomas, and Stelmach's (1998) or Nyberg's (2017) findings of intraindividual inconsistency in OA, variability in ageing may be masked by whole-group analysis. Therefore, previous research (e.g. Mata et al., 2009; 2013) may indeed be 'correct' that OAs with deficits are more exploitative, but as a measure of more severe decrements in ageing rather than an overall necessity to one ageing. Mukaetova-Ladinska et al. (2022) proposed that two-dimensional foraging tasks could be employed as predictive batteries of neurodegeneration, and perhaps, evidenced by the intra-older adult results, the present results could be supportive. However, as discussed above, YA were also found to be more exploitative, and therefore further research into the explicit nuances of two-dimensional foraging tasks is clearly required. Further, it was anticipated that exploitation would show similar results across the Leapfrog task and VR, but this was not the case. It is supposed that some degree, two- and three- dimensional foraging rely on different processes to guide the trade-off between exploration and exploitation—perhaps the three-dimensional implementation masks or erases effects, or supports compensatory processes, than those that underpin two-dimensional exploitation.

4.4.2 Neural correlates

It was investigated whether younger and older adults displayed white matter tract integrity and brain FA and MD differences, and whether these differences related to performance across tasks. Integrity and connectivity between YA and OA were first compared, and then the OA cohort was split based on episodic memory and executive function z-scores. Differences between YA and OA were identified in the corpus callosum, where the body, genu, and splenium all revealed lower FA in OA than YA, indicating greater integrity in YA. Similar results were identified in the tract-based FA and MD values, where lower FA and higher MD were identified in OA as compared to the YA cohort. Previous research has found increasing FA in the corpus callosum throughout one's lifespan, peaking in adulthood but then decreasing as one continues to age (McLaughlin et al., 2007). Tract-based FA has also been found to be negatively associated with age, where overall, FA is sensitive to ageing processes (Schilling et al., 2022). However, both cohorts revealed a similar number of PT completions bidirectionally. This is suggested to show a clear relationship between the selected seed-to-target regions to measure search and foraging behaviour- overall, OA performed similarly to that of their younger cohort, and therefore it may be unsurprising that white matter integrity would also reflect such similarities. But, when the OA cohort was divided by abnormal z-scores on the episodic memory and executive functioning tasks, differences in white matter integrity arose in the NA and vmPFC, ACC and vmPFC, and NA and ACC tracts. This suggests that the OA cohort showed relatively high white matter integrity, and those with greater degradation were masked when analysing whole group. This also suggests that performance is reliant on connectivity. The percentage of cued inspections, the number of patch inspections, and Lexploit were identified to be significantly lower in the group defined by abnormal episodic memory scores than normal, which are some of the key aspects to search and foraging performance. Generally, if one makes greater cued inspections, this will lead to more information about the environment, and therefore greater success. Episodic memory is necessary for greater cued search when template creation is required (Võ & Wolfe, 2015), as this allows one to disregard distractors and recognise the target, but also enables more similar template representations to guide one to the target more precisely, also requiring executive control. Therefore, pathways such as between the NA and vmPFC, and ACC and vmPFC, which were the two bidirectional pathways differentiated by episodic memory, may be predictive of search success. As such, findings reveal that the NA and vmPFC, ACC and vmPFC, and NA and ACC connections greatly contribute to episodic memory and executive functioning, as well as simple exploitative behaviour.

Considering the predictive tracts separately for the two age groups, there were few associations between the selected tracts and performance in YA. Connectivity between the NA and vmPFC predicted more patch visits, and Lexploit was associated with connections between the LC and ACC, and vmPFC and LC. Previous research has suggested that in healthy younger adults, regions such as the medial PFC and ACC have been linked to reduced cognitive control, inhibitory control, and self-monitoring (Li et al., 2015). Berry, Shah, and Jagust (2018) discovered that functional connectivity in the DMN mediates dopamine influence on a YA brain, suggested to benefit executive functioning, effecting behaviours of cognitive flexibility such as switching (like one might find in the trade-off between exploration and exploitation). Thus, connections between LC and ACC, and vmPFC and ACC in the present YA cohort supports research suggesting exploitative influences (e.g. Spreng & Turner, 2021; Wyatt et al., 2024). Additionally, FA was calculated in the body, genu and splenium of the corpus callosum; in YA, the callosal body predicted higher organisation and fewer cup revisits, and the splenium predicted fewer cup revisits. Corpus callosum FA has been shown to peak in young adulthood (McLaughlin et al., 2007), reflecting the maturation of white matter tracts. Further, tract-based FA predicted less exploitative behaviour. Per the adaptive gain model (Spreng & Turner, 2021), the DMN facilitates the trade-off between exploration and exploitation, where associations between mean FA throughout the selected regions (i.e. vmPFC, LC, NA, ACC) predict such behaviours. These findings collectively highlight the complex interplay between neural connectivity, cognitive functions, and foraging behaviours in YA and suggest potential predictive neural mechanisms.

Additionally, white matter tract integrity was predictive of the search and foraging behaviours in the OA cohort. Greater connectivity between the NA and ACC predicted MoCA success. The NA and ACC, NA and vmPFC, and the ACC and vmPFC were all associated with greater target collection and total cup inspection. Clearly, the NA, ACC and vmPFC all support search behaviour, as greater white matter integrity led to search success. These were also the same region-specified tracts differentially identifying the normal and abnormal groups by episodic memory and executive functioning. The vmPFC is associated with top-down control, where it has been suggested that visual search is guided by top-down control (Cohen, McClure, & Yu, 2007; Pantazatos et al., 2012). Further, the vmPFC is involved in value-based choices, shown to guide stimulus-reward associations (Pollmann et al., 2016), such as the choice between a target and distractor. Dynamic coupling between the vmPFC and ACC have previously been associated with adaptive switching in younger adults (Economides et al., 2014), and therefore strengthened connectivity between the two regions as one ages facilitates continued search success. On the other hand, it has been proposed that degraded connections between the ACC and vmPFC have been suggested as a biomarker of AD (Sachdev, 2022), indicating that degraded large-scale search behaviours may provide predictive and early contributions to pathological ageing. Further, connections between NA and ACC promote attentional focus (Spreng & Turner, 2021), and research (Domingues et al., 2022; Fatahi et al., 2023) has shown that impaired connectivity between the NA and ACC leads to disruptions in value-based decision-making, albeit revealed using rat models. The NA is known to facilitate motivation and reward processing, and the ACC has been identified to control decision-led information processing in humans (Magno et al., 2009), guiding goal-directed behaviour. Thus, lower white matter integrity underlies visuomotor deficits, and greater connectivity between the NA, ACC, and vmPFC regions supports greater visual search success as the associations between search behaviours reveal interlinked tracts between regions.

Not only does greater integrity facilitate greater search success, but in terms of foraging behaviour, higher connectivity between the LC and ACC predicted lower organisation. Spreng and Turner (2021) have showed that together the ACC and LC integrate NE signals as a function of the salience network, promoting attention. The ACC has been correlated with increased dwell time in patches, suggesting a possible increase in exploitative behaviour (Lloyd et al., 2023), and the LC has been suggested to control the trade-off between exploration and exploitation (Cohen et al., 2007). Should one have a greater tendency toward exploitation and therefore increased dwell time in patch, included with lower attention, this would certainly lead to lower organisation. It has been suggested (as discussed by Magno et al., 2009) that in rule shift tasks, where participants were not informed of target location, the ACC activates in response to the utility of response option (e.g. the informative value of potential outcomes) mediated by whether the response would lead to a positive or negative outcome. If information is derived purely from whether a target is present, then one may trade information gain with lower organisation. However, although the LC has been associated with tau pathology (Spreng & Turner, 2021), and therefore anticipated to be predictive of search and foraging success associated with AD, it has been shown to be difficult to reliably image (Wyatt et al., 2024) and it is queried whether the lack of additional correlations and low PT completions in the present study are due to such difficulties with imaging.

The mean FA of the body, genu, and splenium of the corpus callosum was correlated against measures of search and foraging behaviours. In the OA cohort, it was found that higher mean FA in the body of the corpus callosum predicted greater organisation and patch inspections, and age. The DMN has been specified to integrate knowledge disseminated from the NA (Spreng & Turner, 2021), promoting attention. This is an integral aspect to organising one's forage, and as the corpus callosum is a part of the DMN, a network integral to foraging success (Liu et al., 2021), then likely the callosal body contributes to greater organisation through attention allocation and knowledge integration. Executive function was a significant predictor of lower callosal body FA, and it has been speculated that executive function ability is closely linked to callosal size (Frederiksen & Waldemar, 2012). As callosal body size has been linked to age-related changes (Ota et al., 2006), it can be tentatively suggested that the link between executive function and callosal body would indeed facilitate greater organisation of one's space, and thus number of patch inspections, especially with the contribution of the attentional network, predicted by one's age.

Higher FA in the corpus callosum genu predicted several aspects of search and foraging success: greater organisation, more targets collected, and higher total, cued, patch inspections, and ageing. It has been shown that the greatest levels of degradation to microstructural connectivity in the corpus callosum is to the genu (as compared to the other regions of the corpus callosum), relative to healthy older adult controls as well as AD patients (Frederiksen & Waldemar, 2012). However, there are relatively few studies that assess the corpus callosum in terms of visual search and foraging behaviour, in humans. Bennett et al. (2012) found that the genu showed the strongest relationship between search speed and accuracy and two-dimensional visual search behaviour, however this was not dependent on age. In the present study, the genu (as compared to callosal body and splenium associations) particularly contributed to search and foraging success. Greater executive function ability was associated with higher genu connectivity. Research has found evidence for greater connectivity between frontal regions and the body and genu of the corpus callosum linking to better executive function ability (Johnson et al., 2017). This would align with the present findings where both callosal body and genu were associated with executive functioning ability, and executive function has been evidenced to support search and foraging behaviour. As ageing was also associated with degradations of the body and genu of the corpus callosum, the corpus callosum contributes to search and foraging success, as predicted by ageing. Kennedy and Raz (2009) implicated differential contributions of the genu and splenium to cognitive performance, influenced by age. They suggested that the degradation of callosal fibres reduced successful bilateral compensation in OA, affecting multiple areas of cognitive functioning, but suggested to stem from multiple factors rather than one area or region of degradation.

The callosal splenium predicted organisation, target collection, and total patch inspections in the current experiment. Research has suggested that age-related changes are not associated with changes in the splenium (Ota et al., 2006). Liu et al. (2021) found an anterior to posterior direction of degradation, and therefore predictive factors associated with the splenium may not become evident until later in the typical, or pathological, ageing process. As a posteriorly-located region and therefore more protected from degradation, perhaps greater sparing of the splenium, or subtle decline, may be evident. Bennett et al. (2012) suggested that the splenium was associated with interhemispheric communication, more closely related to motor speed than a specific visual search measure. Perhaps the same could be suggested in the present study, where behavioural measures may be related to motor speed rather than a mechanism of visual search and foraging behaviour. Further, it has been identified that occipital tracts associated with the splenium showed equivalent integrity to that of the younger controls (Delvenne et al., 2021). Further, FA in callosal splenium was not predictive of any cognitive measures, nor ageing, possibly equating visual search performance between younger and older adults, as has been identified in overall between-group comparisons. It has been shown that the splenium is relatively preserved (Fan et al., 2019), and as ageing was not associated with splenium, nor were there differences identified between the group with abnormal cognitive results and normal, relative preservation in the present cohort was supported.

OA success over the course of the task revealed several associations that were masked by overall performance. OA exploitation across trials was predicted by the genu and splenium corpus callosum. As previously discussed, the genu is associated with executive functioning (Johnson et al., 2017), and links have been suggested between executive functioning and the trade-off between exploration and exploitation (Spreng & Turner, 2021). Therefore, learning over time reveals greater executive requirements, and thus associations with exploitative and exploratory behaviour. The callosal splenium has been associated with motor speed (Bennet et al., 2012), where the present relationship could be related to a preference to exploit due to reduced motor abilities rather than a specific preference or selection of exploitation explicitly. The splenium overall is suggested to be relatively preserved in ageing (Fan et al., 2019), with very little research supporting associations with callosal splenium and foraging ability. Perhaps the genu and splenium provide support of general corpus callosum contribution.

Finally, tract-based mean FA was associated with cued inspections and patch inspections, and mean MD further contributed to predict not only cued and patch inspections but also targets collected and item inspections in single feature trials and within-patch organisation in conjunction trial. Spreng and Turner (2021) proposed that whilst specific mechanisms are still being investigated, NE signalling from the LC creates a prepotent model of choice for exploratory or exploitative behaviour. Whilst some of the components of search behaviour may require decision-making requirements, ultimately the search measures were correlated with mean FA and MD whilst the foraging measures were not related (with the slight exception of within-patch organisation). The salience network mediates transference between the DMN and frontoparietal control networks, suggested to guide response accuracy to stimuli (Wyatt et al., 2024). This would support the present contributions of the tract-based

FA to cued inspections and greater organisation in more difficult conditions. Further, a large amount of individual difference exists in cognitive capacity degradation, including acquiring new information as an especially vulnerable mechanism (Brown et al., 2022). Therefore, as the present tracts have been suggested across the literature to support the exploration-exploitation trade-off as a form of information gathering, then indeed higher tract integrity would support greater information gathering by inspecting greater numbers of items and patches. Although not an explicit measure of exploitation, greater integrity leading to higher number of inspections found in the present experiment may suggest more exploitative-type behaviours, and overall greater tract integrity leads to greater search performance.

4.4.3 Individual differences in younger and older adult performance

Measures of individual difference indicated that YA relied on episodic and spatial working memory, but moreso executive function, with reaction time contributions to facilitate visual search success. It was similarly found in the OA cohort that across search measures, executive function, working memory, episodic memory, and reaction time was associated with success. Reaction time is strongly associated with search success (Wolfe, 2018), and is slowed by ageing processes (Hahn & Buttaccio, 2018). Likewise, episodic memory has been shown to degrade in older adults with intraindividual variability (Nyberg, 2017), where steeper decline is associated with dementia risk (Tromp et al., 2015). As episodic memory is integral to search and foraging success (Wiegand, Seidel, & Wolfe, 2019), the relationship between episodic memory and search success may be indicative of predictive factors associated with measuring search ability in a three-dimensional space. However, episodic memory was only associated with a higher percentage of cued inspections across both cohorts, with an additional contribution to target collection in YA, indicating that additional processes are being utilised to guide search efficiency. Episodic and spatial memory provide support in template creation and search guidance (Van der Stigchel &

Hollingworth, 2018; Wolfe, 2021). As participants were required to create a target representation to guide search, it therefore necessitated spatial and episodic memory, with greater abilities leading to greater success. Declines in working memory, executive function, attention, and processing are interlinked (Naveh-Benjamin & Cowan, 2023). Executive functioning supports goal-directed behaviour (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2021), shown to contribute to younger adult success more than older adult. As such, great variability was revealed between cohorts. Older adults have been shown to employ compensatory strategies to facilitate search success (e.g. Potter et al., 2012) and therefore the integration of working memory and executive functioning may provide insight into contributions derived from concurrent systems facilitating search. It perhaps can be suggested that participants may need to employ various strategies, neither indicating a uniform strategy nor different strategies, but instead a range of changing strategies throughout the task as one learns, or becomes more comfortable, to facilitate search success.

When cognitive measures were associated with learning over the course of the task, similar behaviours arose for both YA and OA. The biggest difference noted was the increase in contribution to target collection in the conjunction condition for OA. When assessed over trials, not only did working memory continue to contribute, but executive function and verbal memory guided success. Further, both executive function and verbal memory CANTAB tasks include a learning-over-time component to the measure, therefore indicating that greater abilities facilitate greater learning, especially to enable successful search. Executive function is essential to aspects of learning and performance monitoring (Baggetta & Alexander, 2016) and implicit learning and procedural memory are preserved in healthy ageing (Madden et al., 2017). Perhaps the associations in learning reflect similar cognitive contributions to OA learning presently where greater executive function and preservation of lead to better learning. However, what is less understood is the lack of relationship between cued inspections over trials and cognition. Previous research has suggested that incomplete template representations impede decision-making and attention, hindering search success (Hout & Goldinger, 2015). It might be suggested that OA learned incomplete or partial templates, leading to target collection success but not cued inspection accuracy, reflected in trial-by-trial successes.

Foraging success in the YA cohort was associated with episodic memory, verbal working memory, executive functioning, with a few contributions from aspects of reaction time or spatial working memory. OA success revealed better reaction time scores, spatial working memory errors and the latency executive function measure across exploitation and revisits, and verbal memory contributed to search organisation in conjunction of feature conditions. Jabès et al. (2021) suggested that spatial working memory differentially separates YA and OA cognitive abilities, and as it has been presently found that spatial working memory contributes to both YA and OA success, with differences identified in foraging performance, then perhaps one of the predictive factors in search success is spatial working memory. Further, as has previously been discussed, the vmPFC contributed to foraging success, and executive function has been shown to reside within the vmPFC (Domenech & Koechlin, 2015). As such, the present results support previous findings in the contribution of executive functioning and frontal neural pathways to foraging success, in both YA and OA cohorts.

Kristjánsson, Ólafsdóttir, and Kristjánsson (2020) suggest that in foraging studies where targets do not disappear, as is found in the present experiment, spatial memory can be more closely investigated. This can provide insight into the ageing process, such that measures of cognitive control, necessary for successful foraging, provide mediation between the exploration and exploitation process (Engle, 2010; Hills et al., 2010). A decline in spatial working memory ability (i.e. greater errors) predicted greater exploitation, suggesting a decrement in cognition control. Finally, results showed that OA with greater verbal memory strength were more organised in their between-patch searching. Hills et al. (2012) suggested that foraging can also occur in semantic memory, where ‘patches’ of animals (for example) can be explored and exploited following aspects of animal fluency tasks for verbal memory contributions. Therefore, it is perhaps a strategy, or an allocation of cognitive resources, to utilise verbal memory in organising one’s forage, especially in ageing when cognitive resources residing in the frontal regions may not be as available as younger adults. Võ and Wolfe (2013) suggested that available form of search guidance (e.g. episodic memory and target templates) compete against one another to facilitate attention, and therefore the process with greatest signal enables success. Cognitive control mediates search and foraging behaviours, displaying reciprocal relationships where areas of cognitive strength facilitate greater success in the present study, however, there are also clearly individual difference contributions, as not all areas of cognition that might be expected to guide success were found to contribute. Perhaps a greater variety of cognitive measures to assess specific contributing factors, or a modelling approach to minimise individual difference interactions (such as Clarke, Hunt, & Hughes, 2022), may provide greater granularity to cognitive control contributions in older adults.

4.5 Conclusion

The present study replicated the paradigm from Experiment 5 and extended it by comparing the performance of older adults to younger adults, whilst examining intra-group differences among older adults, and incorporating additional measures of cognitive and neural markers. It was found that measures of search (i.e. targets collected; cued, total, and patch inspections) were predicted by structural connectivity in regions of the corpus callosum and tracts between frontal and temporal lobes, whereas foraging measures (e.g. exploitation, revisits), with the exception of organisation, were not predictive of success. Cognitive measures revealed differential contributions between the younger and older adults to facilitate success, where younger adults appeared to rely more greatly on several areas of cognition including reaction time, executive functioning, episodic memory, and spatial working memory, whilst older adults relied more exclusively on reaction time, episodic memory and working memory. Results encompassing overall search and foraging behaviour indicated that younger and older adult participants generally did not differ in performance, however when success was analysed on a trial-by-trial basis, significant differences arose across the search, but not foraging, measures. Recent literature (e.g. Wiegand & Wolfe, 2020; 2021) suggests that older adults may not be as poor on visual search and foraging tasks as once believed, where present results may support the translation from two- to three- dimensions, providing the opportunity for older adults to deploy compensatory strategies in order to facilitate greater foraging success. However, this was not the same for search measures. The present results do not support Wiegand and Wolfe (2020; 2021) when performance is analysed on a trial-by-trial basis. Further, comparing older adults within-groups separated by cognitive ability similarly reflected significant differences in search measures but not foraging behaviour. As such, the present experiment has found predictive measures of success where measures of search (i.e. targets collection, cued inspections, total item inspections, and patch inspections) differentiate older adults with lower episodic memory and executive function abilities and degraded white matter integrity in the ACC, NA, and vmPFC tracts.

Observed differences may be due to the present cohort of participants. Age-related differences were identified to correlate with a few measures of search, however, age did not greatly contribute as a covariate. Older adults recruited from the community may show greater levels of cognitive ability or preservation as they are required to show interest in the research, willingly contribute several hours of time, and have a relative ability to embrace change or experience new methods. Especially those who choose to volunteer for research studies, these older adults may have a greater interest in health-related topics, ageing, or contributing to scientific knowledge. Their motivation to participate may stem from personal or altruistic reasons, leading to a self-selection bias among research participants. Further, the older adults who participated may have been healthier than one might expect from the general population with higher levels of physical ability. These are especially true for the present study, which required participants to attend a session for two hours (or two sessions), have the physical ability to walk around a large space, and be willing to try immersive virtual reality, which many of them had never experienced (as gathered colloquially). Therefore, a more varied population, with explicit MCI and AD diagnoses and tighter exclusionary criteria, may be required to fully elucidate the predictive factors between neural structures associated with ageing and search and foraging behaviour. This would provide greater insight into the typical and pathological ageing process. Areas of relative strength however reside in the discrimination between those with abnormal cognitive scores and relationships elucidating differences in search and foraging performance. Despite these potential limitations, it can still be clearly observed that certain neural tracts and cognitive weaknesses are predictive of search and foraging performance. These results, with further clarification from clinical populations, may be able to identify early markers of pathological ageing.

Chapter 5. Experiment 7

5.1 Introduction

Experiments 3-6 identified that uncertainty drove foraging performance, associated with executive functioning (EF) strengths in organisation and exploitation. Domain general processes essential to EF modulate core aspects of cognitive control (e.g. attentional allocation, inhibition, switching, cognitive flexibility, working memory; Baggetta & Alexander, 2016; Barceló & Cooper, 2018). EF contributes to goal-directed behaviour (Friedman & Robbins, 2022), and is essential to task monitoring or regulation (Baggetta & Alexander, 2016). Many networks reside within the prefrontal cortex, impacting EF, which are integrally linked with cognitive control and mediate task performance (Friedman & Robbins, 2022). These networks, including the DMN, are associated with uncertainty, such as the uncertainty described in previous chapters that defines how one searches and forages within their environment (Lloyd et al., 2023). Specifically, uncertainty is suggested to lead to greater exploratory choice (Blanco et al., 2016), and therefore greater EF ability can provide more efficient or successful responses (e.g. exploration) in the face of uncertainty. Residing in the PFC, EF relies on a distribution of networks and thus engages with regions facilitating working memory, set shifting, and planning (Rabinovici, Stephens, & Possin, 2015). This creates an architecture that combines processes such as planning and reasoning, which facilitates exploration and exploitation in uncertain environments (Koechlin, 2016), providing implications that for one to organise, plan their movements, search, forage, or otherwise, and to learn from such behaviours, EF contributions are required.

The contributions of EF on aspects of search and foraging performance have been evident throughout previous chapters; EF has been shown to guide search for greater cued inspections, for example, and facilitate balance between exploration and exploitation. Experiments 3 and 4 (see *section 3.5* and *3.6,* respectively) revealed that greater EF ability played a significant role in achieving success, and Experiment 6 (see *section 4.4*) identified that younger adults relied on EF for success, but older adult success could be predicted by it. It has been discussed that EF mediates foraging-like behaviours (Hills et al., 2010) by preventing revisits through working memory provisions and utilising spatial attention to guide conjunction of feature searching. EF specifically mediates the exploration-exploitation trade-off by moderating motor planning and inhibition, supporting goal-directed behaviours that are required for successful foraging (Woods et al., 2013), as well as facilitating planning and task control (Remington et al., 2021). These flexible adaptations to changing environments reside at the very basis of foraging literature (Kolling et al., 2012) as a measure of EF. S*ection 3.5* and *section 3.6* identified that template formation was mediated by EF, indicating that EF contributed to rule creation, facilitating success. EF has been suggested to comprise of six independent factors, including set-shifting and interference management, prospective working memory, self -monitoring and -maintenance, response inhibition, task analysis, and strategy generation and regulation (Testa, Bennett, & Ponsford, 2012). Peterson, Beck, and Wong (2008) found that loading EF systems leads to a decrement in visual search efficiency, revealing that one role of EF is to prevent early shifts in attention. Ólafsdóttir, Gestsdóttir, and Kristjánsson (2019) further identified within a conjunction visual foraging array that older children and adults searched one feature before switching to a different feature, suggesting that EF mediates switching behaviour between features. As such, implementing an array where hidden targets switch location based on a rule would place greater executive requirements on participants in order to guide success. Accordingly, elucidating the components within large-scale search subserved by EF will provide finer-grain insights into the cognitive demands underpinning three-dimensional tasks, especially when one is required to learn search rules, and how such rules are learnt and flexibly shifted as they change over time.

Set-shifting tasks are one way to measure aspects of EF including cognitive flexibility (Oh et al., 2014), visual discrimination, and the maintenance, shifting and flexibility of attention (Heinzel et al., 2010). The Wisconsin Card Sorting Task (WCST) is the most widely used and well-known set shifting paradigm (Milner, 1963). The WCST requires one to sort cards based on a rule and after a series of successful sorts, the rule changes, requiring a shift in set. The core elements of the WCST encompass stimuli across three features—colour, shape, and number. This requires flexible adaptation to shift rules based on feedback (receiving an “incorrect” response requiring set shifting or a “correct” response to continue the current set). The outcomes of the test are determined by the number of sets achieved, perseveration, inhibition, and the maintenance and shifting of attention. Across several studies utilising the WCST (as described by Oh et al., 2014), the ACC and prefrontal cortical regions were associated with shifting success, regions also associated with search and foraging success, by measuring the brain activity changes. The requirement to shift from one stimulus to another triggered greater brain activity than non-shifting. Further, the processes involved with attentional shifting have been associated with the dopaminergic network, including depletions in the frontal regions, where direct manipulation of the circuitry resulted in increased susceptibility to task-irrelevant stimuli (Jazbec et al., 2007), similarly associated with the exploration-exploitation trade-off. Inhibitory responses are essential for goal-directed actions, facilitated by EF and working memory abilities, and perseverated responses have been associated with EF deficits, with frontal degradation implications (Potter & Grealy, 2006). The ACC contributes to set shifting via the salience network (Dajani & Uddin, 2015), which is the same network that has identified alterations in NE signalling leading to disruptions in flexibility (Wyatt et al., 2024). As the ACC promotes attention (Spreng &

Turner, 2021), set shifting behaviour may reside in similar regions to some search behaviour mechanisms, such as searching for targets amongst distractors. Therefore, set shifting requires contributions from similar networks to that of search and foraging behaviour, suggesting that cognitive flexibility and EF can be quantified by aspects of set shift tasks.

Alternative paradigms to assess set shift mechanisms include the intra-dimensional extra-dimensional set shift task (such as the CANTAB IED test as described in *section 2.3.3*). An intra-dimensional shift includes shifting from one feature to another with the same featural properties (i.e. colour: yellow to blue). An extra-dimensional shift is outside of the featural properties (i.e. colour to form). The CANTAB IED test, for example, has been applied to a great number of cohorts and disorders (see Oh et al., 2014 for a brief overview) and is considered analogous to the WCST. It is suggested that the intra-dimensional extra-dimensional set shift task (IED) is a two-step process. First, one must identify which stimulus aspect is important for receiving reinforcement (e.g. colour). Then, it is associated with individual examples of that aspect with their reinforcement value (Rogers et al., 2000). This first learnt stimulus dimension (e.g. colour: yellow) is relevant, and therefore attention is directed and biased. The initial development of the bias can be tested by presenting a similar stimulus dimension but novel stimulus (e.g. colour: blue; intra-dimensional shift). The bias can be probed (and thus overridden) by shifting to a different dimension (e.g. shape; extra-dimensional shift). The extra-dimensional (ED) shift is more difficult than an intra-dimensional (ID) shift (Rogers et al., 2000). Implementing an IED-type task may shed light on behaviours relevant to search and foraging as a proposed controlled model of EF and cognitive flexibility. Quantifying executive contributions to large-scale tasks defined by shifting rules may offer finer-grained insights into the mechanisms underlying large-scale search and cognition, which are crucial for flexible rule shifting and acquisition.

Therefore, to further elucidate the EF underpinnings to the large-scale search paradigm as described in previous chapters, executive requirements were increased by requiring participants to follow a set-shift task rule. The visual search literature classically shows that individual differences associated with search behaviour are underpinned by memory and control. This experiment manipulated target location rules to specifically investigate executive control in a visual search context. As such, following an IED design, this framework serves as the foundation for distinguishing between ID shifts and ED shifts. By comparing shifts within the same dimension (ID) and shifts between different dimensions (ED), this allows for a more detailed examination of the role of EF and where its effects are most pronounced.

Previous experimental manipulations of the large-scale search task identified that participants did not organise their search as anticipated. Experiments 1-5 revealed that in difficult conditions (i.e. lack of template provision, unequal distribution), search organisation did not differ between single feature and conjunction conditions. Experiment 6 identified that younger and older adults did not differ in their search organisation. Therefore, an additional neuropsychological measure was implemented to further assess organisation and planning. Planning ability is fundamental for search and foraging success (Bocchi et al., 2020), and for one to plan and execute organised search is facilitated by EF ability (Woods et al., 2013). One such neuropsychological measure is the Rey-Osterrieth Complex Figure Test (RCFT; Meyers & Meyers, 1995), which assesses spatial organisation, constructional abilities, and visual memory, evidenced to investigate EF, planning, and organisational strategy (Weber, Riccio, & Cohen, 2013). The RCFT copy condition has been suggested to elucidate planning and organisation by providing insight into visuospatial processing (Wilson & Batchelor, 2015). Uncertainty is suggested to guide search strategy, and those with greater strategy, such as planning and organisation, show greater ability to gain information when uncertainly increases (Walker et al., 2022). Therefore, the RCFT was selected to further assess planning and organisation ability in the present experiment, requiring participants to reproduce a complex figure via copy and from memory. Further, Experiments 1-5 also identified that there were potential verbal underpinnings contributing to success, and therefore an additional verbal assessment was included to investigate whether aspects of verbal ability guides search or foraging behaviour. It was supposed that rapidly changing templates may invoke greater reliance on verbal support, as Rideaux and Edwards (2016) suggested that consolidation requires forming working memory representations, such as templates, and Hills et al. (2012) proposed that foraging-like behaviours also occur in semantic memory, requiring verbal contributions. As such, an additional neuropsychology measure to explicitly investigate verbal contributions was employed. The California Verbal Learning Test (CVLT; Delis et al., 2017) measures verbal list learning from a list comprising of four semantic categories. As spontaneous semantic clustering reveals an organised learning style related to successful acquisition (Shear, Wells, & Brock, 2000), the CVLT was anticipated to allow for greater insight into the relationship between foraging behaviour and semantic memory, alongside verbal underpinnings to search success.

As such, a rule shift task was created to measure the executive contribution to search and foraging behaviour in a large-scale space. It was anticipated that participants who learned the rule would collect more targets throughout each set than those who did not, and participants with greater EF abilities would learn the rule more efficiently. It was further predicted that the shifts between rules would be easier (and more successful) in an ID shift whereas the ED shift would be more difficult and therefore participants would show greater difficulty by making fewer cued inspections and collect less targets. Participants were expected to forage more accurately, as guided by the rule, therefore leading to greater success, indicated by greater organisation through the space and fewer revisits. Participants with greater executive control and flexibility would show greater success overall. Finally, task success would be associated with greater performance across measures from the CVLT and RCFT.

5.2 Methodology

5.2.1 Participants

As described in *Chapter 2. General Methodology*, twenty participants were determined to provide sufficient power per experimental manipulation utilising G*Power F-test for between-within interactions. As the present experiment was devised to elucidate factors following a similar design, the number of participants collected was matched to *Chapter 3* Experiments 1-5. A post-hoc power analysis was conducted based on the above assumptions. Using a two-tailed t-test, G*Power identified that, based on the post-hoc one-sample case using the mean difference from the constant, with a medium effect size, the power (P = .72) was sufficient for the determined sample size. As such, twenty participants aged 19-26 (M = 21.1, SD = 1.94) were collected (female: N = 9, male: N = 11) through the University of Plymouth's participant recruitment system where participant time was compensated for course credit.

5.2.2 Design

In an immersive VR environment, as described in *Chapter 2. General Methodology*, participants searched an array of containers for hidden targets. The specific environment followed that of the conjunction condition in *Chapter 3. Experiments 1-5*, where objects were defined by a conjunction of features (i.e. yellow and blue cups and boxes). However, the task was designed to follow an IED rule shift. Therefore, the targets were beneath one object type, which was represented by a conjunction of colour and form features (e.g. yellow cup). After three trials, the association changed and that was either to an object that only differed along one dimension (e.g. new colour, blue cups) or both dimensions (e.g. new colour and a new feature, blue boxes). The task followed the same order for all participants. Akin to the previous VR paradigms, participants were presented with an array containing 24 tables, and each table contained 12 interactable objects. These objects were defined by a conjunction of features (three yellow cups, three blue cups, three yellow boxes, three blue boxes). Each trial would last 60 seconds, and following time termination, all the cup/box items would disappear, but the tables would remain present. Participants were required to return to a green disc at the centre of the array and press the trigger on the controller to begin the next trial. Like Experiments 1-5, participants were presented with a 30s practice trial, and no participant required a second attempt. Task instructions, akin to Experiments 3 and 4 read: *"You will now complete a series of trials. Each time, your task is to find as many hidden Red balls as possible. The balls change colour when found, so if you find a grey ball you have already searched there. You will have 60 seconds to complete each trial. Remember to search as efficiently as you can."* Three consecutive trials would follow a rule, lasting a total of 24 trials. After the third trial, the rule would shift either intra- or extra- dimensionally, without communication to the participant. All participants began with the target hidden under the yellow cup. Following every three trials, the rule would shift either within ID or ED, and this pattern followed across all 24 trials (see Figure 5.1 for a pictorial description of rule shifting). In total, there were four ID shifts (two by colour, two by shape) and three ED shifts. The order was determined by equating the number of ID and ED shifts with equal ID shifts between colour and shape.

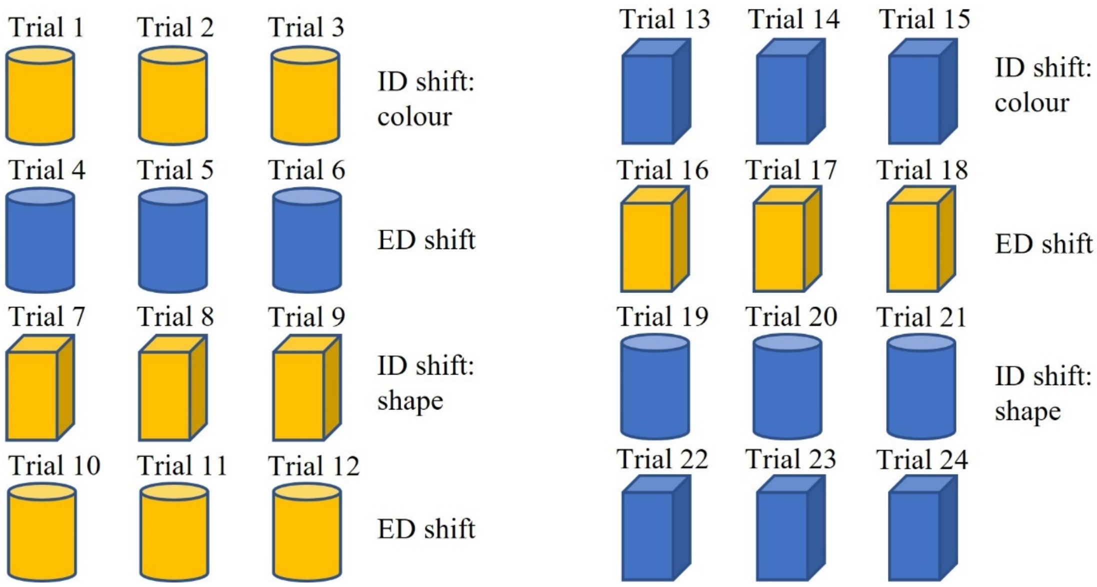

Figure 5.1. Pictorial representing the intra-dimensional extra-dimensional set shifts throughout the task. Three-dimensional shapes represent the stimuli that the target location was defined by per trial, and trials denote the sets of three before a shift (described on the right of the set).

5.2.3 Rey-Osterrieth Complex Figure Test (RCFT)

The RCFT was employed to investigate planning and organisation ability. The complex figure (see Figure 5.2) was presented on a laminated A4 sheet in portrait orientation. Participants were first instructed to copy the figure onto an A4 piece of paper, presented in portrait orientation, and were given as much time as required. Participants were given a pen to copy the figure, and therefore erasing misdrawn lines was not possible. Per the guidelines provided in the testing manual, participants were instructed: *"Look at this figure. I would like you copy that figure onto this sheet of paper. Copy it so that I would know that this is the figure you drew. Do a good job."* After the participant indicated completion, both the figure and copied drawing were taken away. After a short delay of approximately 3-minutes (the RTI was used as a filler task), participants were then presented with a blank sheet of A4 paper in portrait orientation and were instructed to reproduce the figure from memory. Participants were not warned of the delay trial. Specifically, participants were asked: *"A short time ago I had you copy a figure. I would like you to draw that figure again, but this time from memory. Draw that figure here."* Additional components of the full RCFT protocol were not administered.

Scoring of the RCFT is divided into 18 units, which coincides with a different piece of the whole complex figure (see Figure 5.2). Each unit is scored for accuracy and placement: for successful accuracy *and* placement a unit will receive two points, for successful accuracy *or* placement a unit will receive one point, and for *unsuccessful* accuracy and placement a unit will receive no points. There is also the option to score 0.5 on accuracy and placement if the unit was drawn and placed incorrectly but is still *recognisable*. Therefore, each drawing can achieve a maximum score of 36.0 points, and normative *T*-scores and percentiles are derived based on the participant's age. Copied drawings measure visuospatial construction ability, where lower scores indicated reduced spatial organisation and planning. Immediate memory reproductions assessed encoding and short-term memory ability.

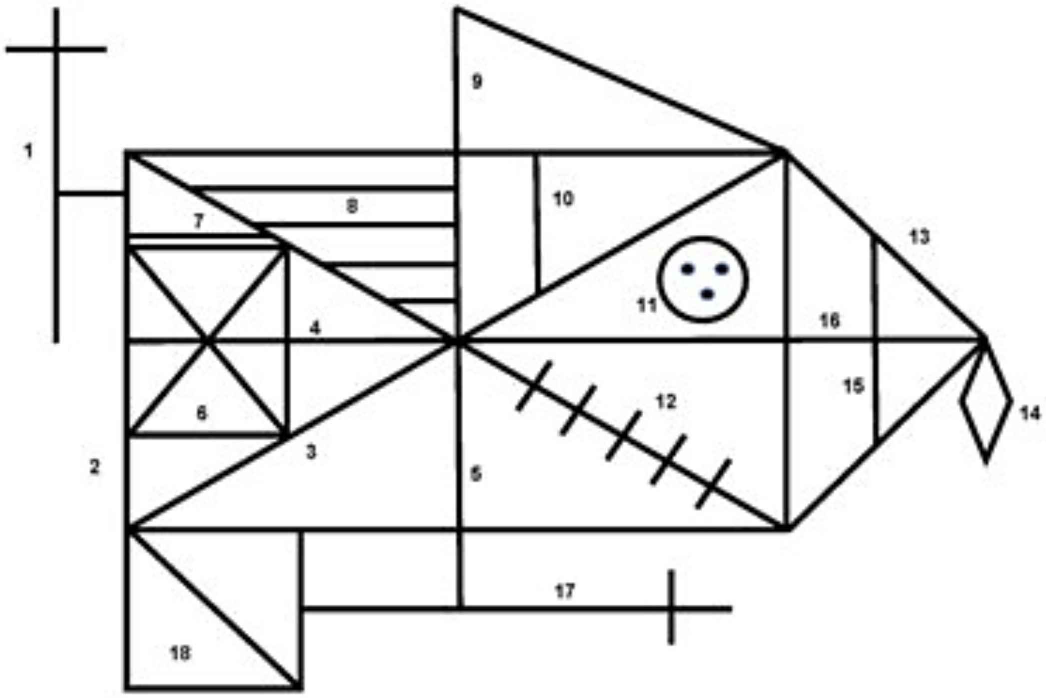

Figure 5.2. The Rey-Osterrieth Complex figure with numbered scoring units from the RCFT Scoring Manual (Meyers & Meyers, 1995).

5.2.4 California Verbal Learning Test- 3rd edition (CVLT)

The CVLT is a measure of verbal learning and memory, where a participant is read a 16-item word list (List A) five times, and after each presentation they must recall as many words as possible. The list comprises of four words each from four categories (i.e. animals, vegetables, ways of travelling, furniture) totalling 16 words. Following the CVLT manual, participants were instructed: *"I'm going to read a list of words to you. Listen carefully, because when I'm through, I want you to tell me as many of the words as you can. You can say them in any order, just as many as you can. Are you ready?"*. Immediately after reading the entire 16-word list, participants were prompted to recall as many words as possible. Following Trial 1 recall, and when participants identified that they could not recall any more words, participants were then instructed: *"I'm going to read the same list again. Like before, tell me as many of the words as you can, in any order. Be sure to also say the words from the list that you told me the first time."* This similar pattern of list delivery, immediate response, and instructions were followed for Trials 3-5. Following the five trials, the participant was presented with a second list of words which acted as 30s distractor and intrusion list (List B). Before the presentation of List B, participants were instructed: *"Now I'm going to read a second list of words to you. When I'm through, I want you to tell me as many words from this second list as you can, in any order. Don't tell me words from the first list, just this second list."* After recalling as many words as possible from List B, participants were prompted to free recall words from List A, and then were provided with semantic cues in a cued recall. Specifically, they were directed: *"Now I want you to tell me all the words you can from the first list, then one I read to you several times. Don't say any words from the second list, just the first list. Go ahead."* For the cued recall, participants were instructed: *"Tell me all the words from the first list that are [furniture/vegetables/ways of travelling/animals]."* Additional measures of the full CVLT were not administered. Table 5.1 describes each of the measures derived for analysis.

Table 5.1. Description of measures derived from the CVLT assessment.

Measure	Description
Trial 1 success	The number of words recalled after the first List A presentation; assesses auditory attention and working memory
Total recall (Trial 1-5)	The total number of words recalled across all five List A presentations providing a global index of verbal learning ability; assesses memory function
Short term memory (Trial B)	The number of words recalled from List B after the presentation; assesses the degree of proactive interference. Higher scores on Trial B than Trial 1 may indicate understanding of task demands or deficits in List A encoding
Short term delay free recall	The number of freely recalled items from List A without item presentation; assesses short term memory retention
Repetitions	Whether participants repeated the same word multiple times within the same trial; assessed as revisit-like errors or inhibition
Intrusions	Total number of words not included in List A when presenting List A, not included in List B when reading List B, or not included in List A when free- or cued- recalling; assesses recall errors
Semantic clustering	Consecutive recall of words from the same semantic category (i.e. animals, akin foraging like behaviours as described by Hills et al., 2015); assesses auditory and verbal episodic encoding and retrieval
List B Semantic clustering	Consecutive recall of words from the same semantic category (i.e. animals, akin foraging like behaviours as described by Hills et al., 2015) from List B only; assesses auditory and verbal episodic encoding and retrieval
Recall consistency	Consistent recall of the same words across consecutive presentations; assesses changes in strategy and measures frontal lobe involvement
Learning slope	The average number of new words per trial; assesses changes in rate of learning throughout Trials 1-5

5.2.5 Procedure

Sessions followed a similar format to that of previous experiments. In the present experiment (akin to *Chapter 2. General Methodology*), participants received all methods in the same order: following written consent, participants were administered the MoCA, RCFT, and CVLT. The short-delay between the copy and immediate recall of the RCFT was filled with the CANTAB's RTI, which is a 3-minute task. Participants would then undertake the VR rule shift paradigm following the CVLT short-delay administration, and finish with the rest of the CANTAB battery. The whole session took approximately 75-90 minutes, depending on participant speed.

5.2.6 Analysis

The behavioural variables were as described in the *Chapter 2. General Methodology*: the search variables were defined by the participant's score, percentage of cued inspections, total inspections, and the number of patches visited. Foraging variables were quantified by within- and between- patch organisation measured by best-*r*, exploitation, and percentage of cup and patch revisits. It was determined in *Chapter 3* that cup revisits did not require further investigation due to the low occurrence. This was also followed presently as very few participants revisited previously inspected cups (M = 3.71%, SD = 2.05%; min = .82%, max = 8.29%). It is important to note that as a shift did not occur until the start of Trial 4, Trials 1 through 3 were excluded from analysis. Each of the search and foraging measures were subjected to analyses quantifying a Shift measure and Trial measure, where each shift and trial were averaged for each behavioural measure. For example, to quantify ID shifts for the number of targets collected, the number of targets collected for each first trial was averaged after all ID shifts (i.e. Trial 4, Trial 10, Trial 16, Trial 22) to get an ID shift Trial 1. ID shifts were then averaged across all second trials of the ID set (i.e. Trial 5, Trial 11, Trial 17, Trial 23), and then third trials. The process was repeated to quantify ED shifts for the number of targets collected. Again, each first trial averaged the number of targets collected after an ED shift to get an ED shift Trial 1 (i.e. Trial 7, Trial 13, Trial 19). Trials were also averaged across the second and third trials from each ED set to get an overall understanding of performance over three trials from each set. The same process was repeated for each of the search (i.e. cued, total, patch inspections) and foraging (i.e. percentage exploit and revisits, between- and within- best-*r*) measures.

It is suggested that colour is easier to identify than shapes (Dzulkifli & Mustafar, 2013) as it requires low level visual attention driven by bottom-up processing (Pike, 2018). Therefore, the type of ID shift was also quantified to assess whether participants were more successful after a colour ID shift or a shape ID shift. As such, following the same procedure as above, for each behavioural measure, first, second, and third trial averages were gathered after a colour or shape ID shift. It was anticipated that colour ID shifts would be the easiest rule shift; the most difficult rule shift was predicted to be the ED shift. Therefore, for each behavioural measure (e.g. number of targets collected) there would be an average number of targets collected across the first, second and third of each ID and ED set, as well as the colour ID and shape ID set.

A repeated measure, within-subjects ANOVA quantified the rule shift per set as a 2 (Shift: ID, ED) x 3 (Trials: Trial 1, Trial 2, Trial 3) design. To further explore whether there was difference between colour ID and shape ID, a repeated measure, within-subjects ANOVA was run to quantify the rule shift in a 2 (Shift: colour ID, shape ID) x 3 (Trials: Trial 1, Trial 2, Trial 3) design. Pearson’s correlations were used to identify relationships between behavioural and cognitive measures.

5.3 Results

5.3.1 Search behaviour

2 x 3 ANOVAs for each behavioural measure are found in Table 5.2, which describes the *F*-ratio and partial eta squared. First assessing ID and ED shift effects on search performance across three trials, ANOVAs revealed that that the type of shift significantly impacted the total number of targets collected, the percentage of cued inspections, and the number of patches inspected. One should note that there were no two-way interactions between shift type and trial number. Specifically, more targets were collected when the shift was an ED shift (M = 44.51, SD = 3.80) than ID shift (M = 42.96, SD = 3.57, *p* = .018). Significantly more targets were collected in the third trial (M = 45.29, SD = 3.73) of the set than the first (M = 41.80, SD = 3.69, *p* < .001), significantly more targets were collected in the second trial (M = 44.12, SD = 3.67) than the first (*p* = .025), however targets collected between the second and third trials did not statistically differ (*p* = .23). Significantly more cued inspections were made when the shift was an ED shift (M = 73.37%, SD = 6.65%) than ID shift (M = 70.35%, SD = 6.22%, *p* = .027; see Figure 5.3a). A significantly greater percentage of cued inspections were made in the third trial (M = 74.34%, SD = 6.58%) than first (M = 67.89%, SD = 6.24%, *p* < .001), and a significantly greater percentage of cued inspections were made in second trial (M = 73.36%, SD = 6.47%) than first (*p* < .001), however cued inspections did not differ between third and second trials (*p* = .32). Significantly more patches were inspected when the shift was an ED shift (M = 15.47, SD = 1.24) than ID shift (M = 15.05, SD = 1.16, *p* = .042). Significantly more patches were inspected in the third trial (M = 15.64, SD = 1.21) of the set than the first (M = 14.70, SD = 1.20, *p* = .002), and significantly more patches were inspected in the second trial (M = 15.45,

SD = 1.19) than the first (*p* = .015), however patch inspections between the second and third trials did not statistically differ (*p* = .84).

Table 5.2. *F*-ratio and partial eta squared for ID and ED shifts over trials.

	Shift		Trial		Shift x Trial	
	F	η_p^2	*F*	η_p^2	*F*	η_p^2
Score (total number of targets found)	6.72*	.26	12.70**	.40	.29	.02
Percentage of cued inspections	5.73*	.23	28.51**	.60	.19	.01
Total inspections	.29	.02	.54	.03	.35	.02
Number of separate patches inspected	4.75*	.20	10.69**	.36	.48	.03
Within-patch best-*r*	.003	.000	.48	.03	.05	.003
Between-patch best-*r*	.02	.001	.31	.02	.52	.03
Exploitation	4.12	.18	1.58	.08	.31	.02
Total number of patches revisited	.36	.02	.13	.01	.43	.02
Runs	5.30*	.22	8.03**	.30	.16	.01

NB. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **

2 x 3 ANOVAs for each search measure investigated whether colour or shape assisted participants in ID shifting across trials (see Table 5.3). Analyses revealed that participants collected more targets when the shift was a shape ID (M = 46.39, SD = 3.88) than colour ID (M = 39.53, SD = 3.40, *p* < .001) shift. Significantly more targets were collected in the third trial (M = 44.24, SD = 3.59) of the set than the first (M = 41.23, SD = 3.58, *p* = .008), significantly more targets were collected in the second trial (M = 43.43, SD = 3.59) than the first (*p* = .013), however targets collected between the second and third trials did not statistically differ (*p* = .11). Significantly more cued inspections were made when the shift was a shape ID shift (M = 75.48%, SD = 6.60%) than a colour ID shift (M = 65.21%, SD =

6.14%, *p* < .001; see Figure 5.3b). Significantly greater percentage of cued inspections were made in the third trial (M = 73.04%, SD = 6.36%) than first (M = 66.46%, SD = 6.05%, *p* < .001), and significantly greater percentage of cued inspections were made in second trial (M = 71.53%, SD = 6.36%) than first (*p* < .001), however cued inspections did not differ between third and second trials (*p* = .20). Significantly more patches were inspected when the shift was a shape ID shift (M = 16.09, SD = 1.27) than a colour ID shift (M = 14.02, SD = 1.10, *p* < .001). Significantly more patches were inspected in the second trial (M = 15.21, SD = 1.16) than the first (M = 14.61, SD = 1.16, *p* = .017), however patch inspections between the second and third trials (M = 15.34, SD = 1.17, *p* = 1.00) did not statistically differ nor did inspections between the first and third trials (*p* = .059).

Table 5.3. *F*-ratio and partial eta squared for ID shifts between colour ID and shape ID shifts over trials.

	Shift		Trial		Shift x Trial	
	F	η_p^2	*F*	η_p^2	*F*	η_p^2
Score (total number of targets found)	20.10**	.51	10.80**	.36	.77	.04
Percentage of cued inspections	13.80**	.42	16.91**	.47	.40	.02
Total inspections	.65	.03	.11	.01	.21	.01
Number of separate patches inspected	15.55**	.45	5.82*	.23	.84	.04
Within-patch best-*r*	1.17	.06	.71	.04	.81	.04
Between-patch best-*r*	.86	.04	.14	.01	.92	.05
Exploitation	20.03**	.51	1.24	.06	2.42	.11
Total number of patches revisited	1.01	.05	.65	.03	.49	.03
Runs	19.09**	.50	7.14*	.27	.74	.04

NB. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **

5.3.2 Foraging strategy

2 x 3 ANOVAs assessing the effects of ID and ED shift on foraging behaviour across trials revealed that none of the foraging measures rose to significance (see Table 5.2). Therefore, to investigate whether participants organised their search based on visual properties alone, rather than the foraging constructs of the array, "runs" (Kristjánsson et al., 2014) were assessed. Kristjánsson and colleagues (2014) described that humans select their targets in non-random sequences, or "runs". They found that most of their participants collected conjunction of feature-defined targets in two long runs, rather than switching. This was suggested to indicate that participants were unable to maintain two conjunction templates simultaneously and therefore collected one conjunction between switching to the second. As such, the number of times a participant inspected one conjunction consecutively (e.g. yellow cup) before switching to the next conjunction was counted and summed for each trial. For example, if a participant inspected "yellow cup", "yellow cup", "blue cup", that would be considered a run of one as there was one consecutive inspection. Run data was subjected to the same procedure as described for the above measures, where averages were gathered and the first, second, and third trials of each set, for both ID and ED, and then for colour and shape ID. It was revealed that the longest run was 81 consecutive cued inspections across trials (M = 39.48). A 2 x 3 ANOVA for run data (see Table 5.2) revealed that runs were longer when the shift was an ED shift (M = 43.40, SD = 4.23) than ID (41.87, SD = 3.96, *p* = .033; see Figure 5.3c) shift. Runs were significantly longer in the third (M = 43.90, SD = 4.23) trial than first (M = 40.89, SD = 4.01, *p* = .004), and runs were significantly longer in the second trial (M = 43.12, SD = 4.09) than first (*p* = .032). Runs did not statistically differ between second and third trials (*p* = .91).

A 2 x 3 ANOVA of foraging behaviour between colour ID and shape ID shifts revealed that the type of ID significantly affected exploitation, but not over trials (see Table

5.3). As such, participants were significantly more exploitative when the shift was a shape ID shift (M = 99.36%, SD = 1.11%) than colour ID (M = 95.18%, SD = 1.23%, *p* < .001) shift. Run data revealed that participants had significantly longer runs when the shift was a shape ID shift (M = 45.72, SD = 4.37) than colour ID (M = 38.02, SD = 3.72, *p* < .001; see Figure 5.3d) shift. Runs were significantly longer in the third trial (M = 42.88, SD = 4.03) than first (M = 40.21, SD = 3.97, *p* = .021), and in the second (M = 42.51, SD = 3.96) than first (*p* = .009) trial, however, runs did not differ between the second and third (*p* = 1.00) trials.

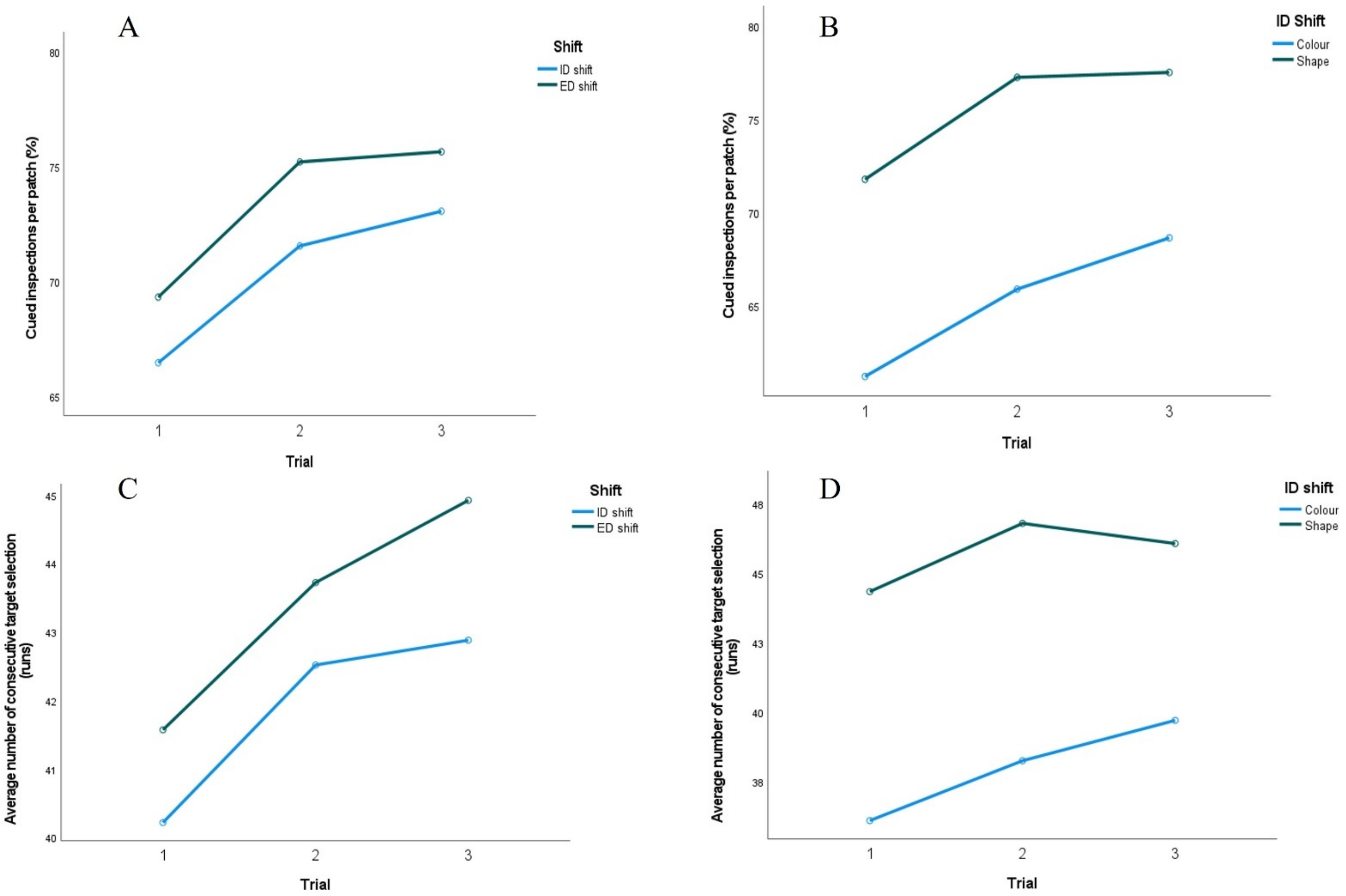

Figure 5.3. Percentage of cued inspections per patch across shift trials between: A) ID and ED shifts and B) colour and shape ID shape. The average number of targets collectively selected in runs for C) ID and ED shifts and D) colour and shape ID shape.

5.3.3 Individual difference

Individual difference was assessed across each of the derived search and foraging measures for ID and ED shifts, ID colour and shape shifts, and across each of the trials. This resulted in a large amount of correlational data. For brevity, general relationships are summarised below, and the complete correlation matrices are found in Appendix C. It was overall found that measures of EF were significantly associated with the number of targets collected, cued inspections, total patch inspections, and run behaviour across all shift-types and trials. EF was also associated with aspects of between- and within-patch organisation, and exploitation. Reaction time was slightly associated to within- and between- patch organisation. Episodic memory was mostly associated with the total number of targets collected, patch inspections and revisits, and it was found that greater episodic memory contributed slightly to longer run behaviour. Verbal memory contributed slightly to within-patch organisation and exploitative behaviour, and spatial working memory was slightly associated with between-patch organisation and patch revisits. It is important to note that all associations are positive in nature, where greater success on the behavioural tasks was associated with greater cognitive abilities.

5.3.4 RCFT

The RCFT was implemented to further clarify any planning and organisational underpinnings of search and foraging behaviour. It was found that the RCFT copy was only associated with a greater number of total item inspections across total ID (first trial: $r = .50$, $p = .027$; second trial: $r = .47$, $p = .036$; third trial: $r = .50$, $p = .026$), colour ID (first trial: $r = .47$, $p = .037$; third trial: $r = .46$, $p = .039$), shape ID (first trial: $r = .49$, $p = .029$; second trial: $r = .49$, $p = .027$; third trial: $r = .51$, $p = .022$), and ED (third trial: $r = .45$, $p = .05$) shifts, where greater copies indicated more item inspections across shift types and trials. Therefore, in a population of young adults, visuospatial planning contributed to successful executive control for item inspection. RCFT success was investigated more closely; RCFT copy scores (M = 32.83, SD = 2.05; min = 29.0, max = 36.0) revealed that 45% (N = 9) of participants achieved normal results (>16 percentile) for their age range. Of the 11 participants who organised their copy at lower than anticipated ability, 25% (N = 5) participants achieved scores lower than the first percentile.

The Immediate recall of the RCFT was associated minimally with shifts: within-patch organisation in the third trial was associated with ID shifts (ID total: $r = .52$, $p = .019$; ID colour: $r = .53$, $p = .018$), and higher exploitation after the third trial of an ED shift ($r = .47$, $p = .037$) and colour ID shift ($r = .46$, $p = .04$) was correlated with greater immediate recall. The Immediate recall scores (M = 21.7, SD = 6.72; min = 10.0, max = 31.0) were anticipated to be lower than the copy condition due to the implementation of memory and interference; this was supported by paired t-test ($t(19) = 7.38$, $p < .001$, $d = 1.65$) where the copy condition showed scores significantly higher than the short-term memory condition. 35% of participants (N = 7) achieved below average short-delay recall scores. However, established cut-offs indicating failure at the copy did not necessarily indicate immediate recall failure (i.e. some participants who failed the copy achieved results within average ranges in the immediate condition, and some participants who achieved normal copies proceeded to fail the immediate recall). This was supported by a lack of correlation between the copy and immediate condition: copying success was not associated with immediate memory success ($r = .14$, $p = .55$). It is important to note that all participants were healthy undergraduate students at the University of Plymouth, and therefore theoretically should achieve ‘within average’ results as all results were normalised and interpreted based on participant age. Two participant copy and immediate RCFT reproductions (Figure 5.4) depict the some of the organisational struggles. For example, Figure 5.4a illustrates initial organisational issues which then affected proceeding memory recall (Figure 5.4b); the participant did not utilise anchoring units to guide organisation (i.e. Figure 5.1, units 2, 3, 4, 5).

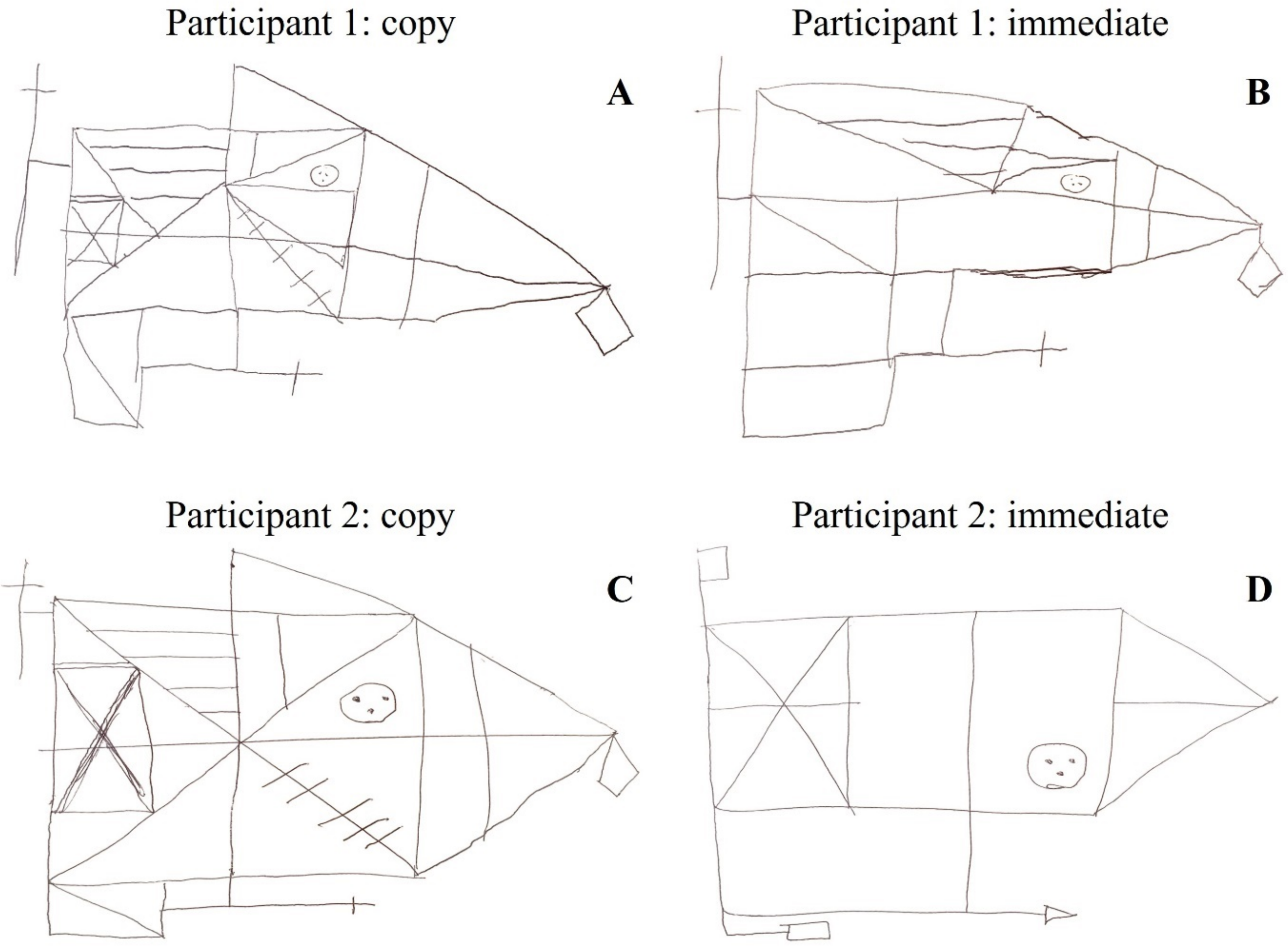

Figure 5.4. Figures A and B depict one participant's copy and immediate drawings, respectively. Figure A) represents the lowest scoring copy (raw = 29.0/36.0, < 1 centile) and B) depicts the respective immediate recall (raw = 16.5/36.0, T-score = 28, 1st centile). Figures C and D portray a second participant's copy and immediate reproductions, respectively. Figure C) illustrates an average copy (raw = 34.0/36.0, > 16 centile) however Figure D) represents severe forgetting or lack of attention (raw = 10.0/36.0, T-score = 19, < 1 centile).

Additional analyses investigated whether performance on the RCFT was associated with measures of cognition. Interestingly, the copy was not associated with any cognitive measures, however, the immediate recall of the RCFT was related to better performance on the interference task (List B; CVLT: $r = .44$, $p = .05$), greater spatial working memory (PALTEA: $r = .62$, $p = .004$; PALFAMS: $r = .6$, $p = .006$; PALTE: $r = -.79$, $p < .001$) and executive functioning (IEDYERTA: $r = .48$, $p = .031$; IEDTTA: $r = -.45$, $p = .049$).

5.3.5 CVLT

Previous manipulations of the VR paradigm identified verbal underpinnings. To further illuminate the nature of such contributions, the CLVT was added as an additional verbal measure. Appendix C details the association between the CVLT and search and foraging behaviour following ID and ED shifts across trials (see Tables B1-B4). In summary, fewer Intrusions were associated with more cued inspections following total ID and colour ID shifts across trials; within- and between-patch organisation across ID and ED shifts were associated with several measures of the CVLT including List B success, Intrusions, and Learning Slope; exploitative behaviour too revealed correlations with semantic clustering and free recall across ID and ED shifts, as did revisits to previously inspected patches. Finally, run behaviour when a colour ID shift occurred revealed correlations with Intrusions. Pearson's correlation was utilised to assess cognitive relationships between CANTAB and CVLT measures of interest. Total recall across CVLT Trials 1-5 was related to all three measures of verbal working memory (VPAERTOT: $r = -.48$, $p = .032$; VPAMWDST: $r = .48$, $p = .033$; VPAERSDR: $r = -.46$, $p = .04$) where greater success across the CVLT indicated fewer verbal errors, higher difficulty achievement, and fewer delayed total errors, respectively. Participant ability to cluster learnt words by semantics (akin to organising one's foraging; e.g. Hills et al., 2015) significantly correlated with fewer spatial working memory errors for both List A (SWMWE: $r = .53$, $p = .017$; SWMDE: $r = .51$, $p = .021$) and List B (SWMWE: $r = .5$, $p = .024$; SWMDE: $r = .51$, $p = .023$).

5.4 Discussion

Previous experimental manipulations revealed that search and foraging behaviour was adjusted in response to environmental manipulations such as template provision and target distribution. Visual search literature traditionally demonstrates that individual differences in search behaviour are influenced by memory and control. To specifically examine executive control within a visual search context, Experiment 7 manipulated target location rules to deliberately engage executive control. As consistent templates are suggested to be controlled differently than inconsistent ones, it was anticipated that nuanced individual differences would be observed when the search task required greater control than previous manipulations. Specifically, it was investigated whether participants were able to update their target templates in response to shifts in rules, and use such information to successfully guide their search, thus improving performance over the course of non-switch trials, in anticipation that ID shift sets would reveal greater success than ED shifts. Participants who were able to learn the rule were expected to search and forage more successfully over the three trials, supported by greater executive control. Further, as previous experimental manipulations identified a lack of organisational and planning differences as was expected, and verbal underpinnings supporting search behaviour, participants with greater copy and immediate recall on the RCFT, and greater number of words recalled over trials and short-term delay on the CVLT task, were anticipated to show greater associative performance.

5.4.1 Rule shift

Results revealed that search performance, but not foraging, was supported by executive control in a rule shift-type task. The number of targets collected, percentage of cued inspections, and number of patches inspected all revealed significant contributions following shifts in rules. Run behaviour was investigated, following the suggestion from Kristjánsson et al. (2014) that runs reveal greater insight into template creation. It was found that across all three search measures and run behaviour, performance was greater when the set followed ED shift, not an ID shift, in contrast to hypotheses and previous literature. Therefore, increased search performance indicated that the present rule shift task placed executive requirements on participants' search success. Participants with greater executive control, and therefore participants who were able to create new templates based on shifts in rules, were more successful across measures of search, including more targets collected, more cued inspections, and more patch inspections. Previous research has suggested that rule switching tasks are mediated by a rule-activation stage of executive control, and the rules (or templates) created are effectively 'switched on and off' in distinct operations (Rubinstein, Meyer, & Evans, 2001). Additional research into the neural underpinnings of shifting and inhibitory behaviour revealed a largely unified network of support from prefrontal and parietal regions subserving the executive control processes (Hedden & Gabrieli, 2010). These findings were generally supported by Lemire-Rodger et al. (2019), who identified that several aspects of executive control (e.g. working memory, inhibition, and task switching) all activated common regions of the brain: frontoparietal control and dorsal attentional networks. This not only supports an executive control requirement in order to successfully shift between templates, but also for domain general contributions to facilitate such successes. Further, the combined contributions of both task switching and working memory support a system that can create and maintain templates to facilitate success. Working memory is considered necessary for template creation and maintenance (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2021). Therefore, greater executive control, subserved by working memory, facilitates greater success when task demands require template creation and maintenance, rule learning and shifting over time.

However, unexpectedly, findings consistently revealed that participants displayed greater success following an ED shift rather than an ID shift. This is contrary to previous literature (e.g. Rogers et al., 2000), where it has been suggested that intra-dimensional shifts are easier than extra-dimensional. The findings might be due to attention, where more overt differences (i.e. switching both features) become more salient over smaller shifts. It has been proposed that target templates originating from visual working memory are subjected to attentional deployments (Drigas & Karyotaki, 2017). If attention is particularly drawn to the novelty of the conjunction feature shift, then perhaps ED shifts would be better supported by the overt salience in the novelty of both features. Research on novelty and attention suggests that novel stimuli or task features can enhance cognitive processing and performance. For example, studies by Bunzeck and Düzel (2006) and Wittmann et al. (2007) found that novel stimuli elicited increased activation in brain regions associated with attention and memory, suggesting enhanced cognitive processing. Further, research into IED task switching in rats has supported the finding that ED shifts may be more easily learned than ID shifts. Trobalon and colleagues (2003) suggested that spatial relationships between reward and non-reward targets may be a mediating factor in the ease of ID or ED shift learning. Whilst the location may not play as large a role across equally distributed patches, the underpinnings of spatial attention and learning may be relevant, such that episodic memory in previous experimental manipulations (and presently) facilitates search success. The other aspect that may contribute to ED shift success is that of binding (i.e. the combination of two feature maps to create one exemplar; Treisman, 1986). Successful binding has been shown to mediate efficient and successful conjunction of feature search (Wyatt et al., 2024) as the conjunction of features becomes a single exemplar, and therefore if the participants created a target representation defined by a conjunction of features, then the shifts would reside along a single dimension. If successfully bound items mediate search success, the difficulty of the ED shift may decrease. Perhaps then if novelty increases salience, the ED shift might make stimuli salient to the attentional systems more effectively than ID shifts. Clearly however, further research into the mechanisms underpinning greater success following an ED shift is required to clarify the presently novel findings.

Results also revealed that participants learned over time across the three search measures (i.e. targets collected, cued and patch inspections), where the third trials revealed greater means than second trials, and both trials were significantly more successful than first trials, as one might expect when successfully learning over trials. Ravizza and Carter (2008) observed that rule shifting was characterised by larger target repetition effects, such that greater repetition of targets supported greater success. This supports the present findings that exposure to targets over time facilitates greater success. Reinforcement, or the reward when successfully discovering a target, is integral to search (Paeye, Schutz, & Gegenfurtner, 2016). The more a participant discovered a target, the more they were able to learn the target location, and therefore the more successful they would be. Reinforcement learning (adjusting one's behaviour based on outcomes) is suggested to facilitate learning of optimal behaviour in uncertain situations (Koechlin, 2016), supporting present findings that participants learnt target location throughout shift sets. The significant differences from the first to second and first to third trials reveals a steeper learning curve that flattens as participants continued to learn, and the first trial representing greater knowledge acquisition with later trials revealing greater target acquisition.

Although it has been suggested that colour identification is easier than shape (e.g. Dzulkifli, & Mustafar, 2013), results revealed that participants were more successful on a shape ID shift than colour ID shift. In a study assessing the contribution of shape to visual search, it was found that global shape information captured the most relevant featural dimensions for guiding search, however colour was not investigated (Alexander, Schmidt, & Zelinsky, 2014). Wolfe and Horowitz (2017) further supposed that shape guides visual search with the caveat that research is less clear on how, but Kim and Cho (2016) evidenced reliable memory-based attentional capture for targets defined by shapes as opposed to colour. As such, it is clear that there is not enough evidence to clearly describe why participants may have been better supported by shape ID shifts than colour. Perhaps this study presents novel findings that shape may be more salient, or at least discriminable, than colour, despite previous suggestions for colour salience. It could also be considered that as this present experiment was conducted in the third dimension, contributions from 3D shapes may provide greater search support than colour, due to factors such as "real world" or naturalistic relevancy. Recent research investigating the contribution of real-world objects found significant contributions to working memory and visual search success when the objects were recognisably real-world as compared to unrecognisable objects (Chung, Brady, & Störmer, 2023). Perhaps therefore three-dimensionality provides additional support not yet investigated in greater detail, and further research into such underpinnings would prove beneficial.

5.4.2 Run behaviour

Run behaviour was also investigated as an additional behavioural measure. Runs were found to be predictive of success similarly to search measures—ED shifts revealed longer runs than ID shifts, run length increased over the three trials per set, and shape ID shifts facilitated longer runs than colour ID shifts. Whilst considered a foraging measure (i.e.

Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020), runs inherently quantify one's template implementation, investigating the number of active templates and the frequency of switching behaviour between multiple templates. Kristjánsson, Ólafsdóttir, and Kristjánsson (2020) describe that traditionally, when targets are defined by a conjunction of features, runs are longer where participants tend to exhaustively forage one type of target before switching to the next, consistent with the single template proposal. The present experiment supports such findings, where runs became longer over time as participants learnt the rule and were therefore able to search under the cued items exclusively. Prpic et al. (2019) too found in an iPad foraging game that participants increased their run behaviour in conjunction conditions as compared to single feature. They suggested this to mean that run behaviour does not rely on single feature and conjunction manipulation, but instead elucidates additional characteristics of foraging behaviour. In the present study, whilst the stimuli were defined by conjunction of features, the targets were only hidden under one feature, and therefore longer run behaviour would indicate greater learning of target location. This does not reveal the same information as Kristjánsson et al. (2020) or Prpic et al. (2019), but it does provide support that aspects of run behaviour can be quantified by executive control and reveal similar insights identified by the search measures (e.g. target collection, cued inspection, etc). Participants with greater control learned the location of the targets, and therefore only collected the targets consecutively, revealing longer runs.

5.4.3 Individual difference

Measures of individual difference were found to support search and foraging behaviour in the present rule shift task. Primarily, EF was greatly associated with measures of success, where across shifts and trials, all measures of EF (i.e. errors, adjusted errors, latency, total trials achieved, and adjusted total trials) were associated with total number of targets collected, cued inspections, patch inspections, exploitation and runs, with a few relationships identified between total item inspections, and between- and within- patch organisation. EF is known to engage with set shifting tasks (Rabinovici, Stephens, & Possin, 2015). As set-shifting tasks are one way to measure EF and cognitive flexibility (Oh et al., 2014), the strong associations between the task and measures of EF reveal that participants with greater cognitive flexibility were more successful in set-shift tasks, particularly supporting search behaviour, but not foraging to any great degree. This supports predictions that search behaviour is underpinned by executive control, with greater control guiding search performance. By moderating top-down information (Funahashi & Andreau, 2013), participants with greater control were able to create more successful search templates to guide behaviour, and therefore shift between search templates as the target location rule switched. It was also predicted that greater control would support foraging behaviour. Indeed, some associations were identified, inconsistently across within- and between- patch organisation. Greater learning of target location led to higher acquisition rates, reducing revisits, but possibly diminishing the necessity for organised movement. Participants with higher cognitive flexibility (indicated by greater executive functioning) sample information to learn target locations, enabling them to shift more effectively between rules or dimensions. This might result in a seemingly disorganised approach focussed on target acquisition. Additionally, the allocation of attention and stronger working memory abilities may allow participants to create stronger target templates, facilitating a more dynamic but disorganised search strategy. However, relationships were more prominently identified in exploitative behaviour. It has been suggested that exploitation can be optimal (Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020) if one has created a successful template, therefore acquiring more targets with minimal energy expenditure. As such, greater control leads to more complete templates, greater ability to switch between templates in response to task demands, and therefore more exploitative behaviour for greater target acquisition.

Additional measures of individual difference were found to support success in the rule shift task. Episodic memory was associated with success across most of the search measures, including target collection, cued inspection, item inspection, and to a lesser degree, patch inspections. Episodic memory also minimally contributed to foraging measures, with some associations identified in exploitative and revisit behaviour. Episodic memory has been shown to be integral to feature binding (Van der Linden et al., 2000), supporting participants in creating a representation of target location to guide search. Research has evidenced that colour-shape associations are stored in episodic memory (Kerzel & Andres, 2020), and therefore should the participant display greater episodic memory, templates will be more precise based on the greater associations developed between colour and shape. Goldstein and Beck (2018) investigated the effects of changing compared to stable templates across trials and found that processes did not necessarily rely on a consistent template to facilitate success, indicating that changing templates (e.g. shifting templates based on rules) over time does not have to indicate success decrements. Further, to facilitate search and foraging success, Sestieri et al. (2014) demonstrated that the DMN promoted episodic memory to guide search, and Chiu and Yantis (2009) evidenced that task switching recruited from a domain-general control mechanism. This would support the mutual contribution of episodic memory alongside executive control to facilitate search success.

Finally, spatial working memory, reaction time, and verbal memory minimally contributed to organisation between- and within- patch, revisits, and exploitation. This clearly reveals the executive control and episodic memory requirements for search success, and the slight contributions of spatial working memory, reaction time, and verbal memory to foraging success in rule shift-like tasks. As the purpose of the rule shifting task was to place executive demands on participants to quantify control, it is unsurprising that additional aspects of cognition do not greatly contribute to search but instead foraging success. Smith and De Lillo

(2022) summarise the relationship in spatial span tasks between systematic visits to target locations and subsequent recall, which require both spatial abilities as well as working memory. Organisation in the present experiment can be similarly associated with systematic inspections, therefore supporting a spatial working memory requirement in successful organisation. The more systematically one forages throughout their space, the less likely they are to revisit previously inspected locations. This reflects the findings in Experiments 1-5, which identified associations between organisation, revisits, exploitation, and spatial working memory. Therefore, despite the executive load placed by the rule shift requirements of the task, the patchy array and motile requirement in the large-scale environment still require cognitive mechanisms to facilitate successful foraging. This certainly reflects the cognitive flexibility participants employ in response to task demands, evidencing cognitive control in the mediation between search and foraging success within a large-scale environment.

The secondary purpose of the present experiment was to investigate planning, organisation, and verbal contributions. Previous experimental manipulations identified verbal underpinnings to success, with deficits in organisation, and therefore the RCFT and CVLT were additionally added to investigate such influences. The RCFT copy measured planning and organisation, and immediate recall determined visuospatial short-term memory. It was found that participants performed poorly on the RCFT overall, worse than would be expected for their age. 55% of participants performed suboptimally in the copy condition and 25% of that scored lower than the first percentile. RCFT copying ability was only predictive of item inspections in the behavioural task, and the immediate recall of RCFT was only slightly associated with within-patch organisation and exploitation. Although the task was presented in a visually guided, large-scale space, and the array was similar to previous iterations, perhaps the factors driving success relied more heavily on executive control and episodic memory, rather than planning and organisation ability. This was supported by non-significant contributions of within- and between- patch organisation throughout the task, indicating that participants did not organise their movements. EF encompasses a range of psychological constructs (Anderson, 2010) and loading of EF factors have shown that set-shifting is a separate executive process from planning and organisation (Testa, Bennett, & Ponsford, 2012), and so despite large-scale implementation, clearly participants did not use such mechanisms to guide success but rather focussed on control to learn the rule. Perhaps greater insight might have been elucidated from implementing the RCFT in *Chapter 3*. However, it was an interesting, incidental finding that university-educated young adults performed poorly on the RCFT. Very little research has been conducted on that of young, healthy adult performance on planning and organisation, especially in term of RCFT performance. It is clear that levels of variability exist in ability, where individual differences play a large role in young adult performance.

The final point of interest was that of CVLT performance, which was implemented to explore potential verbal underpinnings to search and foraging success. CVLT verbal measures revealed associations with all aspects of the VPA subtest but with very few aspects of the behavioural paradigm. Specifically, greater cued inspections and runs were associated with fewer list intrusions, between- and within- patch organisation revealed scattered associations between List 1-5, List B, learning slope, and intrusion. Exploitation and patch revisits too were minimally associated with List B, free recall and semantic clustering. CVLT intrusions likely has an underpinned executive component to inhibit incorrect responses, and therefore it is unsurprising that intrusions were associated with cued inspections and run behaviour, which were also highly correlated with EF measures. The rest of the measures however revealed scattered associations with the CVLT, like the varied contributions of success in verbal memory, spatial working memory and reaction time. This indicates that success is not necessarily supported by verbal ability (or at least exclusively), but there are additional factors in the verbal correlations found in previous chapters. The CANTAB VPA measures verbal ability, but associative, episodic, and working memory also contribute, and therefore associations previously found do not necessarily indicate a verbal underpinning but multiple contributions including working memory. Working memory tasks involve the maintenance and manipulation of information, such as verbal or spatial stimuli, over short periods (Han & Kim, 2009). However, these tasks are not pure measures of a single cognitive process; instead, participants can draw on additional mechanisms to facilitate success. Indeed, previous research has supported a domain-general integration of working memory with verbal and spatial memory (Morey, 2009), implying that such processes are flexible and adaptable. This strategic selection of maintenance mechanisms suggests that working memory tasks allow participants to draw on their individual cognitive strengths, such as verbal or attentional abilities, to facilitate task success. These two systems have been found to be strategically selected in experimental investigations based on task requirements, allowing participants to utilise cognitive strengths (Camos, 2015), thus suggesting a possibility that the present task allowed for a strategic selection of verbal or attentional ability and therefore allowing for the participant to rely on individual cognitive strengths to facilitate task success.

5.5 Conclusion

The present experiment investigated whether a novel, large-scale intra-dimensional extra-dimensional set shift-type task could elucidate EF control underpinnings to search and foraging success, with the inclusion of additional planning and organisation and verbal tasks to address queries in earlier chapters. Results indicated that participants with greater executive control showed greater search success, with ED shifts facilitating greater success than ID shift, and participants learning across the three trial sets. Following suggestions from the visual foraging literature, runs were also quantified, revealing similar associations with executive control as the search variables. Greater control revealed greater search success. However, foraging measures were not predicted by shift or learning performance. Executive control facilitated search success, but additional measures investigating verbal, planning and organisational underpinnings minimally contributed to success. The implementation of a task to investigate executive control allowed for a finer grained analysis into younger adults' ability to use cognitive control resources in a large-scale, three-dimensional task. Target location defined by rule shifting revealed suggestions of participants utilising reactive control, guiding the creation and maintenance of goal-relevant information in a cognitively demanding task to facilitate search success as a domain general strategy.

Chapter 6. Drawing organisation and planning

6.1 Introduction

Measures of graphic production were included in the cognitive assessment batteries administered in Experiments 1-7 (as described in preceding chapters), and some unexpected findings were noted. The Rey-Osterrieth Complex Figure Test (RCFT; Meyers & Meyers, 1995) was administered to younger adults as a measure of organisation and planning and as *Chapter 5* revealed, some university educated younger adults performed suboptimally, below expected levels of performance for their age. In particular, 55% of participants copied the RCFT in a substandard fashion, and 25% of those achieved scores below the first percentile. Further, *section 4.2.1* highlighted surprising results during the administration of the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005) in the clock drawing subtest, where younger adults revealed poor clock representations. Drawing tasks, or graphic productions, can assess a multitude of cognitive functions including memory, attention, action, and visuospatial perception (Trojano, Grossi, & Flash, 2009). As visuospatial organisation and planning have been shown to be integral for search and foraging behaviours (e.g. Kosovicheva et al., 2020; Smith & De Lillo, 2022), assessing decrements utilising well-validated assessments may be able to provide greater insight. RCFT findings revealed surprisingly poor performance, which was also qualitatively observed on the clock drawing subtest. Therefore, this Chapter will explore these performances in greater detail to quantify the underpinnings of these unexpected results.

The MoCA was developed to screen for underlying dementia processes (Siqueira et al., 2019) and has been evidenced as a sensitive measure for early diagnosis (Dautzenberg, Lijmer, & Beekman, 2020). The MoCA assesses visuospatial and executive skills, memory, and attention, amongst others. This test has been utilised widely across a variety of disorders (e.g. substance use; Bruijnen et al., 2019) and age ranges (e.g. healthy young adults compared to young adults with congenital heart disease; Pike, Poulsen, & Woo, 2017). With recent research into retesting and psychometrics, the MoCA has yielded mixed results into its generalisability (Bruijnen et al., 2020), but despite poor loading onto some cognitive domains (e.g. language), the MoCA is particularly sensitive to the visuospatial and executive subtest for predictive accuracy assessing impaired verses unimpaired older adults (Moafmashhadi & Koski, 2013). The MoCA has been shown to reflect interindividual differences in cognitive reserve. A study by Sammer and Lenz (2020) assessing brain structure in relation to MoCA scores in both younger and older adults found that participants with lower cognitive performance, regardless of age, exhibited structural changes compared to those with higher performance scores. This was suggested to indicate that cognitive performance was associated with brain structure, and that differences in brain structure, even for young adults, would result in differences in MoCA performance. Further, there have also been debates surrounding the cut-off criteria of the MoCA. Nasreddine et al. (2005), who devised the MoCA, suggest a cut-off of 26 points of 30 to indicate “normal” performance, and therefore scores of 25 and below indicate neurodegenerative processes. There have been suggested cut-offs and ranges for diagnosing MCI (22/30, range 19-25) and mild AD (16/30, range 11-21), however these are suggested tentatively due to overlap in disease progression (Nasreddine et al., 2005). A recent review has suggested, based on nine studies, that Nasreddine et al.’s cut-offs may result in inflated rates of false positives in clinical populations and therefore the cut-off should be 23/30 (Carson, Leach, & Murphy, 2018). This was supported by Yang et al. (2021) who furthered that a range, leading to degradation monitoring, rather than a singular cut-off score, would provide better screening criterion.

One aspect of the visuospatial and executive component of the MoCA includes a clock drawing element, where one is required to reproduce a clock based purely on verbal instruction. This task places executive, visuospatial and constructional demands on the examinee (Price et al., 2011), specifically requiring conceptualisation, planning, visuoconstructive skills, and symbolic representation (Julayanont & Nasreddine, 2017). Clock drawing is popular amongst the medical field and researchers alike due to its quick and simple administration and innocuous nature and is ubiquitous with quantitative measurement of visuospatial cognition (McDaniel et al., 2024). Sensitive to visuospatial reconstruction and memory, graphomotor skills, executive functioning, and top-down knowledge (Mainland & Shulman, 2017), clock drawing is suggested to be less susceptible to potential confounds such as premorbid intelligence, educational attainment, or ethnicity (Tuokko et al., 2000). Despite its popularity, clock drawing administration (see Mainland, Amodeo, & Shulman, 2014 for a review) and scoring systems (e.g. 18-point scoring: Babins et al., 2008; 7-point scoring: Freund et al., 2005; 38-error scoring: Nyborn et al., 2013; 10-point scoring: Rouleau et al., 1992) differ among many lines, including whether the circular outline of the clock face is provided, or drawn by the respondent. Clock drawing has been a predominant measure in screening, however young adults show deficits in clock drawing abilities.

McDaniel and colleagues (2024) approached 80 young adults, aged 18-30, asking participants to draw clocks (utilising the Clock Drawing Test; CDT). Participants were first provided with an empty circle on an otherwise blank sheet of paper and were asked to place numbers to resemble a clock and then set the time to ‘ten past eleven’. Then, to assess time-telling ability, participants were asked to draw five different times, with the circle of the clock and times provided (11:10, 2:45, 6:35, 9:52, 12:27) on a sheet of paper, and then after state the time shown of five different clocks (4:29, 7:50, 8:08, 1:17, 6:16), presented on a second sheet of paper. Accuracy was determined on a 5-point scoring system, with clocks receiving 4- or 5- points considered within normal limits. Points were awarded based on the following criteria: a perfect clock received 5 points, minor visuospatial errors received 4 points, acceptable visuospatial organisation but inaccurate representation of requested time received 3 points, 2 points were allocated for clocks that had moderate visuospatial disorganisation of numbers, 1 point was given for severe level of visuospatial disorganisation, and 0 points were given for the inability to make a reasonable attempt. 25% of participants scored below the expected range, receiving 3 or fewer points. This led the authors to advise against using the CDT as the sole diagnostic tool in the future, especially as younger adults age and begin to require neuropsychological assessment. As such, McDaniel et al. (2024) suggested that clock drawing may be below the standard that scoring systems may expect. Therefore, the large amount of younger adult data collected through Experiments 1-7, alongside an ageing sample, allowed for a calibration of clock drawing against additional measures of cognition associated with the MoCA. One aspect that may be an important distinction between McDaniel et al. (2024) and the present Chapter is clock outline- the quality of the circle might affect what one produces with the rest of clock. Not all clock drawing administration and scoring is the same, and therefore clear distinctions in abilities are crucial.

In young adults, it could be proposed that clock drawing performance can serve as a sensitive indicator of cognitive abilities and potential cognitive deficits due to the high demands required by the test (e.g. Julayanont & Nasreddine, 2017). High levels of accuracy and efficiency in completing these tasks suggest intact visuospatial skills, executive function, and attentional control. In contrast, errors, or difficulties in completing the tasks may indicate underlying cognitive impairments or developmental differences that warrant further evaluation and intervention. McDaniel et al.'s (2024) young adult findings provide a basis to draw distinctions between several aspects of clock drawing including planning and construction abilities, one’s stored visual knowledge, and the symbolic conception of how an analogue clock works. Whilst McDaniel’s study investigated time-telling, other aspects were not explored including the requirement to draw a contour, and a specific set of scoring instructions (e.g. it can be suggested that “moderate visuospatial disorganisation of numbers” is subjective; see Salo et al., 2024). Assessing these factors will facilitate greater understanding into the areas where young adults may show greater difficulty. Thus, the context of the MoCA alongside clock drawing provides additional insights. The MoCA systematically allows one to understand each aspect of the drawn clock (i.e. contour, numbers on the clock face, time-telling accuracy), alongside performance across other cognitive domains, providing insight into executive and visuospatial abilities compared to global cognition, especially following the assumption that young adults should perform within normal ranges across MoCA performance (i.e. the MoCA was developed as a dementia screen and therefore intact young adults should pass). With the inclusion of additional contour measurements, greater insight into its contributions to clock drawing may be revealed. For example, the box for participants to place their clock drawings measures 5.5 x 5.5 cm, which could guide the sizing of the clock face. Therefore, this Chapter reports an in-depth analysis of clock drawing performance from the MoCA, in an exploratory investigation, to understand the deficits found in younger adult clock drawing behaviour alongside, and in comparison, to older adult performance. It was expected that despite the qualitative deficits noted in previous Chapters, younger adults would have higher clock drawing and overall MoCA scores than older adults, however a subset of younger adults would perform poorly on the clock drawing subtest, and this would correlate with overall MoCA scores. Findings will provide insight into the MoCA as a screening test, as well as the ability of younger and older adults on visuospatial, construction, and graphic production.

6.2 Methodology

6.2.1 Participants

The MoCA was administered to all participants across Experiments 1-7 (C*hapters 3, 4, 5*). Therefore, the total young adult cohort included 165 participants (18-35; M = 21.96, SD = 3.65; female = 106, male = 58, non-binary = 1), where a majority were University of Plymouth undergraduate students (N = 140). There were 53 older adult participants (65-93; M = 74.77, SD = 5.99; female = 32, male = 21). The MoCA from the five older adults who were excluded from analyses in Experiment 6 were included presently. As the excluded participants had requested to stop their participation rather than withdraw, this meant that not enough data was collected to satisfy Experiment 6 comparisons, but the MoCA could still be included for analyses in the present investigation. Further participant demographics are described in their respective Chapters.

6.2.2 Design and procedure

All participants were administered the MoCA. Found within the visuospatial/executive section (see Figure 6.1), the Cube and the Clock were selected to represent visuospatial and perceptual abilities associated with search and foraging requirements. Denoted to assess visuoconstructional and perceptual skills, the Cube task required participants to copy a three-dimensional cube: *"Copy this drawing as accurately as you can"*. Worth one point, the copy must contain the following components: residing with three dimensions, all lines drawn and meeting with little-to-no space, no extraneous lines, lines are relatively parallel with similar lengths, and orientation preserved in space. Also assessing visuoconstructional ability, the Clock drawing subtest required participants to draw a clock without visual prompts. They were instructed to: "*Draw a clock. Put in all the numbers and set the time to 10 past 11."* As denoted by the scoring instructions from the

MoCA manual (Nasreddine et al., 2005), participants are given one point for contour (either circle or square) with only minor distortions, one point of numbers placed correctly and upright in approximate quadrants, and one point for hands placed at the “2” and “11” with the hour hand clearly shorter than the minute hand and meeting close to the centre of the clock, totalling three points. The complete MoCA is scored out of 30 points, dependent upon the scoring protocol of each individual subtest. Following the cut-off criteria as determined by the MoCA manual (Nasreddine et al., 2005), participants with a score of 26 or greater fall within a “normal” range. Any participants with an education of less than 12 years are awarded an extra point to their total score. It is important to note that the MoCA has only been validated for older adults aged between 55-85 years.

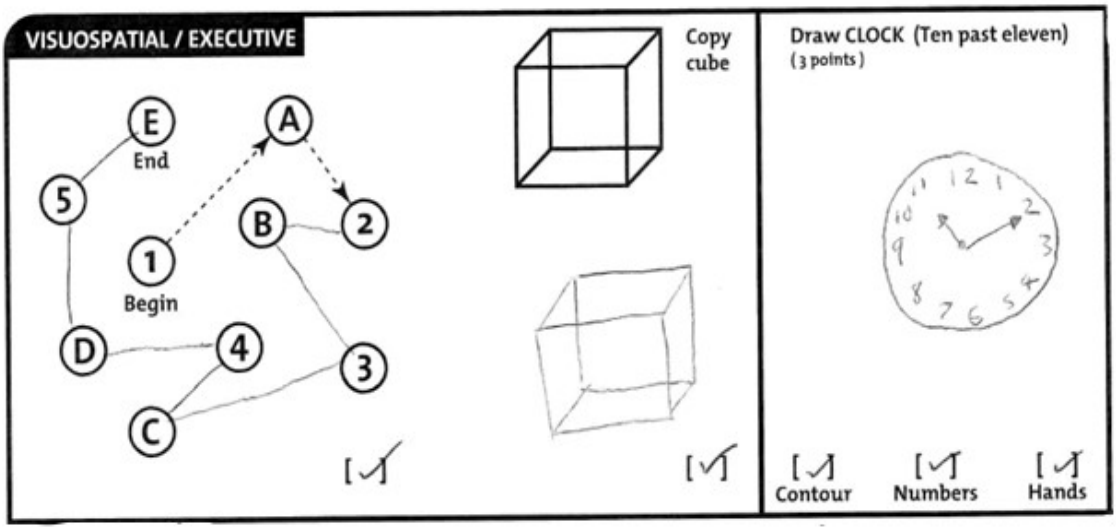

Figure 6.1. Example of the visuospatial/executive section of the MoCA, showing the trail-making (worth 1 point), cube (worth 1 point), and clock drawing component (worth three points in total), respectively. This depicts one participant’s attempt, which received maximum points (5/5) for the visuospatial/executive section.

6.2.3 Analysis

Following the MoCA criteria, one point was given for a correctly drawn Cube. Participants were not allowed to erase lines, however participants were allowed additional attempts (see Figure 6.2). One point was awarded for each correct Contour, Numbers, and Hand placement. The summation of all three points created the Clock total. Smith (2009) discussed the importance of assessing drawing scaling: patients with neglect, for example, have been shown to systematically shrink circles, which was suggested to provide finer-grained differentiation for diagnosis. It has also been suggested that sizing errors are the result of executive and visuospatial function deficits, such that patients with AD show higher incidences of expanded clocks (Eknoyan, Hurley, & Taber, 2012). Scaling measurements have since been applied to healthy younger and older adult populations, revealing that greater difficulty resulted in expanded drawings (Salo et al., 2024). As such, to further quantify Contour success, maximum height and width of the drawn contour were measured in millimetres from the widest and tallest point on the vertical and horizontal plane, respectively. This allowed for the categorisation of different types of error to ascertain potential sources of variation. The ratio of Contour size was also derived from the maximum width and height, where “1” would indicate a near-perfect circle. This would allow for analyses into systematic expansion or shrinkage of the Contour. Due to the multiple potential error points for both Numbers and Hands, any incorrect response was scored as zero, with the specific error noted. This allowed for all errors to be captured without predetermined measures. Number errors were therefore indicative of planning deficits (Eknoyan, Hurley, & Taber, 2012). Hand errors revealed deficits in critical understanding of time-telling (e.g. conceptual deficits; Eknoyan, Hurley, & Taber, 2012) and memory recall (McDaniel et al., 2024). Table 6.1 reveals the errors observed across younger and older adult cohorts. By noting the errors made, it allowed for greater understanding into the specific deficits in clock drawing between and within each age group. Finally, in order to compare the completed MoCA against the visuospatial and executive elements, five points (equating to the visuospatial/executive section total) was subtracted from each participant's total MoCA score to create a non-executive MoCA score. This allowed for the comparison of MoCA success against the visuospatial and executive success, and specifically the clock drawing elements. Descriptive statistics were utilised to understand the percentage of success and difference (e.g. the percentage of participants who were successful or erroneous per measure) independently between the older and younger cohorts. Independent sample t-test assessed the differences between age groups. Pearson's correlation was used to assess the relationship between the derived MoCA score and the visuospatial/executive subtests and their components.

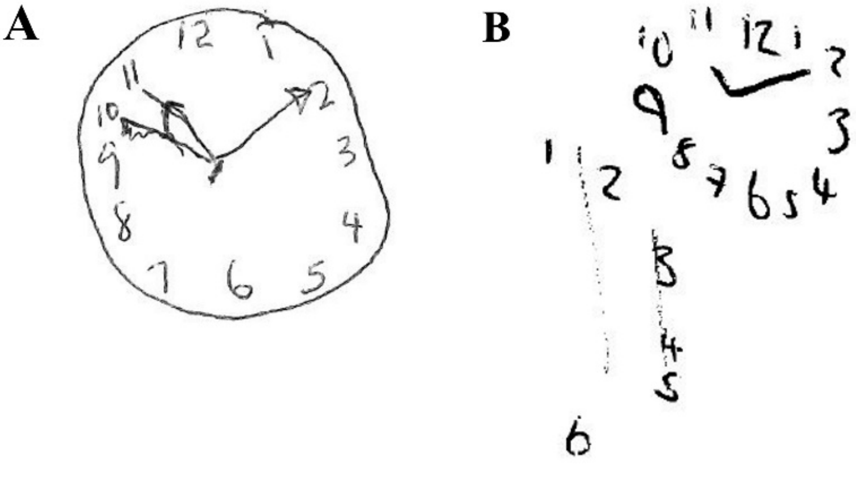

Figure 6.2. Examples of a(n): A) successful; B) unsuccessful self-correction.

Table 6.1. Summary of observed clock drawing errors across younger and older adults.

Criterion	**Measure**	**Description**
Numbers	1 at top	Instead of a 12 placed at the top of the contour, a "1" was denoted
	0 at top	Instead of a 12 placed at the top of the contour, a "0" was denoted
	Incorrect anchors	Clock anchors (i.e. "3", "6", "9", and "12") were placed incorrectly outside of approximate quadrants
	Numbers placed both in/out contour	The numbers of the clock face reside both inside and outside of the drawn contour
	Mixed orientation	Numbers placed upright and upside down
	24 hours	Numbered in 24 hours
	Missing numbers	A total of 12 numbers are not placed on the clock face
Hands	Same length	Hour and minute hands drawn at same length, but time is correct
	Hour and minute swapped	The hour hand is drawn longer than the minute hand, but time is correct
	Hands not centred	The two hands do not meet in the centre of the clock
	Three hands	Three hands are present on the clock
	Minute to 10	The minute hand is pointing to the "10"
	Minute to 11	The minute hand is pointing to the "11"
	Minute to 12	The minute hand is pointing to the "12"
	Minute to 1	The minute hand is pointing to the "1"
	Minute to 3	The minute hand is pointing to the "3"
	Minute to 4	The minute hand is pointing to the "4"
	No hand at 11	Neither hour nor minute hand points to the "11"
	Hour to 10	The hour hand is pointing to the "10"
	Hour to 1	The hour hand is pointing to the "1"

6.3 Results

Clock drawings were scored independently by two experienced raters. Initial agreement between raters based on the younger (Contour: α = .98, Numbers: α = .92, Hands: α = .94) and older (Contour: α = 1.0, Numbers: α = .94, Hands: α = .96) cohorts were high. Maximum size and width were compared, where any discrepancies greater than 2mm were remeasured and discussed. Disagreements across contour, numbers, or hands were discussed and answers were agreed upon to produce the final Cube and Clock scores. Across both cohorts, the Numbers measure displayed the greater disagreement between raters. This will be further discussed in the Discussion section.

6.3.1 Younger adult performance

Firstly, it is important to note that as a majority of the younger adult sample were University of Plymouth undergraduate students, the following findings may not generalise to the general population, or even of undergraduates elsewhere. That said, total MoCA scores revealed that young adult scores ranged from 17- 30 (M = 26.53, SD = 2.32). 29.7% (N = 49) of participants did not meet cut-off (score < 26). First considering the Cube, 22.4% (N = 37) of participants failed to correctly copy the Cube (77.6%; N = 128 received one point for a correct copy). Results for the Clock drawing showed that 63.6% of younger adults achieved the maximum result on the Clock (3 points; N = 105) but 7.9% (N = 13) only received one point for Clock accuracy and 28.5% received two points (N = 47). No participants received zero points for the Clock drawing. Contour maximum width ranged between 16-49mm (M = 31.49, SD = 6.29) and maximum height ranged between 15-51mm (M = 31.95, SD = 6.85) for the younger adults, and the ratio of the Contour ranged from .66-1.00 (M = .93, SD = .06). 4.8% (N = 8) of younger adults did not successfully draw a Contour (either circle or square;

see Figure 6.3), where points were lost for not drawing the Contour at all (N = 6) or for misshaping the Contour (N = 2).

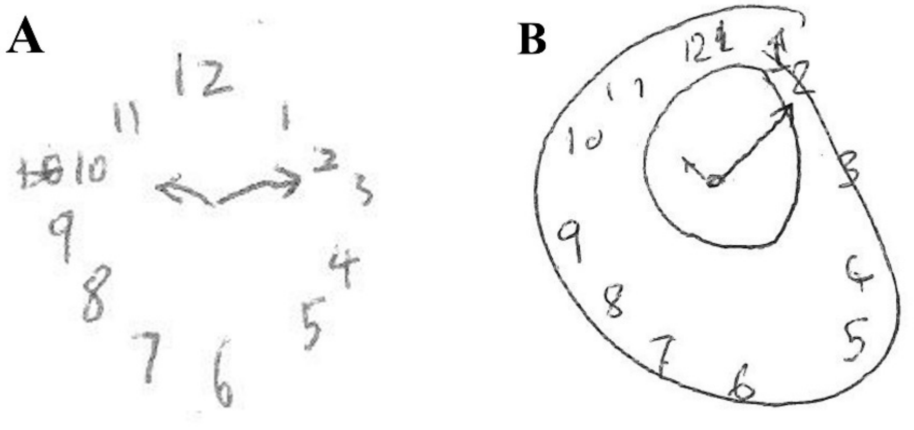

Figure 6.3. Examples of Contour mistakes found across young adult clock drawing: A) missing the Contour entirely; B) misshaping the Contour.

12.1% (N = 20) of participants did not achieve a point for Numbers (87.9%; N = 145 accuracy drew in numbers). Of the 20 participants who did not achieve a point for Numbers (see Figure 6.4), 15% (N = 3) placed a "1" at the top rather than "12", and 5% (N = 1) placed a "0". 65% (N = 13) placed their anchors incorrectly and 5% (N = 1, each) placed the numbers inside and out of the contour, mixed the number orientation, or produced a 24-hour clock. Finally, 20% (N = 4) of participants did not place twelve numbers on the clock face. It is important to note here than these measures are not mutually exclusive; participants may have produced multiple errors within their clock drawing (see Figure 6.4b, for example, the numbers are incorrect, and the hands are pointing to the incorrect time).

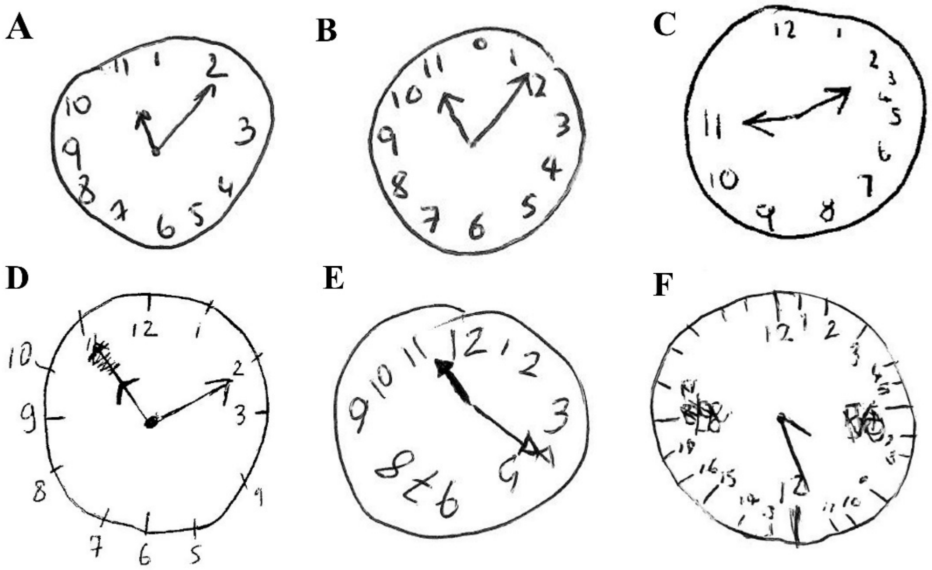

Figure 6.4. Examples of several Number mistakes found across young adult clock drawing: A) “1” placed at the top of the clock face; B) “0” placed at the top of the clock face; C) incorrectly placed anchors; D) mixed contour orientation; E) mixed number orientation; F) attempt at a 24-hour clock.

For the Hands measure, 27.9% (N = 46) of participants failed to receive a point for placing the hands correctly (see Figure 6.5). Of those 46 unsuccessful participants, 28.26% (N = 13) either drew the hands the same length or swapped the hour and minute hand. 6.52% (N = 3) placed the minute hand at “10”, 10.87% (N = 5) positioned the minute hand at “11”, 2.17% (N = 1) placed the minute hand at “12”, 17.39% (N = 8) had the minute hand pointing at the “1”, 4.35% (N = 2) positioned the minute hand at “3”, and one participant (2.17%) pointed the minute hand at “4”. Analysing the hour hands, 17.39% (N = 8) pointed the hand at “10”, and 2.17% (N = 1) pointed the hour hand at “1”. One participant (2.17%) did not point any of the hands to the “11”. Pearson’s correlation revealed that for the younger adult cohort, MoCA success predicted greater Width ($r = .22$, $p = .005$) and Height ($r = .21$, $p = .008$). The Cube was associated with the total Clock score ($r = .17$, $p = .025$), but none of the subcomponents individually. Success on the derived MoCA score revealed associations with better Cube copies (*r* = .38, *p* < .001), more accurately drawn clocks (*r* = .52, *p* < .001), and more accurately drawn Contours (*r* = .26, *p* < .001), and Number (*r* = .26, *p* < .001) and Hands (*r* = .41, *p* < .001) placement.

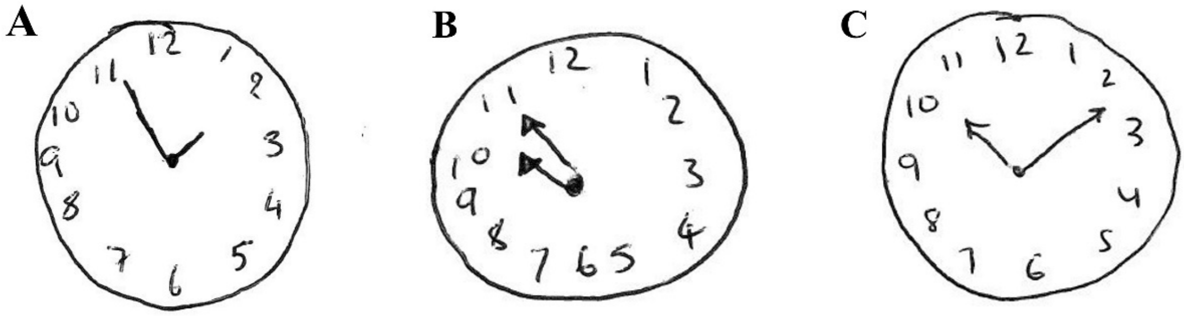

Figure 6.5. Examples of several Hand placement errors found across young adult clock drawing: A) minute and hour hands are swapped; B) hands are pointing to the incorrect time; C) neither hand points to “11” or “2”.

6.3.2 Older adult performance

Total MoCA results revealed that participant scores ranged from 16 - 30 (M = 25.62, SD = 2.83). 45.3% (N = 24) of participants did not meet cut-off (score < 26). The Cube copy revealed that 39.6% (N = 21) of older adult participants were not able to accurately copy the three-dimensional cube (60.4%; N = 32 received one point for an accurate copy). Overall results showed 3.8% (N = 2) of participants only received one point on the overall Clock drawing score, but no participants received a score of zero. Most participants (54.7%; N = 29) received all three points for their production (two points: 41.5%: N = 22). For older adults, Contour maximum width ranged between 16-51mm (M = 34, SD = 6.83) and Contour maximum height ranged between 16-50mm (M = 33.64, SD = 6.32); the ratio of a perfect circle ranged from .74-1.00 (M = .91, SD = .06). Figure 6.6 represents an example of older adult errors. Only two participants (3.8%) failed to accurately draw the Contour (96.2%; N = 51 received one point for an accurately drawn circle). Of the two participants, both did not draw any Contour around the perimeter of the clock face. 7.5% (N = 4) of participants struggled to place the numbers correctly (92.5%; N = 49 correctly drew in the numbers). Of the four participants that did not place the numbers correctly on the clock face, 75% (N = 3) placed a “1” at the top of the clock rather than the “12” and 25% (N = 1) did not place twelve numbers on the clock. Again, one should note that errors are not mutually exclusive (e.g. see Figure 6.6b; Hands are the same length, pointing to the incorrect time, with clock face Numbers placed incorrectly).

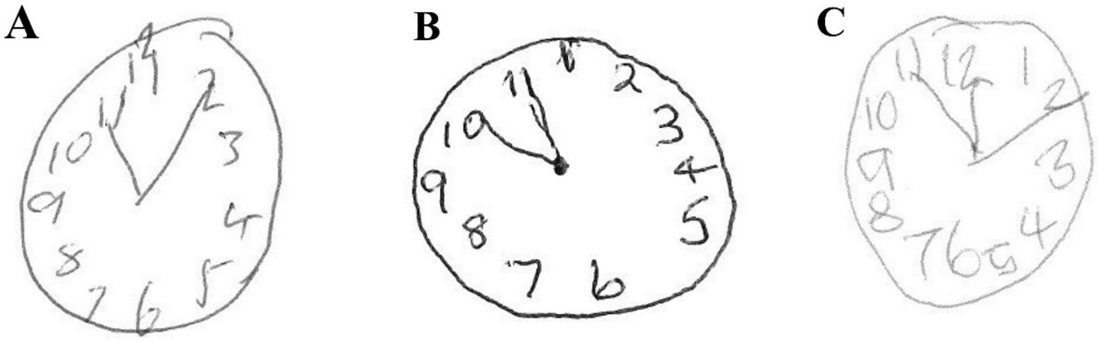

Figure 6.6. Examples of errors found across older adult clock drawing; A) Number placement errors; B) Hand placement and length errors; C) three hands present on the clock.

For the Hands measure, 37.7% (N = 20) of participants incorrectly placed one or more of the hands (62.3%; N = 33 placed both hands in the correct placement). Of the 20 participants that did not receive marks for hand placement, 85% (N = 17) drew the hands at the same length and 10% (N = 2) swapped the hour and minute hands. 10% (N = 2) placed the minute hand at “10” and 5% (N = 1) placed the minute hand at “11”. One participant

(5%) did not place the junction of the two hands at the centre of the clock, and one participant (5%, see Figure 6.6c) drew three hands. Pearson's correlation assessing the relationship between the total MoCA score and Contour sizing revealed greater Width (*r* = .36, *p* = .008) and Height (*r* = .28, *p* = .045) were associated with greater MoCA success. However, the Cube did not correlate with Clock drawing accuracy. Success on the derived MoCA revealed relationships with more accurately drawn clocks (*r* = .39, *p* = .004) and more accurately placed clock Hands (*r* = .37, *p* = .007).

6.3.3 Between group comparisons

Performance was compared between younger and older adults. Two-tailed, independent sample t-tests revealed that younger adults were more successful on the complete MoCA than older adults by achieving a significantly higher score (*t*(216) = 2.36, *p* = .019, *d* = .37). Younger adults drew the Cube more accurately than older adults (*t*(216) = 2.59, *p* = .01, *d* = .41) and older adults drew the width of the contour significantly larger than younger adults (*t*(216) = -2.47, *p* = .014, *d* = -.39). However, older and younger adults did not differ across the rest of the measures, including the total Clock score (*t*(216) = .49, *p* = .63, *d* = .08), correct Contour (*t*(216) = -.32, *p* = .75, *d* = -.05), maximum height (*t*(216) = -1.59, *p* = .11, *d* = -.25), correct Numbers (*t*(216) = -.92, *p* = .36, *d* = -.15), and correct Hands (*t*(216) = 1.36, *p* = .18, *d* = .21).

6.4 Discussion

In this exploratory investigation of younger adult performance on visuospatial and executive aspects of the MoCA, the Clock drawing subtest was explored after a qualitative observation that younger adults struggled more than was expected for university-educated students. It was found, overall, that a proportion of young adults produced a drawing that was not as accurate as one might expect, and this was reflected in the MoCA score. Younger adult performance was assessed across clock drawing errors as compared to a derived MoCA score in order to evaluate the impact of the visuospatial and executive contributions to MoCA success alongside specific clock drawing errors. The inclusion of older adult results allowed for a comparison in performance between age groups, as well as analysis into older adult performance on clock drawing. Although younger adults performed significantly better at the MoCA overall, the executive and visuospatial subtests did not reveal significant differences between age groups.

It was first identified that in the younger adult cohort, almost one third (29.7%) did not meet the cut-off score representing ‘within normal range’ on the MoCA. Although a large portion of younger adults clearly struggled, the MoCA is currently only validated for ages 55-85 (Nasreddine et al., 2005). Yet, some research (e.g. Bruijnen et al., 2019; Dautzenberg, Lijmer, & Beekman, 2020; Pike, Poulsen, & Woo, 2017) have suggested that the MoCA may be appropriate to identify cognitive difficulties throughout one’s lifespan, but these are yet to be further supported. Considering that the MoCA is a screening assessment for dementia, and the purpose of the MoCA is to identify early signs of degradation, young adults should perform within a normal range. If one considers that the derived MoCA score revealed success across all primary and subcomponent measures of visuospatial and executive ability for the younger adult cohort, perhaps then the present findings may suggest a decrement in younger adult’s qualitative appraisal of a clock, and not necessarily as a measure of cognitive status. As such, decrements in clock drawing ability in the younger adult cohort may be predictive of failing MoCA scores, indicating that the deficit is within the visuospatial and executive component exclusively which results in abnormal MoCA total scores.

It has been shown that younger adults do understand the basic concept of clock drawing, where a consistent representation across all participants included a circular form, with Arabic numerals and a general identification that the hands should either point at "10", "11" or "2". It was further observed that the contour of the clock guided response, where imperfections in the circle steered the placement of numbers. This led to incorrect anchoring as a common mistake, distorting the clock contour relative to a circular representation. This possibly represents a distinction between knowing what the clock *is* and understanding its *function*. It can generally be stated that a majority of the population knows the concept of the clock as a similar canonical schematic was created across participants (i.e. circular contour with numberings around the inside edge). Participants were not overtly wrong, but systematically wrong, displaying a lack of understanding. Even the most incorrect representations of a clock still resembled a clock, and could be identified as such, but the systematic re-creations of the clock displayed inaccuracies. Overall, participants were not able to utilise their knowledge of a *clock* to create an accurate depiction. McDaniel et al. (2024) discuss the influx of digitalised time-telling in the modern young adult population. It was reported that from a survey of 602 millennials, 70% reported they 'occasionally' to 'never' wore a wristwatch. Even then, with the advent of fitness trackers and similar wrist-based technology, the watch may not present as an analogue-style clock. A further point McDaniel and colleagues (2024) considered was the use of language. One aspect of their clock drawing study assessed younger adult ability to draw a clock (as discussed in the *Introduction*) where the phrasing required for the Clock Drawing Test (and the MoCA) specifies for one to set the time to *"ten past eleven"*. This turn of phrase may no longer be used, or at least unfamiliar, to some younger adults and therefore inconsistencies and errors in hand placement may occur. Moreover, if one is not guided by a systematic depiction, then conceptualising unfamiliar phrasing within the context of an incomplete representation may lead to greater difficulties. It should also be highlighted that as introduced in the *Methods* section, a majority of the younger adults were University of Plymouth undergraduate students. As such, the deficits identified in clock drawing ability in younger adults may not generalise to the wider population within the UK, or even across other universities. Additionally, university students may have different cognitive and developmental profiles compared to their non-student peers. To fully conceptualise young adults' ability to draw and understand a clock, it would be beneficial to gather further data from a wider young adult sample.

Older adult performance was also assessed on the visuospatial and executive measures of the MoCA. Almost half (45.3%) of the older cohort did not meet the MoCA cut-off score but just over half (54.7%) received all three points for a success Clock. However, the derived MoCA score revealed a significant relationship with the clock total score and Hands, but not Contour and Numbers, indicating that MoCA scores were affected by visuospatial/executive elements, but not exclusively. Incorrectly placed Hands was also the factor that more older adults struggled on, where 37.7% of participants placed the Hands incorrectly. Clock drawing tests have been evidenced to sensitively identify decrements in ageing (Talwar et al., 2019), as has the MoCA (Freitas et al., 2014), and present MoCA scores follow the literature for variability in older adult success (e.g. Hubbard et al., 2008) with some discriminability as a screening measure for cognitive decline. However, as the MoCA was employed in this experiment as a cognitive screening tool rather than for diagnostic purposes, underlying disorders may still be present in participants, and below cut-off results may indeed suggest potential cognitive impairments that warrant further investigation.

When comparing Clock drawing performance between the younger and older adults, it was found that younger adults received higher MoCA scores and copied the Cube more accurately than older adults. Conversely, older adults drew the width of the contour significantly larger than younger adults. However, the rest of the measures did not statistically differ between age groups. It is unsurprising that younger adults received higher scores on the MoCA overall; the MoCA is sensitive to ageing and numerous studies have supported the findings that MoCA total score negatively correlates with age (e.g. Bruijnen et al., 2019; Julayanont & Nasreddine, 2017). Relatively few reports have explicitly analysed copying ability between younger and older adults; Salo et al. (2024) found no statistical difference between age group copying ability, and Gagnon et al. (2003) found minor inaccuracies suggestive of relative organisational preservation. The present discrimination between groups in Cube copying therefore may reflect visuospatial and frontal decrements in the ageing process; previous research has highlighted the sensitivity of the three-dimensional cube copy for detecting cognitive ability and poor cube copying has been determined as a risk factor in atypical ageing processes as a stand-alone measure (Bu et al., 2013). However, Clock drawing, including the subcomponents, did not differ between age groups presently. Hubbard et al. (2008) analysed clock drawing across several scoring systems utilising a large sample of ‘cognitively normal’ older adults. Results indicated that the participants fell within the normal ranges of performance, however rates of variation between scoring systems indicated that some normal subjects could be misclassified, leading the authors to suggest that the range of ‘normal’ performance may reveal greater variability than previously considered. Clock drawing has also been assessed in young adults, using 10-point scoring criteria, where it was similarly found that nearly 30% of young adults did not achieve a full Clock drawing score (Winstead & Holman, 2021). However, when Winstead and Holman (2021) compared the young adult data to published older adult normative data using the same scoring system, younger adult drawings were significantly higher scoring. Whilst the authors did not expand on the implications of younger and older differences, it can be assumed that one might expect older adults to perform less accurately. And yet, present results do not reveal statistical differences. Talwar and colleagues (2019) found in a comparison of neural structure and brain function, alternative neural pathways develop as one ages, despite age-related changes, protecting cognitive function in a domain general capacity. Perhaps then the decrements identified in younger adult ability is reflective of not knowing a clock, and deficits in older adult clock drawing is reflective of cognitive functioning, as is assessed in the MoCA. If one evaluates non-conceptual related stimuli, Salo et al. (2024), for example, identified significantly less accurate reproductions from memory on abstract stimuli in the older adult cohort as compared to younger adults. As such, perhaps the CDT, and all forms of clock drawing assessment, need to be reevaluated as the present younger generations age.

One finding not addressed throughout most of the clock drawing literature was that of the systematic sizing of the clock drawing. It was found that older adults drew significantly wider Contours than younger adults. There have been suggestions that changes in vision lead to systematic sizing differences of circles (Zelaznik & Lantero, 1996), which can provide insights into how visual perception influences spatial representation and fine motor control. Previous research has addressed clock contour in the context of hemineglect patients (A. Smith et al., 2006), and in comparison to patients with right-sided brain damage, healthy controls produced larger and more circular and intact contours (Chen & Goedert, 2012). In the present study, the systematic sizing (ratio of width and height) of clock contours in younger and older adults revealed no significant differences between groups. However, one might recall that the Contour size was constrained within a 5.5 x 5.5mm space. As such, perhaps greater differences would be identified should participants be offered an A4 sheet of paper, for example, to freely draw an unrestrained Contour. Further research is required to specify the underlying mechanisms not only in sizing, and possibly constraining factors associated with sizing differences, but in relationship to cognition and ageing. Salo et al. (2024) identified a discrepancy between copying and memory reproductions where age-related differences only arose in memory conditions, and not copying. Further, Smith (2009) highlighted differences between patients (e.g. case examples including HJA, DW, etc) where utilising a copy condition provided greater insight into size accuracy as an objective gauge of decrements in visuospatial abilities. At minimum, research into clock drawing should continue to allow participants to draw the contour, as greater information can be derived than a pre-drawn contour.

A final consideration is that of the scoring procedure of the Clock drawing subtest. Relatively high interrater reliability was found in the present Chapter, however this is not consistent across the literature. Cumming et al. (2020) highlighted quite a large discrepancy in MoCA clock drawing subcomponents between raters, and when novice raters were analysed on MoCA scoring consistency, it was clear that repeat training was required (Price et al., 2011). Salo et al. (2024) emphasised the potential subjectivity in scoring drawings, pointing out the implications of varying interpretations of unclear instructions. For example, to quantify successful clock hand placement, a distinction is required between length of hands and centre point. The MoCA instructions state that the hands must have *"… their junction close to the clock centre"*. It can certainly be subjectively interpreted what quantifies as 'close'. This leads to a consideration: how does one quantify the centre of the clock, by height or width (exampled in Figure 6.7a)? Surely both, but how far from the horizontal centre and vertical centre can the junction be to still be considered correct? Further, it can be difficult to judge hand length as end point is critical—there is an implication of proximity rather than literal length. By that, one should consider Figure 6.7b, which presented as a point of difference between the two raters. The hands of the clock appear to be similar in length, however the relative proximity of the hand pointing to the "2" can be determined as marginally closer than the hand pointing to the "11" (however, if one measured the length of the hands with a ruler, it would be found that the minute hand was longer). Yet, the MoCA is advertised as a quick screen (Dautzenberg, Lijmer, & Beekman, 2020), explicitly stated to not necessitate ruler measurements. Price and colleagues (2011) contend that the MoCA instructions are too vague and brief, therefore leading inexperienced administrators to greater inter- and intra- rater variability. Indeed, Cumming et al. (2020) found that inter-rater reliability on clock hands (as compared to numbers and contour) revealed especially low agreement (κ = .46). Discussed further below, Mainland et al. (2014) say simpler scoring is better, but rater disagreements are rife through the scoring literature. Salo et al. (2024) concluded by stating greater knowledge is gained from specific quantifiable metrics, with greater importance placed on explicit scoring descriptives. Considering the full MoCA test, a rater incorrectly scoring the Clock impacts up to 10% of the total MoCA score, which could have severe implications for diagnosis. As such, the neuropsychological literature requires greater quantification of scoring metrics (as discussed by Leek et al., 2000; Salo et al., 2024; Smith, 2009). Further quantification of clock drawing performance was attempted in this assessment of the Clock drawing MoCA subtest, which revealed greater insight for both younger and older adults.

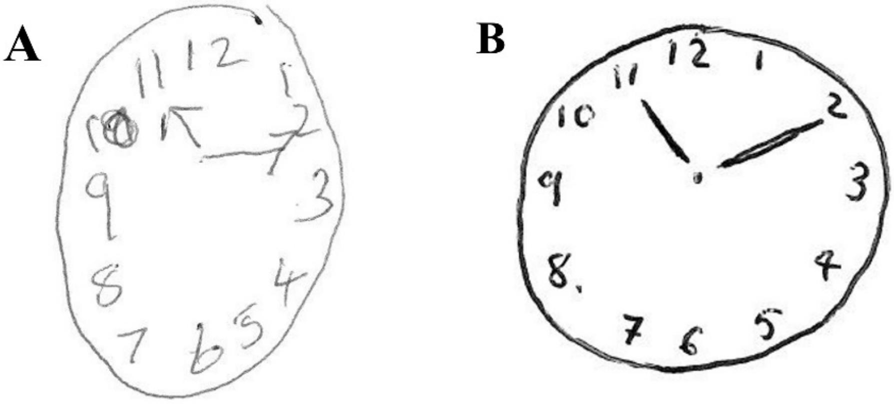

Figure 6.7. Examples of potential scoring subjectivity: A) the Hands junction meets at the vertical centre but not the horizontal centre; B) the minute hand to the “2” than the hour hand to the “11” insinuates closer proximity.

An additional component of scoring is that of the selected system. Hubbard et al. (2008) compared three different scoring systems to measure clock drawing, finding that there was performance variation in each CDT scoring, leading to possible misclassifications. However, it was also revealed that "normal" performance included a wider distribution of results than had previously been reported. With an influx of scoring systems, as highlighted by Mainland et al. (2014), it appears that one must find a balance between sensitivity and predictive validity, and administration and scoring times. Mainland et al. (2014) compared scoring systems via literature review, concluding that simpler systems are better due to similarities in psychometric properties, accounting for enough to offset the time it takes to administer and score more complex systems, especially in a clinical context. The highlighted 'simpler' system was a binary discrimination between a 'normal' and 'abnormal' clock drawing, allowing clinicians to 'eyeball' the clock for sufficient information on clock quality. However, the intention behind the binary system was to establish those requiring comprehensive cognitive testing. The present findings may support such an overt decision, as the total Clock was associated with success on the MoCA in both age groups, however whether such suggestions are tenable require insight into the purpose of the CDT. If one's intention is to assess visuospatial ability and executive function, amongst construction, planning, and conceptual abilities, then a binary system would not provide enough information. Further, if healthy, young adults are failing the clock component, perhaps then greater nuance is required.

6.5 Conclusion

In summary, younger adults do not perform as well as expected on the Clock drawing subtest of the MoCA, but when one compares the performance between younger and older adults, results are similar. It is therefore suggested that the clock drawing subtest of the MoCA reflects degradation in the older adult cohort, but a clear deficit in conceptual knowledge in younger adults. This deficit may additionally be reflective of a modern shift in time-telling and accessibility to electronic assistance. Further, by the addition of observed error categorisation assessing Contour, Hand, and Numbers, greater insight into strengths and weaknesses of both cohorts were able to be elucidated and discussed, where both cohorts had the greatest deficit in Hand placement. The clock drawing subtest correlated with the MoCA in both cohorts but not all subcomponents. This was taken to reflect that deficits on the MoCA in young adults reflect the inability to produce an accurate clock as all clock metrics were also correlated, whereas only the total Clock score reflected MoCA success in older adults. As such, the present findings follow the literature that the MoCA is suitable for older adults. However, younger adults do not appear to hold a conceptual understanding of a clock as one might have used to, and therefore further research is required to develop appropriate clock-like measurements of success as the present younger generation ages. This may include examining the language used to discern whether terminology lessens conceptual knowledge, assessing the knowledge of function with finer-grained systematicity, or consistency of clock use, which will provide greater understanding to younger adults' success.

Chapter 7. General Discussion

This thesis reports a series of experiments that were designed to elucidate whether the integration of visual search and foraging behaviours could identify early neurocognitive correlates of typical and atypical ageing. *Chapter 3* introduced a novel, three-dimensional paradigm that integrated visual search and foraging properties. Over several experimental manipulations on healthy young adults, it was discovered that visually guided large-scale search reflected similar distinctions between single feature and conjunction of feature search as previous two-dimensional paradigms. Foraging-like properties of the task (i.e. patchy array, idiothetic requirements) were also reflected not to diminish the utility of visual cues, and instead provide additional behavioural contributions to search strategy and success. Measures of individual difference revealed that attentional systems, spatial working memory, executive function, and working memory were integral to success, irrespective of task demands (i.e. template provision and target distribution). These findings indicated that properties of visual search and foraging in one domain can indeed be reliably translated and extended from two-dimensional contexts to three-dimensions.

Chapter 4 revealed predictive mechanisms underpinning older adult behaviour, suggesting that visual search performance can identify decrements associated with typical and atypical ageing processes. Specifically, measures of visual search were predicted by bidirectional connectivity between the NA and ACC, NA and vmPFC, and ACC and vmPFC tracts, FA in the body, genu, and splenium of the corpus callosum, and whole brain FA and MD. However, foraging-like decisions were largely unrelated to neuroimaging data: participant organisation in the task revealed several associations (LC and ACC connectivity, callosal body and genu FA, mean MD), but not from additional foraging measures (e.g. exploitation, revisits). Contrary to predictions, search and foraging revealed similar performance between the younger and older adults across all behavioural measures. Cognitive control metrics contributed to older and younger adult success differently: variability in older adult performance on reaction time, episodic memory and working memory was more likely to relate to visual search success whereas younger adults utilised executive functioning, episodic memory, spatial working memory, and reaction times. Of this, both age groups revealed task associations with reaction time. As an indicator of psychomotor coordination, reaction time revealed that individuals with better coordination and faster movement speed collected more targets and visited more patches. This finding aligns with existing literature (e.g. Barrett et al., 2022; Wiegand & Wolfe, 2020) which confirms that older adults generally have slower reaction times compared to younger adults, affecting search performance. As such, overall results support recent findings of Wiegand and Wolfe (2020), who suggested that aside from reaction time, older and younger adults did not differ in performance. However, collective analyses masked between group differences that arose when trials were analysed separately. Over the course of the task, the unfolding of behaviours revealed performance differences between the two age groups. These variations in strategy led to greater success for the younger adults. Research supports the existence of strategic differences between younger and older adults (e.g. Agnew et al., 2020; Wiegand et al., 2019). Consequently, it was revealed that variations in strategy (or compensatory methods, as noted by Wiegand & Wolfe, 2020) emerged between the two age groups over the course of the trials, although these differences did not impact overall performance. It was also revealed, when analysing group behaviour, that older adults were not more exploitative than younger adults, in contrast to previous literature (e.g. Louâpre et al., 2010; Mata et al., 2009; Smith & De Lillo, 2022), over the course of the task. Perhaps the ability for older adults to utilise idiothetic contributions, and therefore possibly allowing for compensatory mechanisms to support success in a domain general capacity, provides support to the cognitive underpinnings that guide successful search and foraging behaviour across the lifespan.

Chapter 5 described a rule shift task where the array was defined by a conjunction of features and employed to investigate the executive function and control underpinnings of visual search-like behaviour. Target location was guided by a rule that shifted every three trials across either intra- or extra-dimensions, where efficient performance was defined by greater cognitive control guiding participants to learn shifts in rules over time. It was revealed that performance across measures of visual search (i.e. target collection, cued inspection, patch inspection, and run behaviour) was greater following an extra-dimension shift than intra-dimension. Further, when intra-dimensional shifts were analysed more explicitly, participants performed better when the rule shift was defined by the object's shape rather than its colour. Most strikingly however were the associations with executive function abilities. Across all trials and rules, behavioural measures were significantly correlated with all measures of executive functioning. These findings indicated that younger adults with greater executive and cognitive control were able to switch their representational target template more successfully in response to the task manipulations for greater target acquisition and search success. Greater executive control provided maintenance of goal-relevant information and ease of response to rule shift, whilst inhibiting uncued inspections. Connecting these findings to Experiments 3, 4, 5, and 6, each experiment collectively revealed that the less information participants were provided with, or the more they had to learn in order to gain information about their space, the more success relied upon executive abilities. Chapter 5 also found that individual difference, assessed by the RCFT and CVLT, revealed that planning, organisation, and verbal learning did not predict success. There were slight contributions from episodic memory, but these were only associated with the third trial in both the intra-dimensional and extradimensional sets. As such, perhaps when executive demands are eased, as in the third trial where the rule has been learnt, episodic memory then becomes the primary process to continue to guide search success in a balance of cognitive load and search success.

Chapter 6 discussed an exploratory investigation into clock drawing performance as a subtest of the Montreal Cognitive Assessment (Nasreddine et al., 2005) in younger adults after unexpected deficits were observed. A derived MoCA score that excluded the visuospatial/executive section of the MoCA revealed significant associations with total clock drawing, as well as sub-measures, in younger adults. This was supposed to suggested that younger adult performance revealed conceptual deficits in clock drawing abilities, whilst older adults revealed ageing deficits as detected by the MoCA. Specific errors across both age groups included incorrectly placed clock hands, which often pointed to “11”, indicating some understanding of the concept, whilst minute hand length and time were erroneous. As such, MoCA success in younger adults was primarily reliant on the executive and visuospatial component of the MoCA, where greater executive success led to greater MoCA total scores. It could be considered that this executive component may not necessarily reflect a deficit in control, but instead a lack of conceptual knowledge. That being said, as has been clear across the aforementioned experiments, executive control facilitates greater success, and perhaps this too has been reflected in MoCA scores.

Throughout the seven experiments, the significant contribution of executive functioning to younger adult success has become apparent. These experiments, which examined various factors such as the use of templates, equal and unequal distribution, rule shift requirements, and conceptual clock representations, demonstrated that younger adults primarily relied on executive function control to achieve success. This reliance on executive functioning was more prominent than the influence of other individual differences. General processes across domains that are crucial for executive functioning regulate fundamental elements of cognitive control (Baggetta & Alexander, 2016; Barceló & Cooper, 2018). The capacity to switch between tasks and suppress automatic or conflicting responses has been demonstrated to make a significant contribution to cognitive control, particularly in understanding differences in performance related to age, such as those between younger and older adults (Schnitzspahn et al., 2013). It has been suggested that cognitive control is closely linked with executive function (Friedman & Robbins, 2022), and research has demonstrated that younger adults tend to rely on executive function for success when faced with demanding cognitive tasks (Isingrini et al., 2015). Further, Ólafsdóttir, Gestsdóttir and Kristjánsson (2021) identified that children completed single feature foraging tasks similar to adults, but were significantly worse at conjunction tasks, which led to the conclusion that executive function is essential for successful foraging over other measures of individual difference (such as working memory). Friedman and Robbins (2022) argued that executive functioning encompasses a set of higher-order cognitive processes that are involved in the control and regulation of other cognitive processes, such as attention, working memory, and decision-making. Within this framework, cognitive control is viewed as one of the primary mechanisms through which executive function operates, allowing individuals to manage their thoughts, behaviours, and emotions in order to achieve goals and adapt to changing circumstances. Therefore, the present series of experiments can suggest that younger adults with greater cognitive control perform more successfully on foraging-like large-scale search—across measures of target collection, template creation leading to cued inspection, exploitation, prevention of revisits—and rule shift-type tasks. For instance, individuals with greater executive function abilities demonstrate more efficient search strategies, quicker adaptation to changing environmental demands during behavioural tasks, and enhanced ability to acquire and apply complex rules in cognitive tasks. This suggests that cognitive control, a key component of executive function, underlies younger adult performance. A point of caution, and one limitation of this thesis, is the reliance on straightforward statistical techniques such as t-tests and Pearson’s correlations to assess individual differences. Whilst these methods are easy to interpret and provide clear distinctions in cognition and behaviour, they also result in a large number of individual statistical tests within each study and across the thesis, increasing the risk of Type 1 errors. However, this risk was somewhat mitigated by the repeated replication of key findings throughout the body of work.

One consideration across the series of experiments detailed throughout the thesis is that of domain generality. As has been addressed, executive functioning and control was heavily relied upon to facilitate success. Previous research has suggested that executive functioning is modulated by domain general processes (Barceló & Cooper, 2018), which may reflect the identified trade-off of greater cognitive contribution between executive function and episodic memory identified on the third trial per shift set in Experiment 7, particularly as domain generality has been suggested to moderate dynamic switching from one region to another (Hills et al., 2015). Perhaps the observation that executive function was relied upon until the third trial of the set, where episodic memory was utilised more heavily (and then back to executive functioning again on the next trial), reveals the domain general dynamic switching between areas of cognition to best support success whilst maintaining cognitive load and demand. As the third trial per shift set would represent the first point participants can apply an anticipatory response to cued inspection at the beginning of the trial, then recalling target location from episodic memory would indeed be necessary, rather than relying on executive function for target location information.

Experiments 1-6 revealed that other than executive function, different task demands seemed to highlight the contribution of different cognitive abilities, further supporting a domain general argument for success. Especially in Experiment 6, with the inclusion of older adult performance, there were clear similarities across age groups, whilst episodic memory (known to degrade throughout ageing; Korkki et al., 2020) revealed predictive differences within older adult performance. As described previously, older adults performed similarly to younger adults overall, but differences were identified over the course of the task. And, when the older adult cohort was analysed separately, participants scoring normally on episodic memory and executive functioning tasks revealed greater behavioural performance. This was suggested to indicate that to facilitate success, older adults utilised compensatory mechanisms. Agnew et al. (2020) suggested that differences in search strategy reflected compensation for reduced response times, and Wiegand and Wolfe (2020) furthered that top-down contributions to success were preserved in older adults, proposed as compensatory strategies to guide search despite possible cognitive or motor decrements. Further, the compensatory mechanisms employed by older adults to facilitate search and foraging success provides support to domain generality (Kan et al., 2013), where present results showed that multiple systems contributed to success despite potential decrements associated with ageing. As Hills (2011) summarised, humans have a cognitive control process that works across different situations. This facilitates following smaller goals within larger plans, such as the sequence of inspections within one's strategy. The cognitive control process can be traced back to spatial foraging abilities, where this broad aspect of cognition provides greater understanding into the basic elements of cognitive control, allowing insight into its different parts and subsequent integration. Therefore, reflective of the fact that both older and younger adults were similarly successful across visual search and foraging measures, despite evidence that measures of individual differences were dissimilar between the two groups, this suggests domain general processing to facilitate success.

A further prediction of the thesis was that domain generality would contribute to foraging success, and specifically the exploration-exploitation trade-off (Hills et al., 2010). It has been suggested that connections across different domains leading to success indicates domain generality (Anvari & Marchiori, 2021), and as such, considering multiple cognitive contributions across search and foraging behaviours, it can be suggested that domain general processes are supporting success. The literature heavily emphasises domain generality mediating the exploration-exploitation trade-off (as discussed in *section 1.4.1*). Hills, Todd, and Goldstone (2008) proposed that similar dopaminergic processes modulate both exploration and exploitation, resulting in similarities between physical and mental search processes. Hills and colleagues (2010) further found that executive search processes aid in switching between subgoals, supporting the idea that cross-domain systems contribute to success. Although older and younger adults did not exhibit the expected trade-off between exploratory and exploitative behaviours, it was revealed that exploitation was more prevalent in single feature conditions regardless of age. This suggests a strategy where fully exploiting a patch increases target acquisition and minimises energy expenditure when the target location is accurately identified and in more difficult conditions, to sample for information gain. Successful search requires creating a cognitive representation, or target template, to guide the process, which is a domain-general function (Hills et al., 2015). Mata et al. (2015) proposed that the trade-off between exploration and exploitation is guided by domain-general mechanisms, supported by norepinephrine and dopamine, which modulate attention and learning across species. Dopaminergic signalling contributes to the adaptive gain model, which describes the exploration-exploitation trade-off and involves the NA, ACC, LC, and prefrontal regions (Spreng & Turner, 2021). These regions were also associated with search and foraging success in both age groups in Experiment 6, particularly among older adults. Foraging organisation was correlated with connectivity, as were item inspections. Although initially classified as a search measure, greater item inspections may indicate more movement within the environment. Effective foraging organisation leads to greater target collection, meaning more item inspections correlate with increased movement. Thus, greater foraging ability is determined by the interplay between organisation, target collection, and item inspection, highlighting the role of domain-general regions in achieving success.

7.1 Current insights and future directions in research

7.1.1 Considerations of present literature

A debate that has persisted is whether visual search and foraging requires memory. This is a considerable discussion as researchers such as Wolfe (2012) follow a memoryless search model and thus coin 'hybrid search' as search with the inclusion of memory whereas researchers such as Klein and MacInnes (1999) state that memory is inherently linked to search, and therefore hybrid search is a superfluous specification. Recent research by Li and colleagues (2018) supports the argument that memory is required within visual search, but further supposing that previous two-dimensional models may not require memory as would a three-dimensional model. It was overall found (Li et al., 2018) that participants employed visual search strategies reliant of spatial memory, and, when compared against a two-dimensional paradigm, participants were more efficient at learning the target and distractor items, and therefore increasing success over time. As such, it was concluded that not only is memory required, but so are additional processes such as attention. Although the debate considered whether memory was necessary for search, it ultimately led to the introduction of individual differences in visual search. The present series of experiments supported the necessity of memory, attention, and additional forms of cognition and cognitive control in order to guide search and foraging. Simply, the clear associations between behavioural tasks and the CANTAB measures indicated the use of spatial working memory, episodic memory, working memory, and verbal memory. Across the seven experiments, a complex interplay between regions of cognition guided success, such that executive function and memory contributed to more complex manipulations (e.g. Experiment 4—without template provision and with unequal distribution—episodic memory was found to guide attention for template creation and executive functioning facilitated patch visit success) where single feature search in Experiment 1, for example, only revealed associations with spatial working memory. The determinants of search can be understood by different processes depending on the complexity of the array. Executive control and memory have been found to be relied upon for complex or novel arrays whilst fixed sequences of search, or the creation of a basic schema, facilitate a less demanding and simple search (Smith & De Lillo, 2022). The modulation of strategy to decrease executive and memory load increases target acquisition and is guided by cognitive control processes.

Clearly, whilst this thesis adds to the expanding literature on combining visual search and foraging, more research is needed to comprehensively grasp the factors influencing search alongside foraging. There have been various suggestions of combined paradigms, including hybrid search (Wolfe, 2012), hybrid foraging (Wolfe et al., 2016), or visual foraging (Kristjánsson, Jóhannesson, & Thornton, 2014). It has been suggested that these concepts extend classic visual search, and implement further variables, with the addition of memory, multiple targets, or individual difference. However, whilst each concept broadly investigates search behaviour across various domains, the differences in the hybrid literature reside within the specific domain being studied. Hybrid search (Wolfe, 2012) was designed to investigate the inclusion of memory to visual search, deviating away from the classic ‘pop out’ where one’s attention is drawn to a singular target. This was suggested to address the integration of visual search for multiple targets outside of working memory limits. Hybrid foraging (Wolfe et al., 2016) was then devised to look how one makes decisions to stop searching in one location and move onto the next. Economic decision-making, defined by MVT properties, was investigated by implementing multiple instances of multiple targets.

Whilst also utilising memory, hybrid foraging required one to hold multiple target instances in mind in order to search patchily distributed items. Finally, visual foraging (Kristjánsson et al., 2014) is like hybrid foraging where multiple instances of multiple targets are presented within an array, but visual foraging is suggested to focus more specifically on the implementation of visual search properties utilising single feature and conjunction of feature defined displays. Instead of following the MVT or reaction time to quantify a search slope, visual foraging implements organisation and systematicity to search and foraging through measures such as run behaviour, best-*r*, and inter-target time. In this sense, the present series of experiments described in the thesis appears to follow a visual foraging-type paradigm by the implementation of single feature and conjunction defined arrays. However, visual foraging does not distribute targets patchily, and therefore perhaps in a novel combination of hybrid foraging and visual foraging, this thesis presents a foraging-like search. Only has a visual foraging display been integrated into a three-dimensional setting; hybrid search and hybrid foraging still reside within two-dimensions. Across each of these aforementioned paradigms, the addition of cognitive resources (and therefore individual difference) to guide search is required for success. As such, whilst conveyed and utilised as separate tasks measuring slightly different things, it appears cognitive control and strategy underpin the varying iterations of integrated search and foraging.

Treisman and Gelade (1980) initially devised their search task for the target to 'pop out'—one does not need to search. As the visual search field has progressed, the additional targets and cognitive resources necessary for success may more closely represent *visual search* where one is required to search the space for a target—it is not automatically attended to by salience. As such, the commonality across hybrid search, hybrid foraging, and visual foraging is that of cognitive control and strategy. Clarke et al. (2022) suggest that strategy is the search behaviour one chooses to guide them, which differs across individuals. This strategic allocation of cognitive resources is guided by cognitive control processes, which enable individuals to regulate their attention, inhibit distractions through executive functioning, create memory-based target templates, and adapt their search strategies based on task demands and goals. As described by Smith and De Lillo (2022), cognitive control is defined by the complexity of the array and whether someone is required to implement executive control and memory or a basic schema. As a task progresses through trials, even if the search begins as complex, by information acquisition, it may transition into a simple process guided by a basic schema or fixed search sequence. This defines the integration between search and foraging: *how* one searches their environment (the search sequence) reveals the underpinnings of behaviour mediated by cognitive control, executive function, and planning. For example, imagining the conjunction of feature task from Experiments 1-6, it begins as a complex task where sampling items almost exclusively would be required to acquire information. Over time, those participants with greater cognitive control and strategy may begin to discern that the targets are only under the yellow cups and blue boxes. Throughout this process from sampling to concise acquisition, participants must continuously update their strategy to increase success. By observing how one executes a search sequence, this may reveal insights into the underlying mechanisms of behaviour and cognition, elucidating how executive functions influence decision-making and goal-directed behaviour, guided by cognitive control processes.

One way to elucidate strategy, as suggested by Clarke et al. (2022) and Kristjánsson et al. (2020), is the measure of run behaviour. Comparing longer runs to frequent switching (although both strategies may reveal the same number of targets acquired), one strategy may be to collect all the yellow cups, and then the blue boxes, guided by one template that switches to another. An alternate strategy may be to collect one yellow cup, one yellow cup, one blue box, etc, guided by proximity of one item to the next. However, what run behaviour does not provide is strategy in patchy environments. Should one know that the targets are under yellow cups and blue boxes, it would be beneficial to collect all hidden targets, per patch. This would reveal quite short runs, whereas Kristjánsson et al. (2020) discovered that in a conjunction of feature condition, participants tend to exhaustively forage one type before switching to the second type. And so, whilst run behaviour indeed reveals strategy, it is not adapted to patchy environments as one might expect to define foraging environments. Clarke, Hunt and Hughes (2022) discuss that the proximity of targets relative to each other and the number of distractors within an environment affects target switching. This variability poses challenges when comparing findings across studies with different target distributions and categories. This is especially true in unequally distributed arrays. Further, relying solely on run statistics to assess efficient foraging fails to capture the cognitive processes underlying foraging behaviour. It has been proposed that this approach overlooks the intrinsic spatial aspects inherent to foraging (Clarke, Hunt, & Hughes, 2022).

A further consideration of foraging is the presiding method of using the MVT to measure behaviour. As has been discussed (see *section 1.2.1*), utilising the MVT has been the primary method of quantifying foraging behaviour. However, it is difficult to apply the MVT to 'real world', or at least, motile paradigms. As exampled recently across the literature, human behaviour was found to be complex and did not follow a singular rule (Wolfe, 2013), and, due to the simplistic nature of the MVT, the theory does not lend to environmentally influenced behaviour (Fougnie et al., 2015). Foragers do not have optimality knowledge, nor perfect understanding of optimal profitability, particularly within unequally distributed patches, and are limited in their computation ability to calculate an optimal decision (Chin et al., 2015). It has been suggested (e.g. Bettinger & Grote, 2016) that the MVT relies on assumptions such as diminishing returns, which may not reflect all foraging scenarios, or assumptions of equal distribution, which presents difficulty when applying the theorem accurately. Calcagno et al. (2014) identified that optimal time in patch did not show any trend with patch quality, for example, where one might expect to spend longer in reward rich patches as compared to poor. As a novel implementation of motile foraging, the present set of experiments found that the MVT could not be applied, despite the expectation that the MVT should be applicable in an immersive and motile environment. The theorem was unable to discern the nuances associated with unequally distributed patches or account for cognitive abilities such as memory, learning, and decision-making that influence large-scale search behaviour. Certainly, if the MVT represents optimal behaviour, then the theorem should reflect real world situations across all foraging contexts.

Additional ways to measure aspects of foraging behaviour have been developed, including best-*r*, as utilised presently, but also (as highlighted by Kristjánsson, Ólafsdóttir, & Kristjánsson, 2020) measures such as inter-target times, run behaviour, or switch costs, to name a few. Kristjánsson, Ólafsdóttir, and Kristjánsson (2020) acknowledge the seemingly daunting number of measures available to quantify foraging, with a note that as the visual search literature appears to reduce its' measures, foraging provides greater options for analyses. However, this begs the question as to the 'right' measure to quantify search and foraging behaviour. Kristjánsson, Ólafsdóttir, and Kristjánsson (2020) name ten different measures to quantify visual foraging. Amidst this plethora of options, one might question whether researchers across the field are indeed studying the same phenomenon when it comes to visual search and foraging. For example, Kristjánsson et al. (2022) identified that although both best-*r* and inter-target latency measure foraging organisation, they unexpectedly revealed differing results. Are we truly measuring foraging behaviour or are we inadvertently capturing different aspects of the process, leading to fragmentation rather than unity in our understanding? Clarke et al. (2022) suggest that *behaviour* as such does not provide much information, and instead strategies that are identifiable by fixation (target collection) sequences provide greater nuance. As described above, one can discern patterns of behaviour by observing the strategy adopted by a participant, as this may yield greater information about their approach to the search process. Along a similar vein, Treisman and Gelade (1980), amongst many others, employed search slopes to measure the effectiveness of one's visual search. However, Wolfe (2018) cautioned against interpreting fully linear searches as confirming theoretical explanations of search, as the concept of a search slope presupposes a linear correlation between search time and the quantity of items in the display. As mused by Kristjánsson (2015, p. 10): "…the field still has not figured out how visual search works" and later: "no concrete theory accounts for all visual search findings". Therefore, if one looks beyond the behaviours of search and foraging as discrete accounts and rather focus more specifically on strategy, then perhaps one can compare across the variations in paradigms.

If one's underpinned strategy elucidates search and foraging better than behavioural measures, then it becomes integral to devise a method to quantify strategy across paradigms. As discussed previously, runs, MVT, and best-*r* do not capture all aspects of search environments, cognitive control, or individual strategy. Clarke, Hunt, and Hughes (2022) propose that Bayesian multilevel modelling may provide greater nuance into individual strategy as the model parameters are independent of the number of targets present or number of targets to be collected whilst estimating underlying biases of run behaviour including proximity. Whilst this modelling approach provides a closer representation of individual difference and strategy, it was noted that inter-target times were not yet considered, nor were distractors, and the model was developed based on two-dimensional visual foraging data. As such, three-dimensional implementations are still required to quantify and understand participant large-scale search and foraging strategy.

7.2.2 Further considerations

The use of virtual reality is becoming increasingly more popular, with literature such as Kristjánsson, Ólafsdóttir, and Kristjánsson (2020) specifically highlighting the benefits of virtual reality to increase ecological validity in search and foraging paradigms. Investigating the translations from two- dimensions to three- is essential as the field moves toward more ecologically valid research. Combining search tasks with movement introduces additional factors that contribute to success, but also making it more challenging to distinguish individual behaviours within a large-scale task. With reliance on both idiothetic and foveal influences, particularly in three dimensions, specific contributions become more intertwined and less distinct, making them harder to identify. Plainly, when someone can use various support mechanisms to guide their search and foraging, it is difficult to discern which mechanism contributes to which aspect of success. However, this complexity might be the essence of ecologically valid research. For instance, when searching for lost keys at home, people naturally employ physical movement, rotation, and utilise their entire field of view. In this context, explicitly pinpointing specific contributions might not be crucial, as the integration of these mechanisms mirrors typical search and foraging behaviour.

Further, virtual reality allows for research to implement cognitive and physical resources to facilitate success, however one must also be vigilant for potential difficulties that different participants might have with the apparatus. Some research has highlighted concerns in using virtual reality with older adults (e.g. Schöberl et al., 2020), however others have provided support (e.g. McAvan et al., 2021), and indeed *Chapter 4* emphasised the usability of virtual reality across the lifespan with successful data collection of participants aged 18-93. In conversation with the older participants, most shared how novel, but enjoyable, they found the experience, with some excitedly offering to “come back next week”. There was a huge influx in the number of interested older adults to be added to a participant database “if this was the direction of psychological research". It is especially noted that the 93-year-old participant particularly enjoyed the VR task with aplomb. These are promising and inspiring anecdotes in the movement towards ecologically valid laboratory-based experiments, where older adults can, and will, continue to be interested in participating. Clearly, as identified in *Chapter 4*, this also facilitates the collection of previously unobserved behaviours and provides greater insights into ageing and underpinned compensatory mechanisms. McAvan et al. (2015) evidenced, using immersive VR, that older adults were able to employ various navigational strategies which facilitated greater success than has previously been observed on monitor-based studies. Further research into the explicit strategies older adults used to guide success in the present study may provide insight into some of the compensatory mechanisms that may be at play and provide more information about any domain general processes, but at minimum, this can certainly be achieved using fully motile virtual reality.

A final point of consideration is the physicality between older and younger adults. It was clearly observed (and evidenced through the greater number of patches inspected in younger adults) that older adults moved throughout the space significantly less, and this may be irrespective of strategy. Experiment 6 may have benefitted from including a measure of speed or movement in VR to covariate against task performance. Reaction and movement time was addressed in Experiment 6's discussion (see *section 4.4.3*), however it was also noted that the RTI was an iPad-based reaction time task and may not reflect the same reaction and movement time differences as observed in the large-scale task. Whilst it is likely that if participants are slower on the iPad measure, then they too will show reduced reaction and movement time in VR, it should still be considered that movement, and compensatory systems, are not identical. An additional measure in the visual search literature is eye tracking, which could provide greater nuance into participant visual search behaviour alongside idiothetic requirements when search success may be hampered by movement speed. Malcolm and Henderson (2009) posited that eye tracking provided real world processing insights. Therefore, the present series of experiments may have benefitted from implementing eye tracking alongside the large-scale search task, which may have provided greater understanding into not only strategy between participants, but also into the search ability of older adults beyond physical constraints. Hollingworth and Bahle (2020) found that by employing eye tracking, they were able to derive greater nuance to search, as compared to traditional two-dimensional search, such as attention allocation, prioritisation of visual information, or gaze revisits without inspection revisits. It was also suggested that eye tracking provided more information about temporal and spatial aspects of visual search behaviour, including temporal dynamics of attention over time, systematic scanning, and the impact of distractors. As a cypher for visual attention, pairing eye tracking with the idiothetic cues facilitated by immersive VR may elucidate finer-grained detail to large-scale, visual search behaviour, as well as provide greater information into the domain generality of search across the lifespan.

7.1.3 Future research

A primary concern is that of older adult data and how it is utilised and understood within visual search and foraging. It is known that the effects of ageing are not linear (Verdú et al., 2000) and older adult performance is not as categorically worse than younger adults as has been previously suggested (see discussions around older adult search and foraging performance in *section 1.5*). As ageing and degradation is known to be individualistic, a suggested way to quantify ageing is by one's 'brain age' rather than chronological age (Franke & Gaser, 2019). It has recently been suggested that computing 'brain age' may better reflect the deviation from normal population (Smith et al., 2019). This is done by finding the difference between brain age and actual age (termed 'the delta'). Degradations in brain age may be determined by a high degree of atrophy, for example. However, large amounts of data are required to accurately quantify brain age (e.g. Smith et al. (2019) accessed N = 19,000 data from UK Biobank). As such, larger sample sizes may allow for specific measurements of brain age. This seems difficult at best for behavioural data acquisition. Therefore, perhaps future works into specific biomarkers and neural substrates that underpin specific deficits, rather than encompassing whole populations, may provide greater nuance into decrements in ageing and how this may present. Further, as was discussed in *section 4.4.5*, there is also large variability assumed in older adult participants who engage in psychological research as compared to older adults who may be less interested, mobile, or active in a community. Experiment 6 revealed a particular strength in the range of ages (i.e. 65-93) in the older adult participants, however these participants may reflect relative preservation in ability. Perhaps, with the implementation of mobile technology, and therefore administering the battery to a more diverse group of older adults in more accessible locations outside of a laboratory context, including those who have neurodegenerative diagnoses, may provide greater insights.

A final consideration to elucidate further differences between older adults would be to employ the large-scale task with a specific group of AD-diagnosed participants, or those identified to hold the APOE-ε4 allele (the gene known to be associated as the strongest genetic risk factor in developing Alzheimer's disease; Serrano-Pozo, Das, & Hyman, 2021). Research has suggested that early tau pathology, the protein known to maintain neuronal structural integrity, originates in the LC (Mather & Harley, 2016). This is thought to mediate shifting between exploration and exploitation through noradrenergic signal alterations, and with the emergence of exploitation biases, this may reflect reduced attentional flexibility in AD (Wyatt et al., 2024). As it has been found that the LC is difficult to identify on structural brain imaging (Wyatt et al., 2024), perhaps the lack of connections with the LC in Experiment 6 were reflective of scanning difficulties rather than preserved connections. As such, methods to efficiently scan the LC, such as sequences optimised to detect neuromelanin (i.e. a pigmented polymer that accumulates in the LC) or higher-resolution brain imaging, may provide greater nuance to LC connectivity (Mather & Harley, 2016), and therefore greater understanding of exploitation in association with neural degradation and performance. Additionally, it is possible that not only can visual search and foraging behaviour predict AD, but they may also be able to discriminate between forms of dementia. Behavioural-variant Frontotemporal Dementia (bvFTD) is characterised by significant atrophy in the anterior insula, and anterior and frontal temporal lobes (Seeley, 2019). As compared to healthy controls, those suffering from bvFTD tend to show affected stimulus-reinforcement learning and decreased exploration (Strenziock et al., 2011). There have been recent identifications in the literature that the different forms of dementia can be difficult to discriminate between, with misdiagnosis presenting as a common issue, such as between bvFTD and frontal variant Alzheimer's disease (as reviewed by Brown, Salo, & Savage, 2023). As such, implementing the present large-scale task on a cohort of participants with a variety of diagnoses may provide greater nuance into the specific behavioural deficits that present within each neurodegenerative disorder in a non-invasive but specific manner.

7.2 Conclusion

In summary, this thesis described whether neural and cognitive underpinnings of search and foraging behaviour could be predicted by a large-scale, immersive VR task. Indeed, decrements in frontal and temporal regions, and episodic memory and executive function, predicted worse visual search on measures of success and foraging decision performance. More research is needed to further elucidate finer-grained detail, especially in populations with diagnosed dementia, however these series of experiments provided support to the large-scale implementation to quantify search and foraging behaviour across the lifespan as predictive measures to neurodegeneration. This serves as a foundation to guide healthcare practices in ageing populations and stimulate additional scientific and theoretical investigation.

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Appendix A

Table A1. Pearson's correlations between behavioural measures and episodic and executive functioning measures in Experiment 1.

	PALTEA	PALFAMS	PALNPR	PALTE	IEDEEDS	IEDYERTA	IEDTT	IEDTTA	IEDTL
Within patch best-r_f	-0.34	-0.25	-0.18	0.27	-0.08	-0.20	0.06	0.13	-0.14
Within patch best-r_c	0.25	0.26	0.31	-0.37	0.25	0.20	-0.20	-0.22	0.06
Between patch best-r_f	-0.24	-0.18	-0.07	0.12	-0.20	-0.23	0.14	0.19	0.10
Between patch best-r_c	0.20	0.20	0.18	-0.18	-0.13	-0.11	0.17	-0.01	0.13
Targets collected_f	0.27	0.30	0.08	-0.17	0.25	0.30	-0.29	-0.33	-0.21
Targets collected_c	0.33	0.30	0.17	-0.32	0.31	0.22	-0.14	-0.16	-0.03
Total inspections_f	0.27	0.30	0.08	-0.18	0.25	0.30	-0.28	-0.32	-0.20
Total inspections_c	0.14	0.14	-0.05	-0.07	0.23	0.18	-0.11	-0.13	-0.23
Percentage cued_f	-0.06	-0.08	-0.11	0.28	-0.06	-0.01	-0.14	-0.06	-0.17
Percentage cued_c	$.54^{*}$	$.48^{*}$	$.51^{*}$	$-.62^{**}$	0.36	0.21	-0.11	-0.18	0.39
Patch visits_f	0.21	0.24	0.03	-0.09	0.25	0.28	-0.30	-0.32	-0.26
Patch visits_c	0.02	-0.02	-0.05	-0.05	0.12	-0.07	0.02	0.12	0.00
Exploit_f	0.33	0.41	0.34	-0.43	0.25	0.37	-0.14	-0.38	0.12
Exploit_c	0.31	0.37	0.29	-0.43	0.26	0.32	-0.09	-0.25	0.13
Patch revisits_f	-0.26	-0.35	-0.34	0.35	-0.31	-0.39	0.11	0.41	-0.09
Patch revisits_c	0.28	0.19	0.06	-0.07	0.13	0.10	-0.14	-0.14	-0.10

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **.

Table A2. Pearson's correlations between behavioural measures and verbal memory and working memory in Experiment 1.

	VPAERTOT	VPAMWDST	DGSFMAXP	VPAERSDR	VPAMWDSD
Within patch best-r_f	0.23	-0.26	-0.34	0.22	-0.10
Within patch best-r_c	-0.40	0.32	0.07	-0.40	-0.11
Between patch best-r_f	0.17	-0.23	-0.18	0.04	-0.24
Between patch best-r_c	-0.08	0.06	-0.07	-0.23	0.11
Targets collected_f	-0.07	0.11	0.15	0.00	0.29
Targets collected_c	-0.12	0.10	0.16	-0.14	-0.08
Total inspections_f	-0.06	0.09	0.15	0.01	0.29
Total inspections_c	0.12	-0.08	-0.10	0.17	0.14
Percentage cued_f	-0.02	0.09	0.12	0.08	0.21
Percentage cued_c	-.45*	0.31	.47*	-.62**	-.44*
Patch visits_f	-0.03	0.08	0.05	0.08	0.31
Patch visits_c	0.02	-0.05	0.06	0.02	-0.24
Exploit_f	-0.13	0.10	0.27	-0.23	0.23
Exploit_c	0.00	-0.06	0.09	-0.16	-0.07
Patch revisits_f	0.08	-0.06	0.03	0.12	-0.21
Patch revisits_c	-0.31	0.38	0.17	-0.16	0.25

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **.

Table A3. Pearson's correlations between behavioural measures and spatial working memory in Experiment 1.

	SWMTE	SWMBE	SWMWE	SWMDE	SWMS
Within patch best-r_f	-0.12	0.33	-0.02	0.09	-0.01
Within patch best-r_c	-0.36	.45*	-0.06	-0.31	0.12
Between patch best-r_f	-0.11	0.31	-0.22	-0.14	0.00
Between patch best-r_c	-0.30	0.41	0.18	-0.02	0.00
Targets collected_f	-0.26	0.24	-0.03	0.08	0.31
Targets collected_c	-0.27	0.20	-0.21	-0.20	0.11
Total inspections_f	-0.25	0.23	-0.03	0.08	0.29
Total inspections_c	-0.03	0.01	-0.07	0.12	-0.08
Percentage cued_f	-0.08	0.10	0.08	0.13	0.31
Percentage cued_c	-.55*	0.42	-0.25	-.62**	.48*
Patch visits_f	-0.21	0.21	0.05	0.16	0.28
Patch visits_c	-0.02	0.03	0.01	-0.07	-0.10
Exploit_f	-0.44	0.37	-0.13	-0.08	.44*
Exploit_c	-.48*	0.37	-.47*	-0.27	0.28
Patch revisits_f	0.44	-0.43	-0.06	-0.06	-.45*
Patch revisits_c	0.20	-0.23	0.30	0.05	-0.04

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A4. Pearson's correlations between behavioural measures and episodic and executive functioning measures in Experiment 2.

	PALTEA	PALFAMS	PALNPR	PALTE	IEDEEDS	IEDYERTA	IEDTT	IEDTTA	IEDTL
Within patch best-r_f	0.26	0.24	0.15	0.00	0.22	0.25	-0.31	-0.31	-.54*
Within patch best-r_c	0.12	0.01	0.30	0.24	-0.09	0.08	-0.06	-0.06	-0.16
Between patch best-r_f	-0.20	-0.23	-0.18	0.26	0.04	-0.03	0.03	0.03	-0.28
Between patch best-r_c	0.23	0.10	0.43	0.13	-0.39	-0.36	0.36	0.36	0.32
Targets collected_f	0.28	0.28	-0.07	-0.18	0.42	0.17	-0.22	-0.22	0.00
Targets collected_c	-0.20	-0.17	-0.05	0.15	0.13	0.04	0.08	0.08	-0.08
Total inspections_f	0.32	0.31	0.01	-0.16	0.43	0.20	-0.22	-0.22	-0.05
Total inspections_c	-0.27	-0.25	-0.10	0.15	0.14	0.03	0.10	0.10	-0.04
Percentage cued_f	0.07	0.13	-0.10	-0.23	-0.14	-0.06	0.01	0.01	0.34
Percentage cued_c	0.07	0.09	-0.02	0.01	0.02	-0.07	0.07	0.07	-0.01
Patch visits_f	0.24	0.22	0.03	-0.02	0.35	0.16	-0.19	-0.19	-0.05
Patch visits_c	-0.43	-0.44	-0.16	0.36	0.02	0.03	0.07	0.07	-0.31
Exploit_f	0.30	0.30	-0.19	-0.22	0.40	0.02	-0.06	-0.06	0.00
Exploit_c	0.00	0.02	-0.09	-0.12	0.23	-0.06	0.10	0.10	0.15
Patch revisits_f	0.08	0.14	0.19	-0.22	0.14	0.33	-0.24	-0.24	-0.10
Patch revisits_c	-0.09	-0.04	0.08	0.29	-0.08	0.11	-0.02	-0.02	-0.10

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A5. Pearson's correlations between behavioural measures and verbal memory and working memory in Experiment 2.

	VPAERTOT	VPAMWDST	DGSFMAXP	VPAERSDR	VPAMWDSD
Within patch best-r_f	0.27	-0.32	-0.04	-0.19	0.20
Within patch best-r_c	-0.12	0.06	-0.21	-0.23	0.31
Between patch best-r_f	0.44	-0.39	-0.14	0.35	-0.34
Between patch best-r_c	-0.10	0.07	-0.04	-0.38	.48*
Targets collected_f	-0.40	0.33	-0.09	-0.38	0.22
Targets collected_c	-0.35	0.29	0.04	-0.32	0.19
Total inspections_f	-.46*	0.39	-0.11	-0.43	0.29
Total inspections_c	-0.39	0.33	0.07	-0.29	0.14
Percentage cued_f	0.01	0.01	0.07	0.15	-0.14
Percentage cued_c	0.05	-0.03	-0.13	0.12	-0.07
Patch visits_f	-0.31	0.28	-0.25	-0.31	0.22
Patch visits_c	-0.24	0.24	-0.22	0.05	-0.12
Exploit_f	-0.24	0.14	-0.03	-0.44	0.19
Exploit_c	-0.11	0.01	0.21	-0.36	0.19
Patch revisits_f	-0.43	0.37	.48*	-0.38	0.35
Patch revisits_c	-0.20	0.24	-0.13	-0.09	0.10

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A6. Pearson's correlations between behavioural measures and spatial working memory in Experiment 2.

	SWMTE	SWMBE	SWMWE	SWMDE	SWMS
Within patch best-r_f	-0.11	0.08	-0.11	-0.07	-0.24
Within patch best-r_c	0.12	-0.18	0.09	0.11	0.02
Between patch best-r_f	0.04	-0.02	0.16	0.12	$-.47^{*}$
Between patch best-r_c	0.32	-0.37	0.30	0.29	0.19
Targets collected_f	-0.23	0.15	-0.24	-0.12	0.32
Targets collected_c	-0.06	0.04	-0.21	-0.02	0.06
Total inspections_f	-0.18	0.10	-0.20	-0.11	0.30
Total inspections_c	0.01	-0.03	-0.25	-0.06	0.03
Percentage cued_f	-0.08	0.04	0.03	0.18	0.18
Percentage cued_c	$-.54^{*}$	$.47^{*}$	-0.10	0.19	0.00
Patch visits_f	-0.20	0.14	-0.11	-0.07	0.24
Patch visits_c	-0.01	0.01	-0.09	-0.02	-0.24
Exploit_f	-0.06	0.00	-0.22	-0.11	0.15
Exploit_c	-0.38	0.31	-0.38	-0.01	0.26
Patch revisits_f	0.04	-0.06	-0.21	-0.17	0.35
Patch revisits_c	0.43	-0.40	0.11	-0.10	-0.17

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A7. Pearson's correlations between behavioural measures and episodic and executive functioning measures in Experiment 3.

	PALTEA	PALFAMS	PALNPR	PALTE	IEDEEDS	IEDYERTA	IEDTT	IEDTTA	IEDTL
Within patch best-r_f	0.05	0.08	0.37	-0.19	0.34	-0.09	-0.43	0.06	-0.28
Within patch best-r_c	0.09	0.12	0.18	-0.06	0.13	0.12	-0.33	-0.17	-0.44
Between patch best-r_f	0.10	0.10	0.37	-0.15	-0.03	-0.11	-0.20	0.22	-0.19
Between patch best-r_c	0.02	-0.05	0.27	0.00	0.12	-0.27	-0.20	0.39	-0.10
Targets collected_f	-0.17	-0.13	-0.34	0.38	-0.15	0.21	0.03	-0.29	-0.04
Targets collected_c	-0.18	-0.12	-0.15	0.15	-0.21	0.25	-0.06	-0.31	-0.28
Total inspections_f	-0.21	-0.24	-0.22	0.38	-.48*	0.03	0.21	-0.12	0.10
Total inspections_c	-0.23	-0.23	-0.15	0.22	-.51*	0.12	0.14	-0.20	-0.04
Percentage cued_f	0.15	0.23	-0.03	-0.14	.59*	0.36	-0.46	-0.37	-0.38
Percentage cued_c	0.05	0.14	-0.03	-0.04	0.25	0.11	-0.24	-0.13	-0.41
Patch visits_f	0.04	0.07	-0.26	0.24	-0.05	0.28	-0.04	-0.36	-0.14
Patch visits_c	0.12	0.16	-0.09	-0.06	-0.09	0.14	-0.01	-0.23	-0.26
Exploit_f	-0.16	-0.17	-0.08	0.20	-0.20	-0.10	-0.08	0.03	-0.13
Exploit_c	-0.28	-0.23	-0.16	0.22	-0.17	0.40	-0.20	-0.43	-0.28
Patch revisits_f	-0.23	-0.23	-0.08	0.06	0.11	0.13	0.33	-0.10	0.48
Patch revisits_c	-0.05	-0.02	0.08	0.03	-0.15	-0.31	0.29	0.36	0.27

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **.

Table A8. Pearson's correlations between behavioural measures and verbal memory and working memory in Experiment 3.

	VPAERTOT	VPAMWDST	DGSFMAXP	VPAERSDR	VPAMWDSD
Within patch best-r_f	-0.19	0.16	0.10	-.50*	0.45
Within patch best-r_c	-0.09	0.04	0.25	-0.28	0.27
Between patch best-r_f	-.47*	.49*	0.35	-.53*	.52*
Between patch best-r_c	-0.34	0.33	0.28	-0.37	0.39
Targets collected_f	0.33	-0.34	0.07	0.11	-0.10
Targets collected_c	0.33	-0.33	-0.01	-0.01	0.01
Total inspections_f	0.44	-0.45	0.09	0.17	-0.15
Total inspections_c	.53*	-.51*	-0.04	0.14	-0.14
Percentage cued_f	-0.08	0.07	-0.08	-0.11	0.10
Percentage cued_c	-0.12	0.10	0.02	-0.10	0.10
Patch visit_f	0.19	-0.20	-0.30	0.14	-0.15
Patch visit_c	0.24	-0.25	-.49*	0.21	-0.23
Exploit_f	0.33	-0.35	.56*	0.04	-0.02
Exploit_c	0.20	-0.20	0.40	-0.18	0.19
Patch revisits_f	-0.01	0.03	-0.21	-0.05	0.05
Patch revisits_c	-0.15	0.19	-0.02	-0.06	0.06

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A9. Pearson's correlations between behavioural measures and spatial working memory in Experiment 3.

	SWMTE	SWMBE	SWMWE	SWMDE	SWMS
Within patch best-r_f	-0.42	0.22	-0.21	-0.21	0.34
Within patch best-r_c	-0.40	0.18	-0.36	-0.34	0.23
Between patch best-r_f	-0.03	0.05	-0.20	-0.25	0.26
Between patch best-r_c	-0.28	0.35	-0.20	-0.27	0.40
Targets collected_f	-0.26	0.16	-0.18	-0.18	0.10
Targets collected_c	-0.14	0.02	-0.18	-0.12	0.08
Total inspections_f	-0.19	0.16	-0.27	-0.28	0.00
Total inspections_c	-0.11	0.09	-0.22	-0.19	-0.06
Percentage cued_f	-0.10	-0.03	0.23	0.26	0.19
Percentage cued_c	-0.11	-0.09	-0.11	-0.04	0.17
Patch visit_f	-0.08	0.00	-0.03	0.03	-0.08
Patch visit_c	0.04	-0.12	-0.03	0.08	-0.20
Exploit_f	$-.47^{*}$	0.44	$-.53^{*}$	$-.57^{*}$	0.37
Exploit_c	-0.17	0.10	-0.29	-0.29	0.27
Patch revisits_f	0.42	-0.44	$.64^{**}$	$.60^{**}$	-0.26
Patch revisits_c	0.13	-0.12	0.10	0.09	-0.06

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **.

Table A10. Pearson’s correlations between behavioural measures and episodic and executive functioning measures in Experiment 4.

	PALTEA	PALFAMS	PALNPR	PALTE	IEDEEDS	IEDYERTA	IEDTT	IEDTTA	IEDTL
Within patch best-r_f	0.19	0.27	-0.06	0.00	0.31	0.20	0.06	-0.21	0.10
Within patch best-r_c	0.08	0.15	-0.15	0.07	0.19	0.08	0.09	-0.06	0.10
Between patch best-r_f	-0.20	-0.13	-0.08	0.15	-0.03	-0.21	0.12	0.23	0.27
Between patch best-r_c	-0.05	-0.09	0.12	-0.02	0.19	0.28	-0.25	-0.23	0.15
Targets collected_f	0.01	0.03	-0.29	0.22	0.09	0.25	-0.08	-0.29	-0.30
Targets collected_c	.48*	.53*	0.08	-0.26	0.15	0.03	0.39	-0.10	0.04
Total inspections_f	-0.02	-0.03	-0.08	0.09	0.13	0.27	0.01	-0.33	-0.17
Total inspections_c	0.32	0.37	0.14	-0.29	0.12	0.10	0.34	-0.17	0.04
Percentage cued_f	0.10	0.12	-0.22	0.13	-0.13	-0.20	-0.02	0.18	-0.08
Percentage cued_c	0.23	0.23	-0.09	0.05	-0.05	-0.25	0.20	0.23	0.12
Patch visits_f	-0.02	0.00	-0.31	0.26	0.14	0.22	-0.06	-0.26	-0.19
Patch visits_c	0.07	0.15	-0.23	0.16	0.18	-0.06	0.27	0.04	-0.03
Exploit_f	0.00	-0.01	-0.25	0.15	0.17	0.26	-0.10	-0.26	-0.30
Exploit_c	.53*	.55*	0.15	-0.37	0.25	0.27	0.17	-0.28	-0.04
Patch revisits_f	0.34	0.32	0.38	-0.39	-.55*	-0.26	0.37	0.15	0.28
Patch revisits_c	0.10	0.02	0.29	-0.22	-.68**	-0.32	0.34	0.16	0.18

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **.

Table A11. Pearson's correlations between behavioural measures and verbal memory and working memory in Experiment 4.

	VPAERTOT	VPAMWDST	DGSFMAXP	VPAERSDR	VPAMWDSD
Within patch best-r_f	-0.12	0.05	-0.12	-0.13	0.13
Within patch best-r_c	-0.13	0.19	0.00	-0.21	0.20
Between patch best-r_f	0.10	-0.31	-0.21	0.16	-0.17
Between patch best-r_c	0.06	-0.11	0.38	-0.26	0.26
Targets collected_f	-0.06	0.23	0.02	-0.26	0.27
Targets collected_c	-0.30	0.41	-0.31	0.27	-0.26
Total inspections_f	-0.15	0.29	-0.06	-0.17	0.20
Total inspections_c	-0.25	0.34	-0.14	0.31	-0.27
Percentage cued_f	0.24	-0.16	0.04	-0.03	0.01
Percentage cued_c	-0.05	0.04	-0.39	0.02	-0.05
Patch visits_f	0.03	0.13	0.06	-0.22	0.23
Patch visits_c	-0.19	0.21	-0.39	0.22	-0.22
Exploit_f	-0.02	0.09	0.02	-0.25	0.25
Exploit_c	-0.20	0.34	0.15	0.06	-0.04
Patch revisits_f	-0.21	0.22	-0.27	0.26	-0.25
Patch revisits_c	0.16	-0.14	-0.38	0.01	0.00

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A12. Pearson's correlations between behavioural measures and spatial working memory in Experiment 4.

	SWMTE	SWMBE	SWMWE	SWMDE	SWMS
Within patch best-r_f	0.01	-0.08	0.07	-0.04	0.07
Within patch best-r_c	-0.06	0.02	-0.11	-0.13	0.35
Between patch best-r_f	0.22	-0.15	0.25	0.27	-0.05
Between patch best-r_c	0.06	0.02	.47*	.46*	0.09
Targets collected_f	0.10	-0.05	-0.05	-0.10	-0.20
Targets collected_c	-0.22	0.14	-0.19	-0.28	0.07
Total inspections_f	-0.07	0.16	0.10	0.09	-0.02
Total inspections_c	-0.29	0.28	-0.21	-0.19	0.21
Percentage cued_f	0.23	-0.29	-0.21	-0.31	-0.31
Percentage cued_c	0.15	-0.27	-0.04	-0.21	-0.23
Patch visits_f	0.19	-0.11	0.08	0.02	-0.23
Patch visits_c	0.11	-0.12	-0.07	-0.13	-0.12
Exploit_f	-0.12	0.13	-0.27	-0.32	-0.24
Exploit_c	-0.39	0.30	-0.30	-0.38	0.17
Patch revisits_f	0.05	-0.19	0.09	0.12	0.01
Patch revisits_c	-0.06	0.01	-0.10	-0.09	0.02

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A13. Pearson's correlations between behavioural measures and episodic and executive functioning measures in Experiment 5.

	PALTEA	PALFAMS	PALNPR	PALTE	IEDEEDS	IEDYERTA	IEDTT	IEDTTA	IEDTL
Within patch best-r_f	0.27	0.13	0.18	-0.29	0.11	-0.09	-0.18	0.08	-0.33
Within patch best-r_c	.49*	.47*	0.34	-0.39	0.38	-0.04	-0.39	0.03	-0.10
Between patch best-r_f	-0.13	-0.23	0.07	-0.05	-0.21	-0.14	-0.31	0.15	-0.46
Between patch best-r_c	0.23	0.15	.54*	-0.31	0.11	0.13	-0.45	-0.16	-0.35
Targets collected_f	0.11	0.16	-0.25	-0.08	0.19	-0.09	0.15	0.13	0.25
Targets collected_c	0.11	0.15	-0.20	-0.05	0.16	-0.21	0.27	0.26	0.35
Total inspections_f	0.03	-0.02	-0.11	0.02	0.03	-0.08	0.04	0.10	0.13
Total inspections_c	-0.02	-0.05	-0.18	-0.02	0.18	-0.01	0.17	0.07	0.14
Percentage cued_f	0.09	0.23	-0.11	-0.12	0.28	0.12	0.05	-0.12	0.08
Percentage cued_c	0.15	0.26	-0.03	0.04	-0.13	-0.20	0.09	0.14	0.38
Patch visits_f	0.10	0.15	-0.22	-0.09	0.20	-0.11	0.13	0.14	0.23
Patch visits_c	0.07	0.13	-0.19	-0.02	0.13	-0.26	0.31	0.30	0.38
Exploit_f	0.09	0.02	-0.17	0.03	0.27	0.06	0.01	-0.02	0.12
Exploit_c	0.26	0.22	-0.10	-0.13	0.39	0.02	0.13	0.03	0.19
Patch revisits_f	-0.03	0.06	0.10	-0.07	-0.41	-0.12	0.04	0.07	-0.04
Patch revisits_c	-0.13	-0.07	0.04	0.02	-.53*	-0.11	-0.11	0.04	-0.06

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A14. Pearson's correlations between behavioural measures and verbal memory and working memory in Experiment 5.

	VPAERTOT	VPAMWDST	DGSFMAXP	VPAERSDR	VPAMWDSD
Within patch best-r_f	-0.15	0.11	0.06	-0.40	$.45^{*}$
Within patch best-r_c	-0.32	0.32	-0.27	-0.19	0.19
Between patch best-r_f	0.21	-0.20	$.46^{*}$	0.08	-0.07
Between patch best-r_c	0.05	-0.06	-0.25	0.09	-0.08
Targets collected_f	-0.30	0.27	-0.05	-0.38	0.40
Targets collected_c	-0.37	0.39	-0.05	-0.37	0.38
Total inspections_f	-0.33	0.29	-0.15	-0.25	0.27
Total inspections_c	-0.35	0.35	-0.06	-0.37	0.39
Percentage cued_f	0.00	0.02	-0.01	-0.07	0.04
Percentage cued_c	-0.16	0.20	-0.04	-0.07	0.04
Patch visits_f	-0.28	0.25	-0.06	-0.41	0.43
Patch visits_c	-0.35	0.37	-0.07	-0.38	0.39
Exploit_f	-0.28	0.27	-0.07	-0.03	0.03
Exploit_c	-0.23	0.25	0.00	-0.29	0.30
Patch revisits_f	0.05	-0.04	0.08	-0.14	0.12
Patch revisits_c	-0.15	0.13	-0.01	-0.06	0.05

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at *p* < .05 is denoted by *; *p* < .001 is denoted by **.

Table A15. Pearson's correlations between behavioural measures and spatial working memory in Experiment 5.

	SWMTE	SWMBE	SWMWE	SWMDE	SWMS
Within patch best-r_f	0.20	-0.28	0.04	0.06	-0.03
Within patch best-r_c	-0.24	0.10	-0.12	-0.14	0.06
Between patch best-r_f	0.06	-0.11	0.26	0.29	0.40
Between patch best-r_c	-0.18	0.03	0.02	0.03	-0.01
Targets collected_f	-0.09	0.19	-0.26	-0.21	0.15
Targets collected_c	-0.12	0.19	-0.28	-0.29	0.15
Total inspections_f	0.14	-0.02	-0.06	0.03	-0.07
Total inspections_c	-0.06	0.18	-0.20	-0.16	0.06
Percentage cued_f	-0.29	0.24	-0.23	-0.31	0.08
Percentage cued_c	-0.14	0.09	-0.21	-0.29	-0.02
Patch visits_f	-0.09	0.17	-0.26	-0.20	0.18
Patch visits_c	-0.10	0.16	-0.30	-0.30	0.14
Exploit_f	0.02	0.21	-0.08	-0.04	-0.02
Exploit_c	-0.17	0.28	-0.15	-0.18	0.15
Patch revisits_f	0.09	-0.23	0.10	0.06	-0.07
Patch revisits_c	0.24	-0.31	0.13	0.16	-0.23

NB. Behavioural measures denoted by _f represents single feature conditions, and measures denoted by _c indicate conjunction of feature conditions. Significance at $p < .05$ is denoted by *; $p < .001$ is denoted by **.

Appendix B

MRI SAFETY PRESCREENING QUESTIONNAIRE

MRI uses a strong magnetic field and radiofrequency energy to create pictures of the inside of your body. Some implants, clothing and objects may be hazardous to you and / or interfere with the scan. Please answer the following questions carefully. A MRI operator will go through the form with you, so you will have the opportunity to ask about anything you are unsure of. **The form is on two sides.**

First Name:	Last Name:	
1st Line of Address:		
Date of Birth: D D M M Y Y Y Y If 0	Weight:	Height:
GP name and contact information (email, phone)		
Mother's first name:	Mother's maiden name:	

Have you had an MRI scan before?	YES ☐ NO ☐
Have you had any operations in the last two months? - If yes, what was the operation?	YES ☐ NO ☐
Have you **ever** had any operations to your head? - Do you have an aneurysm clip? - Do you have a programmable hydrocephalus shunt?	YES ☐ NO ☐ YES ☐ NO ☐ YES ☐ NO ☐
Have you **ever** had any operations to your eyes? - Do you have a false eye? Retinal tacks? Other eye implant?	YES ☐ NO ☐ YES ☐ NO ☐
Have you **ever** had any operations to your ears? - Do you have a cochlear implant? Auditory brainstem implant? Other ear implant?	YES ☐ NO ☐ YES ☐ NO ☐
Have you **ever** had any operations to your heart? - Do you have a pacemaker? - Do you have, or have **ever** had, pacing wires? - Do you have a loop recorder or other cardiac implant?	YES ☐ NO ☐ YES ☐ NO ☐ YES ☐ NO ☐ YES ☐ NO ☐
Do you have anything else implanted in you that you can't completely remove e.g. pain infusion pumps, neuro-stimulators, joint replacements, heart valves, stents, vascular filter, spinal rods or metalwork, tissue expanders, gastric bands etc?	YES ☐ NO ☐
Have you ever swallowed anything that contains metal or electronic / magnetic components, such as a 'PillCam' or other foreign object?	YES ☐ NO ☐
Have you **ever** had an accident or injury where a piece of metal has gone into your eyes? Have you **ever** had an accident or injury where a piece of metal has gone into your body e.g. shrapnel / bullets?	YES ☐ NO ☐ YES ☐ NO ☐

Are you wearing a fentanyl drugs patch? Are you wearing any dressings or patches that have foil rims or contain silver, or ECG dots?	YES ☐ NO ☐ YES ☐ NO ☐
Are you wearing any clothing that contains silver (e.g. antibacterial sports clothing)?	YES ☐ NO ☐
Do you have any tattoos or piercings that you cannot remove?	YES ☐ NO ☐
Is there any possibility that you may be pregnant? Are you having regular periods? When did your most recent period start?	YES ☐ NO ☐ YES ☐ NO ☐
I understand that I must remove all metallic and electronic items before going into the magnet room. This includes watches, jewellery, dentures, wallets, coins, keys, bank cards, mobile phones, hair grips, hair pieces with metallic mesh / fastenings, pen-knives etc.	YES ☐ NO ☐
I understand that I may be asked to change into a hospital gown if my clothing contains silver fibres or metallic threads / fastenings.	YES ☐ NO ☐
I understand that I may be asked to remove eye make-up if having my head scanned.	YES ☐ NO ☐
I would like a staff member to chaperone me during the set up for my MRI scan.	YES ☐ NO ☐

Do you have a **fever** or **temperature** at present? YES ☐ NO ☐

I CONFIRM THAT I HAVE READ AND COMPLETED THIS FORM AND THAT IT IS CORRECT TO THE BEST OF MY KNOWLEDGE. I HAVE BEEN GIVEN THE OPPORTUNITY TO ASK QUESTIONS AND I AM WILLING TO UNDERGO THE MRI PROCEDURE. **Is there anything else you think we should know?** Please write below:

Volunteer Name:	Date:

Appendix C

Table C1. Pearson's correlations between significant CVLT measures and cued inspection across shift types and trials.

	Cued Trial 1 ID shift	Cued Trial 2 ID shift	Cued Trial 1 ED shift	Cued Trial 1 colour ID	Cued Trial 2 colour ID	Cued Trial 3 colour ID	Cued Trial 1 shape ID
List 1-5	0.213	0.162	0.211	0.266	0.217	0.198	0.155
List B	0.249	0.259	0.334	0.226	0.276	0.374	0.254
Intrusions	.507*	.473*	.486*	.512*	.522*	.480*	.473*
Learning Slope	0.203	0.228	0.252	0.240	0.299	0.322	0.159

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C2. Pearson's correlations between significant CVLT measures and between- and within- patch organisation across shift types and trials.

	Between Trial 2 ID shift	Between Trial 2 ED shift	Between Trial 3 ED shift	Between Trial 2 shape ID	Within Trial 1 colour ID	Within Trial 1 shape ID
List 1-5	-0.263	-0.150	-0.022	-0.146	0.221	.463*
List B	0.077	0.016	-.509*	0.138	-0.335	0.194
Intrusions	-.446*	-.465*	-0.083	-.634**	0.208	0.083
Learning Slope	0.153	-0.036	-0.118	0.019	.448*	0.005

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C3. Pearson's correlations between significant CVLT measures and exploitative behaviour across shift types and trials.

	Exploit Trial 2 ID shift	Exploit Trial 1 ED shift	Exploit Trial 2 ED shift	Exploit Trial 2 colour ID	Exploit Trial 3 colour ID
List B	0.222	0.332	0.401	0.156	.533*
Free Recall	-0.362	-.577**	0.108	-0.225	-0.112
Intrusions	0.280	-0.064	-0.009	0.389	0.223
Semantic Cluster	.559*	0.149	.546*	.542*	0.100

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C4. Pearson's correlations between significant CVLT measures and patch revisit and run behaviour across shift types and trials.

	Revisit Trial 2 ID shift	Revisit Trial 3 ED shift	Revisit Trial 2 colour ID	Revisit Trial 2 shape ID	Run Trial 1 colour ID	Run Trial 2 colour ID
List B	0.153	.583**	0.204	0.020	0.230	0.271
Free Recall	0.022	0.079	0.069	-0.080	-0.013	-0.042
Intrusions	0.277	-0.148	0.193	0.409	.452*	.448*
Semantic Cluster	.482*	0.206	.454*	.464*	0.213	0.276

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

Table C5. Pearson's correlations between significant executive function measures and the total number of targets collected across ID and ED shift types and trials.

	Targets Trial 1 ID shift	Targets Trial 2 ID shift	Targets Trial 3 ID shift	Targets Trial 1 ED shift	Targets Trial 2 ED shift	Targets Trial 3 ED shift
IEDEEDS	.651**	.658**	.646**	.586**	.615**	.663**
IEDYERTA	.472*	.495*	.486*	0.431	.446*	.512*
IEDTT	-.580*	-.534*	-.520*	-.521*	-.485*	-.569*
IEDTTA	-0.362	-0.408	-0.399	-0.354	-0.377	-0.407
IEDTL	-.621**	-.549*	-.501*	-.541*	-0.460	-.536*

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

Table C6. Pearson's correlations between significant executive function measures and the total number of targets collected across colour and shape ID shift types and trials.

	Targets Trial 1 colour ID	Targets Trial 2 colour ID	Targets Trial 3 colour ID	Targets Trial 1 shape ID	Targets Trial 2 shape ID	Targets Trial 3 shape ID
IEDEEDS	.622**	.633**	.626**	.643**	.647**	.624**
IEDYERTA	.449*	.479*	0.414	.468*	.486*	.525*
IEDTT	-.594**	-.519*	-0.460	-.537*	-.517*	-.543*
IEDTTA	-0.330	-0.397	-0.346	-0.371	-0.398	-0.426
IEDTL	-.625**	-.495*	-0.403	-.584*	-.566*	-.562*

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

Table C7. Pearson’s correlations between significant executive function measures and the percentage of cued inspections across shift types and trials.

	Cued Trial 1 ID shift	Cued Trial 2 ID shift	Cued Trial 3 ID shift	Cued Trial 1 ED shift	Cued Trial 2 ED shift	Cued Trial 3 ED shift	Cued Trial 1 colour ID	Cued Trial 2 colour ID	Cued Trial 3 colour ID	Cued Trial 1 shape ID	Cued Trial 2 shape ID	Cued Trial 3 shape ID
IEDEEDS	.547*	.530*	.523*	.506*	.512*	.525*	.544*	.531*	.518*	.513*	.497*	.488*
IEDYERTA	.509*	.490*	.487*	.468*	.499*	.495*	.509*	.459*	0.437	.479*	.494*	.505*
IEDTTA	-.481*	-.499*	-.503*	-.474*	-.500*	-.494*	-.454*	-.463*	-.446*	-.476*	-.506*	-.528*
IEDTL	-.625**	-.563*	-.524*	-.574*	-.563*	-.563*	-.619**	-.515*	-.500*	-.588*	-.574*	-.510*

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C8. Pearson’s correlations between significant executive function measures and the number of item inspections across shift types and trials.

	Item Inspect Trial 1 ID shift	Item Inspect Trial 2 ID shift	Item Inspect Trial 3 ID shift	Item Inspect Trial 1 ED shift	Item Inspect Trial 2 ED shift	Item Inspect Trial 3 ED shift	Item Inspect Trial 2 colour ID	Item Inspect Trial 3 colour ID	Item Inspect Trial 1 shape ID	Item Inspect Trial 2 shape ID	Item Inspect Trial 3 shape ID
IEDTTA	.484*	.517*	.533*	.555*	.502*	.469*	.488*	.505*	.523*	.524*	.538*

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C9. Pearson’s correlations between significant executive function measures and the number of patch inspections across shift types and trials.

	Patch Trial 1 ID shift	Patch Trial 2 ID shift	Patch Trial 3 ID shift	Patch Trial 1 ED shift	Patch Trial 2 ED shift	Patch Trial 3 ED shift	Patch Trial 1 colour ID	Patch Trial 2 colour ID	Patch Trial 3 colour ID	Patch Trial 1 shape ID	Patch Trial 2 shape ID	Patch Trial 3 shape ID
IEDEEDS	.656**	.641**	.648**	.606**	.620**	.652**	.639**	.606**	.613**	.633**	.639**	.638**
IEDYERTA	.459*	0.434	.474*	0.403	0.438	.501*	.452*	0.398	0.406	0.440	0.443	.508*
IEDTT	-.552*	-.530*	-.515*	-.526*	-0.459	-.562*	-.554*	-.521*	-0.438	-.516*	-.508*	-.550*
IEDTL	-.586*	-.540*	-.484*	-.533*	-0.415	-.525*	-.559*	-.509*	-0.365	-.571*	-.536*	-.560*

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C10. Pearson's correlations between significant executive function measures and between- and within- patch organisation across shift types and trials.

	Between Trial 2 ID shift	Between Trial 2 ED shift	Between Trial 2 colour ID	Between Trial 2 shape ID	Within Trial 3 colour ID	Within Trial 3 shape ID
IEDEEDS	-.648**	-.534*	-.511*	-.542*	0.387	-0.237
IEDYERTA	-.466*	-0.411	-0.262	-.450*	.509*	0.042
IEDTT	0.317	-0.077	.487*	0.024	-.539*	0.312
IEDTTA	0.436	.474*	0.124	.505*	-0.444	-0.147
IEDTL	0.252	-0.030	0.324	0.076	-0.380	.483*

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C11. Pearson's correlations between significant executive function measures and the percentage of exploitative behaviour across shift types and trials.

	Exploit Trial 1 ID shift	Exploit Trial 2 ID shift	Exploit Trial 1 ED shift	Exploit Trial 2 ED shift	Exploit Trial 3 ED shift	Exploit Trial 1 colour ID	Exploit Trial 2 colour ID	Exploit Trial 3 colour ID	Exploit Trial 1 shape ID	Exploit Trial 2 shape ID	Exploit Trial 3 shape ID
IEDEEDS	0.366	0.414	0.071	0.304	.673**	0.280	0.400	.457*	0.340	0.210	0.177
IEDYERTA	.467*	.572**	0.352	0.230	.484*	0.271	0.441	0.254	.510*	.547*	0.390
IEDTT	-.579*	-0.105	0.260	-0.461	-0.370	-.555*	-0.055	-0.276	-0.393	-0.128	0.196
IEDTTA	-0.385	-.641**	-.482*	-0.148	-0.437	-0.145	-.480*	-0.242	-.508*	-.634**	-.498*
IEDTL	-.630**	-0.204	0.116	-.570*	-0.294	-.749**	0.021	-0.433	-0.251	-0.466	0.138

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C12. Pearson's correlations between significant executive function measures and the number of consecutive inspections (runs) across ID and ED shift types and trials.

	Run Trial 1 ID shift	Run Trial 2 ID shift	Run Trial 3 ID shift	Run Trial 1 ED shift	Run Trial 2 ED shift	Run Trial 3 ED shift
IEDEEDS	.625**	.643**	.621**	.598**	.627**	.659**
IEDYERTA	.494*	.485*	.464*	0.394	0.433	.509*
IEDTT	-.527*	-.522*	-0.456	-.507*	-0.456	-.494*
IEDTL	-.576*	-.595**	-.477*	-.553*	-0.447	-.494*

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C13. Pearson's correlations between significant executive function measures and the number of consecutive inspections (runs) across colour and shape ID shift types and trials.

	Run Trial 1 colour ID	Run Trial 2 colour ID	Run Trial 3 colour ID	Run Trial 1 shape ID	Run Trial 2 shape ID	Run Trial 3 shape ID
IEDEEDS	.621**	.609**	.605**	.592**	.641**	.595**
IEDYERTA	.497*	.480*	0.372	.464*	.467*	.520*
IEDTT	-.539*	-.486*	-0.386	-.483*	-.526*	-.490*
IEDTL	-.544*	-.516*	-0.368	-.565*	-.631**	-.546*

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C14. Pearson's correlations between significant episodic memory measures and the number of targets collection across shift types and trials.

	Targets Trial 2 ID shift	Targets Trial 3 ID shift	Targets Trial 1 ED shift	Targets Trial 2 ED shift	Targets Trial 3 ED shift	Targets Trial 2 colour ID	Targets Trial 3 colour ID	Targets Trial 2 shape ID	Targets Trial 3 shape ID
PALTEA	.454*	.487*	.466*	.485*	.457*	0.438	.469*	.446*	.475*
PALTE	-.455*	-.490*	-.456*	-.510*	-.455*	-.447*	-.472*	-0.439	-.478*

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C15. Pearson's correlations between significant episodic memory measures and the number of patch inspections across shift types and trials.

	Patch Trial 3 ID shift	Patch Trial 1 ED shift	Patch Trial 2 ED shift	Patch Trial 3 colour ID	Patch Trial 3 shape ID
PALTEA	.490*	.459*	.463*	.476*	.471*
PALTE	-.489*	-0.438	-.487*	-.486*	-.459*

NB. * indicates significance at *p* < .05, ** indicates significance at *p* < .001.

Table C16. Pearson's correlations between significant episodic memory measures and the percentage of cued inspections across shift types and trials.

	Cued Trial 1 ID shift	Cued Trial 2 ID shift	Cued Trial 3 ID shift	Cued Trial 1 ED shift	Cued Trial 2 ED shift	Cued Trial 3 ED shift	Cued Trial 1 colour ID	Cued Trial 2 colour ID	Cued Trial 3 colour ID	Cued Trial 1 shape ID	Cued Trial 2 shape ID	Cued Trial 3 shape ID
PALTEA	.508*	.451*	.477*	.509*	.485*	.456*	.533*	.478*	.513*	.456*	0.403	0.408
PALTE	-.55*	-.54*	-.57**	-.59**	-.61**	-.57**	-.53*	-.55*	-.57**	-.54*	-.50*	-.53*

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

Table C17. Pearson's correlations between significant episodic memory measures and the percentage of cued inspections and number of patch inspections across shift types and trials.

	Item Inspect Trial 1 ID shift	Item Inspect Trial 1 ED shift	Item Inspect Trial 2 ED shift	Item Inspect Trial 3 ED shift	Item Inspect Trial 1 colour ID	Item Inspect Trial 2 colour ID	Item Inspect Trial 1 shape ID
PALTEA	-0.250	-0.240	-0.198	-0.212	-0.254	-0.262	-0.229
PALTE	.494*	.490*	.445*	.459*	.494*	.473*	.461*

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

Table C18. Pearson's correlations between significant episodic memory measures and the percentage of exploitative behaviour and patch revisits across shift types and trials.

	Exploit Trial 3 ED shift	Exploit Trial 3 shape ID	Revisit Trial 1 ID shift	Revisit Trial 2 ID shift	Revisit Trial 3 ID shift	Revisit Trial 1 colour ID	Revisit Trial 2 colour ID	Revisit Trial 3 colour ID	Revisit Trial 3 shape ID
PALTEA	0.336	0.191	.534*	.490*	.522*	.569**	.526*	.496*	.477*
PALFAMS	0.272	0.217	.518*	0.439	.498*	.536*	.480*	.480*	.446*
PALTE	-.518*	-.449*	-0.419	-0.322	-0.392	-0.426	-0.325	-0.319	-0.430

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

Table C19. Pearson's correlations between significant episodic memory measures and the number of consecutive inspections (runs) across shift types and trials.

	Run Trial 3 ID shift	Run Trial 2 ED shift	Run Trial 3 ED shift	Run Trial 3 shape ID
PALTEA	.457*	0.444	0.437	.447*
PALFAMS	0.381	0.398	0.346	0.383
PALTE	-.465*	-.463*	-.465*	-.458*

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

Table C20. Pearson's correlations between significant reaction time and verbal memory measures and the between-patch organisation, within-patch organisation, and percentage of exploitative behaviour across shift types and trials.

	Between Trial 3 ED shift	Between Trial 2 colour ID	Within Trial 1 ED shift	Within Trial 2 colour ID	Within Trial 3 shape ID	Exploit Trial 3 ID shift	Exploit Trial 2 ED shift	Exploit Trial 3 colour ID
RTIFMMT	0.344	.450*	-0.099	.604**	0.436	0.111	-0.117	0.164
RTIFES	-.487*	0.099	0.225	0.220	-0.146	0.407	0.220	.542*
VPAERTOT	-0.018	0.297	0.166	0.129	.533*	-0.036	-.508*	-0.214
VPAERSDR	-0.239	0.225	.448*	-0.088	0.277	0.064	-0.272	-0.132
VPAMWDSD	0.438	-0.143	-0.246	-0.293	-0.023	-.482*	-0.192	-.576**

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.

Table C21. Pearson's correlations between significant spatial working measures and the between-patch organisation, within-patch organisation, and patch revisits across shift types and trials.

	Between Trial 1 ID shift	Between Trial 2 ID shift	Between Trial 1 shape ID	Within Trial 3 colour ID	Within Trial 1 shape ID	Within Trial 2 shape ID	Revisit Trial 2 ED shift	Revisit Trial 2 colour ID
SWMTE	-.452*	-0.085	-.621**	-0.419	-0.421	-0.435	-0.431	-0.371
SWMBE	.502*	0.080	.643**	.487*	.536*	0.416	.444*	.465*
SWMWE	-0.024	-0.367	-0.068	0.039	-0.044	-.453*	-0.089	-0.164
SWMDE	-0.090	-.471*	-0.131	-0.015	-0.057	-.479*	-0.107	-0.136
SWMS	0.302	0.033	.485*	.532*	0.375	0.175	0.273	0.142

NB. * indicates significance at $p < .05$, ** indicates significance at $p < .001$.