

**The Search for Structure: An Assessment of the Benefits of Using Structured
Patterns in Human Spatial Memory**

**Thesis submitted for the degree of
Doctor of Philosophy**

**Melissa Kirby
Neuroscience, Psychology & Behaviour
University of Leicester
September 2016**

The search for structure: An assessment of the benefits of using structured patterns in human spatial memory

Melissa Kirby

Abstract

The search for food is directly related to individual fitness, with many cognitive competences thought to be the products of foraging pressures faced by our hominid ancestors. Efficient spatial working memory, which often shows a male advantage, is of particular importance to maximise benefits whilst minimising costs during search. An ability to benefit from spatial structure, which reduces memory load, interestingly shows an inverse relationship with taxonomic distance from humans. Eleven experiments highlighted a propensity to detect and benefit from structure during search, and considered the evolutionary and comparative importance of this high-level cognitive skill. In the first study to disentangle the cognitive and energetic motivations of human search, a preference was found for the reduction of cognitive load by exploiting spatial structure, over the reduction of travelling distance. Further findings suggested that data-reducing strategies exploiting spatial structure may be characteristic of primate cognition. The development of an ecologically valid task based on primate foraging situations, showed a strong tendency in humans to detect and use temporal structure. When adapted for the assessment of older adults and children, older adults were less efficient foragers and showed a deficit in their ability to detect temporal structure, whilst children appeared to show a developmental trend in foraging efficiency. This task afforded a direct comparison between humans and a non-human primate species, which suggested that baboons did not exploit temporal structure during search. The finding that humans show a tendency to promote cognitive over energetic economy, and a strong proficiency to benefit from structure in stimuli, has implications for the evolution of this competency, the role of the dorsolateral prefrontal cortex, and sex differences in spatial memory. These findings have implications for theories which suggest that diet and the requirements of foraging played an important role in the high-level cognition humans possess today.

Acknowledgements

First and foremost, I would like to acknowledge Dr Carlo De Lillo. Thank you for all your help from day one. I am extremely grateful for all of your comments, advice, help, and support with everything from preparing my initial thesis proposal, to listening to presentations, to reading endless drafts. Your guidance over the past four years has been invaluable!

I would also like to acknowledge and thank Kevin McCracken and Jodil Davis for their technical and programming expertise, and Drs Jose Prados and Phil Duke for all the feedback and comments at my yearly reviews. I am also grateful to Dr Joel Fagot for introducing me to the baboons, and for implementing our task which I am grateful to have been able to include in this body of work.

I would also like to extend my gratitude to all the participants who took the time to help with this research, to everyone I have met at the university and at conferences who have offered helpful comments and advice, and to my family who still aren't sure what I do but have always supported me nonetheless.

Finally, thank you Danny for keeping me comfortable during endless days and nights of collecting, analysing, and reporting data. And to our Teddy, for keeping me particularly uncomfortable in the best of ways.

Declaration

The work presented and analysed was carried out by myself and has not previously been submitted for another degree. Experiment 10 was run in Aix, France by Dr Joel Fagot, yet the design, procedure, analyses, and interpretation was carried out by the author. Experiment 1 has also been published in two capacities as part of two papers:

De Lillo, C., Kirby, M. & Poole, D. (2016). Spatio-temporal structure, path characteristics and perceptual grouping in immediate serial spatial recall. *Frontiers in Psychology*, doi: 10.3389/fpsyg.2016.01686.

De Lillo, C., Kirby, M. & James, F. C. (2013). Spatial working memory in immersive virtual reality foraging: Path organization, traveling distance and search efficiency in humans (*Homo sapiens*). *American Journal of Primatology*, 9999, 1-11.

Table of Contents

Table of Figures	9
List of Abbreviations.....	13
Chapter 1: General Introduction	14
1.1 An Evolutionary Perspective	14
1.2 The Comparative Method.....	16
1.3 Primate Diet and Foraging Ecology	17
1.4 Sex differences in Spatial Memory	19
1.5 Spatial Working Memory	21
1.6 Experimental Aims and Methods	26
1.7 The Search for Structure.....	33
Chapter 2: The Role of Distance Travelled in Search.....	34
2.1 Introduction.....	34
2.1.1 Principled and Organised Search Strategies.....	34
2.1.2 Immediate Serial Spatial Recall	35
2.1.3 Path Length	36
2.2 Experiment 1	37
2.2.1 Methods.....	37
2.2.2 Results.....	42
2.3 Discussion	45
2.3.1 Importance of Cognitive Economy	46
2.3.2 Comparative Differences	47
2.3.3 A Male Advantage.....	48
2.3.4 Conclusions.....	48
Chapter 3: Chunking within Spatial Working Memory	50
3.1 Introduction.....	50
3.1.1 Chunking to Reduce Cognitive Load	50
3.1.2 Reducing Cognitive Load or Optimal Foraging?.....	51
3.1.3 Spatial Search Strategies	52
3.2 Experiment 2.....	53
3.2.1 Methods.....	53
3.2.2 Results.....	57

3.2.3 Discussion	61
3.3 Experiment 3	62
3.3.1 Methods.....	62
3.3.2 Results	63
3.3.3 Discussion	67
3.4 Experiment 4.....	68
3.4.1 Methods.....	68
3.4.2 Results.....	71
3.4.3 Discussion	72
3.5 General Discussion	73
3.5.1 Differences in Foraging Strategies	73
3.5.2 Spatial Structure in Search	74
3.5.3 Object Location Memory.....	74
3.5.4 Conclusions.....	75
Chapter 4: Detection of Temporal Structure in Search	76
4.1 Introduction.....	76
4.1.1 Evolutionary Pressures	76
4.1.2 Temporal Structure in Foraging	77
4.1.3 Mental Representations or Associative Learning?.....	77
4.2 Experiment 5.....	79
4.2.1 Methods.....	79
4.2.2 Results.....	81
4.2.3 Discussion	85
4.3 Experiment 6	85
4.3.1 Methods.....	85
4.3.2 Results.....	87
4.3.3 Discussion	92
4.4 Experiment 7	93
4.4.1 Methods.....	93
4.4.2 Results.....	94
4.4.3 Discussion	101
4.5 General Discussion	102
4.5.1 Detection of Structure as an Adaptation.....	103
4.5.2 Acquisition of Spatial Information or Overshadowing?	103
4.5.3 Sex Differences in Foraging	104
4.5.4 Conclusions.....	105

Chapter 5: Effects of Ageing in the Detection of Temporal Structure	106
5.1 Introduction.....	106
5.1.1 A Cognitive Decline	106
5.1.2 Importance of Ecologically Valid Tasks	107
5.1.3 Age-Related Changes in Search	108
5.2 Experiment 8.....	108
5.2.1 Methods.....	109
5.2.2 Results.....	112
5.3 Discussion	118
5.3.1 Detection of Structure.....	118
5.3.2 Foraging Efficiency	119
5.3.3 Use of Ecological Tasks	120
5.3.4 Conclusions.....	120
 Chapter 6: Developmental Changes in Foraging Efficiency	 122
6.1 Introduction.....	122
6.1.1 Evolutionary Developmental Psychology	122
6.1.2 Cognitive Development.....	122
6.1.3 Development of Search Strategies	123
6.2 Experiment 9.....	124
6.2.1 Methods.....	124
6.2.2 Results.....	125
6.3 Discussion	135
6.3.1 A Developmental Trend in Structure Detection?.....	135
6.3.2 Development of Foraging Efficiency	136
6.3.3 Sex Differences in Children’s Search	137
6.3.4 Conclusions.....	137
 Chapter 7: Foraging efficiency and Detection of Structure in Baboons, <i>Papio papio</i> . 139	
7.1 Introduction.....	139
7.1.1 Baboon Lineage and Ecology.....	139
7.1.2 Baboon Cognition	140
7.1.3 Foraging Efficiency of Baboons and Humans	140
7.2 Experiment 10.....	141
7.2.1 Methods.....	141
7.2.2 Results.....	144
7.2.3 Discussion	154

7.3 Experiment 11	155
7.3.1 Methods.....	155
7.3.2 Results.....	156
7.3.3 Discussion	167
7.4 General Discussion	167
7.4.1 Baboon Cognition	168
7.4.2 Detection of Temporal Structure	168
7.4.3 Conclusions.....	169
Chapter 8: General Discussion	170
8.1 Detecting Structure	170
8.2 Experimental Chapters.....	170
8.3 Sex Differences	180
8.4 Value of VR and Touchscreen Methodologies	182
8.5 Final Conclusions	185
Appendix.....	188
Appendix A: Ethical Approval for the VR Experiments	188
Appendix B: Consent Form for Experiment 1, Chapter 2	190
Appendix C: Consent Form for Experiments 2, 3 and 4, Chapter 3	191
Appendix D: Consent Form for Experiments 5, 6, and 7, Chapter 4.....	192
Appendix E: Ethical Approval to Assess Ageing in Young and Older Adults	193
Appendix F: Permission to use the MoCA Questionnaire	195
Appendix G: Consent Form for Older Adults in Experiment 8, Chapter 5	196
Appendix H: Consent Form for Young Adults in Experiment 8, Chapter 5	198
Appendix I: Ethical Approval to Assess Developmental Cognition in Children	199
Appendix J: Consent Form Sent to Children’s Parents in Experiment 9, Chapter 6.....	202
Appendix K: Consent Form for Experiment 11, Chapter 7	205
References.....	206

Table of Figures

Chapter 2

Figure 2. 1 Plan view, configurations and path length sizes for Exp 1.....	39
Figure 2. 2 The eight conditions presented illustrating the clustered and matrix arrays.	41
Figure 2. 3 The mean number of correct responses made within each condition	42
Figure 2. 4 The mean number of correct responses made by each sex within each condition.....	43
Figure 2. 5 The mean reaction time (seconds) taken to select consecutive items within each condition.....	44
Figure 2. 6 The mean reaction time (seconds) taken by males and females in each condition.....	45

Chapter 3

Figure 3. 1 VR environment for Exp 2, 3, and 4.....	54
Figure 3. 2 Configuration of food types and locations within the array.	55
Figure 3. 3 Plan view representations of the food locations in the foraging space.....	56
Figure 3. 4 Exp 2, the mean number of selections to completion of a trial.....	57
Figure 3. 5 Exp 2, the mean number of alternations made between food types.....	58
Figure 3. 6 The locations of the rewarded poles in the matrix.	61
Figure 3. 7 Exp 3, the mean number of selections to completion of a trial.	63
Figure 3. 8 Exp 3, the mean number of alternations made between food types.....	65
Figure 3. 9 The mean number of selections made to completion of a trial comparing Experiments 2 and 3	67
Figure 3. 10 Radial maze in the VR environment.....	70
Figure 3. 11 Exp 4, the mean number of selections and alternations	71

Chapter 4

Figure 4. 1 The virtual room with landmarks and the pole array for Exp 5, 6, and 7. ...	80
Figure 4. 2 Exp 5, the foraging efficiency measures.....	82
Figure 4. 3 Exp 5, the proportion of correct first choices made.	84
Figure 4. 4 Exp 6, the foraging efficiency measures.....	88
Figure 4. 5 Exp 6, the proportion of correct first choices made in the single alternation.....	90

Figure 4. 6 Exp 6, the proportion of correct first choices made in the double alternation.....	91
Figure 4. 7 Exp 7, the foraging efficiency measures.....	95
Figure 4. 8 Exp 7, the proportion of correct locations and never rewarded locations selected within the first 12 choices	99
 Chapter 5	
Figure 5. 1 The array of locations presented on the touchscreen for Exp 8 (and 9).....	110
Figure 5. 2 The mean number of selections made to completion of a trial for each age group	112
Figure 5. 3 The mean number of never rewarded locations selected by each age group	113
Figure 5. 4 The mean number of revisits made by each age group	114
Figure 5. 5 The proportion of correct first choices made in the single alternation by each age group.....	116
Figure 5. 6 The proportion of correct first choices made in the double alternation by each age group.....	117
 Chapter 6	
Figure 6. 1 The number of trials completed by children of each age for Exp 9.....	126
Figure 6. 2 The mean number of selections to the completion of a trial across 8 trials for each age group.....	127
Figure 6. 3 The mean number of selections to the completion of a trial across 20 trials for each age group	128
Figure 6. 4 The mean number of never rewarded locations selected across 8 trials for each age group.....	129
Figure 6. 5 The mean number of never rewarded locations selected across 20 trials for each age group.....	130
Figure 6. 6 The mean number of revisits made across 8 trials for each age group.	131
Figure 6. 7 The mean number of revisits made across 8 trials for each sex and each age group.	133
Figure 6. 8 The mean number of revisits made across 20 trials by each age group.....	132

Chapter 7

Figure 7. 1 The incremental training procedure for Exp 10	143
Figure 7. 2 Exp 10, the mean number of selections to the completion of a trial in the training trials	144
Figure 7. 3 Exp 10, the mean number of selections to the completion of a trial made by each subject in the 25-location array.....	145
Figure 7. 4 Exp 10, the mean number of never rewarded locations selected in the training trials	146
Figure 7. 5 Exp 10, the mean number of never rewarded locations selected by each subject in the 25-location array.....	147
Figure 7. 6 Exp 10, the mean number of revisits made in the training trials	148
Figure 7. 7 Exp 10, the mean number of revisits made by each subject in the 25-location array	149
Figure 7. 8 Exp 10, the proportion of correct first choices made in the single alternation in the training trials.....	150
Figure 7. 9 Exp 10, the proportion of correct first choices made in the single alternation by each subject in the 25-location array.....	151
Figure 7. 10 Exp 10, the proportion of correct first choices made in the double alternation in the training trials	152
Figure 7. 11 Exp 10, the proportion of correct first choices made in the double alternation by each subject in the 25-location array	153
Figure 7. 12 Exp 11, the mean number of selections to completion of a trial for humans	156
Figure 7. 13 Exp 11, the mean number of selections made by humans and baboons. .	157
Figure 7. 14 Exp 11, the mean number of never rewarded locations selected by humans	159
Figure 7. 15 Exp 11, the mean number of never rewarded locations selected by humans and baboons.....	160
Figure 7. 16 Exp 11, the mean number of revisits made by humans.....	161
Figure 7. 17 Exp 11, the mean number of revisits made by humans and baboons	162
Figure 7. 18 Exp 11, the proportion of correct first choices made in the single alternation by humans.....	163
Figure 7. 19 Exp 11, the proportion of correct first choices made in the single alternation by humans and baboons	164

Figure 7. 20 Exp 11, the proportion of correct first choices made in the double alternation by humans.....	165
Figure 7. 21 Exp 11, the proportion of correct first choices made in the double alternation by humans and baboons	166

List of Abbreviations

BW	Blue/White Double Alternation
CC	Chunk Compromised Condition
CM	Chunk Maintained Condition
DA	Double Alternation
DLPFC	Dorsolateral Prefrontal Cortex
EEA	Environments of Evolutionary Adaptedness
HMD	Head Mounted Display
ISSR	Immediate Serial Spatial Recall
LTM	Long Term Memory
ML	Mixed Locations Condition
PG	Purple/Green Double Alternation
SA	Single Alternation
VR	Virtual Reality
WM	Working Memory

Chapter 1: General Introduction

1.1 An Evolutionary Perspective

The necessity of finding food, mates, and resources is an important evolutionary challenge that all organisms face on a daily basis. As such, an understanding of spatial relations enables individuals to locate these resources, and to avoid visits to unprofitable or unfavourable locations. The search for food in particular is directly associated with individual fitness, and the majority of, if not all, animals spend a large proportion of their time involved in the search and procurement of food, more so than in any other activity (Rozin, 1996). A meta-analysis of primate behaviour indicated that the majority of innovative behaviours recorded were observed within a foraging context (Reader & Laland, 2001), highlighting the importance of foraging situations in the assessment of cognitive ability, and supporting ecological explanations of primate intelligence (Reader & Laland, 2002). Today, modern humans have largely avoided the need to hunt, capture, and forage for food, and can simply fulfil their daily nutritional requirements with a trip to the supermarket. However, a long period of evolutionary history saw ancestral humans and other hominids alike faced with the task of finding enough food daily. Among hunter-gatherer tribes today, which allow a glimpse of ancestral societies, a failure to provide food can lead to a loss of status (Hill & Hurtado, 1996) and may also be reason for wives to divorce their husbands (Betzig, 1989). The repercussions of an inability to find sufficient food can have a significant impact on all aspects of an individual's life.

Due to the importance and necessity of successful foraging behaviour, many adaptations that we see in humans are thought to have evolved from the selection pressures required for this during the EEA (environments of evolutionary adaptedness). Napier (1972) notes that primates evolved specialised adaptations for living arboreally, including long fingers and nails instead of claws to aid in the manipulation of objects and to assess the ripeness of foods. Primates evolved forward-facing eyes and lower snouts for clear stereoscopic vision, and colour vision to aid in the recognition of edible fruits and leaves, with an expansion of the occipital region of the brain occurring as a result of a reliance on visual cues (Napier, 1972; Price, 1996). After a shift to a terrestrial way of life, hominins evolved longer legs (Napier, 1976) and specialised foot bones (Harcourt-Smith & Aiello, 2004) to exploit bipedal behaviours, whilst the diets of early hominins expanded and became increasingly more varied to exploit a variety of

habitats (Teaford & Ungar, 2000). Sexual dimorphism is also seen in ancestral hominins and humans today, which is thought to be due to differences in foraging behaviour between the sexes, and the differing requirements for males and females. Males often possess a larger body size and greater strength than females (Fruyer & Wolpoff, 1985), with fossil samples from the Paleolithic period indicating that early hominins also showed sexual dimorphism in the femur and tibia (Ruff, 1987). The physical adaptations of males can be plausibly explained by their role of hunter which favoured large size and strength to capture prey (Buss, 2009). In addition to the physical adaptations that evolved from the selection pressures associated with finding food, the use of sophisticated cognitive skills were also necessary for successful search.

Whilst cognitive ability can be difficult to infer from ancestral species, fossil records show brain size increases along the hominin lineage (Price, 1996; Parker & McKinney, 1999), and does so in terms of relative brain size when compared to body mass (Kappelman, 1996). Cognitive abilities are viewed as adaptations rather than side-effects of a larger brain, primarily due to the great expense an enlarged brain poses (Parker & McKinney, 1999), therefore the fitness benefits of such competences must outweigh the expensive cost of a larger brain. The frontal lobe in particular appears to play an important role in primate intelligence (Dunbar & Shultz, 2007), and ecological hypotheses of primate intelligence further suggest that an enlarged brain and sophisticated cognitive skills emerged as a result of foraging behaviour (Milton, 1981a; 1993; see Fleagle, 2013). Sex differences in terms of spatial ability within a foraging context have also been observed in human (see Silverman & Eals, 1992; Silverman, Choi & Peters, 2007), and non-human species (Gaulin & Fitzgerald, 1986; 1989; Gresack & Frick, 2003). The extent to which foraging has shaped our cognitive ability as humans, and has shaped male and female cognition appears to be an important area of research. Such as a preference for sugar persists in humans and other great apes today due to an abundance of foliage and a scarcity of caloric fruits during the EEA (Breslin, 2013), cognitive relics of such evolutionary pressures can also be seen.

There are difficulties associated with testing cognition within an evolutionary context due to the indirect effect cognitive processes have on individual fitness (Shettleworth, 2010), however, it is undoubtedly important to test cognitive competences under conditions which approximate those where these skills may have evolved. Moreover, the assessment of specific cognitive skills to determine which are uniquely human, and to determine where differences and similarities lie across species,

must be investigated comparatively to consider where these skills evolved throughout evolutionary history, and more specifically, the primate lineage.

1.2 The Comparative Method

Darwin, in the *Descent of Man* (1871), declared that the difference between man and animals is better thought of in terms of degree, rather than absolutes. He was one of the first to consider the behaviour of animals in relation to the understanding of the human mind, and where and when human behaviours may have evolved (see Boakes, 2008). It was this understanding of behaviour and intelligence that sparked the development of the comparative method within psychology. Yerkes (1913) attempted to define comparative psychology as the study of any organism's consciousness and behaviour by using the method of comparison. He believed that to fully understand human behaviour, we must also understand behaviour in other species, including those which are taxonomically close and distant to determine where specific human traits and abilities may have originated (Yerkes 1914). Whilst he acknowledged the benefits of naturalistic studies, he recognised the importance of implementing the experimental method to assess the same behaviours, to complement observational findings (Yerkes, 1914). Yerkes considered the study of non-human primates to be of particular importance as a method to better understand human behaviour and cognition, because of their close taxonomic relatedness with man, which was a sentiment echoed by Kohler. Kohler (1925a; 1925b) carried out the first thorough research program with apes, and saw that chimpanzees showed evidence of insight when completing novel tasks. Chimpanzees made errors that appeared to show a level of understanding of the situation (Boakes, 2008). From this, he concluded that their behaviour could not be explained as purely trial and error. The work of Yerkes and Kohler was in contrast to the traditional behaviourist views of Watson (1903) and Thorndike (1898) who advocated stimulus-response learning, and who did not place higher intelligence in apes. Darwin, Yerkes and Kohler can be considered pioneers of comparative psychology who understood that to fully explore human intelligence, it must be considered within an evolutionary context and therefore across species.

Today, the comparative method is widespread across the different domains of scientific research, and it is widely accepted that the study of cognitive abilities of non-human species at differing taxonomic distance from humans can provide important insights into the cognitive abilities of common ancestors throughout our evolution. The

methods used to study different species however, must be meaningful and relevant to all species being tested in order to accurately assess mental capabilities (see De Lillo, 2012 for a discussion). However, more recently, it has been noted that whilst comparative researchers may focus on the high-level skills animals show akin to humans, we must acknowledge the tendencies in humans to behave in a similar manner to animals (Shettleworth, 2010). For example, humans have been found to show unconscious responses to cues; men are attracted to potential mates on the basis of cues to fitness such as waist-to-hip ratio in women (Singh, Dixson, Jessop, Morgan & Dixson, 2010), in a similar manner as female birds choose mates with brighter plumage (Hamilton & Zuk, 1982). Whilst the similarities between humans and other species must be investigated, we must also consider the dissimilarities (Premack, 2007). It is equally important to consider the extent to which the cognitive abilities observed in humans are unique to us, are high-level skills present in other non-human species, or are behaviours that are instinctual and shared with other animals, to fully understand human cognition.

1.3 Primate Diet and Foraging Ecology

Following the views of Yerkes (1914) and Kohler (1925), comparisons with non-human primates allow us to consider when specific cognitive skills may have evolved, and advocates the investigation of these skills within evolutionarily-relevant contexts. We can only infer what ancestral situations and conditions were like for our hominin ancestors from fossil records and the conditions experienced by extant species today. Before life on a savannah, early humans transitioned from forest environments and had already acquired many adaptations to a forest habitat (Milton, 1981a). Supporting this notion, a relatively recent discovery of fossil remains found evidence for the earliest hominin ancestor, *Ardipithecus ramidus* (White et al. 2009), who appeared to have inhabited a woodland environment (Louchart et al. 2009). Their discovery indicated that *Ar. ramidus* was a terrestrial species, combining bipedalism with arboreal capabilities, with a dental examination showing no strong evidence of frugivory, folivory or carnivory, suggesting an omnivorous diet. White et al. (2009) stated that this early species predated *Australopithecus afarensis*, and appeared to be the first hominin species found since our last common ancestor with chimpanzees, helping to define the evolutionary pathway humans undertook. Their findings largely suggested however that the last common ancestor hominins shared with chimpanzees was considerably different from existing ape species today. Despite this, the ecological

conditions our earliest hominin ancestor faced appears to be similar to the habitats of extant chimpanzees, and so it is plausible to assume that they faced similar evolutionary pressures. Whilst the diet of chimpanzees is primarily frugivorous, humans also share a preference for sugars and fruits (Breslin, 2013), suggesting that fruits played an important part in human evolution. The search for ripe fruits within a wooded environment may not only result in a taste preference, but may also promote enhanced cognition due to the sophisticated cognitive skills required to find these ephemeral resources.

Fruit is a particularly high energy food source, and a frugivorous dietary strategy has significant advantages for those who can exploit it (Milton, 2003). In comparison with a folivorous diet, a frugivorous diet allows a lesser amount of fruit to be consumed than leaves for an equal amount of energy. However, within a tropical forest, the availability of fruit fluctuates across seasons (van Schaik, Terborgh & Wright, 1993), and for species with a frugivorous-based diet to efficiently forage, sophisticated cognitive skills are required to detect these often complex patterns (Milton, 1981a). Milton (1981a; 1993) suggested that it was this evolutionary pressure to efficiently forage on resources which differed in temporal availability and were patchily distributed that triggered the emergence of larger brains and enhanced cognition in primates. Across mammalian species, differences can be seen between frugivorous species who forage primarily on fruit, and folivorous species whose primary diet consists of leaves. Frugivorous, and omnivorous, species show a larger comparative brain size than folivores or non-fruit eating species (Harvey, Clutton-Brock & Mace, 1980; Jones & MacLarnon, 2004) and show differences in digestive morphology (Chivers & Hladik, 1980; Milton, 1981b), suggesting that diet and foraging requirements led to cognitive and physical adaptations. Milton (1981b) studied the food and digestive strategies of the frugivorous black-handed spider monkey (*Ateles geoffroyi*) and folivorous mantled howler monkeys (*Alouatta palliate*) - two species which are very similar in terms of size, social groups, and arboreality, though differ substantially in diet – who were found to show very different digestive strategies. The area of the large intestine was found to be smaller in spider monkeys in comparison to howler monkeys who require more time to process foliage. These findings by Milton (1981b), in accordance with the finding that the former have a larger brain size than the latter, suggest an inverse relationship between intestine area and comparative brain size in frugivorous and folivorous primates. The physical adaptations species show due to their diet, suggests that

cognitive adaptations may also differ between frugivores and folivores. Cognitive differences have been observed between primate species where foraging ecology differs indicating that foraging and diet is a significant selective pressure (Stevens, Hallinan & Hauser, 2005). The benefits of maintaining an expensive and enlarged brain must be considerable (Milton, 1981a), and may be expressed in enhanced cognitive abilities, particularly relating to spatial relations and food distribution.

We can infer from fossil discoveries that early hominins shared a similar ecological environment as extant primates, therefore the assessment of cognitive abilities derived from the requirements primates face during foraging would be beneficial. It has been suggested that to accurately assess cognitive competences, methodologies should be ecologically-valid and consider naturalistic situations (Phillips, Kliegel & Martin, 2006; Burgess et al. 2006). However, the situations humans experience daily in order to find food are vastly different to the environments in which our cognition evolved. It can therefore be suggested that to more accurately assess human cognition relating to spatial memory, it would be important to assess humans in situations tapping the requirements of search within foraging situations ancestral humans would have experienced.

1.4 Sex differences in Spatial Memory

An additional factor that is thought to influence spatial cognition is sex. The literature surrounding spatial memory ability often reports sex differences in the performance of both humans (Silverman & Eals, 1992; Silverman, Choi & Peters, 2007; Moffat, Hampson & Hatzipantelis, 1998) and non-human species (Gaulin & Fitzgerald, 1986; 1989; Jacobs, Gaulin, Sherry & Hoffman, 1990; Gresack & Frick, 2003), which are thought to have evolved when evolutionary pressures contributed to male and female fitness in different ways (McBurney, Gaulin, Devineni & Adams, 1997). Typically, studies conclude that males outperform females in spatial tasks, though when different aspects of spatial memory tasks are considered there are certain tasks in which females surpass males. Two evolutionary theories which attempt to explain this sex difference in humans are the *hunter-gatherer* hypothesis (Silverman & Eals, 1992), and the *twofold selection process* (Ecuyer-Dab & Robert, 2004).

To explain human sex differences in spatial cognition, Silverman and Eals (1992) proposed the *hunter-gatherer* hypothesis based on the division of labour experienced by humans throughout evolutionary history. Bone fragments from the

Upper and Middle Paleolithic periods have shown that the human femur and tibia reveal sexual dimorphism, suggesting that males were better adapted than females to activities needing strength and mobility (Ruff, 1987). Hunting appears to provide a likely explanation for human sexual dimorphism, relics of which are still seen today (Tooby & DeVore, 1987). Modern hunter-gatherer societies show this division where hunting is primarily undertaken by men, and the women gather (Buss, 2009). Silverman and Eals' (1992) hypothesis proposed that due to these roles during the EEA, specific cognitive adaptations as well as physical adaptations necessary for pursuing prey successfully across large-scale environments would have been selected for in males, whereas selection pressures for females would relate to successful gathering in smaller spaces. In support of this, males often outperform females on tasks of mental rotation (Silverman & Eals, 1992; Silverman, Choi & Peters, 2007; McBurney et al. 1997; Astur, Tropp, Sava, Constable & Markus, 2004) and route learning (Lawton, 1994; Moffat et al. 1998), both of which require an ability to orient the self. Consistent with the theory that males evolved specialised adaptations to hunting and tracking prey through large-scale spaces, men outperform women in measures of dynamic spatial ability (Law, Pellegrino & Hunt, 1993), and have been found to place a heavier reliance on geographical and Euclidean information when learning a route, whilst women prefer a smaller-scale, landmark strategy (Lawton, 1994; Saucier et al. 2002). Way-finding through a wooded area was also found to be superior in males and was specifically related to mental rotation ability rather than general intelligence, suggesting that space constancy is the fundamental mechanism that has evolved underlying these specific spatial abilities (Silverman et al. 2000). Females on the other hand show spatial adaptations to a gathering lifestyle. Women show a superiority in object location tasks (Silverman et al. 2007; Levy, Astur & Frick, 2005; Voyer, Postma, Brake & Imperato-McGinley, 2007), show superior plant knowledge (Voeks, 2007) and are able to locate plants and foods more accurately than men (Laiacona, Barbarotto & Capianni, 2006; New, Krasnow, Truxaw & Gaulin, 2007; Pacheco-Cobos, Rosetti, Cuatianquiz & Hudson, 2010).

Ecuyer-Dab and Robert's (2004) *twofold selection process* offers the explanation that a male's spatial cognitive abilities would have been shaped by inter-male competition and sexual selection pressures, whilst a females spatial abilities are due to mothering constraints. In accordance with the hunter-gatherer theory, hunting pressures can be considered a source of male competition, selecting for superior navigational abilities in males which are sexually selected for by females (Geary, 1995).

However, unlike Silverman and Eals' (1992) theory, this account applies to both humans and other mammal species. By competing with one another for access to mates, through hunting or by extending their home range, males are able to increase their chances of successful mating (Ecuyer-Dab & Robert, 2004). Many studies, as described above, provide support for the idea that male hunting in the EEA has resulted in a Euclidean strategy of navigation through large-scale, unfamiliar spaces. Females however, would not have faced inter-sex competition to the same extent as males and so did not face this evolutionary problem. Being the primary caregiver in the majority of mammal species, females were confronted with the challenge of keeping offspring alive, resulting in selection for a strong concern for survival of both offspring and self (Ecuyer-Dab & Robert, 2004), a propensity much stronger in females than males (Campbell, 1999). Thus, this theory proposed that as females are constrained and slowed down by pregnancy and young offspring, spatial navigation based on a low-risk, proximal, landmark strategy to facilitate memory for locations of food resources and nearby hiding places in case of predators, would be more efficacious for females than following a Euclidean strategy where the likelihood of making costly mistakes is higher. Studies indicating that males outperform females on tasks of way-finding, route learning, and use of Euclidean directions support this notion that females faced selective pressures for a lower-risk strategy. Both evolutionary hypotheses appear to explain the sex differences observed in spatial tasks with humans, though the extent to which sex differences occur in spatial tasks which exploit the structure of search environments remains an aspect which is yet untested.

1.5 Spatial Working Memory

It can be inferred from fossil records and extant primate studies that feeding ecology plays an important role in the cognitive adaptations we possess today. To forage efficiently, a number of cognitive competences are required. An ability to learn where and when foods will be available is necessary during search for fruit, in addition to an efficient long-term memory (LTM) capacity to learn which locations are profitable and which never yield fruit. During a foraging bout, spatial working memory (WM) is also important to temporarily store information about spatial locations to support other cognitive functions involved in search, and to avoid the occurrence of revisiting previously depleted locations (see Baddeley, 2003; Baddeley & Hitch, 1974). WM capacity is thought to be associated with higher cognitive skills, and has been suggested

to be an important trigger of enhanced human cognition (Coolidge & Wynn, 2005; Balter, 2010). Enhanced WM ability is considered to be relatively recently acquired within the hominid lineage (Coolidge & Wynn, 2005) though other findings suggest that WM can be traced further back than initially thought (Read, 2008). Due to the non-verbal nature of spatial WM, it is a particularly valuable method to assess cognition across species to provide insights into what is characteristic of human and non-human cognition.

Visual search and foraging. Typically, visual search tasks are used to assess human foraging cognition. For example, Klein and MacInnes (1999) proposed that inhibition of return is an important mechanism in visual search and considered it a foraging facilitator, whilst Wolfe (2013) used a berry-picking visual search task to infer foraging behaviour. However, the question of whether visual search tasks presented in plan-view can accurately assess the competences required during foraging was considered by Gilchrist, North and Hood (2001) in a large-scale foraging task. Gilchrist et al. used arrays of film canisters where participants were asked to find the hidden marble by shaking each canister to check for the presence of the target. In accordance with typical feature-absent visual search tasks where the target and distractors appear similar (Palmer, 1995), Gilchrist et al. found that the time taken to find targets showed a linear increase with the array size. Smith, Hood and Gilchrist (2008) further provided support for this, indicating that in a large-scale space implementing a typical visual search paradigm, feature-absent trials also became more difficult as set-size increased. Additionally, a single green light took longer to find amongst locations showing both green and red lights (feature-absent), compared to the search for a location with both lights lit amongst only green lights (feature-present). These findings suggest that important characteristics of visual search can also pertain to large-scale search where body movement is required through the search space, and may in fact be a useful alternative. However, large-scale foraging tasks often show differences in the number of revisits made to previously searched locations. Gilchrist et al. found that revisits were relatively rare, which was also found by Smith et al., as in their foraging condition - where the target could not be seen unless the location was checked - the majority of participants made no revisits at all. In comparison, Gilchrist and Harvey's (2000) results suggested that refixation on targets in a visual search task is common, and that memory for previously visited locations appears not to be a strong mechanism. Gilchrist et al.

proposed that fewer revisits in a large-scale space could be a result of a larger cost involved in revisiting a previously checked location, which would involve walking to the location again, and is physically more demanding than refixations in visual search. Previous research acknowledges that various types of memory are involved in visual search (Gilchrist et al. 2001; Gibson, Li, Skow, Brown & Cooke, 2000) and foraging in large-scale search (Gilchrist et al. 2001; Smith et al. 2008), and walking through a search space appears to require an increase in WM efficiency to avoid costly revisits.

Simplicity and structure in search. A particular feature of human cognition that appears to aid WM and reduce error is the ability to detect patterns and structure in stimuli. This propensity to detect and process patterns in the world around us is thought to be due to the expansion of the cerebral cortex, and is also often seen in non-human primates (Mattson, 2014). This ability is thought to be an adaptation which may persist if it results in a large fitness benefit to the individual (Foster & Kokko, 2009). The tendency to find patterns has also been considered in relation to simplicity, and has been considered a fundamental cognitive skill in humans (Chater, 1996; 1999; Pothos & Chater, 2002; Chater & Vitanyi, 2003). Chater (1999) proposed that humans have a propensity to search for the simplest pattern or explanation of a situation across a range of psychological domains, including perception and memory, to predict and understand the world. To support this notion of search for simplicity, humans spontaneously organise stimuli into categories based on the simplest choice (Pothos & Chater, 2002), show a preference for simple and easy to understand options when faced with a number of choices (Iyengar & Kamenica, 2007), and tend to find the simplest pathway through arrays of locations (De Lillo, 2012). The simplicity of a pattern can be defined and measured in terms of the length of instruction or the time taken to describe it (Chater, 1999), and was measured in a task by De Lillo (2012). Students were asked to describe pathways that were either made by children, capuchin monkeys, or rats. Participants required significantly fewer words to describe the pathways made by children than by capuchin monkeys, and in turn used less words to describe the route taken by monkeys than by rats, indicating that children were making comparatively more undemanding routes through the search space than the two animal species. This also highlights differences between primates and rodents and implies that an ability to use the simplest route increases as taxonomic distance from humans decreases.

Assessing the search strategies primates deployed in a foraging task, De Lillo, Visalberghi and Aversano (1997) found that capuchin monkeys were efficient at searching arrays of nine baited containers arranged as three clusters, and spontaneously searched each cluster in turn. Capuchin monkeys appeared to hierarchically search the array of clusters by searching one cluster before moving to the next, to exhaustively search the environment, and in turn reducing memory demands. In a later study, De Lillo, Aversano, Tuci and Visalberghi (1998) found that capuchin monkeys also demonstrated organised search when searching containers arranged as a matrix, line, cross or circle, for instance by searching from one end of a line arrangement to the other. An ability to deploy highly organised and principled search strategies appears to be related to taxonomic distance to humans, as mice (Valsecchi, Bartolomucci, Aversano & Visalberghi, 2000) and rats (Foti, Spirito, Mandolesi, Aversano & Petrosini, 2007) did not show principled search to the same extent as monkeys when faced with the same configurations of baited locations. Interestingly, when tree shrews were assessed in this task, Bartolomucci, de Biurrun and Fuchs (2001) observed some evidence of hierarchical clustering in a similar manner to capuchin monkeys. This demonstration of principled search was to a lesser degree than capuchin monkeys yet more principled than rodents. As tree shrews are closely related to primates (Sargis, 2004), this further supports the notion that an ability to benefit from structure is inversely related to phylogenetic distance from humans. Humans have also been found to exploit the spatial structure of arrays, when placed within similar conditions in a virtual environment (De Lillo & James, 2012). Participants spontaneously searched locations arranged as spatial clusters or a matrix, by exhaustively searching each cluster, row or column in turn before moving to the next. However, as these tasks observed free search behaviour within the arrays, a causal relationship between the path taken and performance cannot be inferred. The use of immediate serial spatial recall (ISSR) tasks allows researchers to experimentally assess this relationship.

ISSR tasks are used to experimentally manipulate the paths taken through an array of locations to assess recall accuracy. Traditionally, the Corsi block-tapping task has been used which requires participants to view the experimenter tapping out a sequence across a number of irregularly arranged blocks, before being asked to recall the sequence by tapping the blocks in the same order (Farrell Pagulayan, Busch, Medina, Bartok & Krikorian, 2006). Within a Corsi-type task, Bor, Duncan, Wiseman and Owen (2003) manipulated the structure of sequences to-be-recalled through an on-

screen array of blocks arranged as a matrix. Sequences were more accurately recalled when subsequent locations in the sequence were in the same row, column, or diagonal line, compared to when sequences regularly switched rows and columns within the matrix. Using ISSR within a patchy environment where locations to-be-searched were arranged as clusters, humans were found to recall sequences more accurately when they were segregated by clusters, and accuracy decreased when sequences regularly switched groups of locations (De Lillo, 2004; De Lillo & Lesk, 2010). In a computerised Corsi task with baboons (*Papio papio*), subjects did not appear to benefit from sequences which exploited the structure of the array to the same extent as humans (Fagot & De Lillo, 2011). Sequences which follow the structure of the search space and afford hierarchical organisation have the property of simplifying the cognitive demands of a recall task (De Lillo, 2012), and this difference in ability to exploit spatial structure in ISSR task performance between baboons and humans may reflect differences in the prefrontal cortex. Bor et al.'s (2003) fMRI data indicated an increased activation of the dorsolateral prefrontal cortex (DLPFC) in humans when they experienced structured sequences. Humans have been found to possess a comparatively larger DLPFC than baboons when considering brain volume (McBride, Arnold & Gur, 1999), suggesting that an expansion of this brain region in humans may explain why inter-species differences occur in this domain.

Perceptual grouping. Bor et al. (2003) explained their results in terms of perceptual grouping processes. The array was presented in plan-view, and accurate memory for structured sequences may be explained by chunking proximal locations together to form familiar shapes. Research investigating perceptual grouping in primates has found differences in global-local processing, which shows a local advantage in baboons when viewing targets and locations on screen, whilst humans show a global advantage (Fagot & Deruelle, 1997; Deruelle & Fagot, 1997; 1998). An individual who focuses primarily on local properties during search may fail to see global, structural features of a sequence to-be-recalled. This may explain why humans benefit from the global spatial arrangement of locations whilst baboons do not appear to use this information. Perceptual grouping is particularly evident in arrays of locations presented in plan-view, however ISSR and additional search tasks must also be carried out within navigational spaces which do not easily afford perceptual grouping processes. If

humans also benefit from structure in these situations then this suggests that species-typical differences cannot entirely be explained perceptually.

Immediate serial spatial recall in a navigational space. Superior recall accuracy for structured ISSR sequences has also been observed in tasks where individuals must navigate through virtual environments (De Lillo & James, 2012; De Lillo, Kirby & James, 2013). When required to follow specific trajectories through the search space participants more accurately recalled sequences which followed the structure of the clustered and matrix arrays, and thus subsequent selections were within the same cluster, row, or column before moving to the next, than when sequences violated this rule and frequently switched cluster, row, or column. These findings indicated that within a three-dimensional space where perceptual grouping is not easily afforded, spatial structure persists in playing an important role in easing memory load.

The ability to benefit from spatial structure, particularly when searching spatial clusters, may be a specific adaptation in primates to forage on patchily distributed resources (see Milton, 1981a; 1993). This ecological pressure is thought to have triggered the emergence of primate intelligence, leading to an expansion in memory span and the cognitive skills required to efficiently travel between patches (Milton, 1993; De Lillo, 2012). As such, De Lillo (2012) acknowledged that an ability to benefit from the structure of a search space, and to search locations hierarchically, is the most efficient method to search a large number of locations whilst minimising memory load. In this way, organised and principled search would result in fewer revisits to locations previously searched and reduced travel costs. However, a motivation to maximise cognitive economy and minimise travelling costs are often considered one and the same in foraging models, which the first experimental chapter of this thesis aimed to address.

1.6 Experimental Aims and Methods

The propensity to exploit spatial structure within a search environment appears to be an important aspect of human spatial cognition. Reducing cognitive load by hierarchically and principally organising locations to-be-searched would be evolutionarily advantageous to minimise the effort expended, and previous findings suggest that both humans and non-human primates show this tendency. However, the concept of structure and the part it plays in reducing memory load is yet to be fully characterised, both in relation to the physical structure of the environment and

conceptual structure to be held in memory. Within spatial tasks, reducing cognitive load and minimising energy costs through shorter travelling distances are often considered equivalent principles, however this assumption may not be withstanding. Across six experimental chapters, this thesis aimed to further characterise the human tendency to detect structure, by initially disentangling the two driving principles of efficient search which are often confounded in studies assessing motivation in search; cognitive load and travelling distance. Furthermore, the experiments of this thesis address the use of conceptual and temporal structure to be held in memory, the effects of ageing on the use of structure, how foraging efficiency develops across children, and finally the foraging efficiency and ability of a non-human primate species, *Papio papio*, to detect and use structured information. Across all experiments with humans, sex differences in the use of structure and search efficiency were also considered.

To assess these issues of spatial, conceptual, and temporal structure, the experiments presented employ both virtual reality (VR) and touchscreen-based methodologies. Within Chapters 2, 3 and 4, participants were assessed within egocentric VR environments. VR is a relatively novel method to assess cognition, and is particularly valuable in the assessment of spatial WM, allowing participants to move and navigate through an environment. VR has many benefits, and is considered an ecologically valid and useful alternative to using real-life large-scale spaces. The variables manipulated can be easily controlled within VR, allowing for a more accurate assessment of cognition, which is particularly valuable when assessing variables and cues that cannot be easily disentangled within a natural setting. This methodology also allows for environments to be designed for humans which replicate previous conditions in which non-human animals have been tested; an important contribution to more accurately assess cognitive skills comparatively. To assess spatial memory therefore, VR appears to be an invaluable method to accurately consider the cognitive skills involved in search and the possible benefits of structure in memory.

Whilst the benefits of VR are evident, the latter three experimental chapters employed a touchscreen-based methodology. The foraging paradigm initially designed within VR, was adapted for use on a touchscreen to assess a wider range of participants including older adults, young children, and a non-human primate species, in Chapters 5, 6 and 7 respectively. VR is known to cause motion sickness in some individuals with more nausea symptoms reported when viewing VR through a head-mounted display (HMD) compared to when viewing VR on screen (Sharples, Cobb, Moody & Wilson,

2008), whilst susceptibility to motion sickness is highly variable and differs vastly between individuals (Golding, 2006). VR is therefore not always suitable, most particularly when investigating vulnerable cohorts. The use of a touchscreen methodology extinguishes the risk of motion sickness and also brings new benefits to testing as it is easier to administer and the data collection rate is higher. Participants did not experience an immersion within the foraging space, however, the touchscreen task retained the capacity to assess the essential cognitive skills required for efficient foraging.

The Role of Distance Travelled in Search. Typically in ISSR tasks, sequences to-be-recalled which exploit the spatial structure of locations, and for instance visit locations within a cluster before moving to the next, are shorter than sequences which violate this rule where subsequent selections switch between clusters, and therefore require a further distance to-be-travelled through the search space. Whilst previous research suggests that spatial structure plays a large role in memory to reduce cognitive load (Bor et al. 2003; De Lillo et al. 1997; De Lillo, 2004; De Lillo & Lesk, 2010; De Lillo & James, 2012), the confounding variable of path length is present. Smyth & Scholey (1992) assessed the role of path length in a spatial span task and found that the distance between targets did not have a significant effect on the number of targets recalled, suggesting that the distance travelled between locations would not have an effect on accuracy within a navigational task. However, a robust effect of path length was later demonstrated by Parmentier, Elford & Maybery (2005), who found that performance was more accurate when locations to-be-recalled were closer together on the screen, and thus when the path length was shorter, compared to recall when locations were more distantly spaced. However, this has yet to be assessed within a navigational and three-dimensional space. As the current literature stands, the extent to which spatial structure plays an important role in reducing memory load is unclear whilst the principle of distance travelled through the search space remains intertwined. This first experiment outlined in Chapter 2 aimed to address this issue and disentangle these two principles within large and smaller-scale VR navigational environments.

Chunking Within Spatial Working Memory. In addition to spatial structure, representing items in memory by hierarchically structuring items to-be-recalled also plays a role in reducing cognitive load. Chunking typically refers to the recall of a large

number of items by grouping items into fewer components to be held in memory (Miller, 1956), and has been assessed in humans by the recall of words and lists, which show a spontaneous use of categories of like-items (Cohen, 1963; Servan-Schreiber & Anderson, 1990). An ability to chunk like-items together has also been claimed to exist in rats. Spatial arrangements of locations containing one of three types of food items have been used to assess chunking ability in rats. A 12-arm radial maze was used to demonstrate that rats learned to efficiently search the maze by using a hierarchical search strategy, and organised visits to arms on the basis of the food type found at each location (Dallal & Meck, 1990; Macuda & Roberts, 1995). Rats who were given stable cues to food location used this information to make fewer choices to complete the maze, which was viewed as evidence of chunking. The use of a chunking by food-type strategy here was seen as analogous to human chunking, despite the ecological differences of a foraging task (Cohen, Pardy, Solway & Graham, 2003). Whilst it is important to assess animal cognition within tasks that are meaningful to the species tested, it is equally important to assess humans within the same paradigm. As of yet, human chunking has not been assessed within a search space which includes opportunities to learn where rewarded locations are by use of spatial structure and also contains cues to rewards in the form of differing object types. The extent to which humans exploit the structure of a VR search space to aid memory for reward location, or use a hierarchical chunking strategy in a similar manner to rats was addressed. Chapter 3 therefore considered whether differences exist in the use of structure between rodents and humans, or whether an ability to benefit from this information is an important feature of primate cognition.

Detection of Temporal Structure in Search. Structural information to be held in memory can occur across time as well as spatially, and this is particularly evident within foraging situations. Considering the evolutionary pressures under which our search cognition evolved, observations of primates foraging today provide an approximation of ancestral conditions hominins faced. Foraging tasks derived from these situations can provide an ecologically valid method of assessing the cognitive skills required for efficient search. Primates that primarily rely on fruit to reach their nutritional requirements must know where and when to find ripe fruit, requiring sophisticated cognitive skills to learn regular fruiting patterns across time. Recent observations suggest that frugivorous primate species are able to use spatio-temporal

information relating to when specific trees will be fruiting and where they are located (Janmaat Ban & Boesch, 2013a; Janmaat, Chapman, Meijer & Zuberbühler, 2012). The set of experiments outlined in Chapter 4 initially aimed to assess humans within a VR foraging situation tapping the cognitive skills relevant to efficient search to determine whether humans are able to detect and use spatio-temporal structure within and across foraging bouts.

Within naturalistic foraging environments, non-human primates may use olfactory cues rather than spatial information to find fruiting trees, though Janmaat et al.'s (2012; 2013a) findings led to the conclusion that the likelihood of this was very low. It has been suggested that individuals may acquire cognitive maps (Tolman, 1948) to form mental representations of their foraging environment and the spatial relationships between objects. Research has suggested that chimpanzees may build mental representations of locations and use a flexible Euclidean strategy (Normand & Boesch, 2009), whilst other researchers more cautiously agree that locations are mentally represented in some way (Zuberbühler & Janmaat, 2010; Janmaat, Byrne & Zuberbühler, 2006; Janmaat et al. 2012; 2013a; Ban, Boesch & Janmaat, 2014). However, it is not possible to fully experimentally assess whether spatial information is acquired within a natural environment as olfactory cues and seasonality changes will always be available for an individual to use. It is difficult to assess exactly which cognitive skills are involved in efficient search due to the issue of cue competition. Associative learning theory posits that the acquisition of spatial information during search is not necessary, and individuals may attend to more salient cues, such as visual cues, within the environment despite both cues being predictive of reward availability. This would indicate an effect of overshadowing (Mackintosh, 1971; 1976). The final experiment in this chapter manipulated the cues available to participants to investigate whether spatial information is encoded in the presence of potentially salient visual cues within an ecological foraging task.

Effects of Ageing in the Detection of Temporal Structure. The importance of ecologically valid tasks to assess cognition has been highlighted by previous research (Burgess, Alderman, Evans, Emslie & Wilson, 1998; Burgess et al. 2006; Phillips et al. 2006; Phillips, Henry, Martin & Kliegel, 2008), and is particularly important in relation to ageing. Phillips et al. (2006) found that ageing effects were diminished when a task based on day-to-day experiences was used. However, day-to-day experiences are

evolutionarily recent situations, and an ecological alternative would be to assess effects of ageing within tasks based upon situations our hominin ancestors would have faced. The foraging task developed within the previous chapter, appeared to be a useful paradigm within which to assess cognitive decline. Across humans, a general cognitive decline is often seen with age, with older adults showing a decline in cognitive speed (van Hooren et al. 2007), and executive function and working memory tasks (van Hooren et al. 2007; MacPherson, Phillips & Della Sala, 2002; see Bishop, Lu & Yankner, 2010, for a review). Specifically, MacPherson et al. (2002) found that age-related decline was specific to tasks dependent on the DLPFC, the area of the brain which has shown increased activation when experiencing spatial structure (Bor et al. 2003). As such, an ability to benefit from temporal structure may be reliant on the DLPFC and show a deficit in older adults. In this chapter, the foraging paradigm developed for the set of experiments outlined in Chapter 4 was modified. A touchscreen version was employed to assess the foraging efficiency and ability to detect temporal structure shown by older adults, to determine the extent to which they detect and use spatio-temporal structure in comparison to their younger counterparts.

Developmental Changes in Foraging Efficiency. In addition to testing an ageing population, the foraging task developed afforded the assessment of primary school children. It has previously been found that children with larger WM spans better organised their search in a large-scale search task (Smith, Gilchrist & Hood, 2005), suggesting that spatial WM plays an important role in the search strategies children deploy. Evolutionary developmental psychology asserts that across the stages of ontogeny, different adaptive pressures were faced which conferred different advantages (Bjorklund & Pelligrini, 2000; Bjorklund & Bering, 2002). This is reflected in studies which show a developmental trend in cognitive skills, including WM capacity (Orsini et al. 1987; Luciana & Nelson, 1998; Hamilton, Coates & Heffernan, 2003), ability to use memory strategies (Dempster, 1978), and the use of organised structure (Uttal, Gregg, Tan, Chamberlin & Sines, 2001). Uttal et al. (2001) found that being shown the structure of spatial locations improved children's search performance. A propensity to benefit from structure appears to be related to the DLPFC (Bor et al. 2003), which has been found to continue developing after the age of 7 and into early adulthood (Diamond, 2002), and to show increased activation with age amongst children in a visuo-spatial WM task (Kwon, Reiss & Menon, 2002). Further research by Imbo,

Szmalec and Vandierendonck (2009) found that children aged from 9 years old benefitted from structured sequences in a Corsi-task and recall accuracy was high, though they did not benefit to the same extent as older participants, suggesting that this propensity to detect structure in stimuli continues to develop into adulthood. Chapter 6 aimed to investigate when the cognitive skills involved in efficient foraging develop in children, and whether an ability to detect structured patterns occurs, by employing the touchscreen foraging task described in Chapter 5.

Foraging Efficiency and Detection of Structure in Baboons, *Papio papio*.

The experiments described within Chapters 4, 5, and 6 aimed to assess the cognitive skills humans deploy in a foraging task based upon primate foraging situations. However, this can only provide information surrounding human cognition, and therefore an experimental assessment of non-human primates is required to investigate these competences fully. A primate research centre at the Université d'Aix, Marseille, comprised an ideal set-up with which to test this foraging paradigm with a troop of baboons trained in the use of touchscreen tasks.

Baboons, like humans, are typically omnivorous which allows them to exploit a range of ecological niches (Napier & Napier, 1967; 1985). The divergence of baboons from folivorous species is thought to have occurred within similar habitats and at a similar time when hominins diverged from a common ancestor with chimpanzees (Gilbert, Goble & Hill, 2010; Jolly, 2001; Zinner, Groeneveld, Keller & Roos, 2009). As such, Jolly (2001) notes that conditions that may have impacted human evolution in sub-Saharan Africa, would have had a parallel effect on ancestral baboons unlike for forest-dwelling apes, and this can provide interesting insights into human evolution. Mangabey monkeys, species of the Papionini tribe to which baboons belong, appear to learn which trees in their home range are most likely to be yielding fruit (Janmaat et al. 2006; Olupot, Chapman, Waser & Isabirye-Basuta, 1997). Mangabey monkeys are primarily frugivorous and so may possess higher level cognitive skills due to the requirements of foraging on ephemeral resources (Milton, 1981a; 1993). Chapter 7 considered the cognitive skills baboons possess and aimed to shed further light on this hypothesis. Whilst the previous experiments of this thesis aimed to characterise the benefits of structure in human cognition, this final experimental chapter tested a non-human primate species on a touchscreen-based task to provide further insight into the

cognitive skills primates have acquired, and where along the primate lineage high-level cognitive skills may have evolved.

1.7 The Search for Structure

To further characterise the notion of physical and conceptual structure, and its role in reducing memory load, the following 6 experimental chapters outline 11 experiments. An ability to benefit from the structure found in search environments and to use principled and organised search strategies would be evolutionarily advantageous. By reducing memory load during search, the effort expended during foraging is minimised. The propensity to detect and use structure in search tasks was investigated, assessing both younger and older adults, children, and a non-human primate species. Considering previous research, it is predicted that humans will exploit the spatial, conceptual, and temporal structure present within search environments, whilst the final experiment with baboons aimed to provide further insight into the evolution of this cognitive competency.

Chapter 2: The Role of Distance Travelled in Search

2.1 Introduction

The study of WM, and particularly spatial WM, is a valuable way to assess cognitive functions across species due to its non-verbal nature. WM is a system that stores information temporarily, in order to support other cognitive functions (Baddeley, 2003; Baddeley, & Hitch, 1974), which in relation to spatial WM, enables the temporary storage of locations during search. WM capacity is seen to be associated with higher cognitive skills, and an expansion in this domain has also been considered as an important trigger of hominin cognition (Coolidge & Wynn, 2005; Balter, 2010). Considering this, and the non-verbal nature of spatial WM more specifically, the comparative study of this may provide information about what is characteristic of human cognition and provide insights surrounding the evolution of WM throughout the primate order (De Lillo et al. 2013).

2.1.1 Principled and Organised Search Strategies

To aid WM, the use of principled and organised search strategies have been shown to be spontaneously deployed in non-human primates (De Lillo et al. 1997; De Lillo et al. 1998) and improve recall in humans (De Lillo & James, 2012; De Lillo et al. 2013). De Lillo et al. (1997) assessed capuchin monkeys (*Cebus apella*) within a spatial WM task, in which they were required to search sets of nine baited containers suspended from the ceiling of their enclosure arranged as three clusters (or ‘patches’) or as a matrix in three rows and columns. The monkeys showed principled search strategies when searching the arrays of baited containers, however they were most efficient when searching the clustered arrays, and made less redundant moves than when searching the matrix array. De Lillo et al. (1997) concluded that capuchin monkeys use principled and efficient search strategies here and benefit from the structure of a patchy search space, which may be an adaptation due to foraging on patchy resources within natural environments. These studies support the hypothesis proposed by Milton (1981a; 1993), who initially suggested that the emergence of high level cognitive skills was triggered by the diet of frugivorous primate species and the requirements of foraging on ephemeral resources in a forest environment. This hypothesis offers an explanation as to why frugivorous capuchin monkeys show evidence of effective cognitive skills, and also why they appear to perform exhaustive

searches of locations in a more principled manner in patchy spaces in comparison to linear constructs. Research with other species in a similar set-up using search arrays of clusters and matrices, has shown that mice (Valsecchi et al. 2000) and rats (Foti et al. 2007) do not appear to develop principled search strategies, whilst tree shrews performed the task in a more strategic manner than rodents, though not to the same extent as capuchins (Bartolomucci et al. 2001) – an interesting finding considering tree shrews close genetic relationship to primates (Sargis, 2004).

2.1.2 Immediate Serial Spatial Recall

The studies performed with capuchin monkeys and other species assessing the deployment of organised strategies are observational, and so cannot tell us what motivates systematic searches. To experimentally assess this relationship between the strategies used to search spatial arrays and accuracy of search, ISSR tasks have been used. Bor et al. (2003) initially differentiated between structured and unstructured sequences within a Corsi-type computerised recall task with humans, and found that sequences that visited sequential locations within the same row, column or diagonal line of the matrix array were better recalled than unstructured sequences which violated this rule and regularly switched between rows. Using an ISSR task within a patchy environment, De Lillo (2004) manipulated the spatial arrangement of the locations and the sequences to-be-recalled. Items were presented on-screen to human participants arranged as three clusters of three items and findings indicated that sequences were better recalled when they exploited the spatial structure of the array and were segregated by clusters, compared to when sequences switched between clusters. Bor et al. (2003) paradoxically found that fMRI data showed an increased activation of the DLPFC in human brains when structured sequences which eased memory load, were recalled, suggesting that this area of the brain plays an important role in recognising and benefiting from structure. However, the ISSR tasks described offered participants a plan-view of the array, and perceptual processes may have contributed to recall accuracy. To overcome this, further studies have used three-dimensional, navigational environments to decrease the chance of perceptual grouping.

Using egocentric virtual environments, De Lillo and James (2012; De Lillo et al. 2013) used the equivalent spatial arrangements as De Lillo et al. (1997) and found that humans spontaneously deployed hierarchical and structured search strategies similar to capuchin monkeys when given free search of a clustered array. Results experimentally

confirmed this proficiency to benefit from structure, as findings also showed that when participants were required to use ISSR to follow specific trajectories through the search space, participants more accurately recalled structured than unstructured sequences. These findings highlight the benefits of spatial structure in egocentric navigational spaces in which the viewpoint changes accordingly as the participant walks and turns through the search space, suggesting that perceptual grouping processes may not fully explain this phenomenon. However, a confounding variable which exists in studies manipulating the structure of sequences to-be-recalled is the issue of path length. Structured path sequences exploiting the structure of the locations within the array are typically shorter and therefore the distance to-be-travelled is decreased in comparison with path sequences which are unstructured. Unstructured sequences typically contain path crossings which often increase the distance required to-be-travelled through the search space. Path length must be taken into consideration when interpreting these findings.

2.1.3 Path Length

Manipulating path length has produced conflicting findings, with research finding an effect of path length on the Corsi task (Smirni, Villardita & Zappalá, 1983a) whilst other studies show no significant effect when distances between blocks are changed (Smyth & Scholey, 1992). The path length effect was further tested and defined by Parmentier et al. (2005) in a task requiring participants to recall sequences of dots presented on a screen, where the distance between the locations was manipulated. Their findings indicated that as the distance between the dots increased and thus as path length increased, serial memory for the locations decreased. Sequences were more accurately recalled when the locations to-be-selected were closer together. The robustness of the path length effect was further demonstrated by Guérard, Tremblay and Saint-Aubin (2009), and was again demonstrated in a later study concluding that path length had a greater effect on performance than the manipulation of the display size (Guérard & Tremblay, 2012).

However, the extent to which path length influences recall accuracy in a three-dimensional navigational space is unclear. In navigational spaces, there are energetic costs to consider when traversing a larger distance. Considering optimal foraging, an organism must determine whether an increase in time and energy will result in gain or loss (MacArthur & Pianka, 1966). Bernstein, Kacelnik and Krebs (1991) acknowledge

that travel time between locations should be taken into account when considering foraging; cotton-top tamarins (*Saguinus oedipus*) for example have been found to travel further for a larger reward (Stevens, Rosati, Ross & Hauser, 2005). In addition to a desire to increase food intake, Winterhalder (1981) recognises that amongst humans, there is also a desire to reduce the time and energy spent foraging to increase time for social or leisure activities. In this way, in a VR foraging task, humans are expected to minimise the time and energetic costs that may be expended during search. In the present study, the distance to-be-travelled between locations within a VR environment and the cognitive load required to recall path sequences was manipulated.

2.2 Experiment 1

An ISSR paradigm was employed within an egocentric virtual environment in which participants were required to navigate through and follow structured and unstructured trajectories. To disentangle two motivating factors of search and to therefore assess whether the benefit of structure during recall is due to reducing cognitive load, or due to a shorter path length to-be-traversed, this study manipulated the distance between locations. The performance of male and female participants was also considered.

2.2.1 Methods

Participants. A group of 37 participants (18 female and 19 male), aged between 18-42 years old ($M = 21.81$, $SD = 5.22$) from the University of Leicester took part for course credit or were paid a small fee for their time.

VR Apparatus and Environment. Participants were tested in a VR lab at the university, using Vizard 3.0 software. The virtual environment was presented via a NVIS nVisor stereoscopic HMD, and an Inter-Sense position tracker determined the viewpoint depending on the head movements of the participant. A handheld wand with a thumb operated joystick was used to navigate through the environment and to produce responses by pressing a trigger with the forefinger. The virtual environment was a large, textured hall which consisted of landmarks placed along the walls; two doors, two sofas, a bookcase, and three framed paintings (see Figure 2.1). A set of nine poles was placed in the centre of the virtual room, each surmounted by a white sphere. Poles were either arranged as a 3 x 3 matrix or as 3 clusters each containing 3 poles. The inter-pole

distance within each configuration of poles was manipulated to be either large or small; hereafter referred to as long-path or short-path. The inter-pole distance in the long-path condition was 2.1m, which was three times as long as the inter-pole distance in the short-path condition, 0.7m. The starting distance from the poles in the long-path condition was 14.7m and 4.9m in the short-path condition. Figure 2.1 shows a plan view of the virtual room and the pole configurations.

ISSR in VR. Participants were required to select the poles in a prescribed order. To select a pole, participants navigated towards it in the virtual environment, and when they were within selecting range of the pole, the message ‘Select Pole?’ appeared. Once the wand trigger was pressed, a message confirming that the pole had been visited (‘Pole Selected’) was displayed. No cues were left to mark visited locations. As movement was controlled by the wand, no physical walking movement was required by the participant. The viewpoint of the participant was updated by the tracking system which used the head movements to produce an immersive experience.

Participants were required to follow specific trajectories through the search space using serial recall, and each trial featured a presentation and a recall phase. In the presentation phase, one of the white spheres surmounting the poles turned red until the participants travelled through the environment and selected it. Once selected, the sphere returned to white, and a second pole turned red until selected. This occurred until all nine poles had been visited, then the recall phase began. The starting position was reinstated and participants had to recall the sequence of the presentation phase by navigating through the environment once more and selecting the poles in the same order. The spheres remained white at all times during this phase. Once 9 selections had been made within a trial, the trial terminated and the next trial began.

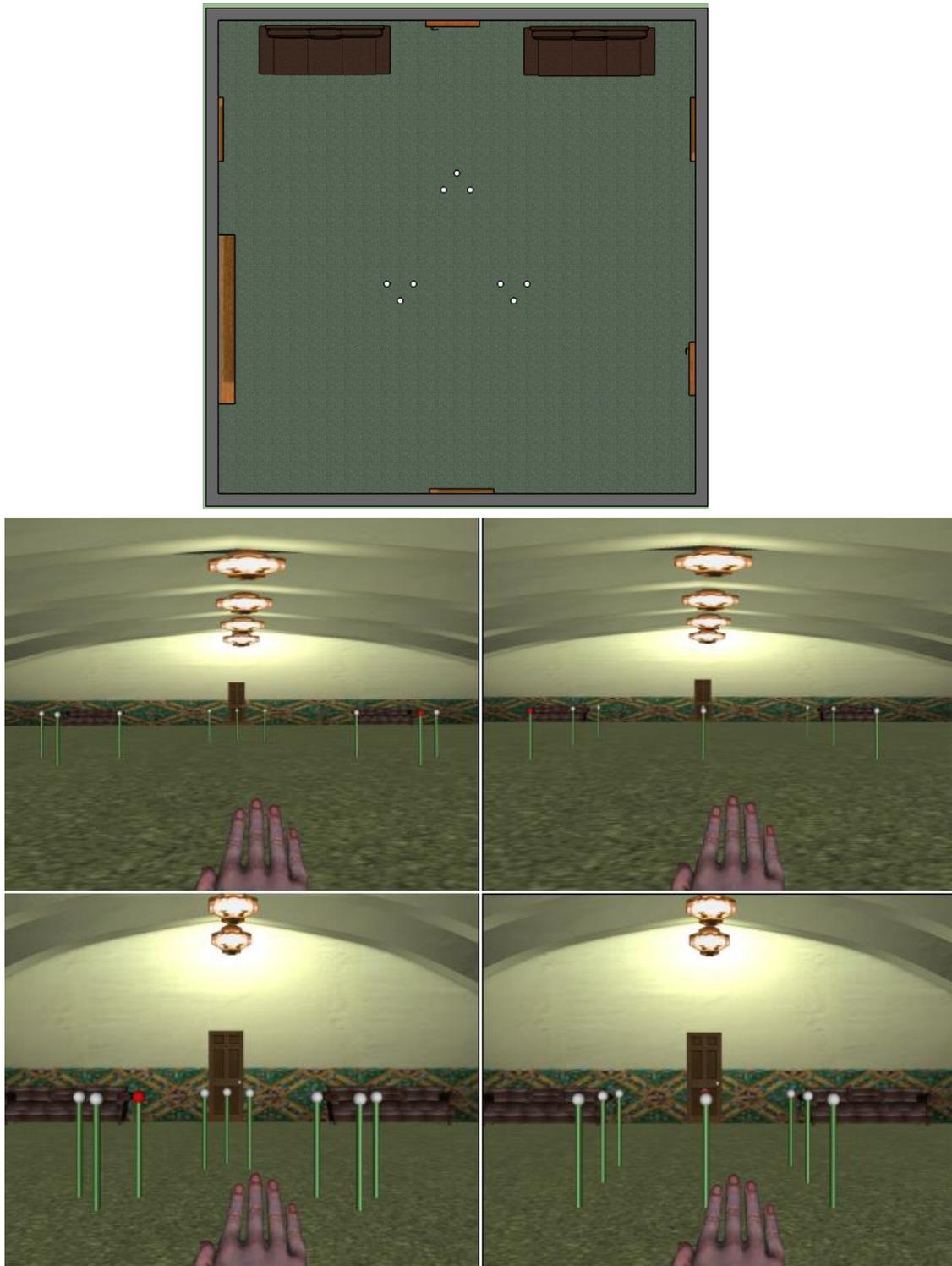


Figure 2.1 A plan view of the VR environment depicting the short-path clustered condition, and below, the configurations and path length sizes. Left; the clustered array in the long-path (top) and short-path (bottom) conditions. Right; the matrix array in the long-path (top) and short-path (bottom) conditions.

Design and Procedure. Each trial featured either the clustered or matrix configuration of poles, and long-path or short-path arrays. The sequences to-be-recalled in a given trial were either structured or unstructured. Structured sequences in the clustered condition featured the selection of consecutive items within the same cluster until the cluster was exhaustively explored, whilst unstructured sequences always had consecutive items to-be-selected within different clusters. In accordance with Bor et al. (2003), structured sequences in the matrix condition had consecutive items within the same row, column or diagonal line, whereas unstructured sequences always violated this rule. The long-path structured trials were designed to require a longer walking distance through the VR environment than the short-path unstructured trials.

There were eight conditions in total (see Figure 2.2). Participants completed alternating trials of the long-path and short-path arrays, with the starting condition randomised across participants. The order in which participants completed matrix or clustered arrays, and received structured or unstructured sequences to-be-recalled was also randomised across the trials. A repeated measures design was used, as participants completed 2 trials of each condition, completing 16 trials in total. Participants were given a short break when required, and a 5-minute break after 8 trials.

Measures. Performance was measured by calculating the mean number of correct responses for each condition. A correct response was defined as any selection to a pole in the recall phase that was selected in the same order as that presented in the presentation phase. In any trial, the optimum number of correct responses was 9, and the highest score a participant could receive was 144. The reaction time between pole selections was also measured in seconds.

2.2.2 Results

Accuracy. The means for each condition are shown below in Figure 2.3. To assess the average number of correct responses made across the conditions, a 2 x (Distance Travelled) x 2 (Configuration) x 2 (Structure) x 2 (Sex) ANOVA was carried out. A significant effect of Structure was found, $F(1, 35) = 41.86, p < .001$, with paired sample t-tests showing that trials which featured structured sequences ($M = 49.49, SD = 13.72$) produced a greater number of correct responses than when unstructured sequences ($M = 39.41, SD = 16.82$) were recalled, $t(36) = 6.55, p < .001$. There was no significant effect of Configuration, $F(1, 35) = 1.51, p = .228$, nor Distance Travelled, $F(1, 35) = .92, p = .343$, showing that overall, recall accuracy in both the matrix and clustered configurations, and the long-path and short-path arrays were similar. There were no significant interactions between Distance Travelled, Configuration, and Structure, minimum $F(1, 35) = 2.93, p = .096$.

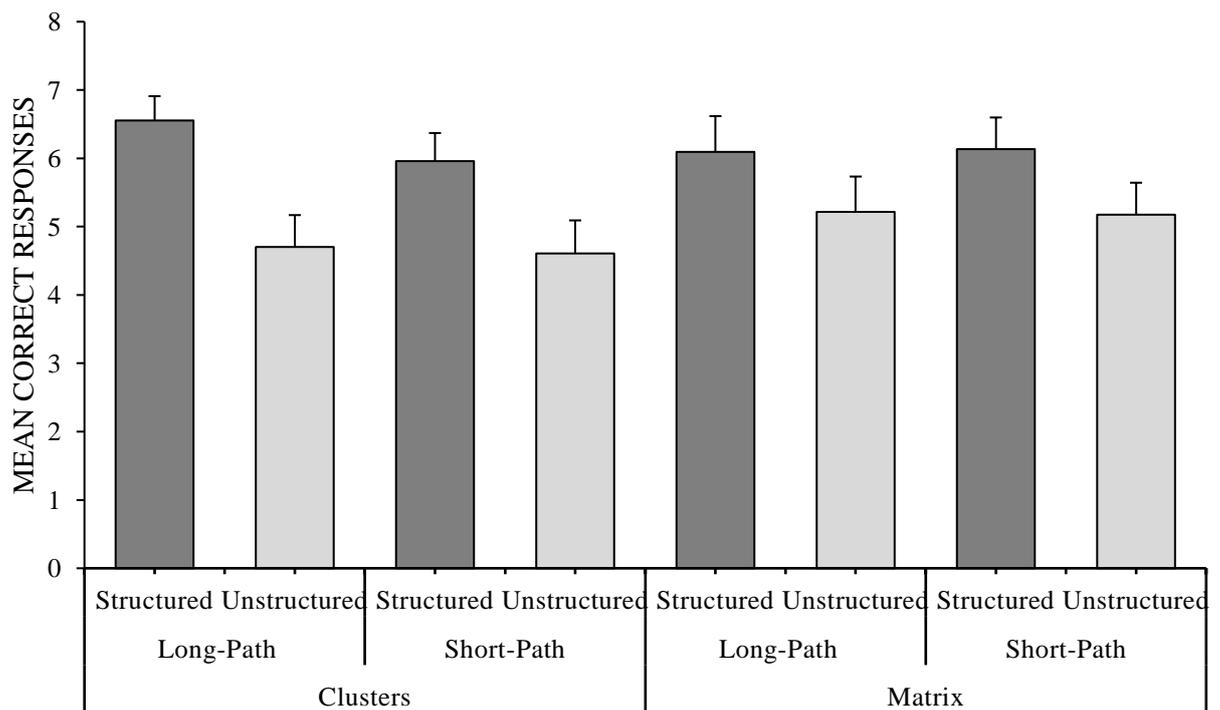


Figure 2.3 The mean number of correct responses made within each condition, with +1 SE bars.

The mean number of correct responses made in each condition by males and females are shown below in Figure 2.4. A significant main effect of Sex was found, F

(1, 35) = 6.50, $p < .05$, with independent samples t-tests indicating that overall, males ($M = 100.00$, $SD = 30.27$) made significantly more correct responses than females ($M = 77.17$, $SD = 23.61$), $t(35) = 2.55$, $p < .05$. A significant interaction of Configuration x Sex was also found, $F(1, 35) = 5.98$, $p < .05$, with independent samples t-tests indicating that in the matrix arrays, males ($M = 52.11$, $SD = 15.27$) made significantly more correct responses than females ($M = 37.83$, $SD = 13.75$), $t(35) = -2.98$, $p < .01$. A trend also emerged for the clustered configuration, though this was not statistically significant, $t(35) = -1.87$, $p = .07$. There were no further significant interactions between the factors, minimum $F(1, 35) = 1.54$, $p = .223$.

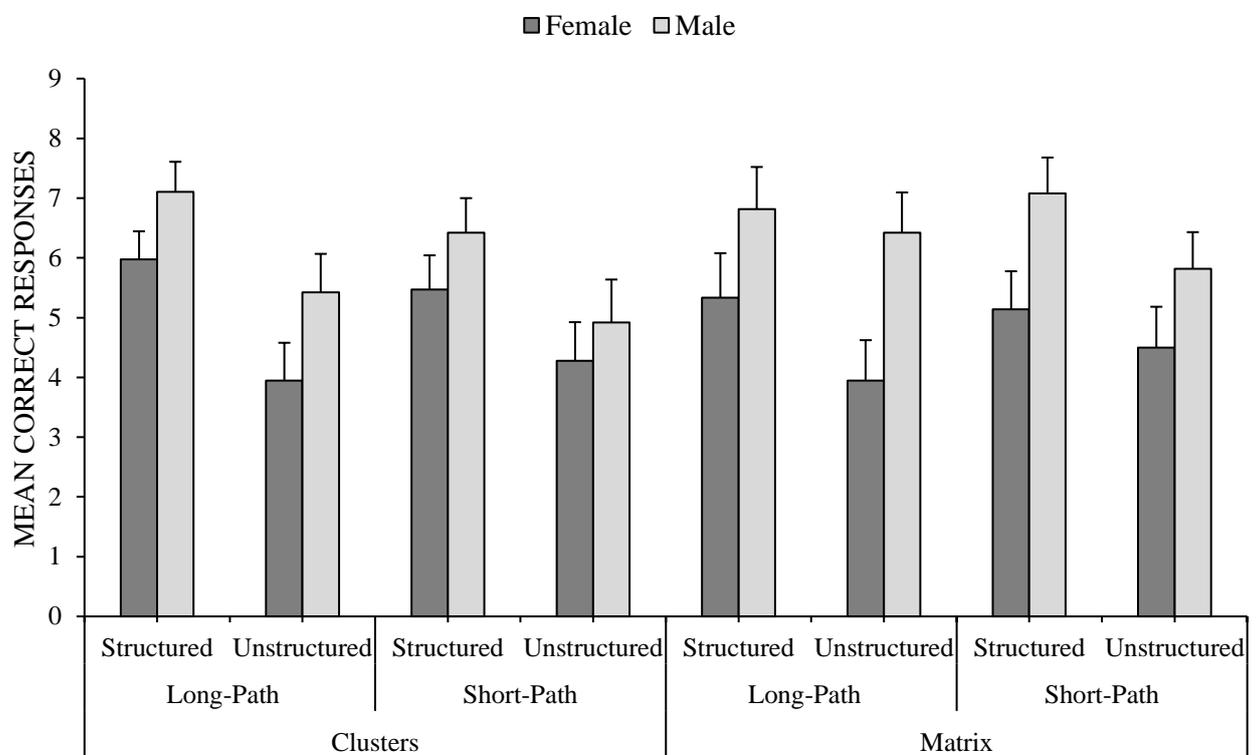


Figure 2. 4 The mean number of correct responses made by males and females in each condition, with +1 SE bars.

Reaction Time. The mean reaction times for each condition are shown in Figure 2.5. A further 2 x (Distance Travelled) x 2 (Configuration) x 2 (Structure) x 2 (Sex) ANOVA was carried out to assess the time taken to select poles in each condition. There was a significant effect of Distance Travelled, $F(1, 34) = 300.33$, $p < .001$, Structure, $F(1, 34) = 103.50$, $p < .001$, and Configuration, $F(1, 34) = 4.65$, $p < .05$. As

expected, paired sample t-tests indicated that long-path sequences ($M = 11.39$, $SD = 2.56$) took significantly longer to recall than short-path sequences ($M = 6.16$, $SD = 1.52$), $t(36) = 17.57$, $p < .001$, and unstructured sequences ($M = 10.45$, $SD = 2.60$) took longer to recall than structured sequences ($M = 7.16$, $SD = 1.63$), $t(36) = -10.47$, $p < .001$. Sequences in the matrix arrays ($M = 9.10$, $SD = 2.25$) also took longer to recall than clustered sequences ($M = 8.49$, $SD = 1.99$), $t(36) = 2.07$, $p < .05$. Additionally, there was a significant interaction of Distance Travelled x Structure, $F(1, 34) = 15.24$, $p < .001$, with paired sample t-tests confirming that in both array sizes, unstructured sequences took longer to recall than structured sequences, minimum $t(36) = 7.90$, $p < .001$. A significant interaction of Configuration x Structure was also found, $F(1, 34) = 35.53$, $p < .001$, with further t-tests indicating that within both configurations, unstructured sequences took longer to recall than structured sequences, minimum $t(36) = 4.01$, $p < .001$. There was no significant interaction of Distance Travelled x Configuration, $F(1, 34) = 2.02$, $p = .164$.

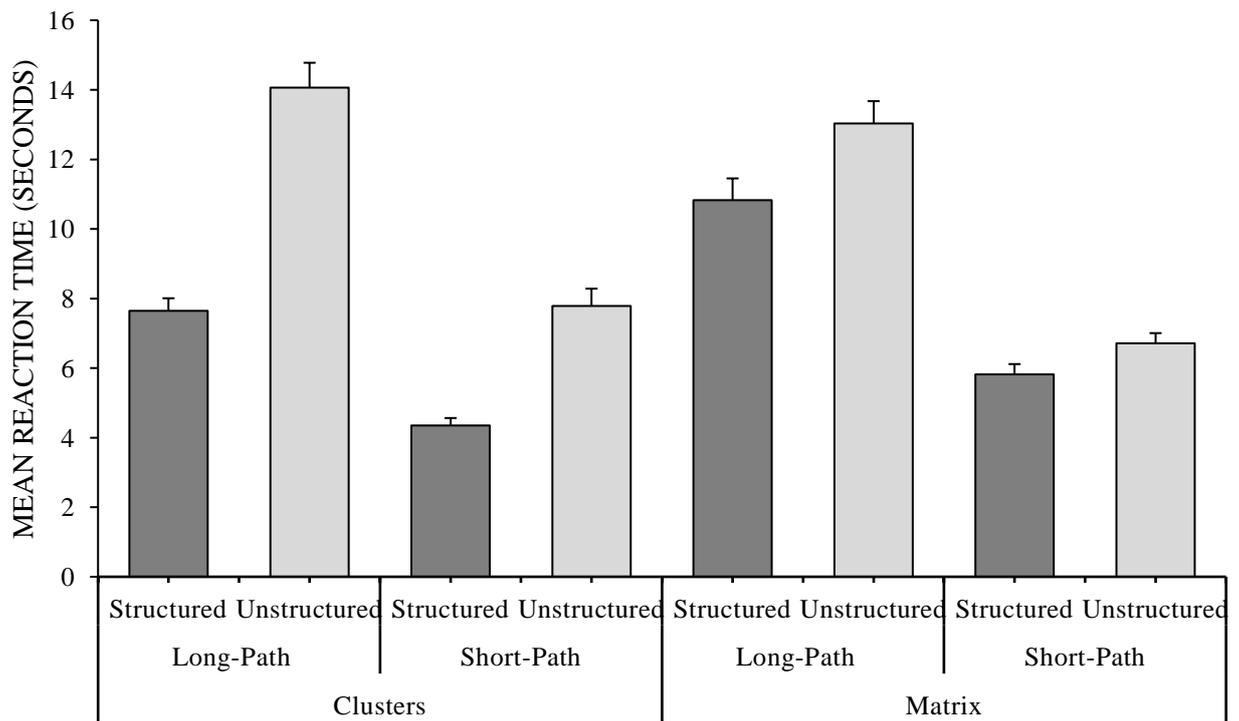


Figure 2. 5 The mean reaction time (seconds) taken to select consecutive items within each condition, with +1 SE bars.

The mean reaction times for each sex are shown in Figure 2.6 for each condition. There was no significant main effect of Sex, $F(1, 34) = 1.75, p = .195$, however a significant interaction of Distance Travelled x Configuration x Sex was found, $F(1, 34) = 8.55, p < .01$. Independent samples t-tests to investigate the interaction showed that females ($M = 6.69, SD = 1.92$) took significantly longer between consecutive selections than males ($M = 5.46, SD = 1.53$) in the short-path clustered condition, $t(35) = 2.15, p < .05$. There were no further interactions between the factors, minimum $F(1, 34) = 3.08, p = .09$.

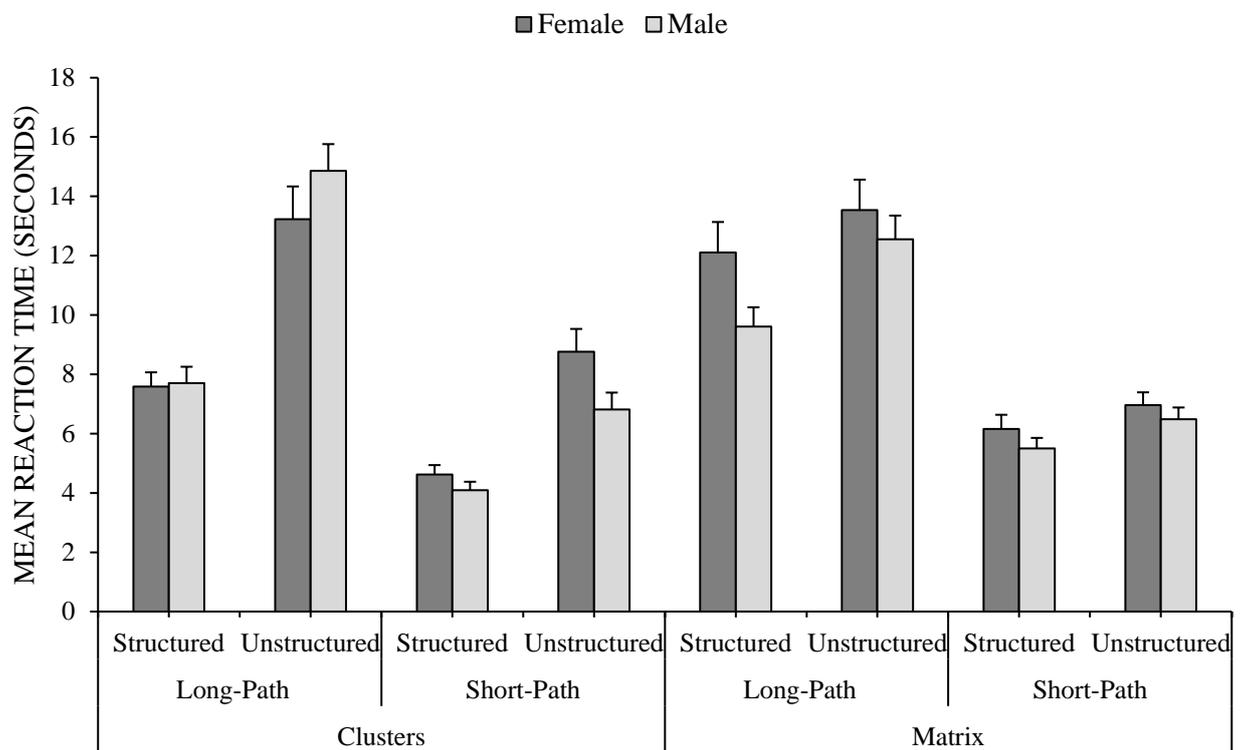


Figure 2. 6 The mean reaction time (seconds) taken to select consecutive items by males and females in each condition, with +1 SE bars.

2.3 Discussion

In an ISSR task which disentangled two motivations of efficient search – a desire to reduce cognitive load and the distance travelled which are often considered equivalent principles – participants were found to benefit further from the structure of sequences to-be-recalled than the distance travelled through the search space. Importantly, no effect of distance was found, indicating that recall accuracy was not significantly affected by a larger distance to-be-travelled. Reaction time analyses

confirmed that sequences in the long-path trials took longer to recall than those in the short-path arrays. Despite a longer time to completion of a trial, recall accuracy was exclusively affected by the structure of the sequences to-be-recalled. Overall, recall accuracy improved when sequences to-be-recalled were structured and exploited the spatial structure of the array, compared to unstructured sequences.

2.3.1 Importance of Cognitive Economy

These findings contrast with the path length effect (Parmentier et al. 2005; Guérard et al. 2009; Guérard & Tromblay, 2012). Guérard et al. (2009) suggested that sequences to-be-recalled which featured a large distance between locations were more poorly recalled as the perceptual organisation of the array was disrupted and would be encoded in isolation as opposed to when there was a small distance between locations which can be processed as a group. This explanation does not appear to pertain to the current results. Path length had no significant effect on recall, consistent with Smyth and Scholey's (1992) findings, whilst the structure of the to-be-recalled sequences showed a robust and consistent effect throughout. Whilst physical energetic costs are minimised in VR tasks, moving through large VR environments replicates the costs involved in walking and is costly in terms of time. However, the current findings strongly suggest that the benefits of reducing memory load by using spatial structure outweighs the costs of travelling a further distance through the search environment.

The findings are consistent with previous research demonstrating that structured sequences are more accurately remembered and recalled than unstructured sequences (De Lillo & James, 2012; Bor et al. 2003; De Lillo, 2004). The ISSR task implemented here successfully disentangled two motivating principles of efficient search, highlighting a propensity for humans to strive for cognitive economy. A proficiency to use structure within search supports the notion that a motivation to reduce cognitive load plays an important role in spatial memory. These findings are consistent with the theory that humans show a propensity to search for simplicity (Chater, 1996; 1999; Pothos & Chater, 2002; Chater & Vitanyi, 2003), and suggests that a desire to use the simplest strategy occurs within spatial memory. Following the structure of the search array provides a cognitively simpler route through the space even when travelling across a larger distance, in comparison to sequences which require switching regularly between clusters, rows or columns within the array. It is possible therefore that this ability to benefit from spatial structure may be an evolutionary adaptation which must

have been associated with large fitness benefits for it to have evolved and persisted in human cognition (Foster & Kokko, 2009). An ability to detect and use structure within an environment may also be related to the requirements of foraging on ephemeral resources (Milton, 1981a; 1993). Frugivorous primates must learn where and when patchily distributed fruits are available within their environment, and therefore a proficiency to use the structure of an environment to reduce cognitive load and to avoid revisiting locations would be highly beneficial. It may be the case that early hominins evolved high level cognitive skills due to these foraging requirements.

2.3.2 Comparative Differences

Studies have shown that mice (Valsecchi et al. 2000) and rats (Foti et al. 2007) do not show principled search when searching clustered arrays. Findings from tree shrews indicate a more principled search than rodents (Bartolomucci et al. 2001), whilst capuchin monkeys' show use of organised strategies (De Lillo et al. 1997; 1998) which do not however reach the same efficiency as humans (De Lillo & James, 2012). It can be suggested that an ability to benefit from spatial structure is characteristic of higher cognition in primates, however ISSR tasks are required to assess this. In an ISSR task, Fagot and De Lillo (2011) found that in comparison to humans, baboon performance was significantly impaired by path length, and subjects did not appear to benefit from the structure of the sequences to-be-recalled. This difference between baboons and humans could be explained by a lack of this ability along the baboon lineage due to a non-frugivorous diet, or a loss if an ability to detect structure became redundant in baboon evolution. However, differences here could also be explained in the task methodology. Baboons completed the task using a touchscreen and therefore differences in human and monkey cognition may be explained by differences in perceptual processing (Fagot & Deruelle, 1997; Deruelle & Fagot, 1997; 1998; Spinozzi, De Lillo & Truppa, 2003) rather than by an inability to benefit from spatial structure. Research assessing capuchin monkeys have used sets of baited containers within their enclosures, and humans have been tested within navigational environments, therefore it is unclear how baboons would behave under similar conditions. However, an ability to benefit from structure as shown in the current task when searching within environments which do not easily afford perceptual grouping, suggests that disparities here are not in themselves due to perceptual differences. Further research with non-human primates would help clarify this.

2.3.3 A Male Advantage

The findings indicated that males outperformed females, consistent with previous studies reporting a male advantage within an ISSR task (Kaufman, 2007; Orsini et al. 1986; 1987). Within the current study males scored higher on recall accuracy than females, suggesting that memory for traversing paths through navigational environments was superior in males. This is in contrast to findings which showed no sex differences on the Corsi task (Smirni, Villardita & Zappala, 1983b; Capitani et al. 1991; Postma et al. 2004). A lack of a significant sex difference on the Corsi task however may be explained by the visual and perceptual grouping processes involved, which may not tap the skills that are required in three-dimensional, navigational environments (Gilchrist, North & Hood, 2001).

A male advantage within this task can be explained by a propensity for males to detect patterns in stimuli (Baron-Cohen, 2002). Whilst Chater (1996; 1999) suggested that an ability to detect patterns was an important aspect of human cognition, Baron-Cohen (2002; Baron-Cohen, Richler, Bisarya, Gurunathan & Wheelwright, 2003) found that this ability was more pronounced in males. However, as there was a male advantage in trials featuring unstructured pathways, it may be the case that this difference was due to a general superiority of male navigational skills. In relation to evolutionary theories, this finding is consistent with the *hunter-gatherer hypothesis* (Silverman & Eals, 1992) which suggests that superior male spatial knowledge evolved due to the division of labour experienced by early humans, where selection pressures favoured advanced navigational and spatial skills in males to find and track prey. The male advantage demonstrated here could also be explained by Ecuver-Dab and Robert's (2004) *two-fold selection process*, which posits that sexual selection pressures and inter-male competition was the trigger for superior spatial skills.

2.3.4 Conclusions

The findings provide further support for the notion that humans have a strong tendency to benefit from the spatial structure of search spaces, and are consistent with theories that humans strive for simplicity (Chater, 1996; 1999). This propensity to benefit from spatial structure despite a further distance travelled, indicates that a motivation to promote cognitive economy outweighs energetic costs. This experiment successfully disentangled these two motivational factors which typically become confounded in models of search. The findings of this spatial recall task also provide

support for evolutionary theories of sex differences, though further investigation of sex differences across species in ISSR tasks would help clarify the extent to which male and female evolutionary pressures have influenced spatial WM.

An ability to detect and use structure during search may be characteristic of higher level cognition in primates (Milton, 1981a; 1993; De Lillo et al. 1997; De Lillo, 2012). Previous studies with rodents have suggested that rats and mice are less able to benefit from the structure of spatial arrays (Valsecchi et al. 2000; Foti et al. 2007) than primate species, however it has been suggested that rats employ a form of cognitive economy during search for food, by chunking like-items together for a more efficient search (Dallal & Meck, 1990; Macuda & Roberts, 1995). This data-reducing strategy has not been assessed in humans within a foraging situation, however the VR apparatus allowed the assessment of this strategy within the next chapter by placing humans within the same conditions experienced by rats.

Chapter 3: Chunking within Spatial Working Memory

3. 1 Introduction

The findings presented in Chapter 2 demonstrated the importance of search strategies which exploit the structure of the search space to ease memory load. This ability to benefit from spatial structure to reduce cognitive cost has been considered characteristic of higher cognition in primates (Milton, 1981a; 1993; De Lillo et al. 1997; De Lillo, 2012), though other studies suggest that rats also show a propensity to reduce cognitive costs in the form of chunking (Dallal & Meck, 1990; Macuda & Roberts, 1995).

3.1.1 Chunking to Reduce Cognitive Load

Bor et al. (2003) suggested that structured sequences are more accurately recalled because humans chunk locations together to form familiar structures. Chunking is seen as a higher cognitive process which aids the recall of a larger number of items from memory by grouping items into fewer components (Miller, 1956), and is an efficient response strategy seen widely in humans. Chunking to aid memory has also been found to occur in non-human primates and pigeons (Terrace, 2001), and rats (Dallal & Meck, 1990; Macuda & Roberts, 1995). Previously, it had been thought that rats do not appear to search arms of a radial maze in an efficient manner (Olton & Samuelson, 1976). However, within a radial maze baited with different food types, Dallal and Meck (1990) claimed that rats deploy a hierarchical search strategy, by chunking locations to-be-searched by the food type found at each location. In their study, each location was baited with one of three food types, and rats were placed in the maze with either stable food cues creating chunks which the rats could use to navigate the environment, or with unstable cues where the food type found at each location did not provide consistent information about location within and across trials. Rats appeared to visit arms which contained their most preferred food type first, followed by arms of their second-preferred food, and visiting the least preferred foods last. Rats also made fewer choices to complete the maze suggesting that the chunking by food type strategy they deployed was an efficient method to ease cognitive load.

Macuda and Roberts (1995) replicated Dallal and Meck's (1990) study, and suggested that chunking is not necessary to attain arm preferences, and a non-chunked mental representation of the arms would allow rats to visit preferred food first. Each of

the 12 arms and the food types found there may be independently represented, rather than forming fewer food ‘maps’ in memory to create chunks. To further assess this, Macuda and Roberts (1995) rearranged the food types after first training rats with stable food cues which created chunks. Food types were rearranged by either exchanging one food type with another whilst maintaining the same chunked locations as learned in the training trials, or by exchanging one food type with the two remaining foods, compromising the previously learned chunks and requiring new chunks to be learned. The chunk maintained group more easily learned the new food locations and were quicker to return to their food preference hierarchy, compared to the chunk compromised group, providing further evidence to support the notion that rats form hierarchical chunked representations in memory.

3.1.2 Reducing Cognitive Load or Optimal Foraging?

In radial maze tasks assessing chunking, rats have been found to often switch chunks before all arms containing a particular food type have been visited (Cohen et al. 2003). Errors of this type may highlight a difference in memory chunking capacity between rats and humans, however as a non-exhaustive search by rats is common due to leaving ‘patches’ before all arms are exhausted, it is difficult to accurately assess a rats WM capacity (Cohen et al. 2003). In humans, short term memory span is acknowledged to be 7 ± 2 (Miller, 1956; Chase & Simon, 1973), whilst Macuda & Roberts (1995) suggested that rats may only have a span of three components. Cohen et al. (2003) suggested that the errors seen in rat performance may be due to the chunking strategy being at odds with an optimal foraging strategy (Charnov, 1976) where rats should aim to visit locations in such a way as to reduce predation and expend less energy. Rats are highly susceptible to predation, and chances of survival are improved if they switch patches more often (Brown, 1999). Thus rats may be more likely to make errors in chunking because all items within a cluster may not be fully explored before they move to the next set of locations. This was illustrated in a study showing that rats were more likely to search adjacent arms within a radial maze when the central arena was large compared to a smaller centre (Yoerg & Kamil, 1982), suggesting that rats perform in such a way as to minimise predation risks. Importantly, Cohen et al. (2003) highlighted the issue that searching for hidden food items within a radial maze is an ecologically different task from those used to assess human chunking. However, the use of a

chunking by food type strategy claimed to be used by rats is seen as analogous to human chunking, despite this ecological difference.

To assess chunking in humans, studies have used words and lists (Cohen, 1963; Servan-Schreiber & Anderson, 1990), sequence learning (Pammi, Miyapuram, Bapi & Doya, 2004; Bor et al. 2003), and chess performance (Chase & Simon, 1973; Gobet & Simon, 1998). Chase and Simon (1973) assessed chess players on their ability to recall the locations of pieces on a board, and found that players appeared to reconstruct boards in groups of pieces. This was explained by the authors in terms of chunking, suggesting that this memory strategy can pertain to visuo-spatial tasks. However, the motivation that rats face during foraging to exploit patches whilst reducing predation risk, are not faced by humans. It is therefore important to assess humans within the same conditions as rats experienced to assess whether humans also show this tendency, or whether we strive to reduce cognitive costs by exploiting the spatial structure of search arrays.

3.1.3 Spatial Search Strategies

Within spatial arrays, humans have been found to search linearly and to benefit from the structure of the search space (De Lillo, 2004; 2012; De Lillo & James, 2012; Bor et al. 2003). Bor et al. (2003) explained this in terms of chunking, as in an ISSR task, sequences with the opportunity to reorganise locations into patterns increased WM capacity, and in turn were easier to recall. Whilst they employed a 2D search space, De Lillo and James (2012) used a VR space in which participants were required to navigate through the environment. Using an ISSR paradigm in accordance with Bor et al. (2003), recall accuracy was higher for structured sequences where the locations to-be-recalled were consecutively in the same row, column or cluster, until that group had been exhaustively explored. The findings presented in the previous chapter (see De Lillo et al. 2013), indicated that superior recall accuracy of structured sequences was present regardless of the distance travelled through the search space, suggesting that foraging strategies in humans are motivated by cognitive economy as opposed to reducing energetic costs. Considering this, it would be important to assess whether or not humans would continue to search linearly and exploit the structure of the search space, in such situations where there is an available cue of food type which rats appear to use to aid memory. In this case, it would be important to dissociate the structure of the search space with the food types found at each location to clearly assess chunking and spatial search preferences in humans. This task also relates to memory for object location, and

therefore the extent to which sex differences occur in this task was also considered (see Silverman & Eals, 1992; Eals & Silverman, 1994; Levy et al. 2005).

3.2 Experiment 2

This experiment aimed to assess the search strategies spontaneously deployed during free search of a matrix array with a proportion of locations containing one of three food types, and whether rearranging the food types found at each location and manipulating chunked locations had an effect on performance. A matrix of locations was used to allow for a portion of locations to remain unrewarded, to avoid a purely linear search strategy.

3.2.1 Methods

Participants. Twelve undergraduate students (7 female and 5 male) from the University of Leicester took part for course credit. Participants had a mean age of 22.17 ($SD = 6.12$), with an age range of 18-39 years.

VR Apparatus and Environment. Participants were tested in a VR psychology lab at the University of Leicester. Vizard 4.0 software was used to present the virtual environment, which participants viewed via a NVIS nVisor head mounted display. A handheld wand with a joystick was used to navigate and produce responses. The virtual environment was the same room as described in Chapter 2, which featured a large, textured hall with landmarks placed along the walls, including two doors, two sofas, a bookcase, and three framed paintings. There were 25 white poles in the centre of the room to be searched, which were arranged as a 5 x 5 matrix. Once a pole was selected, the message 'Pole Selected' appeared, and if a food reward was hidden at that location, a picture of the item found was also shown. Any revisits to locations where the food item had already been collected, only showed the message 'Pole Selected'. The pole configuration and the virtual food reward message is shown in Figure 3.1.



Figure 3. 1 Top; The virtual hall with landmarks and the matrix of locations. Bottom; the message and image shown when a pole was selected.

Design and Procedure. All trials consisted of 12 rewarded locations which contained one of three food types (Figure 3.2). Four poles each hid honey jars (H), apples (A), and carrots (C). The rewarded locations were arranged so that only one of each food type was in the same row or column, dissociating the spatial structure of the search space from the food types.

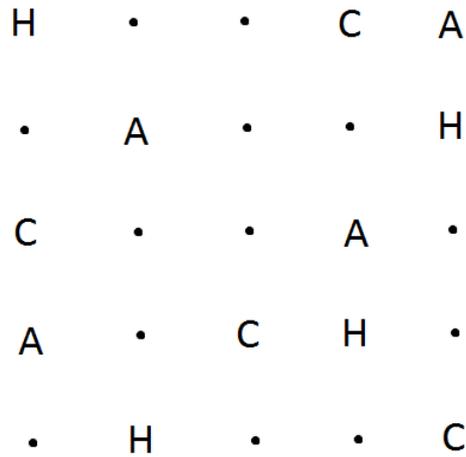


Figure 3. 2 The configuration of food types and locations within the array.

Each participant completed training trials where the locations of the food types were fixed and remained the same throughout, enabling participants to predict where the food types would be found. Participants were then assigned to one of three test conditions. In the test trials, the rewarded locations remained the same, but the food types found at each location were exchanged. In accordance with Macuda and Roberts' (1995) paradigm, the *chunk maintained* (CM) condition retained the locations of the chunks of food items that could be learned in the training trials, though the food types were exchanged. The honey jars were replaced by carrots, the apples were replaced by honey jars, and the carrots were replaced by apples. The *chunk compromised* (CC) condition required participants to learn new chunks in order to chunk by food type. Existing food types were exchanged with both remaining types. The honey jars were replaced by 2 apples and 2 carrots, the apples were replaced by 2 honey jars and 2 carrots, and the carrots were replaced by 2 honey jars and 2 apples. These two conditions are depicted in Figure 3.3. In the third condition, *mixed locations* (ML), the food type found at each location changed from trial to trial and so could not be learned.

Participants were instructed to find the hidden foods and informed that each trial would terminate once all foods had been found. Participants completed 10 training trials, and were then given a short break of 10 minutes. Then, 15 test trials were administered in which the position of the learned food types were manipulated.

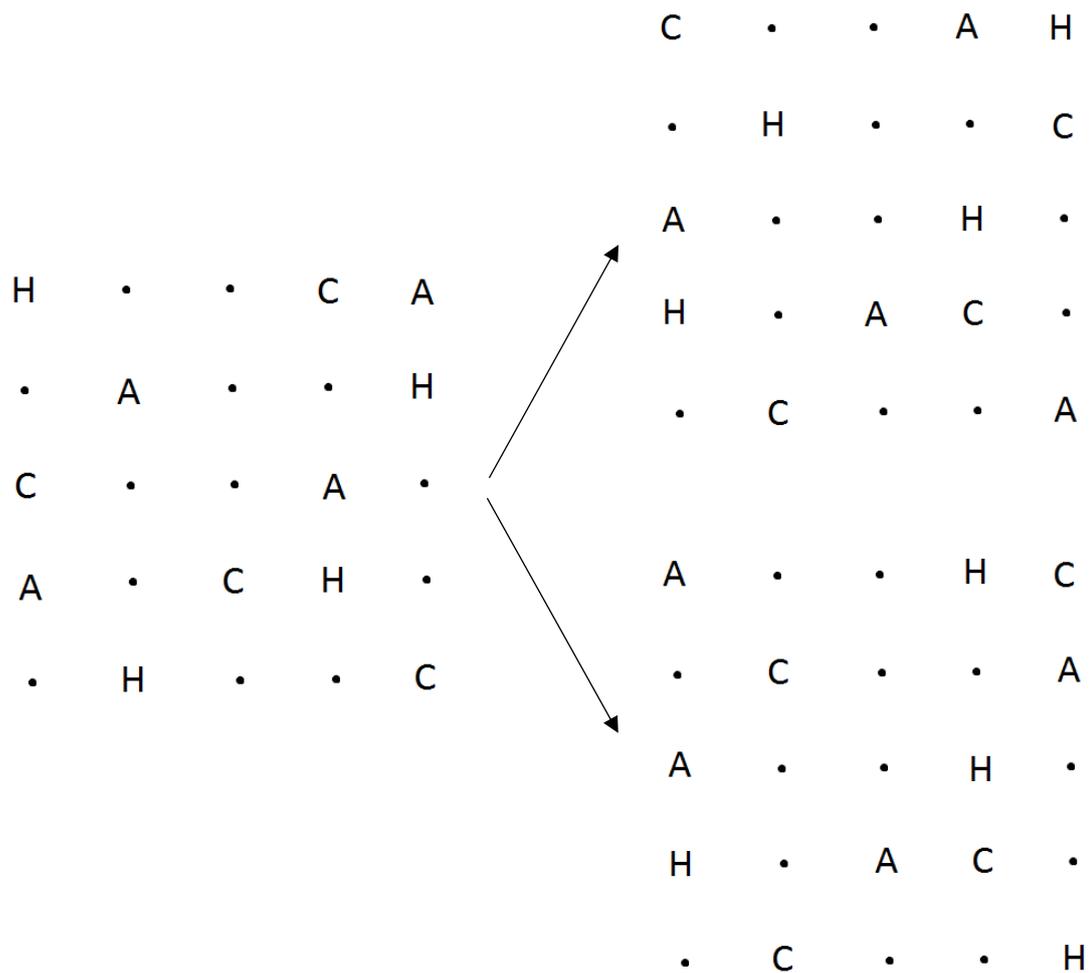


Figure 3. 3 The food locations in the foraging space: Left; the training trials. Top right; the chunk maintained (CM) test trials. Bottom right; the chunk compromised (CC) test trials.

Measures. Accuracy was calculated by analysing the mean number of selections until all foods had been found. As there were 12 foods to be found within the array, the optimum number of selections for each trial was 12. Participants were required to meet a criterion of 15 selections or less by the last trial in order to ensure that the locations of the foods had been learned and to progress to the test trials. In accordance with Macuda and Roberts' (1995) analysis, we calculated the number of alternations between food types during each trial to assess chunking. For this analysis, only selections to rewarded poles were included. For example, if participants selected honey-honey-honey-honey-carrot-carrot-carrot-carrot-apple-apple-apple, then this would consist of 2

alternations; the first from honey to carrot, and the second from carrot to apple. A value of 2 alternations would indicate a chunking strategy using the item found at each location as a cue to chunk. Higher values would be indicative of an alternative search strategy.

3.2.2 Results

Accuracy. Participants became more efficient in their search and made fewer selections until a trial was completed across the experiment. The mean number of selections for all conditions across the training and the test trials are shown below in Figure 3.4.

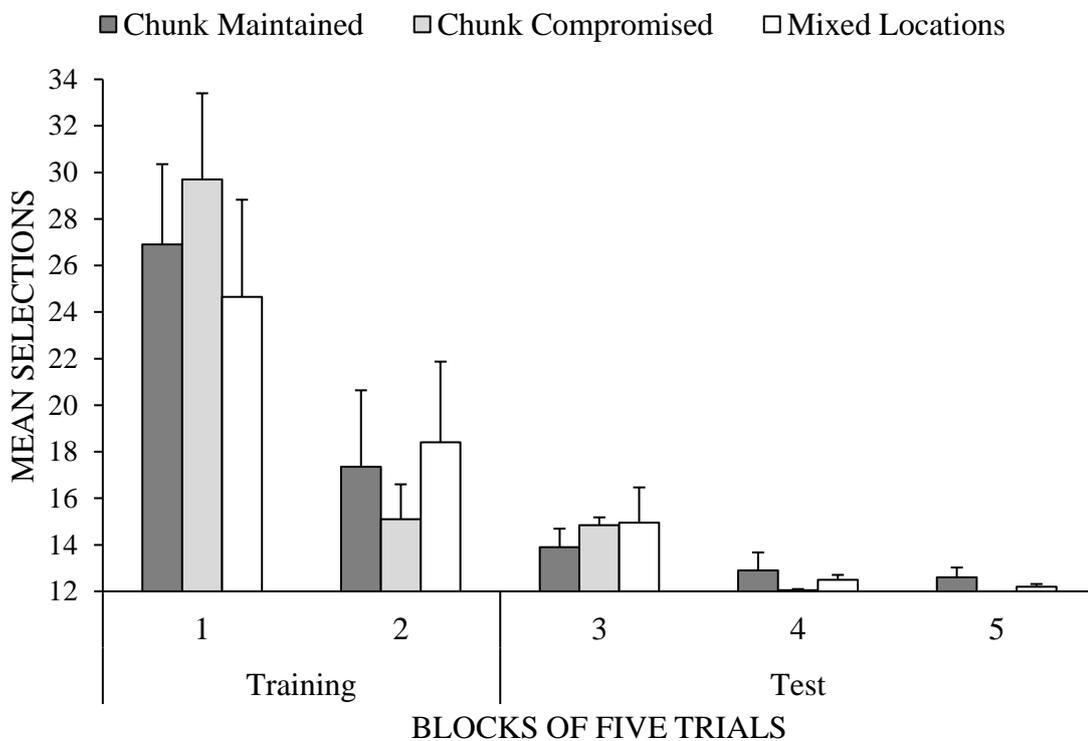


Figure 3. 4 The mean number of selections to completion of a trial in the training and test trials, shown across blocks of 5 trials for each condition with +1 SE bars.

The mean number of selections made in the last 5 training trials was 16.95 ($SD = 5.43$), with all participants reaching the criterion of 15 selections or less. In this block, a one-way ANOVA with Condition and Sex as factors indicated that all participants were performing similarly. There were no significant differences in the mean number of selections made by participants across the three conditions (Condition, $F(2, 6) = .19$, $p = .831$; Sex, $F(1, 6) = .33$, $p = .586$).

A 2 (Blocks) x 3 (Condition) x 2 (Sex) ANOVA was carried out comparing each condition from the last block of training trials to the first block of test trials, which showed no significant effect of Condition, $F(2, 6) = .05, p = .950$. There was no significant effect of Blocks, $F(1, 6) = 1.50, p = .266$, Sex, $F(1, 6) = .03, p = .870$, nor any interactions between the factors, minimum $F(2, 6) = 2.69, p = .147$.

A 3 (Blocks) x 3 (Condition) x 2 (Sex) ANOVA comparing the test trials was carried out. A significant effect of Blocks, $F(2, 12) = 5.46, p < .05$, was found, with findings indicating that the mean number of selections continued to decrease across the trials. There was no significant main effect of Condition, $F(2, 6) = .12, p = .889$, Sex, $F(1, 6) = .71, p = .431$, nor any interactions between the factors, minimum $F(2, 6) = 1.43, p = .310$.

Alternations. To assess chunking by food type, the mean number of alternations made between the food types selected was analysed. Figure 3.5 shows the mean number of alternations across the training and test trials.

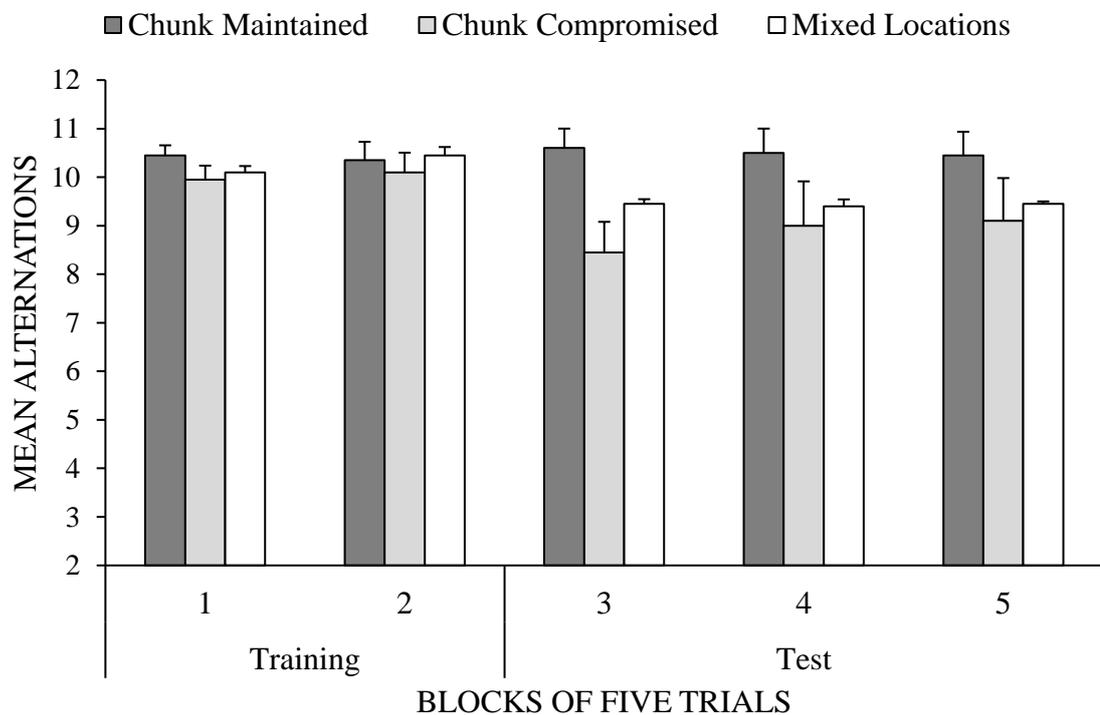


Figure 3. 5 The mean number of alternations made between food types in the training and test trials, shown across blocks of 5 trials for each condition, with +1 SE bars.

The mean number of alternations in the last block of training trials was 10.30 ($SD = .62$) indicating that participants were not using food type as a cue to chunk. A one-way ANOVA with Condition and Sex as factors showed that in this block, the mean number of alternations made by participants in each condition was not significantly different. There was no significant effect of Condition, $F(2, 6) = .41, p = .683$, nor Sex, $F(1, 6) = .41, p = .545$.

To assess changes in search, a 2 (Blocks) x 3 (Condition) x 2 (Sex) repeated measures ANOVA was carried out analysing the number of alternations made by participants in each condition from the last block of training trials to the first block of test trials. There was a significant effect of Condition, $F(2, 6) = 6.05, p < .05$, Blocks, $F(1, 6) = 22.05, p < .01$, and an interaction of Blocks x Condition, $F(2, 6) = 11.35, p < .01$. Pairwise comparisons showed that in the first block of test trials, participants within the CM group ($M = 10.60, SD = .80$) made significantly more alternations than those in the CC group ($M = 8.45, SD = 1.26$), $t(5) = 2.88, p < .05$. There was a significant interaction of Condition x Sex, $F(2, 6) = 5.52, p < .05$, however post-hoc t-test comparisons did not show significant differences, minimum $t(2) = -1.83, p = .207$. There was no significant effect of Sex, $F(1, 6) = .09, p = .775$, nor a significant interaction of Blocks x Sex, $F(1, 6) = 3.39, p = .115$.

Across the three blocks of test trials, a 3 (Blocks) x 3 (Condition) x 2 (Sex) ANOVA was carried out. There was a significant effect of Condition, $F(2, 6) = 6.83, p < .05$, and an interaction of Blocks x Condition, $F(4, 12) = 5.57, p < .01$, with pairwise comparisons indicating that as reported for the previous ANOVA, the difference lay within the first block of test trials, as those in the CM group made significantly more alternations than those in the CC condition. A significant interaction of Condition x Sex was also found, $F(2, 6) = 8.15, p < .05$. Post-hoc t-test comparisons showed that females made fewer alternations ($M = 7.53, SD = .75$) than males ($M = 10.17, SD = .52$), which approached significance, $t(2) = -4.07, p = .055$. There was no significant effect of Blocks, $F(2, 12) = 3.12, p = .081$, Sex, $F(1, 6) = 2.35, p = .176$, nor an interaction of Blocks x Sex, $F(2, 12) = 3.74, p = .055$, despite approaching significance.

The tendency for participants in the CM condition to make more alternations in the test trials than those in the CC and ML groups could be explained by the logistics of dissociating the organisation of the search space from the items found at each rewarded location. As the CM condition exchanged whole chunks, the items found at each location remained dissociated from the structure. The CC condition however, consisted

of switching food types with two other food types, resulting in two apple and two honey jar locations in the same column (Figure 3.3). Similarly, the nature of the ML condition consisted of a number of like-items across the trials appearing in the same row or column, confounding the dissociation from spatial organisation. If participants in these conditions were using a spatial search strategy, they would therefore be more likely to make fewer alternations than the participants in the CM group.

Path Analysis. The low number of selections made by participants and the relatively high number of alternations suggests that humans were searching efficiently throughout the array of locations but were not using food type as a cue to chunk. The proportion of consecutive selections that were in the same row or column was calculated to assess use of spatial structure, and was compared to the proportion of consecutive selections that were to the nearest, unsearched location, to assess whether this could be explained by location proximity. Both measures were calculated using the test trials where the participant had found all foods within 12 selections. A paired samples t-test showed that the proportion of selections to locations in the same row or column ($M = .69$, $SD = .11$) was not significantly different to the proportion of selections to the nearest unsearched location ($M = .67$, $SD = .11$), $t(12) = .379$, $p = .711$, indicating that both strategies may play an important role in search.

To further assess the use of spatial strategies, binomial tests were run to examine whether participants were more likely to select locations within the same row or column before moving to the next row or column, significantly more than chance level. For each participant, all test trials where all foods were found within 12 selections were analysed to calculate a combined probability. After the first selection, the probability that the next choice would be in the same row or column was calculated. For example, using Figure 3.6, if the first choice was to location N, the probability that the second choice would be to S or D, would be $2/11 = 0.18$. If the second choice was to P, then the probability that the third choice would be to U, A, R or S would be $4/10 = 0.4$. The probabilities were combined to provide a mean probability for each trial. These were averaged to calculate an overall probability across the trials for each participant. The first choice on each trial was omitted, and all subsequent observed choices were labelled '1' if that choice was in the same row or column as the previous selection, or '0' if that choice was at another location in the array.

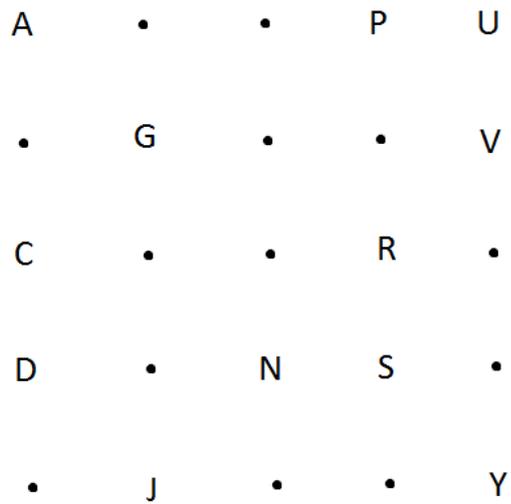


Figure 3. 6 The locations of the rewarded poles in the matrix.

The binomial tests indicated that all participants selected consecutive poles that were in the same row or column more often than expected if all locations were to be chosen equally, $p < .01$.

3.2.3 Discussion

Participants efficiently learned the locations of hidden food rewards and quickly arrived at the optimum number of selections to complete each trial. The high number of alternations made throughout suggested that participants were not chunking food locations together, with the results suggesting that humans spontaneously deploy a spatial search strategy. The results also suggest that humans search using a combination of spatial search strategies and benefit from using the structure of the search space in concordance with searching locations that are nearby, rather than relying on the type of food found at each location to direct search. Taken together with the results described in Chapter 2 that humans are motivated to reduce cognitive as opposed to energetic costs, this suggests that participants place a large importance on the spatial constraints of the search space, which is consistent with the findings of De Lillo and colleagues (De Lillo, 2004; 2012; De Lillo & James, 2012; De Lillo et al. 2013). A marginal effect of Sex was found, indicating that males tended to make more alternations between food types than females, though this only pertained to the CC condition. Generally, no significant

sex differences were found suggesting that both males and females are efficient at foraging under these conditions. The findings suggest that when there is the option to group like-items together, humans show a strong tendency to use a search strategy which exploits the structure of the search space.

Whilst humans do not appear to spontaneously chunk by food type to aid recall of rewarded locations, the extent to which this search strategy benefits or hinders performance remains unclear.

3.3 Experiment 3

During free search, Experiment 2 showed a strong tendency for humans to use the spatial constraints of a search space to aid recall, and participants did not spontaneously use the items found at each location to chunk locations together. It is unknown whether a chunking by food type strategy would be beneficial to search performance or whether participants chose not to deploy this strategy due to greater cognitive costs that may hinder performance. To assess this, Experiment 3 introduced participants to a chunking by food type strategy.

3.3.1 Methods

Participants. A new group of 11 participants took part in this experiment. Undergraduate students and volunteers from the university (5 female and 6 male) took part for course credit or were paid for their time. Participants had a mean age of 22.73 ($SD = 5.00$), with an age range of 18-31 years.

Design and Procedure. The same VR equipment and virtual environment as described for Experiment 2 was employed. This experiment also implemented the same design as described for the previous experiment, however only the CM and CC conditions were used to assess chunking proficiency. As the aim of this experiment was to determine whether participants are able to learn a chunking by food type strategy, the ML condition was not required. Participants were instructed to find the hidden foods, and in addition, they were asked to find the foods in food type order. Participants were required to exhaustively search locations for a specific food type, before switching to search for a different food type. Participants could choose whether to visit carrot, apple, or honey jar locations first, second, or third. It was anticipated that this would be more difficult for participants, thus they completed 15 training trials before the 15 test trials.

To prevent participants from anticipating a change after the training trials, participants completed 3 sessions of 10 trials to ensure that the change occurred mid-session. In this way, they completed 10 training trials, 5 training + 5 test trials, and finally 10 test trials. Participants were assigned to either the CM or the CC condition, and were given a short break after the second session.

Measures. A criterion of 15 selections or less by the last training trial was used, with an additional criterion of 3 alternations or less, to ensure they had learned the locations of the foods and were chunking by food type. Accuracy and the mean number of alternations were calculated as described for Experiment 2.

3.3.2 Results

Accuracy. The mean number of selections until a trial was completed are shown in Figure 3.7 for the training and test trials of the CM and CC conditions.

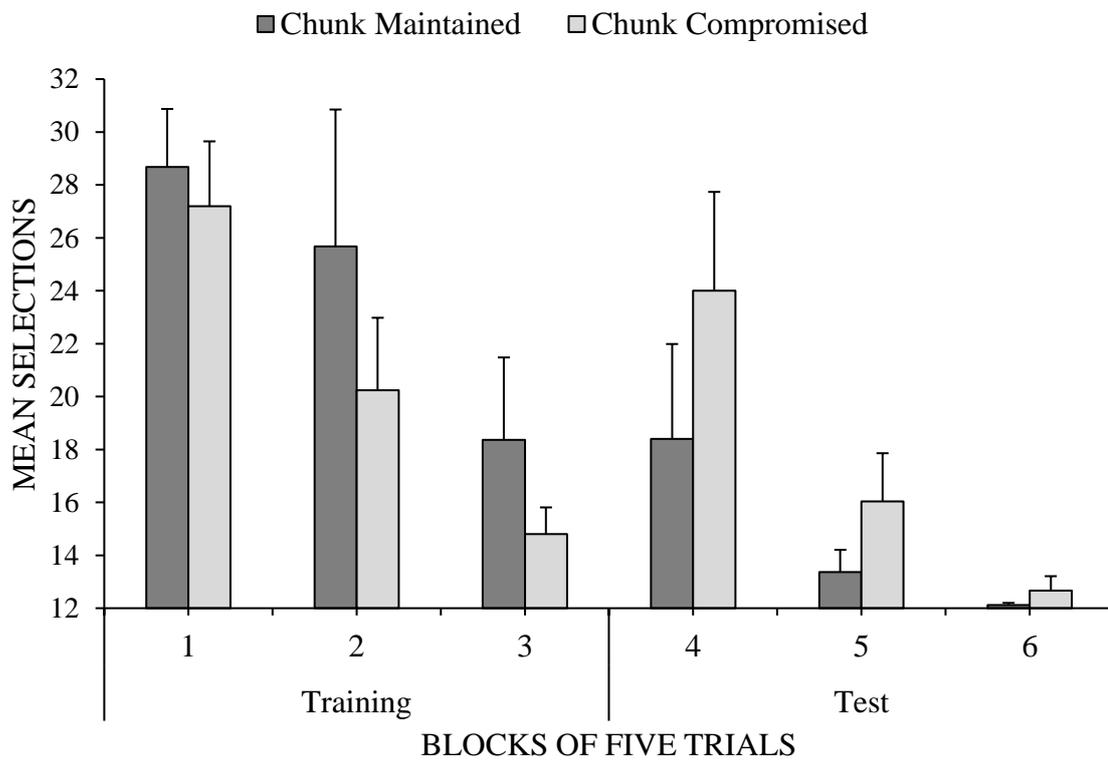


Figure 3. 7 The mean number of selections to completion of a trial in the training and test trials, shown across blocks of 5 trials for each condition, with +1 SE bars.

The mean number of selections in the last 5 training trials was 16.42 ($SD = 4.99$). All participants reached the criteria required of 15 selections or less in the last block. All participants performed at a similar level, as indicated by an independent samples t-test which showed that there was no significant difference between the mean number of selections in the last block of training trials made by participants in the CM and those in the CC group, $t(9) = 1.20, p = .260$. An independent samples t-test further indicated that in this block of trials, there was a trend for females ($M = 19.96, SD = 5.45$) to make more selections than males ($M = 13.47, SD = 1.78$), which approached significance, $t(4.71) = 2.56, p = .054$.

From the last block of training trials to the first block of test trials, a 2 (Blocks) x 2 (Condition) x 2 (Sex) repeated measures ANOVA, showed no significant effect of Blocks, $F(1, 7) = 3.45, p = .106$, Condition, $F(1, 7) = .02, p = .906$, nor interactions between Blocks x Condition, $F(1, 7) = 3.32, p = .111$ and Blocks x Sex, $F(1, 7) = 6.75, p = .202$. A significant effect of Sex was found, $F(1, 7) = 11.73, p < .05$, and a significant interaction between Sex x Condition, $F(1, 7) = 11.00, p < .05$. Post-hoc independent samples t-tests showed a trend across both blocks for females ($M = 22.04, SD = 4.94$) to make more selections than males ($M = 16.35, SD = 3.65$), which approached significance, $t(9) = 2.20, p = .055$. Further t-tests indicated that only amongst males, did those in the CC condition ($M = 19.30, SD = 2.36$) make significantly more selections than those in the CM condition ($M = 13.40, SD = 1.28$), $t(4) = 3.80, p < .05$. Amongst females, this difference was not significant (CM – $M = 25.85, SD = 2.19$, CC – $M = 19.50, SD = 4.71, t(3) = 1.72, p = .184$).

Across the three blocks of test trials, a 3 (Blocks) x 2 (Condition) x 2 (Sex) ANOVA was carried out which showed that there was a significant effect of Blocks, $F(1.06, 7.43) = 20.39, p < .01$, as performance improved across the trials. There was no significant effect of Condition, $F(1, 7) = 1.42, p = .272$, Sex, $F(1, 7) = 1.86, p = .215$, nor any interactions between the factors, minimum $F(1, 7) = 1.49, p = .262$, suggesting that participants in both conditions efficiently learned where the virtual rewards were located once the food types were exchanged.

Alternations. The mean number of alternations between food types is shown below in Figure 3.8 for the CM and CC conditions.

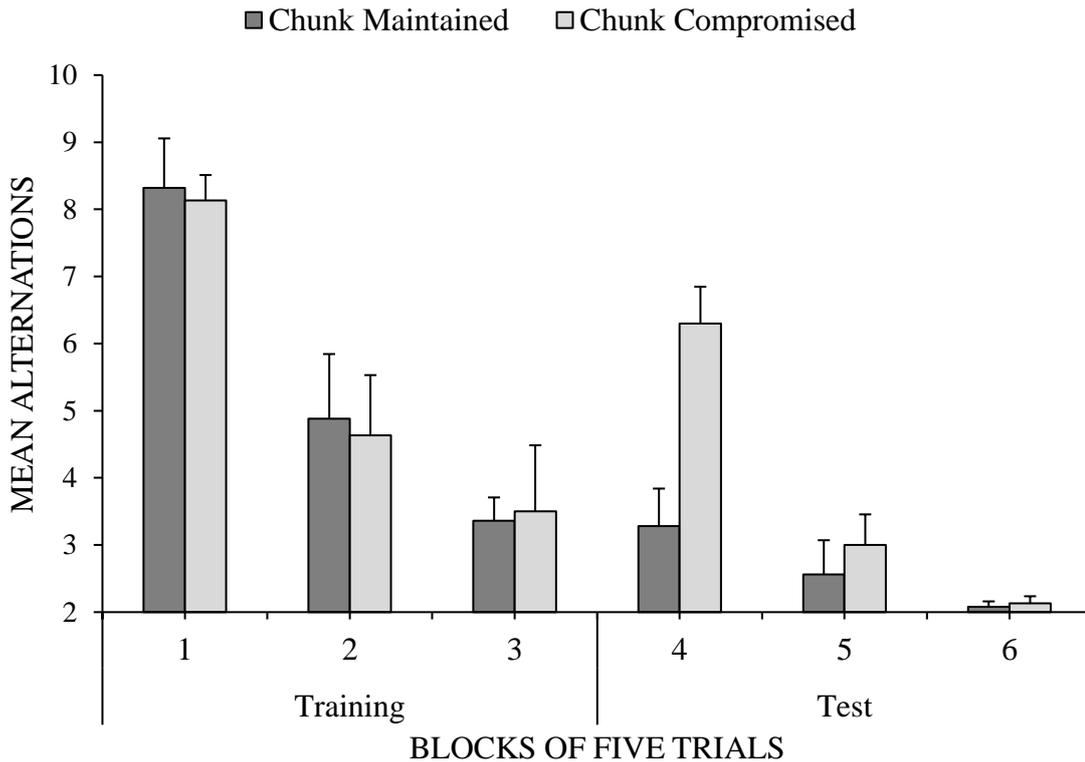


Figure 3. 8 The mean number of alternations made between food types in the training and test trials, shown across blocks of 5 trials for each condition, with +1 SE bars.

In the last block of training trials, all participants reached the required criterion of a maximum of 3 alternations. Participants made a mean number of 3.44 ($SD = 1.48$) alternations, indicating that participants were able to select locations based on a chunking by food type strategy. An independent samples t-test showed no significant difference between those in the CM condition and those in the CC group in training block 3, $t(9) = 1.20, p = .260$, which confirmed that participants efficiently used a chunking by food type strategy before commencing the test trials. A further independent samples t-test indicated that in the last block of training trials, females ($M = 4.08, SD = 1.94$) and males ($M = 2.90, SD = .79$) made a similar number of alternations, $t(9) = 1.37, p = .203$.

A 2 (Blocks) x 2 (Condition) x 2 (Sex) repeated measures ANOVA compared performance from the last block of training trials to the first block of test trials. There was a significant effect of Blocks, $F(1, 7) = 7.12, p < .05$, and an interaction between Blocks x Condition, $F(1, 7) = 7.46, p < .05$. Post-hoc paired-samples t-tests indicated

that participants in the CC condition made significantly more alternations in the first block of test trials when food types were exchanged ($M = 6.30$, $SD = 1.09$) compared to the last block of training trials ($M = 3.50$, $SD = 1.97$), $t(5) = 3.715$, $p < .05$. There was no significant difference for participants in the CM condition between the last training block ($M = 3.36$, $SD = .78$) and the first test block ($M = 3.28$, $SD = 1.25$), $t(4) = .16$, $p = .881$. There was no significant main effect of Condition, $F(1, 7) = 4.60$, $p = .069$, Sex, $F(1, 7) = 2.02$, $p = .198$, nor an interaction of Condition x Sex, $F(1, 7) = .001$, $p = .981$.

Across the test trials, a 3 (Blocks) x 2 (Condition) x 2 (Sex) ANOVA was carried out. There was a significant effect of Blocks, $F(2, 14) = 36.98$, $p < .001$, a significant interaction of Blocks x Condition, $F(2, 14) = 11.32$, $p < .01$, and a significant main effect of Condition, $F(1, 7) = 7.39$, $p < .05$. Independent samples t-tests showed that when the food types were rearranged in the first block of test trials, those in the CC condition ($M = 6.30$, $SD = 1.09$) made significantly more alternations than those in the CM condition ($M = 3.28$, $SD = 1.25$), $t(9) = 4.27$, $p < .01$. All other comparisons were non-significant, suggesting that those in the CC condition quickly returned to an efficient search of the array using a chunking by food type strategy by the second block of test trials. There was no significant effect of Sex, $F(1, 7) = 2.08$, $p = .192$, nor any further interactions, minimum $F(2, 14) = 1.45$, $p = .269$.

Did Chunking by Food Type Benefit Performance? To assess whether this search strategy aided or hindered performance, the mean number of selections made across the first ten training trials of Experiment 2 and 3 were compared, and is shown below in Figure 3.9. A 10 (Trials) x 2 (Experiment) ANOVA was carried out, which showed a significant effect of Trials, $F(4.809, 100.987) = 10.015$, $p < .001$, and a significant interaction between Trials and Experiment, $F(4.809, 100.987) = 2.417$, $p < .05$. Independent samples t-tests indicated that those who were required to use a chunking strategy in the current experiment performed worse than those who could implement their own search strategy in Experiment 2, in trials 3, 6 and 8, minimum $t(21) = -2.16$, $p < .05$. There was no overall significant main effect of Experiment.

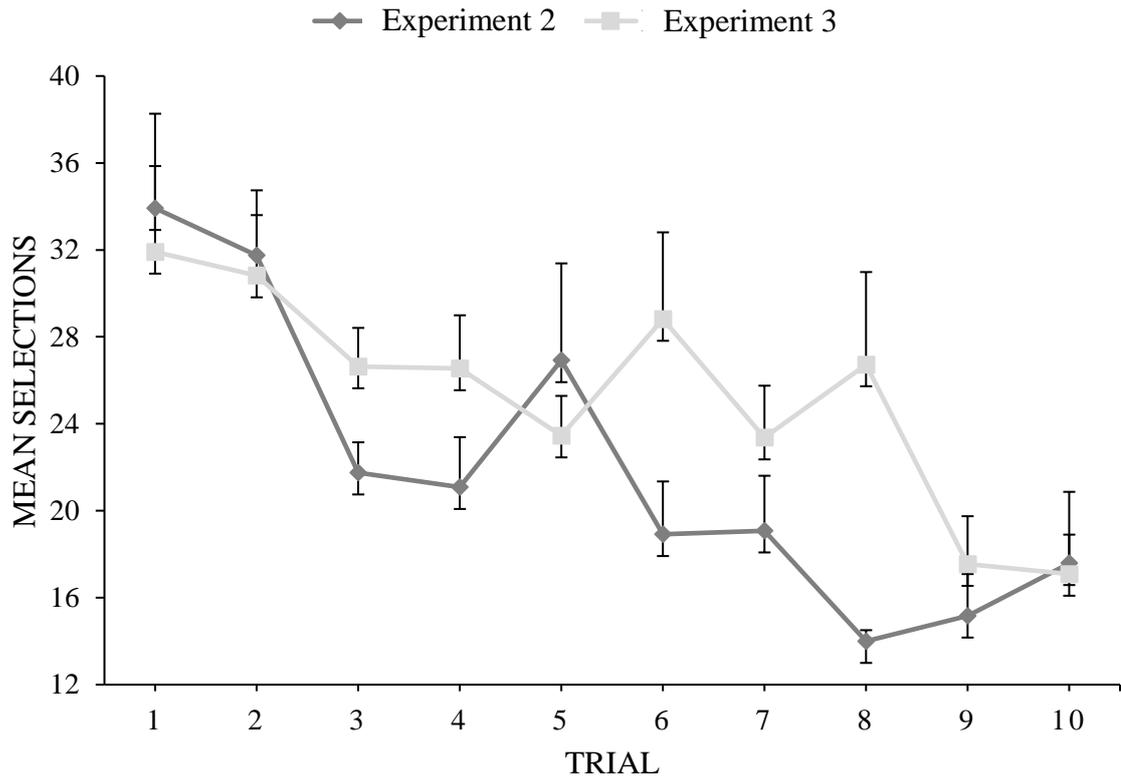


Figure 3. 9 The mean number of selections made to completion of a trial, across the first ten training trials for Experiment 2 and Experiment 3, with ± 1 SE bars.

3.3.3 Discussion

The results of Experiment 3 indicated that humans are efficient at using a chunking by food type strategy. By the end of the training trials, participants made few alternations between food types, and searched by grouping like-items together. The test trials showed that participants in the CC condition who needed to create new chunks once the food types were rearranged were significantly impaired compared to the CM condition, in the first block of test trials only. This suggests that humans efficiently rearrange their memories, and accurately learn new chunks when required to do so, highlighting a difference between human and rat performance (Macuda & Roberts, 1995). Comparing the training trials for Experiments 2 and 3, analyses indicated that participants had a higher accuracy rate during Experiment 2, however humans were able to use and benefit from a chunking strategy. The trend for participants to make more selections in the current experiment suggests that humans needed to learn to chunk by food type and that this strategy may carry a higher cognitive cost.

The results also highlighted a marginal sex difference in the number of selections needed to complete a trial. Females tended to make more selections by the end of the training trials than males, however this did not reach significance. Once food types were exchanged, only males showed a significant increase in the number of selections made. Female performance did not show a significant increase, however, a higher number of selections by females than males may explain why only males were significantly impaired by reorganised chunks. These results suggest that superior object location memory may not serve females specifically in this navigational task (see Silverman & Eals, 1992; Eals & Silverman, 1994; Levy et al. 2005).

A preference to employ a search strategy exploiting the spatial structure of the matrix array is evident, however it remains unclear whether this difference between humans and rats is largely due to the linear search strategy that the matrix array of poles affords. Experiment 3 assessed humans within a radial maze.

3.4 Experiment 4

To assess chunking by rats, a radial maze was used with locations arranged in a circular configuration (Dallal & Meck, 1990; Macuda & Roberts, 1995). The matrix array may have encouraged a linear search strategy, therefore Experiment 4 aimed to replicate the conditions of previous studies with rodents to assess human performance when experiencing the same configuration of locations.

3.4.1 Methods

Participants. A new group of six undergraduate students (3 female and 3 male) from the university took part for course credit. Participants had a mean age of 19.33 years, with an age range of 18-21 years.

VR Apparatus and Environment. The same equipment and virtual hall with textures and landmarks as described for the previous two experiments were used here. A 12-arm radial maze was designed within SketchUp Make 2015, and added to the hall with a pole located at the end of each arm (Figure 3.10). Transparent walls were added between the arms to prevent participants from crossing from one arm to the next and requiring them to return to the central arena before subsequent choices. The dimensions of the maze were based on the maze used by Macuda and Roberts (1995). The central platform had a radius of 60cm, with the arms extending 75cm, and a width of 10cm.

The participants view point was lowered in the virtual environment to replicate the conditions a rat would face in the maze.

Design and Procedure. The same food types as described previously were used here, and each of the poles hid one of the three food types. The foods were arranged so that the same types were not in adjacent locations, dissociating food type from the structure of the search space. As this experiment aimed to assess whether spontaneous chunking would occur in a radial maze, the different conditions were not assessed here. Participants were instructed to find the hidden foods, and completed 10 training trials where food locations were fixed, before completing a further 10 CM test trials in which food items were switched, but retained the chunked locations. Once all foods were found, the trial terminated.

Measures. Performance accuracy and the number of alternations was calculated as described for Experiments 2 and 3.

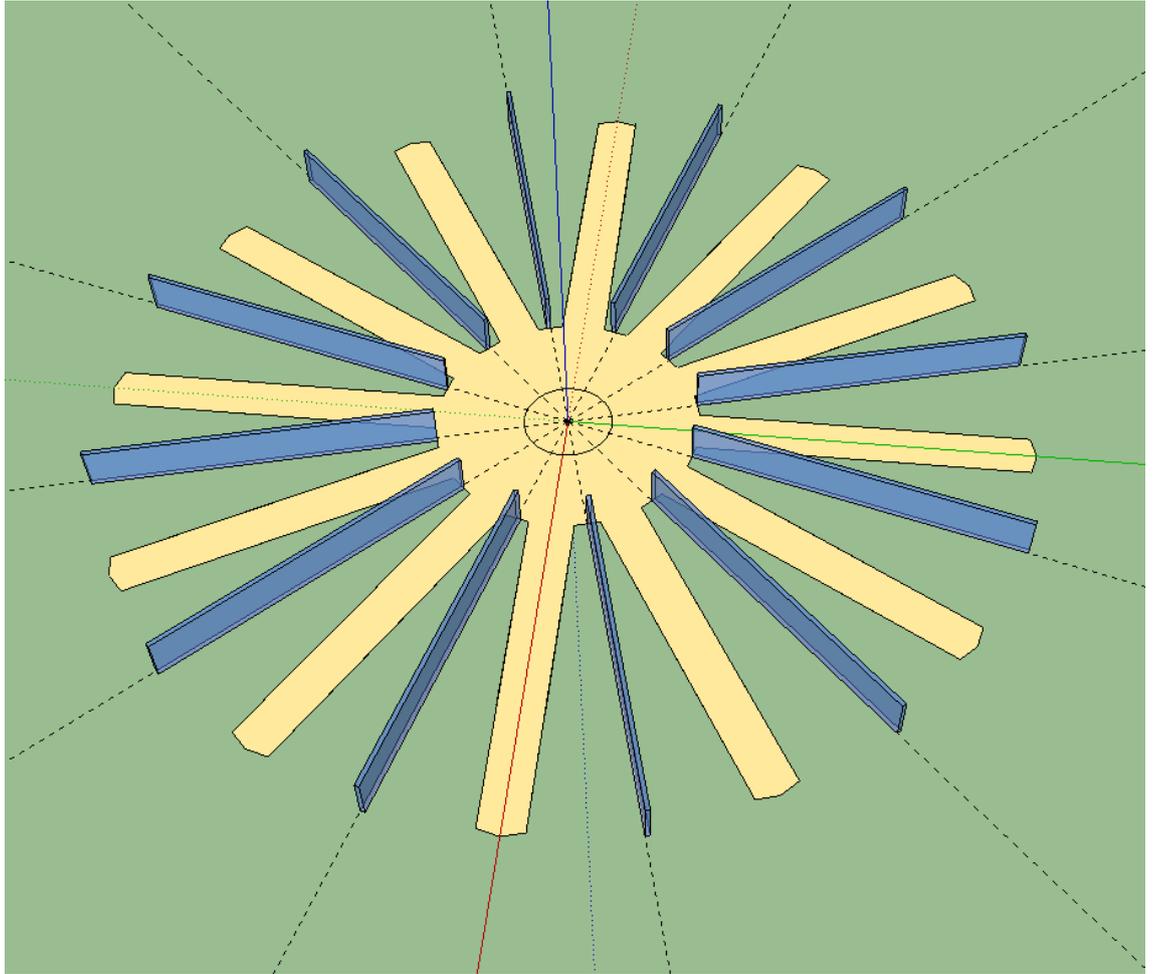


Figure 3. 10 Above: An aerial view of the radial maze as designed in SketchUp; Below: View of the radial maze in the virtual environment.

3.4.2 Results

Accuracy. The mean number of selections in the last 5 training trials was 13.10 ($SD = 1.99$). The means for each block of trials are shown in Figure 3.11. A paired samples t-test was carried out comparing the mean number of selections across the training trials and the CM trials, which showed no significant difference, $t(5) = 1.80$, $p = .132$. Participants were efficient at searching the maze in all trials and performance was not affected by the reorganisation of food types. Comparing male and female performance, independent samples t-tests indicated that in the training trials there was a trend for females ($M = 14.03$, $SD = 1.25$) to make more selections than males ($M = 12.10$, $SD = .17$), which approached significance, $t(4) = 2.65$, $p = .057$. There was no significant difference between females ($M = 12.60$, $SD = .62$) and males ($M = 12.06$, $SD = .12$) in the CM trials.

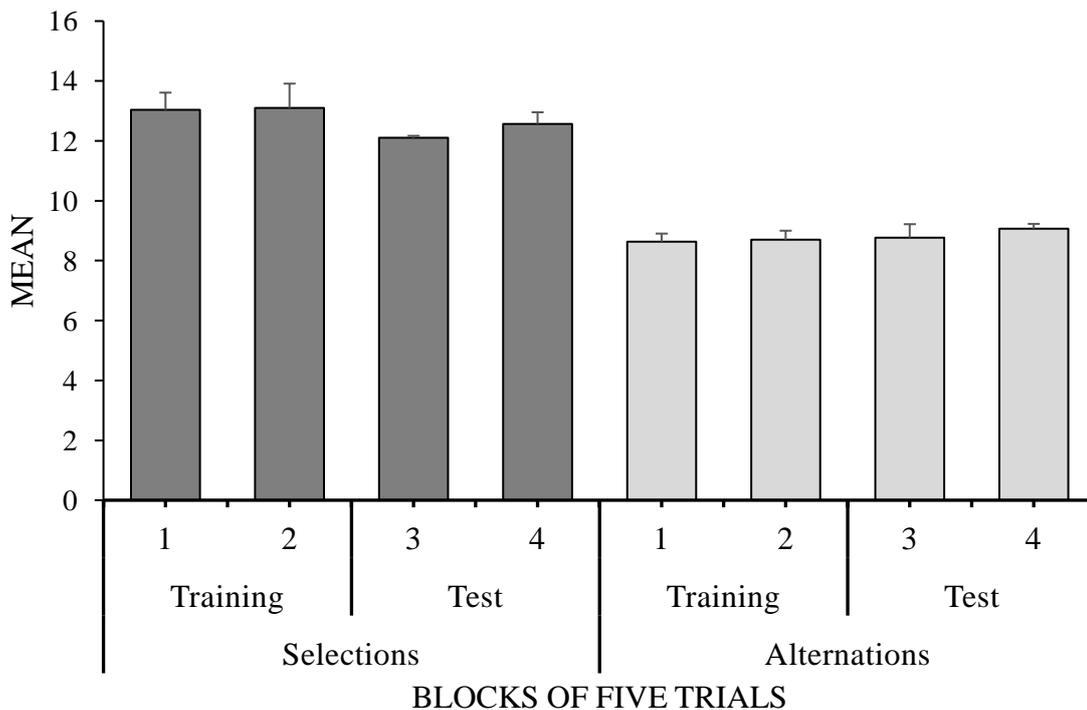


Figure 3. 11 The mean number of selections and alternations made in the training trials and CM test trials, across blocks of five trials, with +1 SE bars.

Alternations. The mean number of alternations across the trials are also illustrated in Figure 3.11. A one sample t-test comparing performance in the last block of training trials ($M = 8.70$, $SD = .73$) against the criterion of 3 alternations set in Experiment 3, showed that significantly more alternations were made, $t(5) = 19.00$, $p <$

.001, indicating that participants were not spontaneously using a chunking by food type strategy. A paired samples t-test further suggested this, as there was no significant difference between the mean number of alternations in the training trials and the test trials when food types were exchanged. To compare differences between the sexes, independent samples t-tests indicated that females ($M = 8.40$, $SD = .95$) and males ($M = 8.93$, $SD = .21$) performed similarly in the training trials, $t(4) = -9.46$, $p = .398$. Performance was also non-significantly different in the CM trials (female – $M = 8.80$, $SD = 1.11$, male – $M = 9.03$, $SD = .06$, $t(4) = -.36$, $p = .735$).

Spatial Search Strategies. As in Experiment 2, the results indicated that participants efficiently searched the locations, though did not appear to search by food type, as shown by the high number of alternations. To assess the search strategies deployed, arm movement was calculated. Arm movement was defined as the number of arms between the arm the participant had just exited and the arm where a pole was next selected. For each pole selection, a value of 1 was assigned to an adjacent arm entry, and values of 2, 3, 4, 5 or 6 were assigned to entries 2, 3, 4, 5 or 6 arms away from the arm just exited. Binomial tests assessed the prevalence of an adjacent arm search strategy. Of the 6 participants, 5 participants were significantly more likely to enter an adjacent arm than a non-adjacent arm, $p < .001$. One participant did not appear to use this strategy, and instead employed an alternative spatial strategy. A further binomial test showed that this participant was significantly more likely to enter opposite arms than adjacent or other non-opposite arms, $p < .001$.

3.4.3 Discussion

There was a strong tendency for participants to spontaneously deploy a spatial search strategy when searching for hidden food items within the radial maze, again supporting previous studies assessing the importance of spatial structure in search (De Lillo, 2004; 2012; De Lillo & James, 2012). The near optimum number of selections made in both the training and test trials showed that humans are very efficient at searching this configuration of locations, whilst the high number of alternations between food types suggested that humans were not using a chunking by food type strategy. The binomial tests confirmed that all participants were using a spatial search strategy, and either searched adjacent or opposite arms to aid recall.

3.5 General Discussion

In this VR task, humans spontaneously deployed a spatial search strategy when given free, unrestricted search of both a matrix of locations and a radial maze and did not appear to use the foods found at each location to direct search. Participants efficiently learned the locations of the hidden food items using this spatial strategy, though the high number of alternations between the different food types indicated that participants did not chunk like-items together, unlike rats who were found to spontaneously deploy a chunking strategy (Dallal & Meck, 1990; Macuda & Roberts, 1995). This finding makes an important distinction between rat and human cognition, and highlights the importance of testing humans within animal paradigms to ascertain where similarities and differences lie. Participants appeared to benefit from employing a chunking by food type strategy when required to do so, and search for the food rewards remained efficient. Once food types were exchanged in the test trials, participants who were required to form new chunks were efficient at reorganising memory in this way and quickly returned to a similar level of performance as participants who experienced trials where chunked locations remained consistent. This differs to the results of Macuda and Roberts (1995) who found that by the end of the test trials, rats in the chunk compromised group did not reach the same level of accuracy as the group where chunk integrity was maintained.

3.5.1 Differences in Foraging Strategies

An obvious difference between the current set of experiments and the studies carried out with rats (Dallal & Meck, 1990; Macuda & Roberts, 1995) is the use of real food items and virtual foods. The search strategy shown by rats, described as chunking, may be due to food preferences. Rats visited their most preferred food first, and this motivational factor would also result in a search strategy which decreases the number of alternations between food types. In a similar task with hidden food items, chimpanzees have been found to direct their searches to locations containing preferred fruit first, before searching for less-preferred vegetables (Menzel, 1973), suggesting that food preference is an important factor. The chunking by food type strategy deployed by rats, and visits to preferred foods first, may be an indication of rats following an optimal foraging strategy to exploit specific patches (Charnov, 1976; Cohen et al. 2003), and to reduce predation risks (Brown, 1999). Memory for where the preferred foods are

located within the maze therefore may be an indirect result of this, resulting in an organised search pattern.

Humans however do not face the same evolutionary pressures during foraging, and this may explain why search strategies differ between humans and rats. Participants completed the maze by searching adjacent or opposite arms, which was a strategy also deployed by marmosets (*Callithrix jacchus jacchus*) in a similar search task requiring hidden foods to be found (MacDonald, Pang & Gibeault, 1994). Roitblat, Tham and Golub (1982) suggested that a high level of performance on a radial maze task however may be simply explained by the use of algorithmic patterns. Their results found that Siamese fighting fish (*Betta splendens*) showed a tendency to enter adjacent arms in a water version of the maze, suggesting that performance may not depend on a high-level cognitive system. These studies and findings suggest that the search strategies a species employs can be explained by the foraging pressures they face. Whilst further studies assessing humans using real food items would be informative, the current experiments suggest that humans appear to minimise the time taken, effort, and memory load, and thus choose the simplest search strategy which follows the structure of the search space.

3.5.2 Spatial Structure in Search

A propensity to use the spatial constraints of a search environment for data reduction appears to be very strong in humans (De Lillo, 2004; 2012; De Lillo & James, 2012; De Lillo et al. 2013). In the current set of experiments, we ensured that the structure of the search space was dissociated from the food type found at each location. However, to chunk by food type would require the participant to cross rows and columns of the matrix, which would in turn increase the distance to-be-travelled through the search space. As the results described in Chapter 2 suggest that a motivation to reduce cognitive load plays a larger role in spatial memory than the energetic cost of travelling a further distance through the search space (see De Lillo et al. 2013), it can be suggested that a preference to search using the spatial structure of the search arrays as opposed to chunking by the items found at each location is unlikely to be due to a reluctance to travel a larger distance.

3.5.3 Object Location Memory

The findings of these studies do not support the notion of a sex difference in ability to search for hidden food items. This finding is in contrast with previous studies

reporting a female advantage in object location tasks (Silverman & Eals, 1992; Eals & Silverman, 1994; Levy et al. 2005), but supports previous studies which did not find an effect of sex in navigational tasks (Astur et al. 2004; Levy et al., 2005; Iachini, Sergi, Ruggiero & Gnisci, 2005). It is possible that the navigational aspect of this task requiring participants to walk through a three-dimensional environment, had an impact on these results. The results reported in Chapter 2 indicated that males outperformed females when recalling pathways through an array of locations, thus in this task, females may be impaired by the spatial aspect and males may more accurately recall the locations of objects within a navigational space. If male performance excels within a navigational space, and females show a proficiency for object location tasks, then this may explain why males and females performed similarly in this task.

3.5.4 Conclusions

The results show that humans have a very strong tendency to use the spatial structure of a search space to guide search, and are most likely to devise the simplest and least cognitively demanding strategy to solve a task. Previous studies show that rats appear to chunk by the food type found at each location to perform a more efficient search, however these findings can also be explained by an optimal foraging strategy to exploit patches of food. The fact that humans do not appear to use this strategy raises questions about the extent to which we can attribute human cognitive competences to non-human species in the absence of experiments testing both study species within the same paradigm.

It may therefore be the case that a cognitive ability to detect and use structure during search is characteristic of primate cognition (Milton, 1981a; 1993; De Lillo et al. 1997; De Lillo, 2012). To further understand this propensity in humans, it is useful to consider the environmental situations within which our cognition evolved. Chapter 4 further considers this in relation to primate foraging and the requirements of foraging within variable forest conditions.

Chapter 4: Detection of Temporal Structure in Search

4.1 Introduction

The findings presented in Chapters 2 and 3 highlighted the importance of spatial structure in search cognition, and suggest that an ability to detect and benefit from structure may be characteristic of high-level cognition in primates. Of particular relevance to spatial cognition, is the notion that many cognitive competences we possess today are thought to have evolved from foraging behaviour. Foraging is directly related to individual fitness and so intuitively, the cognitive skills required for efficient foraging, including WM skills (Coolidge & Wynn, 2005), route planning (Wiener & Mallot, 2003; Noser & Byrne, 2007a; 2010; Janson, 2007), wayfinding (see Golledge, 1999), ability to mentally represent spaces (Tolman, 1948; Noser & Byrne, 2007b; Normand & Boesch, 2009), and a preference for structured pathways to ease memory load during search (Bor et al. 2003; De Lillo & James, 2012; De Lillo et al. 2013), would have been selected for in humans and across the primate lineage.

4.1.1 Evolutionary Pressures

Whilst the exact conditions that our hominin ancestors faced during foraging are unknown, evidence suggests that hominins initially evolved within forest environments prior to savannahs (Lovejoy, 1981; Milton, 1981a). More recently, discoveries have suggested that our earliest hominin ancestor, *Ardipithecus ramidus*, exploited both arboreal and terrestrial competences, dwelling within a wooded habitat (White et al. 2009; Louchart et al. 2009). *Ar. ramidus* is considered to be omnivorous, however, considering this ancestors arboreal abilities and our evolved preference for fruit and sugars that we share with other primate species (see Breslin, 2013), the sophisticated cognitive competences seen in extant chimpanzees today may be a relic of the capabilities that existed in our last common ancestor. The frugivorous diet of ancestral primates is thought to have played an important role in the evolution of complex cognitive abilities (Milton, 1981a; 1993; see Zuberbühler & Janmaat, 2010, and Fleagle, 2013, for a discussion), due to the nature of living and foraging within such complex and variable environments. Comparatively, the brain sizes of primarily folivorous species are smaller than that of species who are frugivorous or omnivorous (Harvey et al. 1980), highlighting a relationship between diet and cognitive capacity. Milton (1981a) hypothesised that it was this propensity to forage on fruit in a forest

environment which triggered cerebral expansion in primates. This suggests that the benefits of feeding on irregular and ephemeral resources must be considerable enough to account for a larger and more expensive brain size (Milton, 1981a).

4.1.2 Temporal Structure in Foraging

Sophisticated cognitive competences are required for efficient search within a forest environment, including LTM to remember which locations are never profitable, WM to avoid revisiting recently depleted locations, and an understanding of ephemeral availability to detect fruiting patterns of different tree species, which taps prospective memory. Primates that rely largely on fruits, therefore must know where to find fruit and when. Chimpanzees in particular have been observed to inspect trees of species which are most likely to yield fruit (Janmaat et al. 2013a), appear to use long-term memory of ‘what-where’ information to guide search (Janmaat, Ban & Boesch, 2013b), and also take into account the amount of fruit they expect to find (Ban et al. 2014). Janmaat and colleagues (Janmaat et al. 2012; 2013a; Ban et al. 2014) have suggested that frugivorous primates use synchronicity information, described as the ‘simultaneous production of fruit in tree individuals of the same species within clustered time periods’ (Janmaat et al. 2013a, p853). Their findings suggested that mangabey monkeys and chimpanzees use this information during foraging, and visit more trees that are in fruiting season than tree species that did not bear any fruit. Janmaat et al. (2012; 2013a) analysed the number of occasions inspections were made to an individual tree of a highly synchronous species but where there were no fruits available, resulting in the likelihood of these species using other environmental cues, such as visual or olfactory cues, as a guide being very low, and provided further support that primates appeared to be using the synchronicity of species to direct their search.

4.1.3 Mental Representations or Associative Learning?

How non-human primates know where to forage is unclear and difficult to assess within natural foraging environments. It is possible that they acquire mental representations of their environment during foraging in the form of cognitive maps. Tolman (1948) proposed that cognitive maps may be used to represent relationships between stimuli in the environment and to signify the different routes an individual could take. Field observations by Normand & Boesch (2009) saw chimpanzees locating specific trees even when travelling from different directions and taking different paths,

suggesting that chimpanzees use sophisticated and flexible mental representations of their environment. Despite the difficulties of assessing mental representations in primates, particularly in natural foraging situations, primate researchers agree that it is likely that primates do mentally represent their environment in one way or another (see Zuberbühler & Janmaat, 2010; Janmaat et al. 2006; 2012; 2013a; Ban et al. 2014).

Menzel (1991) found that when Japanese macaques were presented with the fruit of a vine species, they were more likely to inspect other vines of the same species than alternative food sources. Whilst this may be indicative of an ability to detect information concerning ephemeral availability and synchronicity, this propensity to search items of the same species, may be an associative strategy which uses visual cues to guide search. A number of studies have suggested that visual cues do not play a large role in primate foraging (Dominy, Garber, Bicca-Marques & Azevedo-Lopes, 2003; Sumner & Mollon, 2000), though search strategies which rely on temporal information or visual cues do not necessarily require the acquisition of spatial information for specific trees. Associative learning theory would suggest that in a foraging situation, individuals will attend to salient visual and olfactory cues over the exact spatial location of specific trees, which is equally predictive of reward location yet less salient. Overshadowing therefore occurs when an individual does not learn to attend to secondary, less salient cues (Mackintosh, 1971; 1976). This effect of overshadowing has been demonstrated in rats (Mackintosh, 1971; 1976; Kosaki, Austen & McGregor, 2013), pigeons (Spetch, 1995), and humans (Prados, 2011; Vadillo, Bárcena & Matute, 2006), and has been observed with humans in a virtual Morris water task (Chamizo, Aznar-Casanova & Artigas, 2003). However, the effect of overshadowing found by previous studies has been during the search for a single target. To our knowledge, this has not been tested within a foraging situation where multiple targets must be found.

This set of experiments aimed to assess human ability to detect and predict ephemeral availability within an evolutionarily-relevant task modelled upon real foraging situations. Within natural foraging environments, visual and olfactory cues cannot be separated from the spatial locations of individual trees. However, VR allowed the manipulation of these cues to assess the extent to which visual and spatial information contributes to successful foraging. Considering theories of sex differences in spatial memory, male and female performance was also compared in this foraging task.

4.2 Experiment 5

During foraging, individuals must be efficient to avoid over-expending energy. Foraging efficiency can be decomposed into a number of cognitive competences which include LTM to avoid locations that never yield fruit, WM to remember which locations have recently been visited and depleted during a foraging bout, and an ability to detect fruiting patterns to direct searches to trees that are most likely to be profitable. Experiment 1 solely manipulated the temporal availability of rewards, and presented either a predictable or unpredictable pattern across trials. This experiment assessed efficiency in a VR foraging task, whilst presenting a temporal pattern of food availability across trials, to assess whether humans spontaneously detect and use this information to direct searches to locations yielding virtual fruit rewards.

4.2.1 Methods

Participants. Twenty participants (10 female and 10 male), aged between 18-39 years ($M = 23.15$, $SD = 5.03$ years), were recruited among students and staff from the university. They received course credit or were paid a small fee for their time.

VR Apparatus and Environment. Participants were tested in a VR psychology lab at the university. Vizard 4.0 software was used to present the virtual environment, which participants viewed via Nvidia 3D glasses. A handheld wand with a thumb operated joystick was used to navigate and produce responses by pressing a trigger with the forefinger, which was analogous to chimpanzees checking for the presence of fruit. Janmaat et al. (2013a) assessed the number of occasions chimpanzees checked trees by raising their head and looking up into the canopy for fruit. In a similar manner, the rewards to be found in this task could not be found unless a location was checked by using the wand to select it.

The virtual environment was the same textured hall with landmarks as described within Chapters 2 and 3. This included two doors, two sofas, a bookcase, and three paintings, whilst the locations to be searched were white poles surmounted by a coloured sphere (see Figure 4.1). Bearing in mind estimates of home range sizes with minimum estimates being 50 trees (Zuberbühler & Janmaat, 2010), and task constraints, an array of 36 locations was used. Six colours represented different tree species, with six poles of each colour arranged as a 6 x 6 matrix. In this way, the matrix included six

spheres of blue, white, green, purple, red, and orange poles. The poles were arranged with one of each colour within each row and column of the matrix.



Figure 4. 1 The virtual room with landmarks and the pole array.

Design and Procedure. Each trial in this task represented a foraging bout, and within each trial 12 locations yielded a reward of a virtual apple, thus in any given trial two ‘tree species’, or colours, were rewarded. Once a pole was selected, the message ‘Pole Selected’ appeared, and if a virtual apple reward was hidden at that location, a picture of the apple found was also shown. Participants were informed that they could only ‘take’ the apple once from a rewarded location, and any other selections to that pole would only show the message ‘Pole Selected’.

Participants were alternately assigned to one of two conditions; predictable or unpredictable. The conditions manipulated the predictability of reward availability, which represented the synchronicity of fruiting trees across trials. In the predictable condition, poles were rewarded according to a double alternation, with two species (purple and green, PG) yielding apples for two trials, followed by two other species (blue and white, BW) yielding apples for the subsequent two trials. This pattern was repeated across all trials. In the unpredictable condition, the same pairs of colours were

rewarded together, however, which species would be rewarded could not be predicted at the outset of a trial. The order in which each pair of colours was rewarded changed pseudo-randomly across trials, with no more than 5 trials in a row yielding rewards in the same locations. In both conditions, red and orange poles remained unrewarded. In this way, the sole manipulation was the temporal pattern of food availability across trials, which is where a difference between the two conditions was expected. There were also two patterns that all participants could detect; i) if a pole of one species was rewarded, then all poles of that species will also be rewarded, and ii) if a pole of one species was rewarded, then there will be another species that will be simultaneously rewarded.

Participants were instructed to navigate through the VR environment and search for fruit by checking the poles. They were told that each trial would terminate once all apples had been found, but were not informed of the number of apples hidden. In total, they completed 40 trials and were given a short break of 10 minutes when required.

Measures. An overall measure of foraging efficiency calculated the mean number of selections until all apples were found, with an optimum number of 12 selections. To assess LTM, the mean number of visits in each trial to locations that never yielded a reward was calculated. The number of revisits to poles previously selected within a trial was also calculated to measure WM ability. To assess the extent to which participants predicted the availability and location of fruit on the basis of its cyclical nature, the proportion of correct first choices made was calculated. Using the first selection made in each trial, a score of 1 was given to trials where a rewarded pole was chosen first, whilst a score of 0 was given to selections of an unrewarded pole, which included poles that were rewarded in other trials and also poles that never yielded a reward.

4.2.2 Results

Overall Foraging Efficiency, Long Term Memory, and Working Memory.

Participants in both the predictable ($M = 15.07$, $SD = 1.84$) and the unpredictable group ($M = 15.70$, $SD = 2.10$) made a similar number of selections until the completion of a trial, made few visits to locations which never yielded a reward (predictable, $M = 1.06$, $SD = .68$; unpredictable, $M = 1.24$, $SD = .85$), and made few revisits to locations previously searched within a trial (predictable: $M = .99$, $SD = .30$; unpredictable: $M =$

1.22, $SD = .27$). As shown in Figure 4.2, participants in both conditions became more efficient at searching the array.

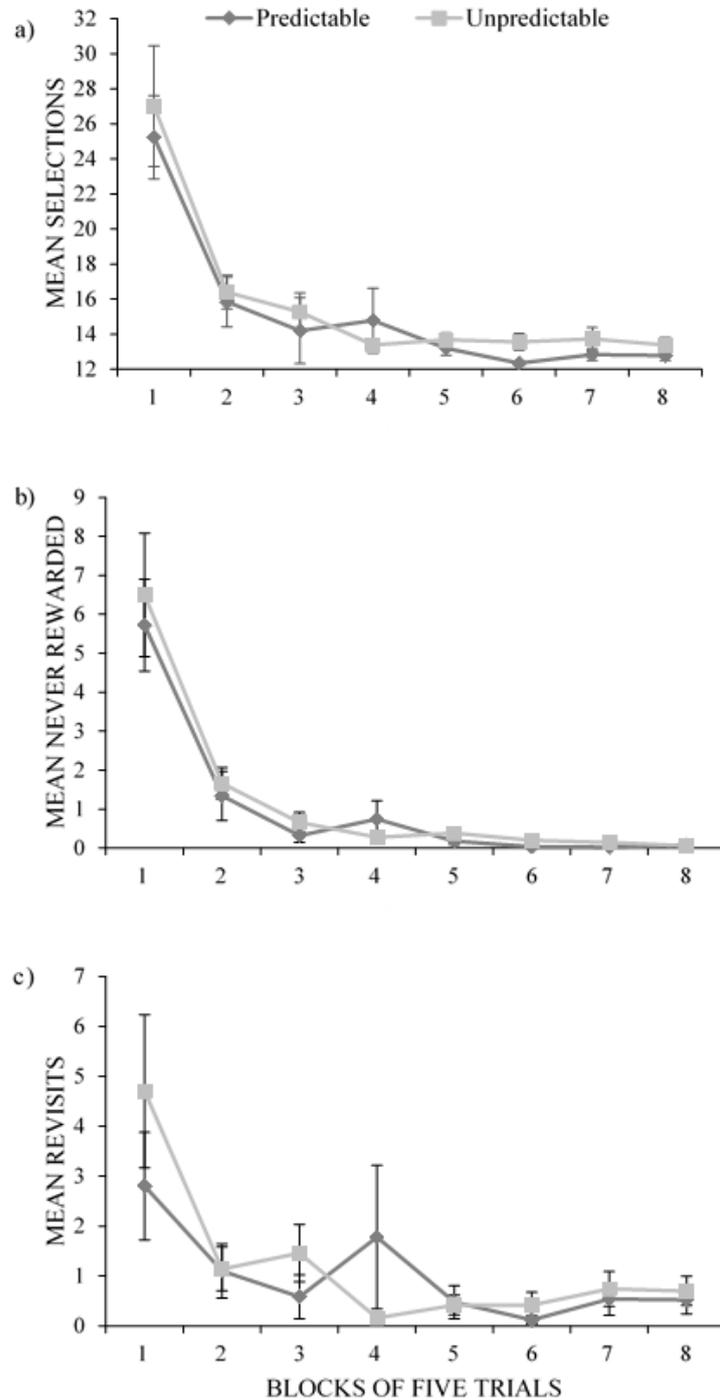


Figure 4. 2 The foraging efficiency measures shown across each block (± 1 SE bars) for the predictable and unpredictable conditions; a) mean selections made until the completion of a trial; b) mean never rewarded poles selected; c) mean revisits.

Three 8 (Blocks) x 2 (Condition) x 2 (Sex) ANOVAS were carried out, which showed a significant effect of Blocks for the mean number of selections, $F(2.43, 38.83) = 24.59, p < .001$, mean number of never rewarded poles selected, $F(1.42, 22.75) = 31.03, p < .001$, and the mean number of revisits, $F(2.81, 44.98) = 5.87, p < .01$. Paired samples t-tests indicated a significant decrease in the mean number of selections from block 1 ($M = 26.12, SD = 9.16$) to block 2 ($M = 16.12, SD = 3.75$), $t(19) = 5.33, p < .001$, which was also found for the mean number of never rewarded poles selected (block 1, $M = 6.11, SD = 4.31$; block 2, $M = 1.50, SD = 1.64$), $t(19) = 5.42, p < .001$. Post-hoc comparisons showed no significant differences between the blocks for the number of revisits, $p > .05$. For all measures, there was no significant main effect of Condition, minimum $F(1, 16) = .46, p = .508$, Sex, minimum $F(1, 16) = .29, p = .598$, nor any significant interactions, minimum $F(2.81, 44.98) = 1.54, p = .220$.

Detection of the Temporal Pattern. The proportion of correct first choices made by participants in the predictable condition was 0.73 ($SD = .15$), whilst those in the unpredictable condition had a mean proportion correct of 0.42 ($SD = .07$), indicating that those in the predictable group were directing their searches to correct locations more often than those in the unpredictable group (Figure 4.3).

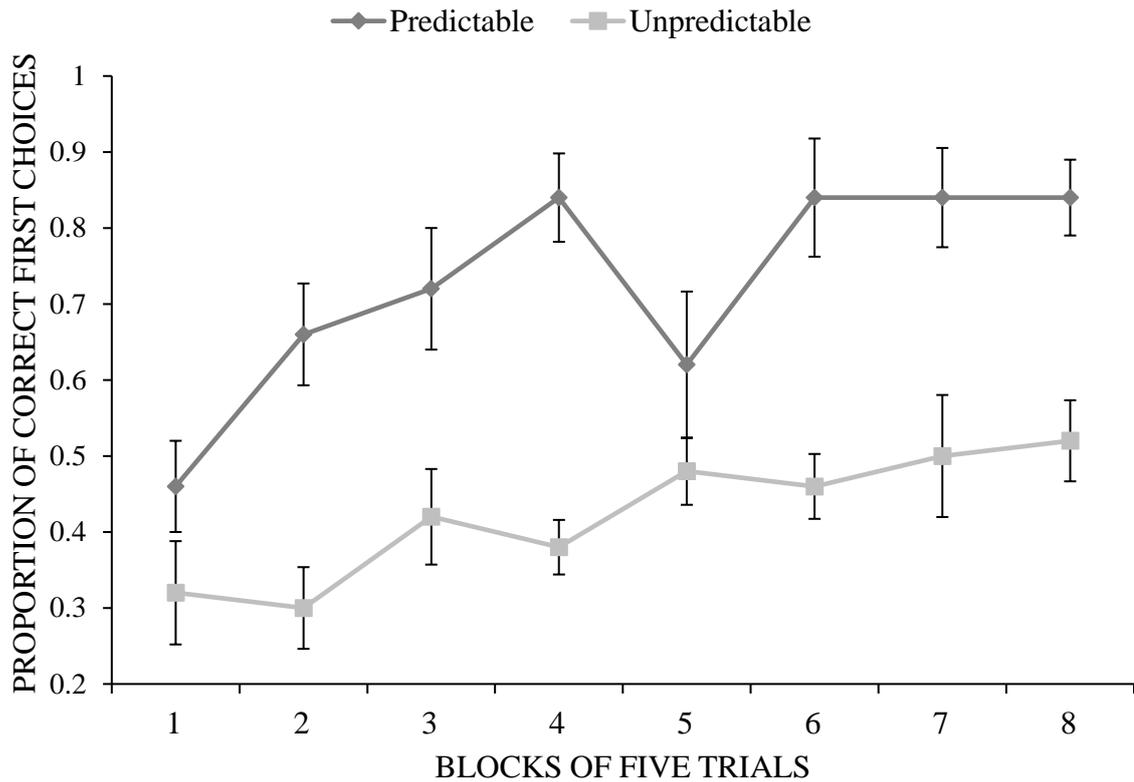


Figure 4. 3 The proportion of correct first choices made across blocks of five trials (± 1 SE bars), for the predictable and unpredictable conditions.

An 8 (Blocks) x 2 (Condition) x 2 (Sex) ANOVA was run, which showed a significant effect of Blocks, $F(7, 112) = 6.02, p < .001$, and a main effect of Condition, $F(1, 16) = 31.04, p < .001$. Independent samples t-tests indicated that when the temporal pattern could be predicted, participants made significantly more correct first choices in blocks 2, 3, 4, 6, 7 and 8, than those in the unpredictable condition, minimum $t(18) = 2.95, p < .01$. There was no significant effect of Sex, $F(1, 16) = .30, p = .591$, nor any interactions, minimum $F(7, 112) = 1.88, p = .080$.

A one-sample t-test, set at .5 under the assumption that participants had learned which locations yielded rewards and thus had a .5 chance at selecting only the rewarded poles, confirmed that by the last block, participants in the predictable condition ($M = .84, SD = .16$) were significantly more likely to direct their search to a rewarded location than chance level, $t(9) = 6.82, p < .001$, and that those in the unpredictable condition did not perform significantly above chance.

4.2.3 Discussion

Humans show a proficiency for efficient foraging, and showed a strong tendency to efficiently and spontaneously detect and use temporal patterns of food availability. Participants in the predictable condition made significantly more correct first choices than chance level, indicating that humans can anticipate which locations will be rewarded across trials and use this information to direct their search. Participants in both conditions efficiently learned which locations were rewarded, and quickly learned to avoid locations that never yielded a reward. Participants were also efficient at avoiding revisits from the outset of trials, highlighting efficient LTM and WM ability. These findings are suggestive of adaptive traits to minimise costs expended during foraging. However, no differences were found when comparing male and female performance, suggesting that in a task requiring the efficient detection and use of structured temporal information, males and females perform similarly.

4.3 Experiment 6

To further assess ability to benefit from temporal structure, Experiment 6 increased the complexity of the task. Within a natural environment, tree species differ in abundance (Hubbell, 1979), and different species follow different fruiting patterns (Chapman, Wrangham, Chapman, Kennard & Zanne, 1999; Anderson, Nordheim, Moermond, Gone Bi & Boesch, 2005). The fruiting patterns of tree species can be complex and can difficult to detect by those without a proficiency to do so, therefore the current experiment introduced two concurrent temporal patterns.

4.3.1 Methods

Participants. A new sample of 26 participants (14 females and 12 males), with an age range of 18-35 years ($M = 22.46$, $SD = 5.26$), took part for course credit.

VR Environment. The virtual reality software, equipment and virtual environment were the same as those described for Experiment 5. A set of 36 poles representing trees were surmounted by coloured spheres representing different species, which determined the locations of the rewards to be found. Poles were arranged as a 6 x 6 matrix, with eight poles surmounted by blue spheres, eight with green spheres, six with purple spheres, six with white spheres, and four each with red and orange spheres. The number of poles of a given colour were altered from those used in Experiment 5, as

in naturalistic forest environments, tree species differ in abundance (Hubbell, 1979) and therefore species that follow different fruiting patterns are likely to be found in varying numbers.

Design and Procedure. Within each trial 12 poles yielded a virtual apple when checked, thus in any given trial two ‘tree species’, or colours, were rewarded. Participants were given the same instructions to check poles for the presence of apples, and the task followed the same procedure as described for Experiment 5 with participants completing 40 trials.

Participants were assigned alternately to one of two conditions; predictable or partially predictable. A completely unpredictable condition would be uninformative here, as a statistically significant difference could occur if participants in the predictable condition detect and monitor only one temporal pattern, regardless of the second. The predictable condition featured two concurrent patterns that could be learned across trials. The first pattern was a double alternation (DA) between poles of two colours (blue and green poles). Blue poles were rewarded in two consecutive trials. Then, green poles were rewarded in two consecutive trials. Simultaneously, a second pattern featured a single alternation (SA) in the availability of fruit at poles of another two colours (red and orange poles). This created a complex pattern of switches between the availability of fruit at poles of different colours across trials. In this way, blue and red poles were rewarded for the first trial, followed by an SA-switch which resulted in blue and orange poles yielding fruit in a second trial. In a third trial, both a DA- and SA-switch took place, which resulted in fruit at green and red poles, followed by a further SA-switch in the fourth trial with green and orange poles yielding fruit. This pattern was repeated across the trials. The partially predictable condition preserved the predictable SA, whilst ensuring the DA could not be learned. This condition prevented participants from predicting whether poles of blue or green would yield fruit at the outset of a given trial, by pseudo-randomising the order in which each species yielded apples. In both conditions, poles of purple and white never yielded rewards.

Measures. The same measures as described for Experiment 5 were calculated; the mean number of selections, locations that were never rewarded, and revisits. As participants in both conditions experienced at least one predictable temporal pattern, it was possible for all participants to direct their searches to rewarded locations at the

outset of all trials, once the pattern had been learned. The first choice measure therefore was divided into the number of correct first choices made to red and orange poles to assess ability to detect the SA, and the number of correct first choices made to blue and green poles to assess detection of the DA. Examining the first selections of each trial, a score of 1 was assigned if a participant visited a rewarded pole in the SA or the DA, instead of or before an unrewarded pole in either pattern, or a never rewarded pole. A score of 0 was given if an unrewarded pole of either pattern, or a never rewarded pole, was visited before a rewarded pole of these two patterns. For example, in a trial where red and green locations were rewarded, if a participant selected poles in the order B-R-G-G-R-G-R-G-R-G-G-G, a score of 0 would be assigned for the DA as blue was selected before green, whilst a score of 1 would be given for the SA as the rewarded red was selected instead of an unrewarded orange pole.

4.3.2 Results

Overall Foraging Efficiency, Long Term Memory, and Working Memory.

Participants showed an improvement in foraging efficiency across the trials. Overall, participants in the predictable condition ($M = 16.07$, $SD = 2.06$) made a similar number of selections until a trial was completed as those in the partially predictable condition ($M = 17.51$, $SD = 3.88$). All participants made few visits to never rewarded locations (predictable: $M = 1.16$, $SD = .91$; partially predictable: $M = 1.66$, $SD = 1.43$), and few revisits (predictable: $M = 1.15$, $SD = .82$; partially predictable: $M = 1.78$, $SD = 1.96$). This can be seen in Figure 4.4.

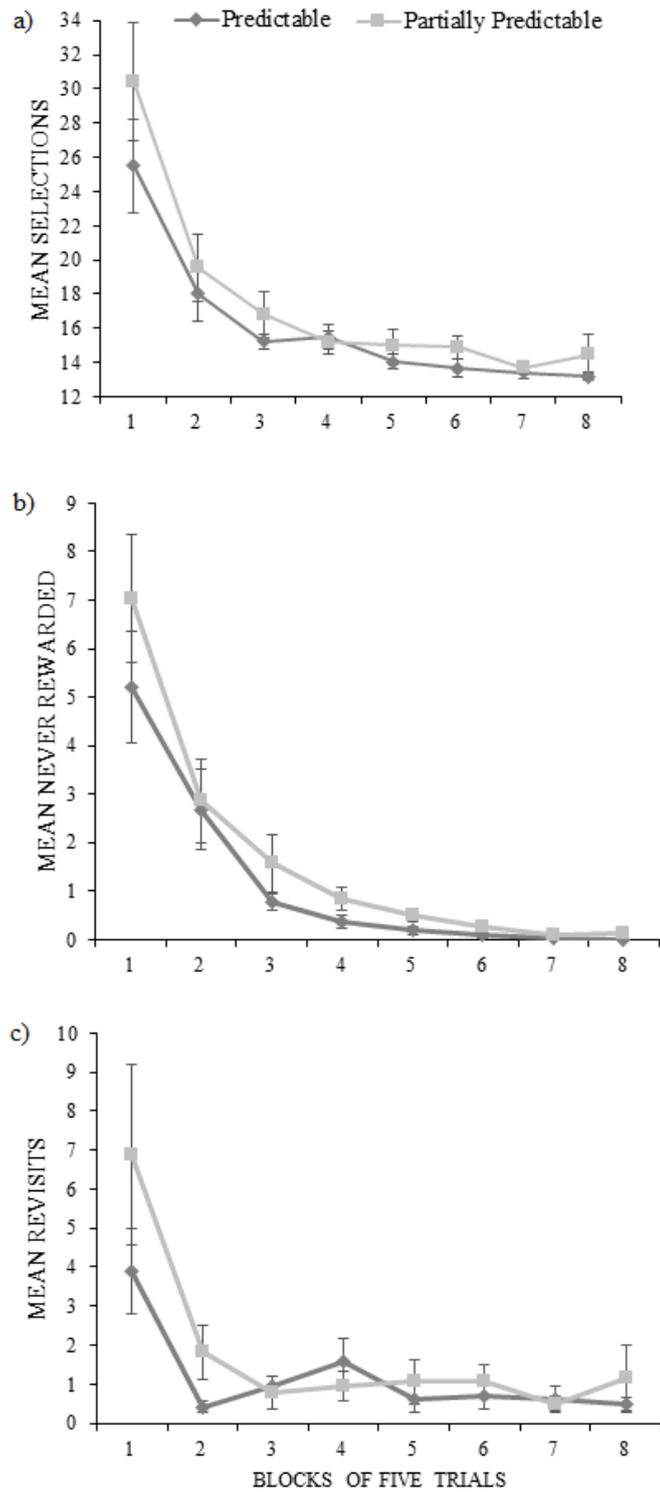


Figure 4. 4 The foraging efficiency measures shown across blocks of five trials (± 1 SE bars) for the predictable and partially predictable conditions; a) mean selections made until the completion of a trial; b) mean never rewarded poles selected; c) mean revisits.

Three 8 (Blocks) x 2 (Condition) x 2 (Sex) ANOVAS were carried out. A significant effect of Blocks was found for the number of selections, $F(1.75, 38.38) = 30.15, p < .001$, number of never rewarded poles selected, $F(1.29, 28.43) = 38.10, p < .001$, and number of revisits, $F(1.69, 37.07) = 9.18, p < .01$. Paired samples t-tests indicated a significant decrease in the number of selections from block 1 ($M = 28.14, SD = 11.50$) to block 2 ($M = 18.83, SD = 6.58$), $t(25) = 7.62, p < .001$, which was also found for the number of visits to never rewarded locations (block 1, $M = 6.19, SD = 4.56$; block 2, $M = 2.78, SD = 2.99$), $t(25) = 3.84, p < .01$, and for the number of revisits (block 1, $M = 5.51, SD = 6.88$; block 2, $M = 1.18, SD = 2.04$), $t(25) = 3.92, p < .01$. For the number of selections, significant interactions were found between Condition x Sex, $F(1, 22) = 4.54, p < .05$, and Blocks x Condition x Sex, $F(1.75, 38.38) = 3.89, p < .05$. Post-hoc t-test comparisons indicated that within the partially predictable condition, females in block 1 ($M = 36.33, SD = 13.94$) made significantly more selections than males ($M = 22.53, SD = 5.31$), $t(12) = 2.28, p < .05$, which was also found in block 2, (females, $M = 22.75, SD = 8.51$; males, $M = 15.27, SD = 1.87$), $t(7.89) = 2.41, p < .05$. All other pairwise comparisons were non-significant, $p > .05$. For the number of never rewarded locations selected, a marginally significant interaction of Blocks x Condition x Sex was found, $F(1.29, 28.43) = 3.77, p = .053$, however there was no significant interaction of Condition x Sex, $F(1, 22) = 3.10, p = .092$. The measure assessing the number of revisits showed no interaction of Blocks x Condition x Sex, $F(1.69, 37.07) = 2.68, p = .090$. There was a significant interaction of Condition x Sex, $F(1, 22) = 4.78, p < .05$. Post-hoc independent samples t-tests however were not statistically significant, and indicated that in the partially predictable condition, females ($M = 2.56, SD = 2.27$) showed a tendency to make more revisits than males ($M = .74, SD = .69$), $t(8.67) = 2.13, p = .063$. In the predictable condition, there was no significant difference (female, $M = .83, SD = .60$; male, $M = 1.48, SD = .93$), $t(10) = -1.44, p = .180$. For all measures, there was no main effect of Condition, minimum $F(1, 22) = .78, p = .387$, Sex, minimum $F(1, 22) = 1.34, p = .260$, nor a significant interaction of Blocks x Condition, minimum $F(1.69, 37.07) = .98, p = .373$.

Detection of Temporal Patterns.

Single Alternation. The proportion of correct first choices of the SA made by participants in the predictable condition was .64 ($SD = .10$), and .62 ($SD = .14$) for those in the partially predictable condition (see Figure 4.5).

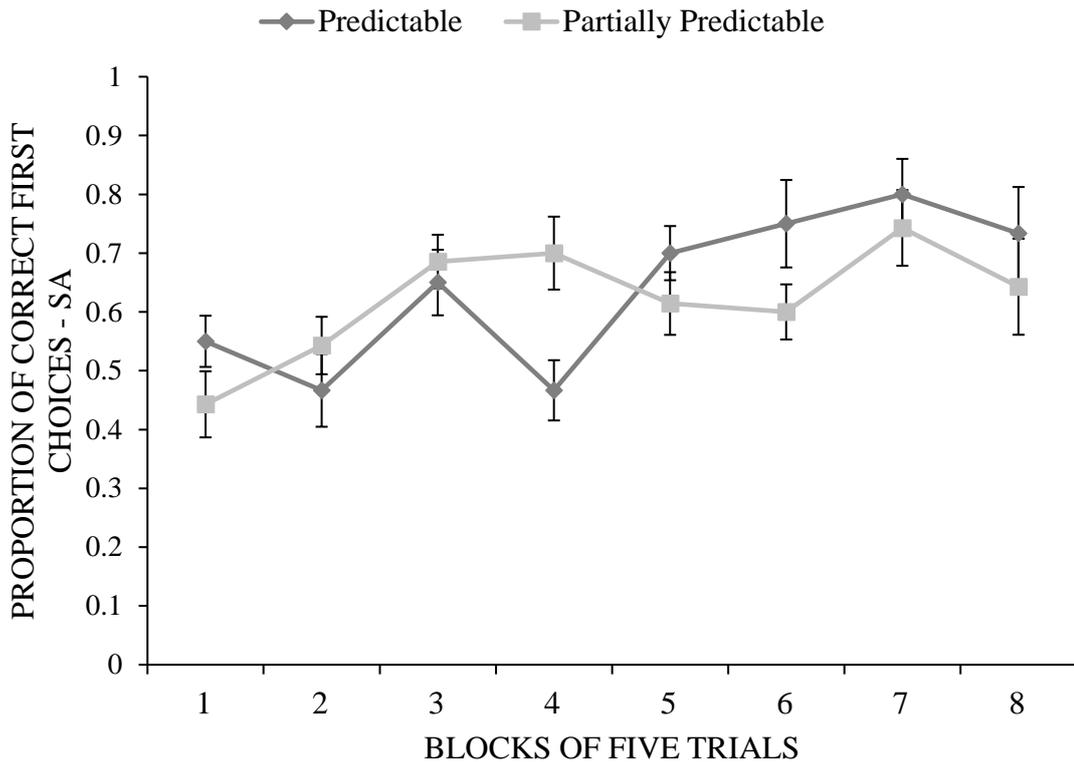


Figure 4. 5 The proportion of correct first choices to poles in the single alternation for the predictable and partially predictable conditions, across blocks of five trials, with ± 1 SE bars.

An 8 (Blocks) x 2 (Condition) x 2 (Sex) repeated measures ANOVA was carried out which revealed a significant effect of Blocks, $F(7, 154) = 6.62, p < .001$, and a significant interaction of Blocks x Condition, $F(7, 154) = 2.90, p < .01$. Independent samples t-tests were carried out to analyse the interaction, revealing that in block 4, participants in the partially predictable ($M = .70, SD = .23$) group made significantly more correct first choices than those in the predictable ($M = .47, SD = .18$) group, $t(24) = -2.84, p < .01$. There was no significant effect of Condition, $F(1, 22) = .07, p = .789$, Sex, $F(1, 22) = 1.95, p = .177$, nor any further interactions, minimum $F(7, 154) = 1.28, p = .264$.

To assess whether participants were making more correct first choices overall than chance level, a one-sample t-test was run with the level set at .5 under the assumption participants had learned the pairs of rewarded colours. Participants in both

the predictable and partially predictable conditions performed significantly better than chance level, $t(11) = 4.74, p < .01$, and $t(13) = 3.34, p < .01$ respectively.

Double Alternation. Overall, participants in the predictable condition ($M = .59, SD = .09$) made more correct first choices than those in the partially predictable condition ($M = .49, SD = .08$). The means are shown in Figure 4.6.

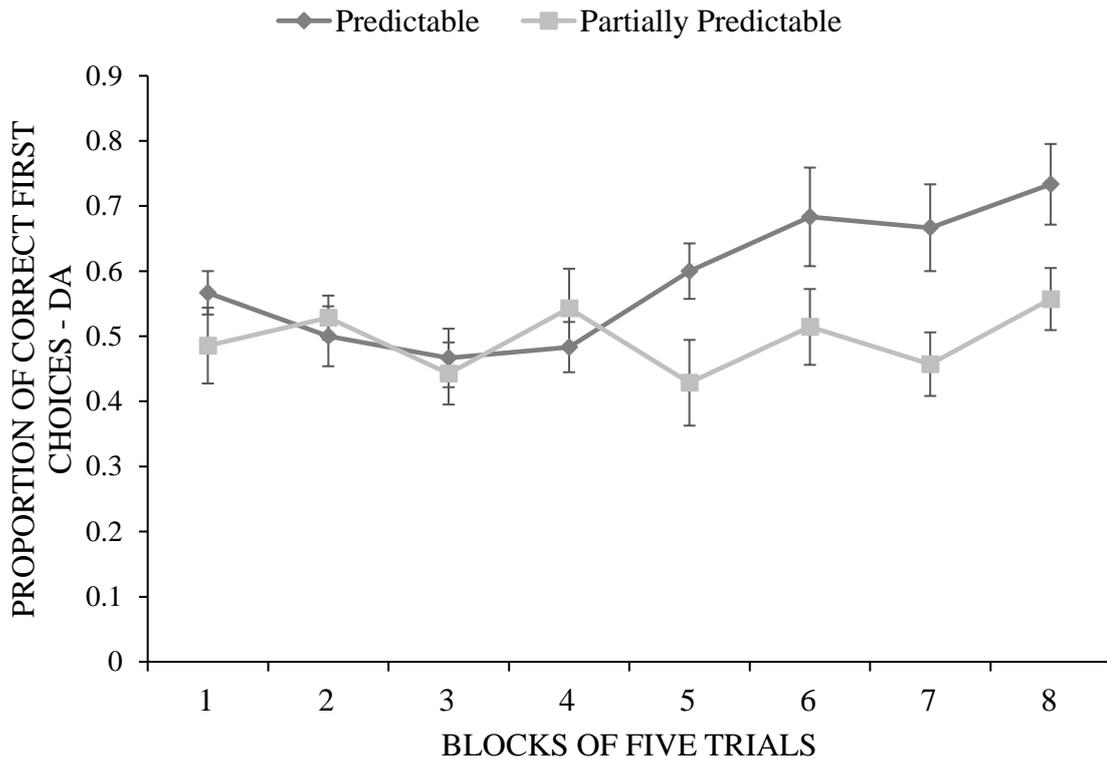


Figure 4. 6 The proportion of correct first choices to poles in the double alternation, for the predictable and partially predictable conditions, across the blocks of trials, with ± 1 SE bars.

An 8 (Blocks) x 2 (Condition) x 2 (Sex) ANOVA was carried out which showed a significant main effect of Blocks, $F(7, 154) = 2.56, p < .05$, and a significant effect of Condition, $F(1, 22) = 8.64, p < .01$. An independent samples t-test indicated that participants in the predictable group made significantly more correct first choices than those in the partially predictable condition, $t(24) = 2.83, p < .01$. A significant interaction of Blocks x Condition was also found, $F(7, 154) = 2.18, p < .05$, with independent samples t-tests indicating that towards the end of the experiment in blocks 5, 7 and 8, those in the predictable condition made significantly more correct first

choices than those in the partially predictable condition, minimum $t(24) = 2.58, p < .05$. There was no significant effect of Sex, $F(1, 22) = .00, p = .987$, nor any further interactions, minimum $F(1, 22) = 2.28, p = .146$.

One sample t-tests comparing the performance overall with chance level (.5) confirmed that the performance of participants in the predictable condition was above chance level, $t(11) = 3.29, p < .01$, whilst participants in the partially predictable condition did not perform significantly differently than chance.

4.3.3 Discussion

Participants spontaneously detected the two available temporal patterns and used this information to direct their searches to rewarded locations. In both conditions, participants were efficient in detecting the predictable SA pattern. The efficiency of this ability is shown in the results of the partially predictable condition, where this was detected despite the presence of a distracting unpredictable temporal pattern. In fact, during the first half of the experiment, the proportion of correct first choices appeared to be higher in the partially predictable group. By the second half, participants in the predictable condition showed a tendency to make more correct first choices than those in the partially predictable group. In accordance with the findings of Experiment 5, participants in both conditions quickly became efficient foragers, showed an improvement in WM performance across the trials by the avoidance of poles already selected within a trial, and showed efficient LTM performance by avoiding locations that never yielded a reward across all trials.

Considering sex differences, males were found to outperform females in the number of selections made at the outset of the trials, whilst this was marginally significant for the measure of WM. There were no significant interactions with sex for the measure of LTM and the two measures of first choice, suggesting that all participants were efficient at learning which locations should be avoided, and that an ability to detect temporal structure within a foraging environment does not appear to be sex-specific.

Overall, simultaneous and complex temporal patterns of fruit availability occur in naturalistic foraging environments, and these findings suggest that this is an evolutionarily-relevant task which accurately assesses foraging competences. This task provides a basis with which to assess the acquisition of spatial information during foraging.

4.4 Experiment 7

It remains unclear whether humans relied on the visual cue of colour to guide search to rewarded locations in this task or whether spatial information was acquired during foraging. Experiment 7 aimed to manipulate the visual cues provided to assess the acquisition of spatial knowledge when competing visual cues were present, and to determine whether salient visual cues overshadow learning of spatial information.

4.4.1 Methods

Participants. The sample consisted of 26 participants (15 females and 11 males), with an age range of 18-36 years ($M = 20.46$, $SD = 3.83$). Participants took part for course credit.

Design and Procedure. The virtual reality software, equipment and virtual environment were the same as those described for Experiment 5. The same 6 x 6 matrix and array of colours as presented in Experiment 5 was employed here, with 12 rewards hidden in each trial. The temporal pattern of rewards followed the same pattern of a PG/BW double alternation with only the predictable temporal pattern presented.

The sole manipulation was the visual cues the participants were presented with, which was manipulated in two conditions; cue-removed and single-cue. To assess whether spatial information was acquired or whether overshadowing occurs during foraging, the conditions followed a typical overshadowing paradigm. Participants in the cue-removed condition were trained with both visual and spatial cues available, as in Experiment 5, before the visual cue of colour was removed from the array and participants completed test trials where the poles turned white and only spatial cues remained available. In this condition, visual and spatial cues were equally predictive of reward location, until only white poles remained and thus only spatial cues could be used to identify the rewarded poles. The single-cue condition required participants to search using only spatial cues from the outset of the experiment, and all poles within the matrix were white. Within this condition, the test trials remained the same as the training trials. The predictable temporal pattern of reward availability remained the same across both conditions and across all trials.

Participants in the cue-removed condition were not told that the visual cues would be removed, and both conditions were given the same instructions. Participants

were asked to search for the hidden apples, and each participant completed 30 training trials and 10 test trials, with a 10-minute break after 20 trials or when required.

Measures. To assess foraging efficiency and detection of temporal information, the same measures as described in Experiment 5 were calculated; mean number of selections, mean number of never rewarded poles visited, mean number of revisits to poles previously searched within a trial, and the proportion of correct first choices. It was anticipated that without visual cues, participants would require more trials to learn the rewarded locations. Participants may acquire spatial information of rewarded locations, and direct their searches there initially, but this may be missed if errors are made and only the number of selections are considered. Therefore, two additional measures were calculated to assess where participants directed their searches regardless of the number of selections made. As there were 12 foods within each trial, the first 12 visits to poles in each trial were analysed. Within these 12 choices, the proportion of correct selections made and the proportion of never rewarded locations selected was calculated, with the optimum values for each measure being 1 and 0 respectively.

4.4.2 Results

Overall Foraging Efficiency, Long Term Memory, and Working Memory.

Across the training trials, participants in the cue-removed condition made fewer selections ($M = 17.20$, $SD = 3.79$), checks to never rewarded poles ($M = 2.06$, $SD = 1.49$), and revisits ($M = .85$, $SD = .91$) than those in the single-cue condition ($M = 26.82$, $SD = 4.80$; $M = 6.74$, $SD = 2.27$; and $M = 1.38$, $SD = .95$ respectively). Across the test trials where the visual cue of colour was removed for those in the cue-removed group, errors by participants in this group showed a marked increase, as participants made more selections ($M = 24.96$, $SD = 6.18$), checks to never rewarded poles ($M = 5.53$, $SD = 2.82$), and revisits ($M = 2.54$, $SD = 2.68$) than those in the single-cue condition ($M = 19.35$, $SD = 8.85$; $M = 2.94$, $SD = 3.63$; and $M = 1.36$, $SD = 2.61$ respectively). This is shown below in Figure 4.7.

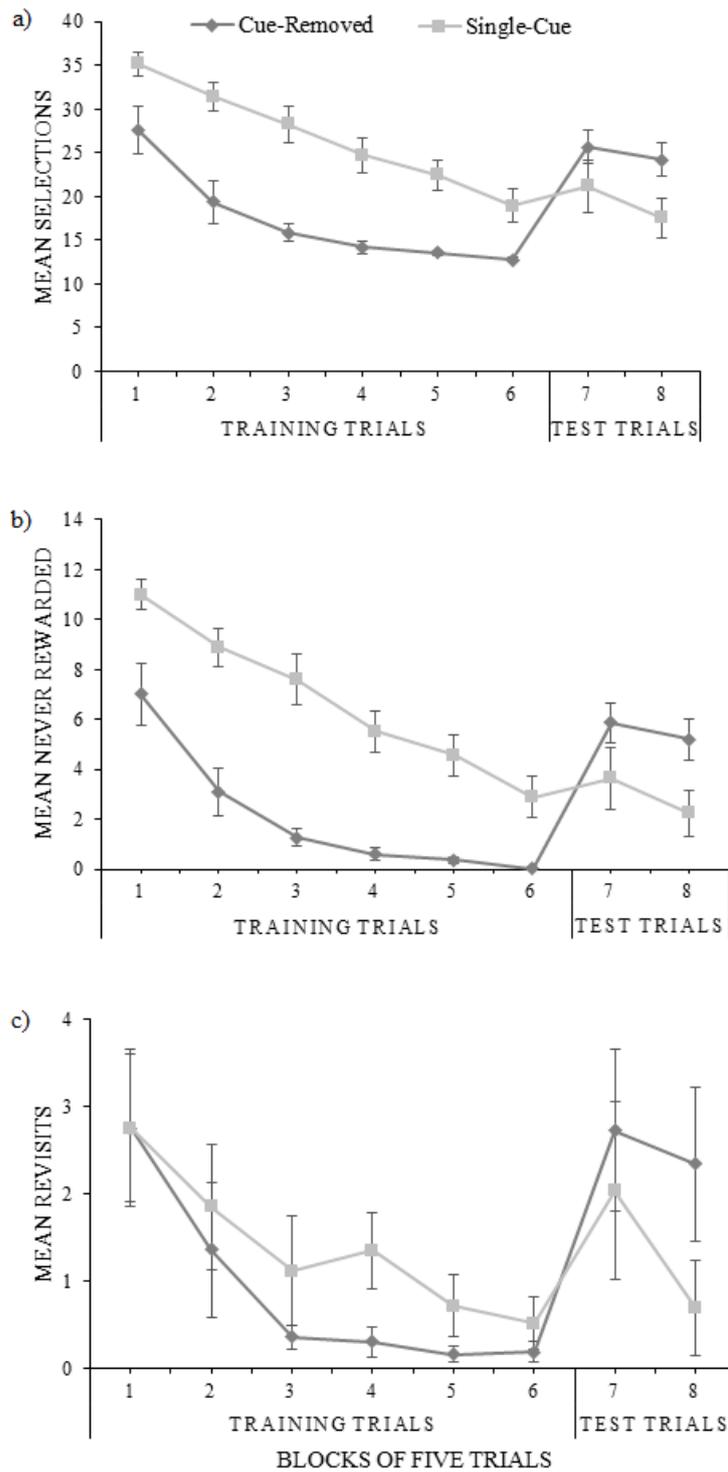


Figure 4. 7 The foraging efficiency measures shown across the blocks (± 1 SE bars) for the training and test trials, for both the cue-removed and single-cue conditions; a) mean selections until completion of a trial, b) mean never rewarded poles selected, and c) mean revisits.

Training Trials. Three 6 (Blocks) x 2 (Condition) x 2 (Sex) ANOVAS analysing the training trials were carried out. A significant effect of Blocks was found for the number of selections, $F(2.18, 47.85) = 36.19, p < .001$, number of never rewarded poles selected, $F(2.18, 47.46) = 41.77, p < .001$, and the number of revisits, $F(2.58, 56.82) = 5.59, p < .01$. A significant effect of Condition was also found for the number of selections, $F(1, 22) = 26.60, p < .001$, and never rewarded poles selected, $F(1, 22) = 32.76, p < .001$, with independent samples t-tests indicating that those in the single-cue condition made significantly more selections and visits to never rewarded locations than those in the cue-removed group, $t(24) = 5.71, p < .001$, and $t(24) = 6.30, p < .001$ respectively. There was no main effect of Condition for the number of revisits, $F(1, 22) = 1.52, p = .231$, suggesting that all participants made few WM errors. For all measures, there was no significant effect of Sex, minimum $F(1, 22) = .81, p = .378$, nor any interactions between the factors, minimum $F(2.16, 47.46) = 2.54, p = .085$.

Test Trials. To assess whether performance was significantly impaired once the visual cues were removed, three 2 (Blocks) x 2 (Condition) x 2 (Sex) ANOVAS for each measure were run, comparing the last block of training trials and the first block of test trials. A significant effect of Blocks was found for the number of selections, $F(1, 22) = 37.92, p < .001$, number of never rewarded poles selected, $F(1, 22) = 39.03, p < .001$, and the number of revisits, $F(1, 22) = 8.56, p < .01$. Significant interactions of Blocks x Condition were also found for the number of selections, $F(1, 22) = 21.65, p < .001$, and the number of never rewarded poles visited, $F(1, 22) = 24.30, p < .001$, but was not significant for revisits, $F(1, 22) = 1.17, p = .290$. Paired samples t-tests confirmed that within the cue-removed group, the number of selections and visits to never rewarded locations significantly increased from the last block of training trials to the first block of test trials, $t(13) = -7.04, p < .001$, and $t(13) = -7.26, p < .001$ respectively. This was not significantly different for the single-cue group, minimum $t(11) = -1.62, p = .133$. For all three measures, there were no significant effects of Sex, minimum $F(1, 22) = 3.49, p = .075$, nor any further interactions, minimum $F(1, 22) = 2.62, p = .120$.

Across the test trials, two 2 (Blocks) x 2 (Condition) x 2 (Sex) ANOVAS were carried out. A significant effect of Blocks was found for the number of selections, $F(1, 22) = 4.85, p < .05$, and the number of never rewarded poles checked, $F(1, 22) = 5.15, p < .05$. A significant effect of Condition was also found for the number of selections, F

(1, 22) = 4.78, $p < .05$, and the number of never rewarded poles visited, $F(1, 22) = 5.16$, $p < .05$. For the number of revisits, there was no effect of Blocks, $F(1, 22) = 1.09$, $p = .307$, nor Condition, $F(1, 22) = 1.80$, $p = .194$. For all measures, there was a significant interaction of Blocks x Sex (selections, $F(1, 22) = 5.85$, $p < .05$; never rewarded, $F(1, 22) = 4.69$, $p < .05$; revisits, $F(1, 22) = 4.93$, $p < .05$). Comparing the first and second blocks of test trials, paired-samples t-tests indicated that in the first block of test trials, females made significantly more selections ($M = 25.77$, $SD = 9.44$ and $M = 21.12$, $SD = 7.65$, $t(14) = 3.62$, $p < .01$), visits to never rewarded locations ($M = 5.59$, $SD = 3.97$ and $M = 3.76$, $SD = 3.34$, $t(14) = 3.42$, $p < .01$), and revisits ($M = 3.35$, $SD = 4.06$ and $M = 1.24$, $SD = 2.13$, $t(14) = 2.84$, $p < .05$). There were no significant differences in male performance across the blocks for all three measures, minimum $t(10) = -.91$, $p = .383$. There were also no significant effects of Sex, minimum $F(1, 22) = 1.66$, $p = .211$, nor any further interactions between the three factors, minimum $F(1, 22) = .659$, $p = .426$.

Detection of the Temporal Pattern. Overall in the training trials, the mean number of correct first choices made by participants in the cue-removed group was .62 ($SD = .12$) and .56 ($SD = .16$) by those in the single-cue group. Across the test trials, the proportion of correct choices was similar for those in the cue-removed group ($M = .74$, $SD = .21$) and those in the single-cue group ($M = .76$, $SD = .18$).

Training Trials. A 6 (Blocks) x 2 (Condition) x 2 (Sex) ANOVA was carried out. A significant effect of Blocks was found, $F(5, 110) = 13.64$, $p < .001$, with a further t-test confirming that participants overall improved and made significantly more correct first choices in the last block of training trials ($M = .74$, $SD = .26$) compared to the first block ($M = .41$, $SD = .14$), $t(25) = -5.97$, $p < .001$. There was no significant effect of Condition, $F(1, 22) = 1.33$, $p = .260$, Sex, $F(1, 22) = .19$, $p = .670$, nor any significant interactions between the three factors, minimum $F(5, 110) = 1.27$, $p = .283$.

One sample t-tests comparing the overall proportion of correct first choices with .5 (chance level), showed that those in the cue-removed group made significantly more correct first choices than chance level, $t(13) = 3.86$, $p < .01$. Across the training trials, participants in the single-cue group did not make significantly more correct first choices than chance would predict.

Test Trials. Comparing the last block of training trials with the first block of test trials across the two groups, a 2 (Blocks) x 2 (Condition) x 2 (Sex) ANOVA was run which revealed no significant effects nor interactions, minimum $F(1, 22) = 1.83, p = .190$, suggesting that when visual cues were removed, a proficiency to direct the first choice to a rewarded location persisted.

Across the two blocks of test trials, the results of a 2 (Blocks) x 2 (Condition) x 2 (Sex) ANOVA also found no significant effects nor interactions, minimum $F(1, 22) = .81, p = .378$, and confirmed that the cue-removed and the single-cue groups did not perform differently in terms of the proportion of correct first choices made across the trials.

One-sample t-tests further revealed that across the test trials, both those in the cue-removed group and those in the single-cue group made significantly more correct first choices than chance level (.5), $t(13) = 4.13, p < .01$, and $t(11) = 5.06, p < .001$ respectively.

Acquisition of Spatial Information. Analysing the first 12 selections made by participants in each training trial, participants in the cue-removed group showed a higher proportion of correct selections ($M = .79, SD = .10$) and a lower proportion of visits to never rewarded poles ($M = .08, SD = .04$) than those in the single-cue group ($M = .55, SD = .14$; and $M = .17, SD = .05$ respectively). In the test trials when visual cues were removed, the number of correct selections made in the first 12 choices of a trial notably decreased for participants in the cue-removed group ($M = .60, SD = .15$) and the number of visits to never rewarded locations increased ($M = .15, SD = .06$), whilst performance on these measures continued to improve in the single-cue group ($M = .76, SD = .25$; and $M = .07, SD = .07$ respectively). This is shown below in Figure 4.8.

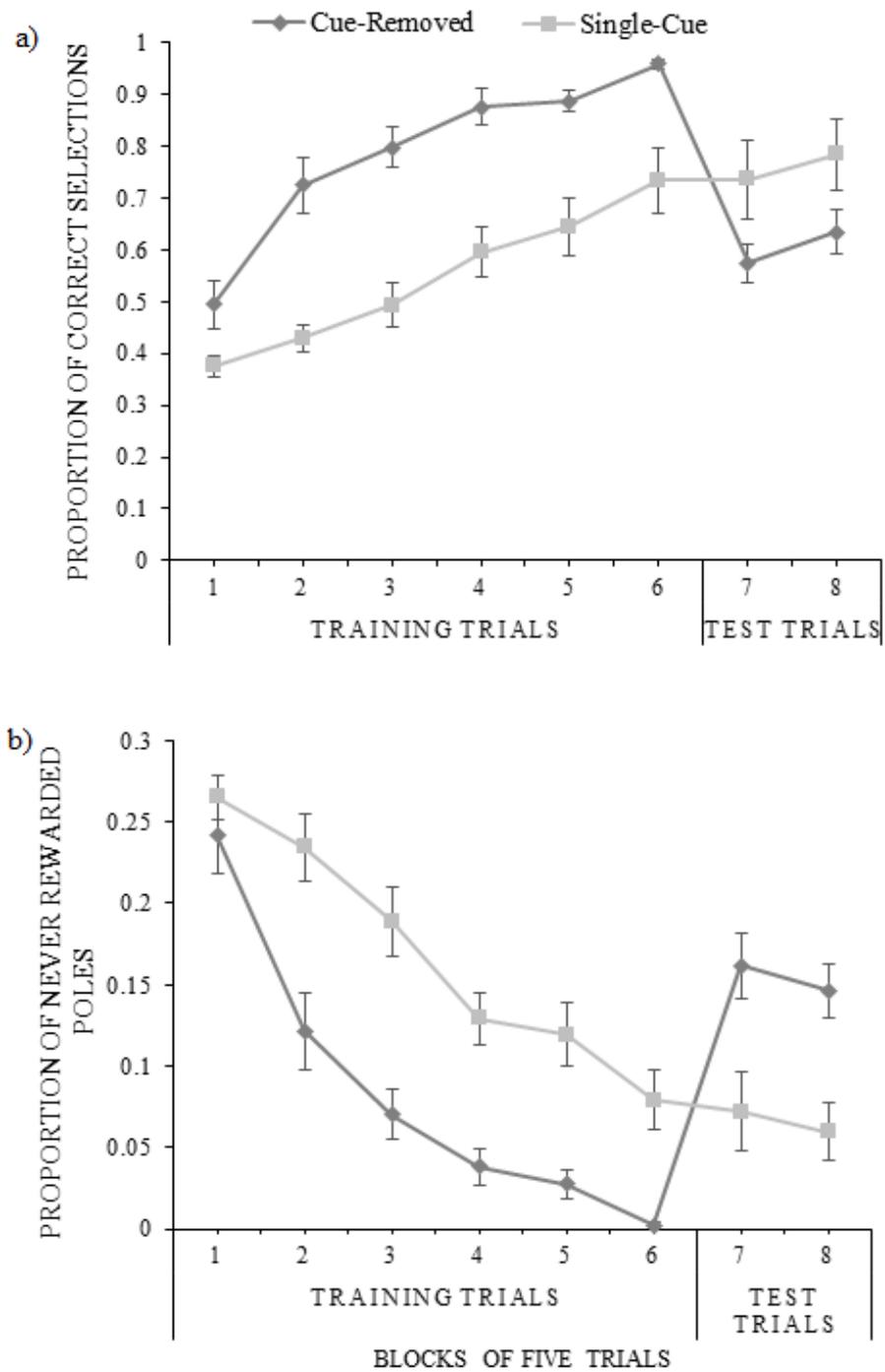


Figure 4. 8 The proportion of locations selected within the first 12 choices that a) were correct selections to poles that yielded a reward, and b) never yielded a reward, shown across blocks of five trials (± 1 SE bars) for each condition.

Training Trials. The results of two 6 (Blocks) x 2 (Condition) x 2 (Sex) ANOVAS revealed a significant effect of Blocks for the proportion of correct choices made in the first 12 searches, $F(2.53, 55.64) = 52.06, p < .001$, and for the proportion of never rewarded locations selected, $F(3.00, 65.88) = 57.45, p < .001$. Significant effects of Condition were also found, $F(1, 22) = 22.65, p < .001$, and $F(1, 22) = 23.32, p < .001$ respectively, whereas a Blocks x Condition interaction approached significance for both the proportion of correct first choices made at the outset of trials, $F(2.53, 55.64) = 2.67, p = .066$, and the proportion of never rewarded poles selected, $F(3.00, 65.88) = 2.54, p = .064$. Post-hoc independent samples t-tests indicated that within the first 12 selections, those in the cue-removed group made significantly more correct first choices, $t(24) = 5.22, p < .001$, and significantly fewer visits to never rewarded locations, $t(24) = -5.18, p < .001$, than those in the single-cue group. A significant interaction of Condition x Sex was also found for the proportion of never rewarded locations selected, $F(1, 22) = 5.05, p < .05$, with post-hoc t-tests indicating that amongst female participants, those in the single-cue condition ($M = .19, SD = .03$) selected significantly more poles that never yielded a reward than those in the cue-removed condition who had both cues available ($M = .07, SD = .04$), $t(13) = 6.21, p < .001$. Amongst males, there was no significant difference between the two conditions ($M = .14, SD = .06$, and $M = .09, SD = .04$), $t(9) = 1.48, p = .173$. For the former measure, this interaction was non-significant, $F(1, 22) = 1.17, p = .292$. For both measures, there was no significant effect of Sex, minimum $F(1, 22) = .88, p = .359$, nor any further interactions, minimum $F(2.53, 55.64) = .40, p = .723$.

Test Trials. To assess whether performance was significantly impaired once visual cues were removed in the test trials, two 2 (Blocks) x 2 (Condition) x 2 (Sex) ANOVAS compared the last block of training trials and the first block of test trials for each measure. A significant effect of Blocks was found for the proportion of correct first choices within the first 12 choices, $F(1, 22) = 73.65, p < .001$, and the proportion of never rewarded poles selected, $F(1, 22) = 34.39, p < .001$. A significant interaction of Blocks x Condition was also found for each measure, $F(1, 22) = 80.32, p < .001$, and $F(1, 22) = 36.23, p < .001$. Paired-samples t-tests indicated that in the first block of test trials, those in the cue-removed group had a significantly lower proportion of correct choices ($M = .57, SD = .14$) and higher proportion of visits to never rewarded poles ($M = .16, SD = .07$) compared to the last block of the training trials (proportion correct, $M =$

.96, $SD = .04$; proportion never rewarded, $M = .00$, $SD = .01$), $t(13) = 10.80$, $p < .001$, and $t(13) = -8.18$, $p < .001$ respectively. Performance was not significantly different for those in the single-cue group from the training to test trials, minimum $t(11) = .46$, $p = .652$.

The results of two 2 (Blocks) x 2 (Condition) x 2 (Sex) ANOVAS indicated that for the proportion of correct selections within the first 12 choices, there was a significant effect of Blocks, $F(1, 22) = 17.62$, $p < .001$, however this was not significant for the proportion of never rewarded poles selected, $F(1, 22) = 2.36$, $p = .139$. For both measures, a significant effect of Condition was also found, $F(1, 22) = 4.53$, $p < .05$, and $F(1, 22) = 11.30$, $p < .01$. For the proportion of correct first choices, independent samples t-tests did not reveal a statistically significant difference between participant performance in the cue-removed and the single-cue groups, $t(17.03) = -1.98$, $p = .074$. Further t-tests indicated that once the visual cues were removed, those in the cue-removed group made a significantly higher proportion of visits to never rewarded locations than those in the single-cue condition, $t(24) = 3.28$, $p < .01$. For both measures, there were no significant effects of Sex, minimum $F(1, 22) = .94$, $p = .343$, nor any significant interactions between the three factors, minimum $F(1, 22) = .72$, $p = .405$.

To assess performance against chance level in the test trials, one-sample t-tests were run for each condition. Out of the 36 locations, participants had 12/36 chances (0.3) to select a rewarded location. Across the test trials, participants in both the cue-removed and the single-cue conditions made more correct selections in the first 12 selections of a trial than chance would predict, $t(13) = 7.82$, $p < .001$, and $t(11) = 6.34$, $p < .001$ respectively. Considering the proportion of never rewarded poles visited, participants made significantly fewer visits to never rewarded locations than expected by chance in both the cue-removed, $t(13) = -8.49$, $p < .001$, and single-cue groups, $t(11) = -11.40$, $p < .001$.

4.4.3 Discussion

The findings suggest that humans acquire spatial information during foraging, despite an effect of overshadowing. In the training trials, all participants became more efficient across the experiment, and made few WM and LTM errors. An ability to detect temporal information persisted across the trials despite the manipulation of visual cues. When both visual and spatial cues were available to participants however, overall

efficiency and LTM performance improved in comparison to when only spatial cues were predictive of reward location. Participants who only had spatial cues available from the outset took longer to reach the same level of efficiency as those who had both cues available.

Once the visual cues were removed for those who had been trained with both cues, performance became impaired. Participants in the cue-removed condition made a higher number of selections and visited more never rewarded locations than those in the single-cue group, even when looking at the outset of trials to ascertain where participants directed their searches initially. This impairment once visual cues were removed, provides support for the concept of overshadowing in associative learning processes (Mackintosh, 1971; 1976). Further analyses however, indicated that despite the removal of visual cues, participants made significantly more correct choices and fewer visits to never rewarded locations than chance would predict. This suggests that humans acquire spatial knowledge of their foraging environment, even when visual cues alone would allow participants to find food efficiently, consistent with the notion that mental representations are acquired during search (Tolman, 1948). WM, and an ability to detect temporal patterns did not appear to be impaired by the removal of colour cues. Overall efficiency in terms of the number of selections made until a trial was completed, and LTM, measured by visits to locations that were never profitable, showed the greatest impairment when visual cues were no longer available.

A sex difference was also evident from the findings. Within the training trials, females were found at the outset of trials to select a high proportion of locations which never yielded a reward. During the first block of the test trials when visual cues were removed, female performance was significantly impaired for measures of overall foraging efficiency, LTM, and WM, compared to block 2, whilst performance between these blocks was not significantly different for male participants. There was no main effect of Sex, suggesting that there was no difference in performance between the sexes. However, female performance showed an improvement across the two blocks of test trials, implying that female performance was initially impaired to a greater degree than male performance.

4.5 General Discussion

In an experimental foraging task derived from naturalistic studies of non-human primates foraging, Experiments 5 and 6 indicated that humans displayed a strong

tendency to detect and monitor complex temporal patterns of resource availability, and used this information to direct subsequent searches to locations that were most likely to yield a reward. Experiment 7 afforded the manipulation of visual cues to determine that humans acquired spatial information during search, despite an impairment in performance when visual cues were removed, showing an effect of overshadowing for the first time within a foraging task. These findings are supportive of the notion that humans may have evolved high level cognitive skills to efficiently find nutrient-rich, ephemeral resources whilst they are available (Milton, 1981a; 1993).

4.5.1 Detection of Structure as an Adaptation

The findings of Experiment 5 and 6 are in support of theories which suggest that humans have a propensity for detecting patterns in stimuli (Mattson, 2014). In search tasks, humans have been found to benefit from the spatial structure within environments (De Lillo & James, 2012; De Lillo et al. 2013), though the findings here further demonstrate that a propensity to benefit from temporal structure is also prevalent in a search task. The findings that humans show a proficiency for detecting temporal structure and that this information is used to direct future searches, has implications for primate cognition. The findings by Janmaat and colleagues (2012; 2013a; 2013b) suggest that frugivorous non-human primates are able to detect fruiting information during their foraging bouts, and use this information to direct their searches to trees that are most likely to be yielding fruit. Our earliest hominin ancestor was thought to have exploited a wooded environment (White et al. 2009; Louchart et al. 2009), similar to environments chimpanzees inhabit today, thus it is possible that humans evolved and retained the cognitive abilities required to forage on ephemeral resources. However, an experimental assessment of non-human primate ability to detect temporal structure is required to provide further insights into whether frugivorous species have evolved high-level cognitive skills.

4.5.2 Acquisition of Spatial Information or Overshadowing?

The acquisition of spatial information may not be required for efficient foraging, as individuals can exploit the synchronicity of fruiting trees to learn which tree species will fruit and when (Janmaat et al. 2012; Janmaat et al. 2013a; 2013b), and can use the visual cues within the environment to direct search, both of which are cognitively less demanding. Whilst it is impossible to control and manipulate the cues available to

foraging primates in natural environments, the VR environment afforded this. The finding that spatial information was acquired during foraging suggests that humans, and perhaps other primates, build spatial representations in the form of a mental map (Tolman, 1948; Normand & Boesch, 2009), however, an experimental assessment of non-human primates within this task is necessary to determine the extent to which primates acquire spatial information. Whether spatial information was learned implicitly, or whether participants used the spatial information during training trials to direct searches cannot be concluded here, though verbal comments at the time of testing of the difficulty of this task and of their reliance on the visual cues, suggests that this knowledge may have been implicitly acquired. Whilst VR allowed the removal of visual information, to fully consider the associative learning principles of blocking and overshadowing, the removal of spatial information was not deemed possible. Spatial structure is fundamental to a navigational space, and in any given foraging situation, it is impossible to dissociate spatial information from an efficient search. For an efficient search, spatial information will always be necessary to determine which locations have already been visited, and therefore cannot be separated.

However, as performance decreased when colour cues were removed, findings suggest that visual cues also play an important role in foraging. In accordance with associative learning theory, the spatial cues available in this task appeared to be less salient than the cue of colour, despite both cues being equally predictive of reward location. An overshadowing effect (Mackintosh, 1971; 1976) was observed here, resulting in poorer learning of the spatial cues when visual cues were present. To our knowledge, this is the first time that an effect of overshadowing has been demonstrated within a foraging situation requiring the search for multiple items within a search array.

4.5.3 Sex Differences in Foraging

The findings of Experiment 5 suggest that both males and females were similar in their overall foraging efficiency, LTM, WM, and ability to detect temporal patterns of reward availability. In this task, evolutionary theories would predict that both males and females would forage efficiently in a small search space requiring both navigational skills which often show a male advantage (Silverman & Eals, 1992; Lawton, 1994; Moffat et al. 1998) and an ability to learn when food items will be available and where they will be found, which often shows a female superiority (Silverman & Eals, 1992; Silverman et al. 2007; Levy et al. 2005). In contrast to this, when two concurrent

patterns were available, females in the partially predictable condition made significantly more selections than males at the outset of trials, suggesting that females initially took longer to complete a trial when the complexity of the task was increased. However, findings indicated that overall, all participants made a similar number of correct first choices across the trials and did so significantly better than chance level. Experiment 7 removed the visual cues, which evolutionary theories would suggest may have been more relied on by females than males, due to a reliance on positional and land-mark based cues (Lawton, 1994; Saucier et al. 2002). Consistent with this argument, females were found to perform worse in terms of overall foraging efficiency, LTM, and WM in the first block of test trials once visual cues were removed compared to the second block of test trials where performance improved, suggesting that females experienced a greater impairment in foraging efficiency. As there was no significant difference between the sexes here, further research into the extent to which females show an impairment on these memory measures when salient cues are removed would be worthy of investigation.

4.5.4 Conclusions

In conclusion, the findings of this chapter indicate that humans have a strong tendency to detect and use structured temporal information during search. These results support the concept that humans possess a propensity to detect structure in search environments, whether this is physical structure of the search space, or structure across time which aids future search. An effect of overshadowing was observed here for the first time within a foraging situation, whilst findings also indicated that humans acquire spatial information, suggesting that the concept of a mental map cannot be ruled out. These results are consistent with the notion that humans evolved sophisticated cognitive skills due to ancestral foraging pressures (Milton, 1981a).

The task outlined within this chapter provided a naturalistic and ecological task with which to assess the cognitive skills required for efficient foraging. It has previously been suggested that ecologically valid tasks are required to accurately assess facets of human cognition (Burgess et al. 1998; 2006), and in particular when assessing effects of ageing in humans (Phillips et al. 2006). The next chapter aimed to implement this foraging paradigm with an ageing population to assess changes in adult cognition across a taxonomy of measures.

Chapter 5: Effects of Ageing in the Detection of Temporal Structure

5.1 Introduction

The experiments outlined in the previous chapter demonstrated the use of a suitable and ecologically valid experimental setup to assess foraging. The foraging paradigm developed allowed the assessment of multiple cognitive competences within a single task, considering human cognition within a situation derived from observations of non-human primate foraging behaviour. Using this paradigm, the experiment described in the current chapter had a unique opportunity to assess the effects of ageing within an ecological and naturalistic paradigm.

5.1.1 A Cognitive Decline

The effects of ageing and the associated deficits in cognition are seen across species, including rodents (Ingram, 1988), zebrafish (Yu, Tucci, Kishi & Zhdanova, 2006), dogs (Milgram, Head, Weiner & Thomas, 1994), and primates (Lacreuse & Herndon, 2009). In humans, a cognitive decline with age occurs in tasks of verbal memory and cognitive speed (van Hooren et al. 2007), memory search performance (Hills, Mata, Wilke & Samanez-Larkin, 2013), and executive function and WM (van Hooren et al. 2007; MacPherson et al. 2002; see Bishop et al. 2010, for a review). A longitudinal study by Park et al. (2002) found a linear decline for tasks including the use of WM, LTM, and speed of processing, indicating that a number of cognitive competences decline in humans as age increases. Research monitoring brain activity of healthy ageing participants has also shown that the large-scale brain system which involves the frontal and posterior brain regions - thought to be related to memory and planning (Vincent, Kahn, Snyder, Raichle & Buckner, 2008) – showed a decline in aged participants across a number of cognitive tasks (Andrews-Hanna et al. 2009). More specifically, it has been found that age-related differences appear to be specific to tasks dependent on the DLPFC, whilst tasks requiring the ventromedial prefrontal cortex did not show any age-related changes (MacPherson et al. 2002). Whilst this postulates that effects of ageing appear to be specific to certain cognitive functions, this also suggests that age-related changes may be found in a foraging task requiring the use of WM and an ability to detect structure, an ability thought to be related to the DLPFC (Bor et al. 2003).

It has also been suggested that cognitive changes may be largely explained by a slowing of information processing with age (Verhaeghen & Salthouse, 1997; Myerson, Ferraro, Hale & Lima, 1992; Bashore, Wylie, Ridderinkhof & Martinerie, 2014). Verhaeghen and Salthouse (1997) performed a meta-analysis which indicated that rather than a loss of capacity, speed of processing explained a large proportion of the variance within age-related changes. Moffat, Zonderman and Resnick (2001) found that after being given learning trials, 76% of older adults were unable to complete a virtual maze without error, compared to only 14% of young adults. These results could also be explained by a slowing of processing speed, as participants were given five learning trials which may not have been sufficient time for older participants to process enough information about the maze.

5.1.2 Importance of Ecologically Valid Tasks

To compensate for slower processing speed, Phillips et al. (2006) suggested that older adults may be using existing knowledge of real-life situations relevant to the experimental task. The ecological validity of such tasks must therefore be taken into account to more accurately assess which aspects of cognition are sensitive to the effects of age (Burgess et al. 1998; 2006; Alderman, Burgess, Knight & Henman, 2003; Phillips et al. 2006; 2008). Within lab-based experiments, research has demonstrated an age-related decline of prospective memory - an ability to plan and perform an action in the future - but does not show the same effect within naturalistic tasks (Rendell & Thomson, 1999; Phillips et al. 2006). The type of task used to assess ageing is of particular importance, and age-related differences may subside when tasks relate to real world situations. Burgess et al. (2006) suggested that an effective approach would be to design a task and a lab-based model which was as close as possible to real-world situations. However, walking through a shopping centre or a supermarket in search for items can be seen as a relatively novel and recent situation. Considering the evolution of hominins (see White et al. 2009) and the sophisticated cognitive skills humans have evolved (see Coolidge & Wynn, 2001; 2005; Ardila, 2008, for a discussion) a task may be more naturalistic and more accurately tap the relevant cognitive competences when based upon conditions under which these skills may have evolved. High-level cognition in primates is thought to have been triggered by the requirement of foraging on ephemeral resources within a forest environment (Milton, 1981a; 1993). To assess

spatial memory therefore, it would be useful to assess humans within foraging tasks, to provide the most ecologically valid task from an evolutionary perspective.

5.1.3 Age-Related Changes in Search

Previous studies assessing the effect of ageing within spatial memory and search, have found differences between older and younger adults. Older adults have shown spatial memory impairments within a large-scale Morris water maze (Newman & Kaszniak, 2000), and performed at a lower level than younger adults within virtual navigational tasks (Zancanda-Menendez et al. 2015; Moffat et al. 2001). Within a foraging task where participants searched for fish, Mata, Wilke and Czienskowski (2009) additionally found that older adults performed worse than younger adults even when shown and asked to use a strategy to improve optimal foraging performance. These findings suggest that the search strategies deployed become less efficient with age.

Foraging tasks are a useful paradigm to assess cognitive ageing as they tap a number of cognitive skills and are based upon evolutionarily-relevant situations. The foraging paradigm outlined for the set of experiments described in Chapter 4, which was based upon naturalistic foraging scenarios of non-human primates (Janmaat et al. 2013a; Janmaat et al. 2013b; Janmaat et al. 2012), was employed in the current experiment. This task afforded the discrimination of cognitive competences deployed during foraging, and therefore allowed the assessment of where age-related changes lie. The search for food items within this task assessed foraging efficiency by measuring the number of moves taken to find the items. Successful search is supported by LTM, WM, and an ability to detect temporal structure, tapping prospective memory, which this task also assessed. As previous findings have suggested that tasks requiring the DLPFC show an impairment with age (MacPherson et al. 2002), it was predicted that older participants may be less able than younger adults to detect the temporal structure across the current task. This experiment therefore aimed to determine where effects of ageing lie in an ecologically valid task which affords the assessment of a number of cognitive competences thought to have evolved from foraging behaviour.

5.2 Experiment 8

A touchscreen version of the VR task described for Experiment 5 of the previous chapter was employed, which presented the stimuli from a plan view. This enabled the

retention of the essential aspects of the task, whilst allowing for a higher number of trials to be completed than within VR to better assess the cognitive ability of older adults. Whilst VR is a particularly useful method which better reflects the skills and cognitive competences required in real-life situations, the touchscreen task removes the need to traverse an environment. However, considering the diagnostic potential of this foraging task to characterise healthy ageing and to detect impairments in one or more measures of cognition, a touchscreen version affords easier administration and was deemed better suited for this task. To assess age-related changes in foraging efficiency, the performance of older adults was compared with younger adults, whilst differences between sexes were also considered.

5.2.1 Methods

Participants. Twenty-four students from the University of Leicester were recruited (15 female, 9 male) aged 17-27 years old ($M = 19.26$, $SD = 1.86$) who took part for course credit. Data was also collected from 28 older adults (16 female, 12 male) aged between 65 and 86 years old ($M = 71.07$, $SD = 4.72$), who were recruited from the Leicester area and paid for their time.

Montreal Cognitive Assessment. To ensure the task measured healthy cognitive changes in the older group and to avoid any results that may be due to cognitive impairment, the Montreal Cognitive Assessment (MoCA, Nasreddine et al. 2005) was administered. The MoCA is comprised of 13 questions tapping visuospatial/executive competences, naming ability, memory, attention, language, abstraction, delayed recall, and orientation. The test has a maximum score of 30, with a score of 26 or over indicating normal cognitive function. All older participants scored above the healthy cut-off point, and were assumed to be performing at a normal level of cognitive ability ($M = 27.58$, $SD = 1.41$).

Apparatus and Environment. The task was configured in Eprime, and presented on a touchscreen. Participants used their fingers to touch the locations and to produce responses. The rewards to be found in this task could not be found unless a location was checked by touching the circle to select it, which was analogous to chimpanzees raising their head and looking up into the canopy to check for the presence of fruit (Janmaat et al. 2013a). An array of 36 locations displayed as circles were

arranged as a 6 x 6 matrix and presented on the touchscreen, with a white background (see Figure 5.1). Six colours were used to represent different tree species. This included eight blue circles, eight green circles, six purple circles, six white circles, and four each of red and orange circles.

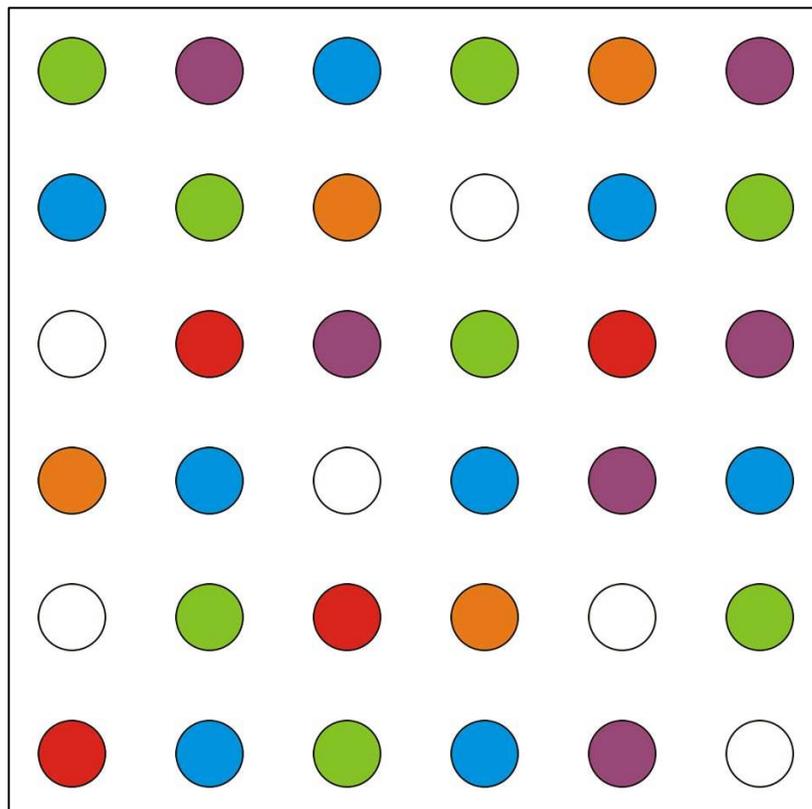


Figure 5. 1 The array of locations presented to participants on the touchscreen.

Design and Procedure. Participants were asked to find the hidden apples by pressing the circles to check for the presence of fruit. Each trial in this task represented a foraging bout, and within each trial 12 locations yielded a reward of a virtual apple, thus in any given trial two ‘tree species’, or colours, were rewarded. Once a circle was selected, it disappeared for 0.5 seconds and an image of an apple appeared in place of the circle if a rewarded circle was selected for the first time in a given trial, or remained blank if an unrewarded circle was selected to show that there was no reward at that location. If a rewarded circle was revisited in a given trial the apple had already been ‘taken’ from that location, and the space remained blank. No cues were left to mark previously visited locations.

Participants were provided with trials featuring a predictable temporal pattern, which consisted of two concurrent patterns that could be learned across trials, in the same way as described for Experiment 6 of the previous chapter. The first pattern was a SA between circles of two colours (red and orange circles), where red circles yielded a reward in the first trial, followed by orange circles yielding rewards in the second trial. Simultaneously, a second pattern featured a DA in the availability of fruit at circles of blue and green. Blue circles were rewarded in two consecutive trials. Then, green circles were rewarded in the subsequent two trials. This created a pattern of switches between the availability of fruit at circles of different colours across trials, and was repeated across all trials. Circles of purple and white never yielded rewards. In addition to the temporal patterns, there were two patterns that were also predictive of reward location; i) if a circle of one species was rewarded, then all circles of that species will also be rewarded, and ii) if a circle of one species was rewarded, then there will be another species that will be simultaneously rewarded.

Participants searched for the hidden apples, and once all apples were found, the trial terminated and they were asked to press the spacebar to start the next trial. Participants completed 120 trials in total, in three blocks of 40 trials with breaks between blocks or when required.

Measures. The same measures as described for Experiment 6 were calculated. The mean number of selections until all apples were found was calculated to assess overall foraging efficiency, where the optimum number of selections was 12. LTM was measured by calculating the mean number of visits in each trial to red and orange locations which never yielded a reward, and WM efficiency measured the number of revisits to circles previously selected within a trial. An ability to detect the availability of fruit on the basis of its cyclical nature, was measured by calculating the proportion of correct first choices made to red and orange circles to assess ability to detect the SA, and calculating the proportion of correct first choices made to blue and green circles to assess detection of the DA. Examining the first selections of each trial, a score of 1 was assigned if a participant visited a rewarded circle in the SA or the DA pattern, instead of or before an unrewarded circle including never rewarded circles. A score of 0 was given if an unrewarded circle of the SA or DA, or a never rewarded circle, was visited before a rewarded pole of these two patterns.

5.2.2 Results

Overall Foraging Efficiency. Across the trials, older adults showed a tendency to make more selections until the completion of a trial ($M = 21.51$, $SD = 7.43$) than younger adults ($M = 16.44$, $SD = 4.26$). Participants within both age groups became more efficient at searching the array, as shown by a decrease in the number of selections (Figure 5.2).

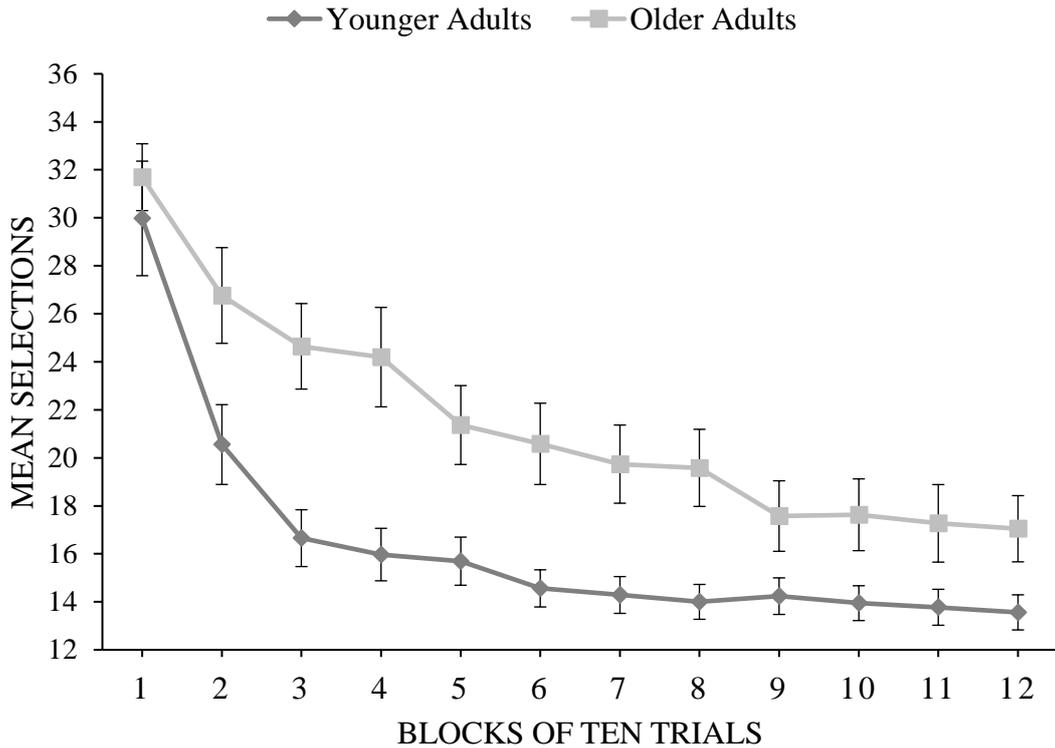


Figure 5. 2 The mean number of selections made to the completion of a trial for younger and older adults, shown across blocks of 10 trials, with ± 1 SE bars.

The results of a 12 (Blocks) x 2 (Age) x 2 (Sex) ANOVA showed a significant effect of Blocks, $F(3.51, 168.32) = 49.59$, $p < .001$, and a significant effect of Age, $F(1, 48) = 8.18$, $p < .01$. An independent samples t-test indicated that overall, older participants made more selections until the completion of a trial than younger adults, $t(50) = -2.95$, $p < .01$. The interaction of Age x Blocks however, approached significance, $F(3.51, 168.32) = 2.38$, $p = .062$. There was no main effect of Sex, $F(1, 48) = .35$, $p = .556$, nor any significant interactions between the three factors, minimum $F(3.51, 168.32) = .46$, $p = .741$.

To compare the slopes of learning across the trials, a linear regression line of each slope was calculated. An independent samples t-test was carried out which showed no significant difference between the slopes of the two age groups (young, $M = -.96$, $SD = .63$; old, $M = -1.17$, $SD = .81$), $F(1, 50) = 1.07$, $p = .306$, suggesting that despite an effect of age, the rates of learning were similar.

Long Term Memory. The mean number of locations selected that never yielded a reward was 3.65 ($SD = 3.65$) for older participants, and 1.18 ($SD = 1.69$) for younger adults. Participants of both age groups became more efficient at avoiding these locations across the trials, with a sharper decrease evident for younger participants (Figure 5.3).

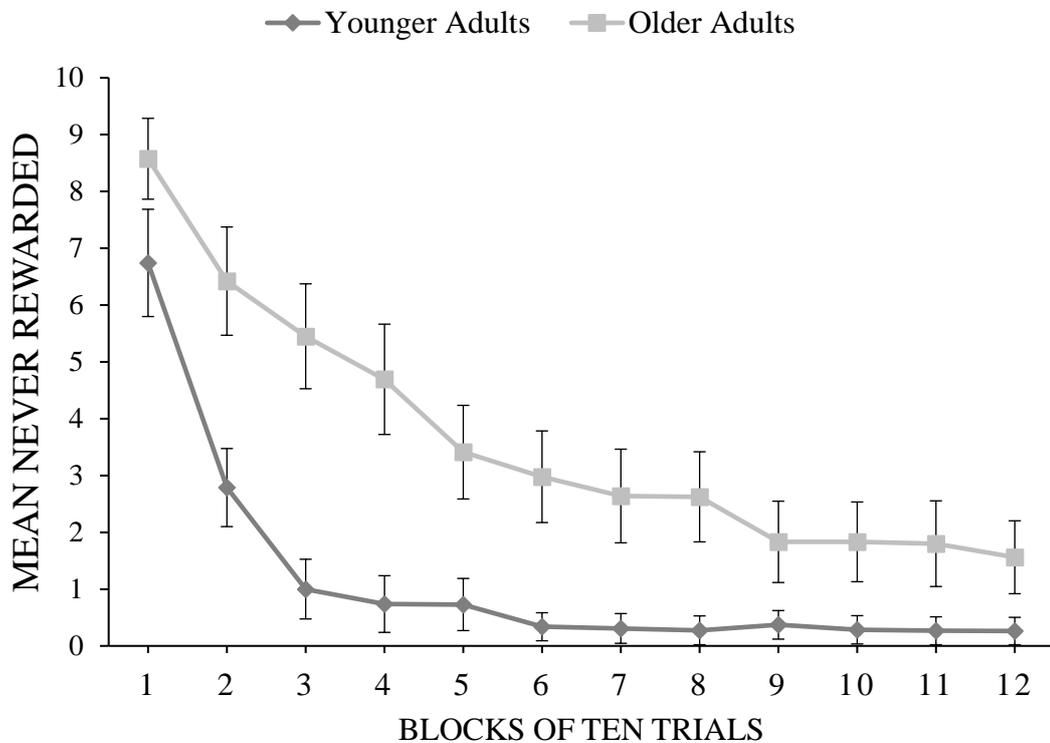


Figure 5. 3 The mean number of never rewarded locations selected by younger and older adults, shown across blocks of 10 trials, with ± 1 SE bars.

A 12 (Blocks) x 2 (Age) x 2 (Sex) ANOVA was carried out which showed a significant effect of Blocks, $F(2.77, 133.09) = 47.06$, $p < .001$, a significant effect of Age, $F(1, 48) = 8.65$, $p < .01$, and a significant interaction of Blocks x Age, $F(2.77, 133.09) = 3.31$, $p < .05$. Independent samples t-tests indicated that in blocks 2, 3, 4, 5, 6, 7, 8 and 10, older adults selected more never rewarded locations than younger adults,

minimum $t(33.61) = -2.08, p < .05$. In blocks 9, 11 and 12, older adults appeared to have reached a level of performance closer to young adult performance, and differences here were not statistically significant, minimum $t(34.37) = -1.89, p = .067$, suggesting that older adults took longer to become efficient at avoiding these circles. There was no significant effect of Sex, $F(1, 48) = .61, p = .438$, nor any further interactions, minimum $F(1, 48) = .06, p = .801$.

The learning rates between the two groups was compared by calculating the linear regression lines. An independent samples t-test showed a significant difference with a significantly sharper decrease in the number of never rewarded locations selected in the younger sample ($M = -.36$) compared to older participants ($M = -.56$), $t(45.03) = 2.09, p < .05$.

Working Memory. Across the trials, both older and younger adults made few revisits ($M = 1.59, SD = 1.52; M = .96, SD = .65$ respectively). Participants of both age groups made fewer working memory errors as the trials progressed, as shown in Figure 5.4.

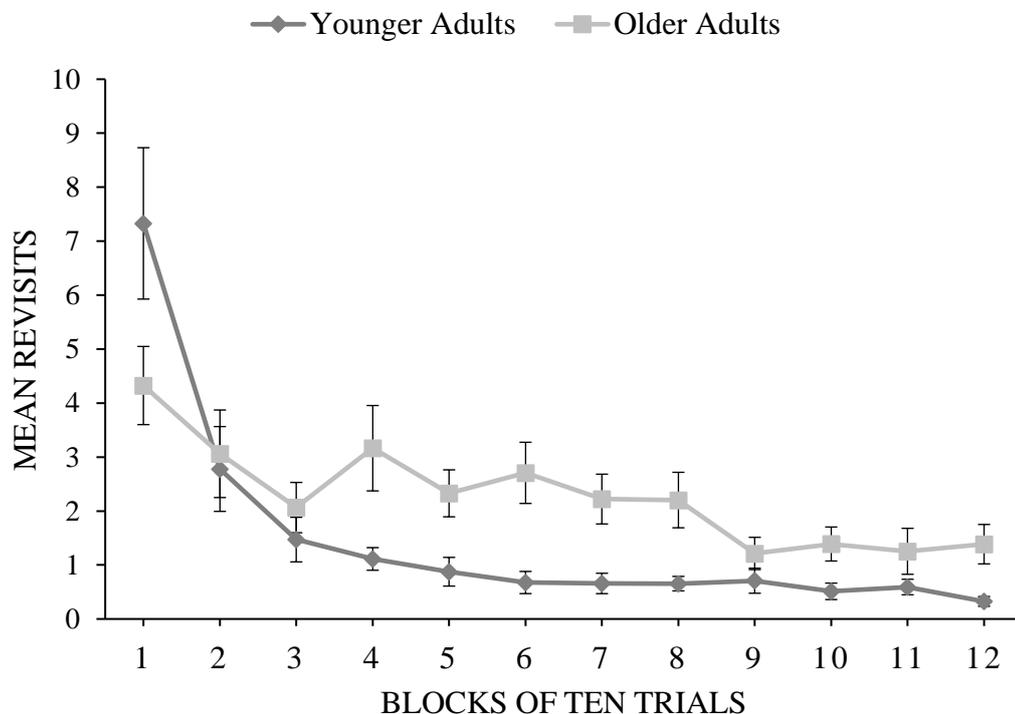


Figure 5. 4 The mean number of revisits made by younger and older adults, shown across blocks of 10 trials, with ± 1 SE bars.

A further 12 (Blocks) x 2 (Age) x 2 (Sex) ANOVA was carried out. A significant effect of Blocks, $F(3.49, 167.28) = 17.80, p < .001$, and a significant interaction of Blocks x Age, $F(3.49, 167.28) = 3.87, p < .01$, was found. Independent samples t-tests showed that older adults made significantly more revisits than younger adults in blocks 4, 5, 6, 7, 8, 10 and 12, minimum $t(30.76) = -2.51, p < .05$. Blocks 1, 2, 3, 9 and 11 were non-significantly different, minimum $t(34.79) = 1.90, p = .065$, indicating that at the start and towards the end of the trials younger and older adults were performing at a similar level. There was no significant main effect of Age, $F(1, 48) = 3.48, p = .068$, Sex, $F(1, 48) = .24, p = .628$, nor any further interactions, minimum $F(3.49, 167.28) = .69, p = .581$.

To compare the slopes of each age group, linear regression lines were calculated. An independent samples t-test showed no significant difference between the two age groups (young, $M = -.18, SD = .14$; old, $-.10, SD = .17$), $F(1, 50) = 3.01, p = .089$, suggesting that rates of learning for both age groups were similar.

Detection of Temporal Patterns.

Single Alternation. The proportion of correct first choices made to circles in the SA was higher for younger adults ($M = .68, SD = .13$) than older adults ($M = .54, SD = .10$). Performance increased across the trials, however this increase was sharper for younger than older adults (see Figure 5.5).

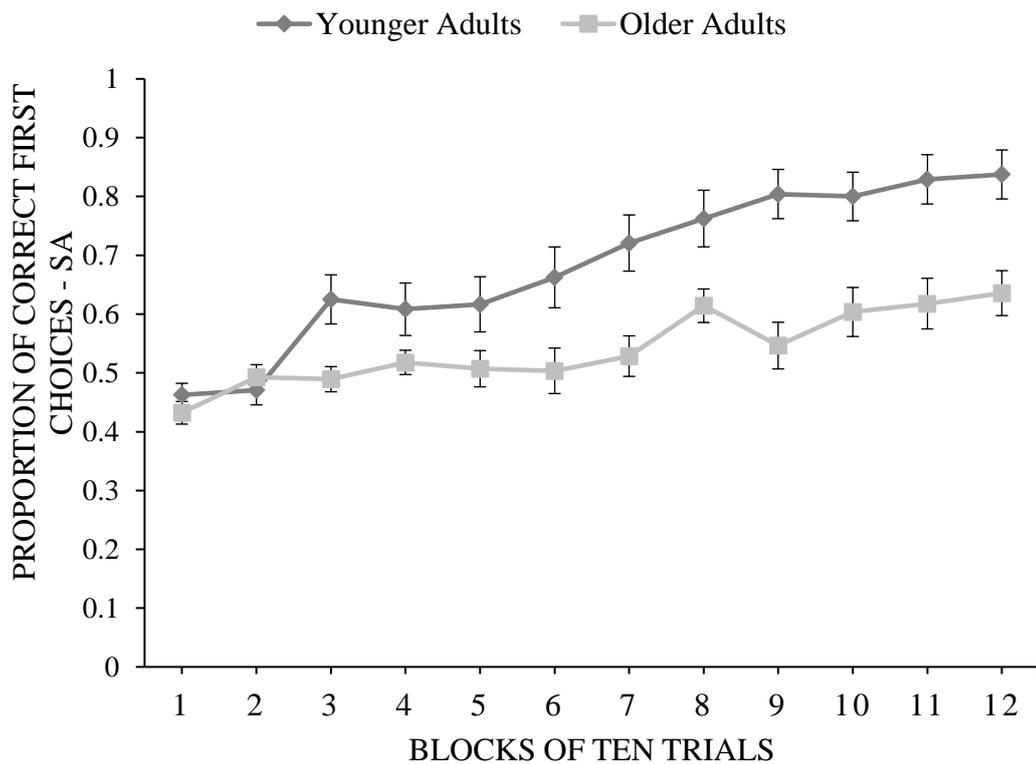


Figure 5. 5 The proportion of correct first choices to locations in the single alternation pattern selected by younger and older adults, across blocks of 10 trials, with ± 1 SE bars.

A 12 (Blocks) x 2 (Age) x 2 (Sex) ANOVA was carried out which found significant effects of Blocks, $F(5.90, 283.29) = 18.79, p < .001$, Age, $F(1, 48) = 16.65, p < .001$, and an interaction of Blocks x Age, $F(5.90, 283.29) = 3.33, p < .01$. Independent samples t-tests showed that older adults made significantly fewer correct first choices of the SA pattern than younger participants in blocks 3, 6, 7, 8, 9, 10, 11 and 12, minimum $t(44.14) = 2.46, p < .05$. Blocks 1, 2, 4 and 5 showed no significant differences, minimum $t(32.60) = 1.84, p = .075$. There was no significant effect of Sex, $F(1, 48) = .68, p = .412$, nor any further interactions, minimum $F(5.90, 283.29) = .70, p = .652$.

To compare the slopes in the rates of learning for each age group, a further independent samples t-test was run using the linear regression lines of each slope. A significant difference was found with a significantly sharper increase in learning found for younger adults ($M = .04$) compared to older adults ($M = .02$), $t(50) = 2.93, p < .01$.

Whilst older adults were making significantly less correct first choices than younger participants, a further analysis determined whether they were making more correct choices than chance level by the end of the trials. Under the assumption that participants had learned which 12 locations to avoid, the probability of selecting a correct location was 12/24, thus using a one-sample t-test the test statistic was set at .5. In the last block of trials, older participants made significantly more correct first choices ($M = .64$) than chance level, $t(27) = 3.55, p < .01$, suggesting that they had detected and were using structured temporal information.

Double Alternation. For the DA pattern, the proportion of correct first choices made was higher for younger adults ($M = .66, SD = .13$) than for older adults ($M = .53, SD = .09$). Both younger and older participants appeared to perform similarly initially, however younger adult performance showed a sharper increase (Figure 5.6).

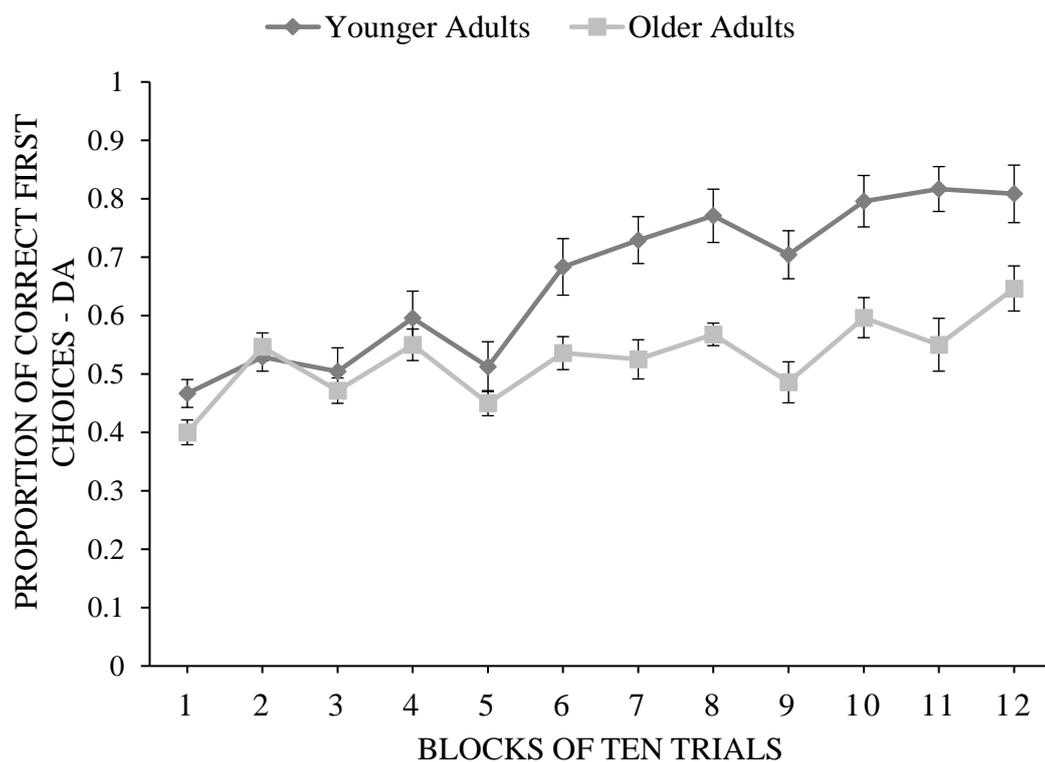


Figure 5. 6 The proportion of correct first choices to locations in the double alternation pattern selected by younger and older adults, across blocks of 10 trials, with ± 1 SE bars.

A 12 (Blocks) x 2 (Age) x 2 (Sex) ANOVA carried out showed significant effects of Blocks, $F(6.20, 297.79) = 18.66, p < .001$, Age, $F(1, 48) = 17.65, p < .001$, and an interaction of Blocks x Age, $F(6.20, 297.79) = 4.70, p < .001$. Independent samples t-tests showed that older adults made significantly fewer correct first choices in the double alternation pattern than younger adults in blocks 1, 6, 7, 8, 9, 10, 11 and 12, minimum $t(50) = 2.10, p < .05$. In blocks 2, 3, 4, and 5, participants performed similarly, minimum $t(34.28) = 1.31, p = .200$. There was no main effect of Sex, $F(1, 48) = .19, p = .662$, nor any further interactions between the three factors, minimum $F(6.20, 297.79) = .65, p = .693$.

To compare the slopes across the trials for the two age groups, linear regression lines were calculated for each age group. An independent samples t-test showed a significantly sharper increase in the performance of the younger adults ($M = .03$) than for older adults ($M = .01$), $t(50) = 3.45, p < .01$.

To assess whether older adults were performing above chance level, a one-sample t-test was carried out, with the test statistic set at .5. In the last block of trials, older participants made significantly more correct first choices ($M = .65$) than chance level, $t(27) = 3.79, p < .001$, suggesting that participants had learned this temporal pattern of reward availability by the end of the experiment.

5.3 Discussion

In a foraging task derived from studies of primate foraging behaviour which simulated the ephemeral nature of cyclically available fruit, older adults were less efficient at searching an array of locations for hidden rewards than younger adults. Older adults showed a slower rate of learning of structured temporal information when linear regression slopes were compared to younger adult performance, and significant differences in the detection of temporal patterns were also apparent by the end of the trials. However, by the end of the trials older participants directed their searches to rewarded locations more often than chance would predict suggesting that they had acquired knowledge of the available temporal information, albeit to a lesser extent than younger adults.

5.3.1 Detection of Structure

The finding that older adults showed a deficit in the detection of temporal structure suggests that competences relying on DLPFC function become impaired with

age. The results suggested that by the end of the trials, for measures of overall efficiency, LTM, and WM, performance by both age groups reached a similar level whilst this was not found for ability to detect and predict temporal structure. An ability to detect and benefit from structure is thought to be reliant on the DLPFC (Bor et al. 2003), and the results of the current study support the notion that the largest age-related differences are specific to tasks dependent on this area of the brain (MacPherson et al. 2002; Andrews-Hanna et al. 2009). McDaniel and Einstein (2011) suggested that in memory, planning load plays an important role and tasks requiring considerable monitoring show the largest decline. The current findings also suggest this, as in this foraging task, a considerable planning component is required to remember which locations were rewarded within the previous trial and to bear in mind where to direct future searches. To further explore this, it would be informative to use fMRI in conjunction with this task to determine the extent to which an ability to detect structure in this task is related to DLPFC function.

5.3.2 Foraging Efficiency

Across all measures, both young and older adults became more efficient as the trials progressed. Differences in overall foraging efficiency and LTM were found, as overall older adults made more selections until the completion of a trial and made more visits to locations that never yielded a reward than their younger counterparts, suggesting that they took longer to learn which locations were profitable. All participants made a similar number of revisits at the start of the experiment, however during the middle blocks, younger adults became more efficient than older adults and made fewer visits to previously selected locations. The finding that older adults show an impairment across these measures of memory, support previous findings also indicating a cognitive decline (Hills et al. 2013; van Hooren et al. 2007; Park et al. 2002). The findings are also consistent with the notion that age-related changes are due to a general slowing of information processing (Verhaeghen & Salthouse, 1997). Older adults became more efficient foragers across the task, though the differences suggest that they take longer to learn and process information. However, comparing the rates of learning across the trials, a significant difference was found for the measure of LTM only. The linear regression lines for each age group for the measures of foraging efficiency and WM indicated that both groups did not differ in learning rate, and by the end of the trials, performance did not appear to be significantly different. This indicates that older

adults had learnt which locations were profitable and which should be avoided, to a similar level as younger adults.

The results also did not indicate any effects of sex, suggesting that males and females performed similarly throughout the task. Additionally, the findings suggested that male and female performance did not differ with age. This is in contrast to previous findings indicating that women's performance deteriorates with age in an object location task (Cashdan, Marlowe, Crittenden, Porter & Wood, 2012). Whilst the current task also requires object location memory, no effect of sex was found amongst the younger or older adults tested.

5.3.3 Use of Ecological Tasks

The use of ecological and naturalistic tasks to accurately assess cognition has been highlighted by numerous researchers (Burgess et al. 1998; 2006; Alderman et al. 2003; Phillips et al. 2006; 2008), and has also been emphasised within a clinical setting for diagnostic use (Barkley, 1991; Burgess et al. 2006; Foreman, Addison, Kim & Dibble, 2011). The current task successfully implemented a paradigm derived from naturalistic foraging behaviour, which tapped a number of cognitive competences required for efficient search. As age-related changes were found across certain measures within this task, it can be suggested that this is an efficient paradigm with which to assess effects of ageing, and aids to further characterise what is typical of healthy ageing in humans. Considering the conditions within which hominin cognition may have evolved (White et al. 2009; Milton, 1981a; 1993), a more accurate assessment of relevant cognitive skills may occur when tasks consider the evolutionary pressures hominins faced. Therefore, it can be suggested that tasks derived from these situations, provide the most ecologically valid task from an evolutionary perspective.

5.3.4 Conclusions

The foraging task developed appears to be an effective paradigm with which to characterise healthy cognitive ageing. In particular, an ability to detect and benefit from temporal structure was affected by age, and older adults did not reach the same level of efficiency as younger participants, suggesting that age-related changes may be specific to cognitive functions relying on the DLPFC. Foraging behaviour is thought to have triggered the emergence of many cognitive skills seen in humans today, thus experimental foraging tasks allow us to assess these skills under evolutionarily-relevant

situations. The results of this chapter indicate that the use of this foraging task is an effective way to ensure ecological validity and helps to further characterise healthy cognitive ageing in humans.

As the foraging paradigm developed appeared to be sensitive to the effects of cognitive ageing, and considering the ease with which this task can be administered, the task therefore afforded the assessment of different populations. The findings presented within this chapter highlighted that young adults are highly efficient during search and demonstrated differences with older adults, however it is unknown when these cognitive competences may develop. The experiment described in Chapter 6 aimed to address this.

Chapter 6: Developmental Changes in Foraging Efficiency

6.1 Introduction

The search paradigm developed in Chapter 4, and which was modified in Chapter 5, is a useful and ecologically valid method to investigate foraging cognition, and appears to be sensitive to the effects of ageing. Whilst it is clear that young adults are highly efficient across a range of measures, it is unknown when these skills develop in humans. This paradigm therefore, further afforded an investigation of when the cognitive skills relevant to efficient foraging behaviour may develop in children.

6.1.1 Evolutionary Developmental Psychology

A relatively recent branch of evolutionary psychology devotes its time to understanding child development. Evolutionary developmental psychology asserts that a long developmental period as experienced by humans is risky and must have strong benefits for it to have evolved (Geary & Bjorklund, 2000). Growth rates across species suggest that developing at a maximum rate may be detrimental, particularly in terms of cognitive development which may not reach full potential if body growth is rapid (Metcalf & Monaghan, 2003). In humans, individuals face a relatively long period of childhood before reaching maturity, suggesting that this developmental period is adaptive. The selection pressures faced by our ancestors varied during the stages of development, and therefore it is thought that some behaviours and cognitive mechanisms serve different advantages across the various stages of ontogeny (Bjorklund & Pelligrini, 2000; Bjorklund & Bering, 2002). In comparison to other primate species, the human developmental period is relatively large, though cognition has become enhanced and stages of development have accelerated during human evolution (Parker & McKinney, 1999). Across hominin species, Bogin (1997) notes that the period of childhood appears to show an increase. As a result, it is logical to assume that childhood is an important and adaptive function of the lifespan.

6.1.2 Cognitive Development

Proficiency in WM tasks often shows a linear increase as children age (Orsini et al. 1987; Luciana & Nelson, 1998; Hamilton et al. 2003; Gavens & Barrouillet, 2004; Bayliss, Jarrold, Baddeley, Gunn & Leigh, 2005; Farrell Pagulayan et al. 2006). Similarly, children show improvements as they age in inhibitory control (Williams,

Ponessa, Schachar, Logan & Tannock, 1999; Bedard et al. 2002; Sinopoli, Schachar & Dennis, 2011; Davidson, Amso, Anderson & Diamond, 2006), and rule use and reasoning (Frye, Zelazo & Palfai, 1995; Zelazo, Frye & Rapus, 1996; Siegler & Chen, 1998). In particular, the ability to use memory and recall strategies appears to show a clear developmental trend (Dempster, 1978).

6.1.3 Development of Search Strategies

Diamond (2002), in a review, considered the development of the frontal lobe and noted that whilst cognitive functions unrelated to the prefrontal cortex are reasonably developed by age 7, the cognitive functions related to the DLPFC continue to develop and improve after the age of 7 years old and often into early adulthood. Supporting this, Kwon et al. (2002) investigated brain activation patterns in participants aged 7-22 years old and found a linear increase in the activation of the fronto-parietal network, including the DLPFC, as age increased when performing a visuo-spatial WM task. The DLPFC is also thought to be related to an ability to benefit from structure (Bor et al. 2003), and further findings by Imbo et al. (2009) in a Corsi task found that all groups of participants, aged 9-19, benefited from sequences which exploited the spatial structure of the blocks, though older participants benefited to a greater degree when a structured strategy could be used. These findings suggest that an ability to detect and exploit structure in search may show a developmental trend as the DLPFC continues to develop throughout childhood.

In a maze task, the search strategies children deploy have been shown to develop with age (Aadland, Beatty & Maki, 1985). Lehnung et al. (1998) found that 5 year old children used proximal cues whilst 10 year olds were able to use distal cues. Children aged 7 years old appeared to be at a stage of transition, and deployed search strategies based on both these cue types. However, in a large-scale search task by Smith, Gilchrist and Hood (2005), no effect of age was found when children were asked to search for a green target light amongst a number of switches positioned on the floor. In a similar way to the paradigm employed in the subsequent experiment and within the previous two chapters, Smith et al.'s search paradigm required participants to check each location for the presence of the target, which more accurately reflects true foraging situations. Unlike natural situations however, Smith et al.'s task featured a single target per trial. The current experiment aimed to further assess the cognitive competences required for efficient foraging in children, in a task requiring the search for multiple items. It is

predicted that developmental trends will be seen across a number of cognitive competences required for efficient foraging behaviour.

6.2 Experiment 9

The task employed in this experiment was the same as that described for Experiment 8. As this task proved to be sensitive to the effects of ageing, this experiment assessed primary school children in the development of foraging cognition, whilst also considering whether sex differences occur within age groups in a foraging task.

6.2.1 Methods

Participants. Data was collected from 63 children (30 female and 33 male), aged 5 to 11 years old ($M = 8.86$, $SD = 1.62$), from a primary school in Staffordshire, UK. Consent forms were obtained from parents two weeks prior to testing, with the children also agreeing to take part on the day of testing.

Apparatus and Environment. The same Eprime touchscreen task as described for Experiment 8 was employed. As testing was carried out at the school, the monitor used to present the task required a stylus to produce responses in place of touching the screen with their finger. A 6 x 6 matrix array of coloured circles was presented on screen. Six colours were used to represent different tree species, which included eight blue circles, eight green circles, six purple circles, six white circles, and four each of red and orange circles.

Design and Procedure. Participants were required to check for the presence of an apple by selecting a circle. A single foraging bout was represented by a single trial, with 12 circles yielding a reward of a virtual apple within each trial. In any given trial, two ‘tree species’ – colours – yielded a reward. When a rewarded circle was selected for the first time in a trial, the circle disappeared for 0.5 seconds and an image of the apple appeared in place of the circle. If an unrewarded circle was selected or a circle was reselected, the space beneath the circle remained blank to show there was no reward or that it had already been taken. No cues were left to mark previously visited locations. The availability of fruit followed the same temporal patterning as described for Experiment 8, which featured two concurrent patterns of a SA between red and orange

circles, and a DA between green and blue circles, whilst purple and white circles never yielded a reward. However, due to time and attention constraints, children's ability to detect the temporal patterns across trials could not be assessed. Within a trial, participants could still detect the two available patterns; i) if a location of one species was rewarded, then all locations of that species will also be rewarded, and ii) if a location of one species was rewarded, then there will be another species that will be simultaneously rewarded.

Children were asked if they wanted to play a game where they had to find the hidden apples by tapping on circles to see if there was an apple hidden there. Once all the apples had been found, the trial terminated and children were asked to press the spacebar to start the next trial. They completed as many trials as they could in 15 minutes.

Measures. Overall foraging efficiency was measured by calculating the number of selections made until the completion of a trial. To assess LTM, the number of never rewarded locations selected was calculated, and to measure WM ability, the number of revisits made within a trial was also calculated.

6.2.2 Results

The number of trials children completed ranged from 3 to 32 trials ($M = 18.60$, $SD = 7.73$), which is shown as a scatterplot in Figure 6.1.

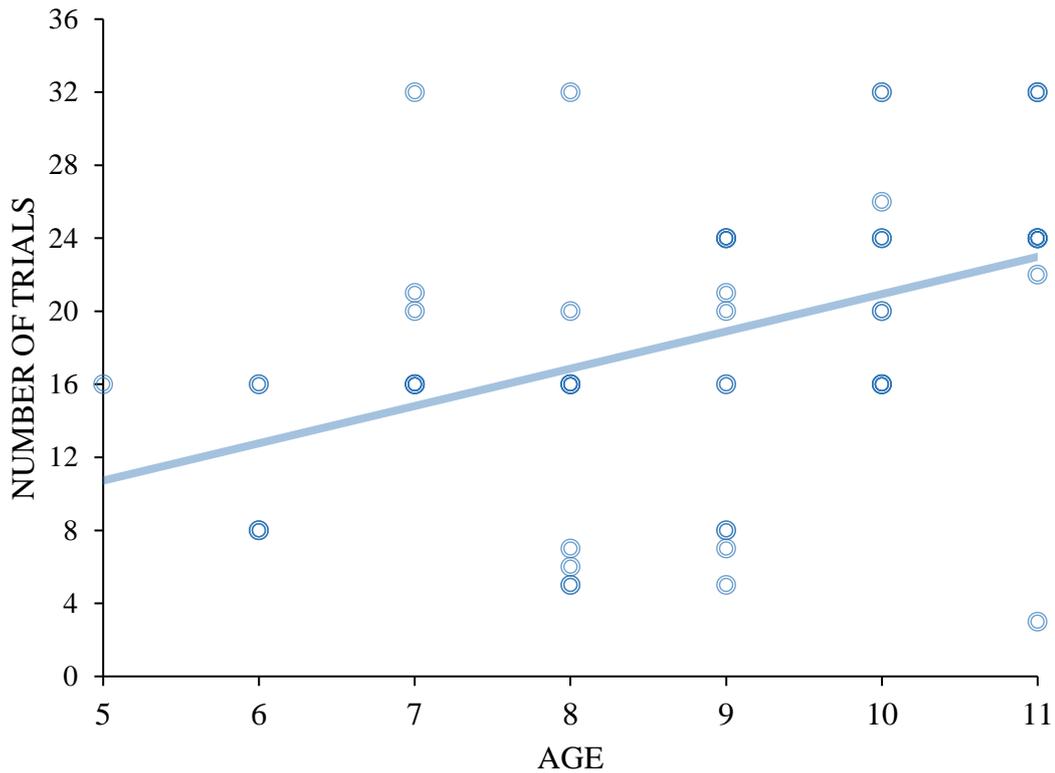


Figure 6.1 The number of trials completed by children of each age.

A Pearson’s correlation showed a significant positive correlation between the age of the participant and the number of trials they completed, $r = .429$, $N = 63$, $p < .001$, indicating that the older a child was, the more trials they were able to complete in the allocated time.

To analyse foraging efficiency, participant data was split into three age groups; 5-7, 8-9, and 10-11 years old. Results were initially analysed across the outset of trials by analysing the first eight trials as the majority of children completed at least this number (5-7 years, $N = 14$; 8-9 years, $N = 18$; 10-11 years, $N = 24$), before analysing the first 20 trials to further assess changes in foraging efficiency (5-7 years, $N = 3$; 8-9 years, $N = 9$, 10-11 years, $N = 19$).

Overall Foraging Efficiency.

Eight Trials. Across the first 8 trials, the mean number of selections made by 5-7 year old children was 35.13 ($SD = 7.89$), 41.88 ($SD = 16.00$) for 8-9 year olds, and 31.61 ($SD = 9.86$) for 10-11 year olds. The means are shown in Figure 6.2.

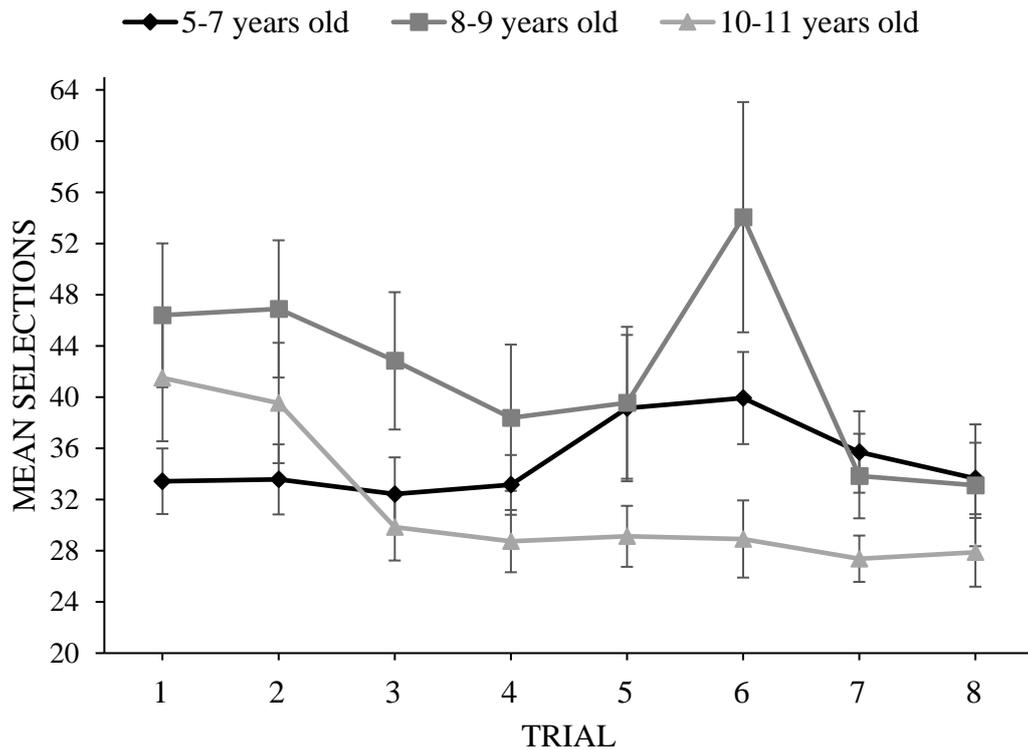


Figure 6. 2 The mean number of selections to the completion of a trial across the first 8 trials for each age group, with ± 1 SE bars.

An 8 (Trials) x 3 (Age) x 2 (Sex) ANOVA was carried out, which showed significant effects of Trials, $F(5.25, 262.24) = 3.53, p < .01$, Age, $F(2, 50) = 6.46, p < .01$, and an interaction of Trials x Age, $F(10.49, 262.24) = 2.16, p < .05$. Independent samples t-tests indicated that in trials 1 and 2, children aged 8-9 years old made significantly more selections than 5-7 year old children, minimum $t(23.48) = -2.10, p < .05$, and significantly more than 10-11 year old children in trials 3 and 6, minimum $t(40) = 2.36, p < .05$. In trials 6 and 7, 5-7 year olds made significantly more selections than 10-11 year olds, minimum $t(36) = 2.46, p < .05$. A significant effect of Sex was also found, $F(1, 50) = 8.65, p < .01$, with females ($N = 25, M = 39.40, SD = 13.03$) making significantly more selections overall than males ($N = 31, M = 32.88, SD = 11.30$), $t(54) = 2.00, p = .05$. The interaction Age x Sex approached significance, $F(2, 50) = 2.77, p = .073$, and all other interactions were non-significant, minimum $F(10.49, 262.24) = 1.34, p = .205$.

The results of a further ANOVA carried out for each age group across the trials indicated that only 10-11 year old children showed a significant linear decline in the

number of selections made across the trials, $F(1, 23) = 11.22, p < .01$. This approached significance for 8-9 year olds, $F(1, 17) = 3.83, p = .067$, and was also non-significant for 5-7 year old children, $F(1, 13) = 1.42, p = .255$.

Twenty Trials. Considering performance across 20 trials, the mean number of selections made by 5-7 year old children was 34.93 ($SD = 2.43$), 31.29 ($SD = 6.67$) for 8-9 year olds, and 26.20 ($SD = 7.04$) for 10-11 year old children (see Figure 6.3).

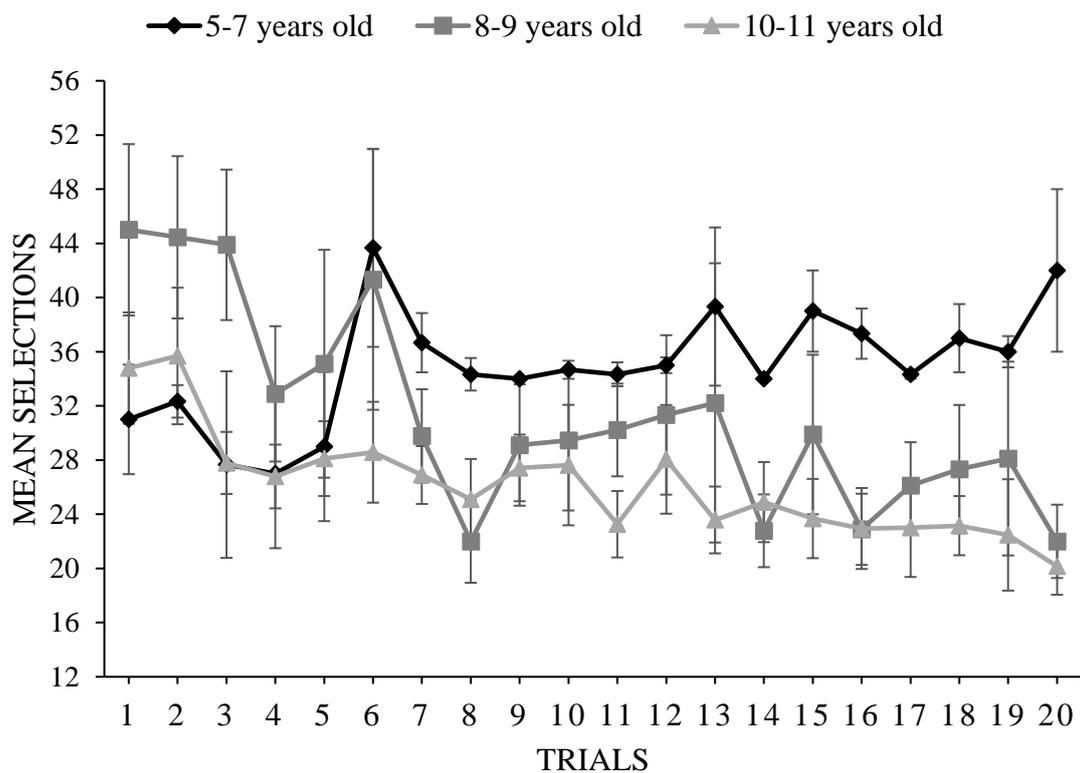


Figure 6. 3 The mean number of selections made to the completion of a trial shown across 20 trials for each age group, with ± 1 SE bars.

A 20 (Trials) x 3 (Age) x 2 (Sex) ANOVA was carried out which showed no significant effect of Trials, $F(8.67, 216.63) = 1.50, p = .153$, Age, $F(2, 25) = 2.74, p = .084$, Sex, $F(1, 25) = .00, p = .951$, nor any interactions between the factors, minimum $F(17.33, 216.63) = 1.28, p = .206$.

A further ANOVA was carried out to assess each age group independently, which indicated that 8-9 year old, and 10-11 year old performance showed a significant

linear decline, $F(1, 8) = 5.91, p < .05$, and $F(1, 18) = 8.26, p < .05$, respectively. There was no significant linear decline, $F(1, 2) = 7.22, p = .115$.

Long Term Memory.

Eight Trials. The mean number of locations selected that never yielded a reward was 9.84 ($SD = 3.86$) for 5-7 year old children, 10.99 ($SD = 4.78$) for 8-9 year olds, and 7.95 ($SD = 4.37$) for 10-11 year olds. The number of never rewarded locations selected within the first eight trials is shown in Figure 6.4.

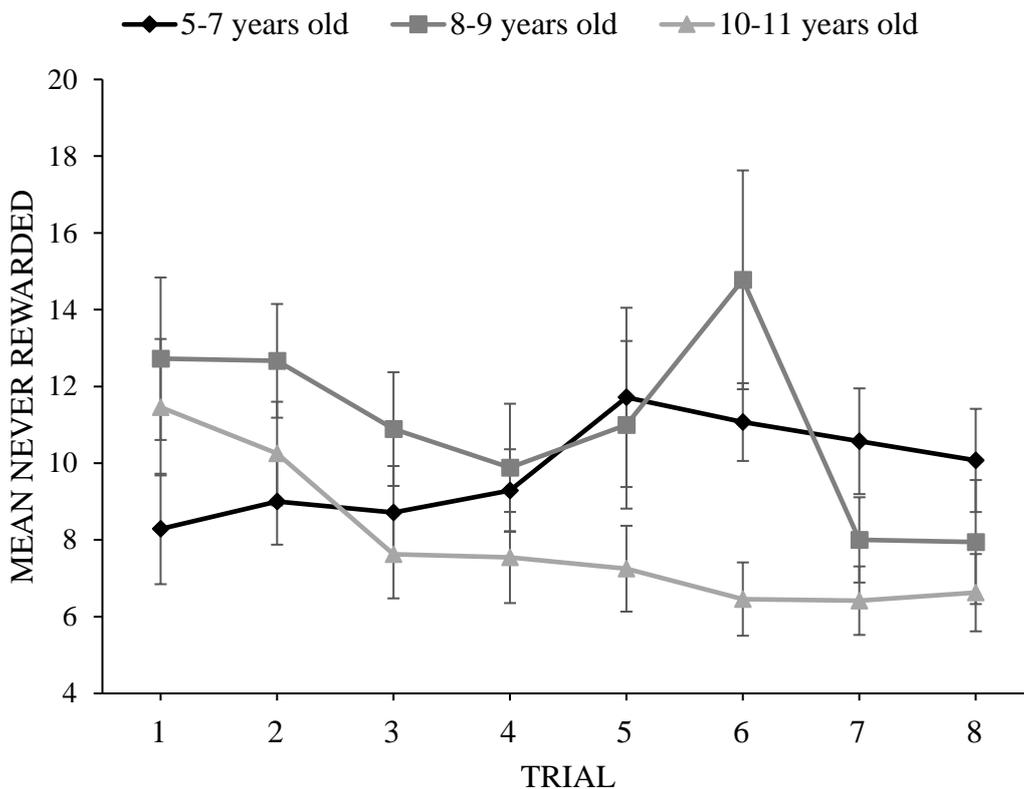


Figure 6. 4 The mean number of never rewarded circles selected across the first 8 trials for each age group, with ± 1 SE bars.

An 8 (Trials) x 3 (Age) x 2 (Sex) ANOVA was carried out, which indicated a significant effect of Trials, $F(4.97, 248.48) = 2.48, p < .05$, Age, $F(2, 50) = 4.00, p < .05$, and a significant interaction of Trials x Age, $F(9.94, 248.48) = 2.44, p < .01$. Independent samples t-tests indicated that 8-9 year old children made significantly more visits to never rewarded locations than 10-11 year old children in trial 6 only, $t(20.84) = 2.77, p < .05$. As the trials progressed, 5-7 year old children started to make significantly more visits to never rewarded circles than 10-11 year olds, in trials 6, 7,

and 8, minimum $t(36) = 2.06, p < .05$. There were no significant differences between 5-7 and 8-9 year old performance, minimum $t(30) = -1.63, p = .113$. The ANOVA also revealed a significant effect of Sex, $F(1, 50) = 6.43, p < .05$, however independent samples t-tests indicated that overall, females ($M = 10.48, SD = 4.24$) did not make significantly more visits to these locations than males ($M = 8.53, SD = 4.61$), $t(54) = 1.62, p = .110$. All other interactions were non-significant, minimum $F(2, 50) = 1.30, p = .283$.

The results of a further ANOVA indicated that only 10-11 year old children showed a significant linear decline in the number of never rewarded locations visited, $F(1, 23) = 12.74, p < .01$. For 5-7 year olds, and 8-9 year olds, this analysis did not reach statistical significance, $F(1, 13) = 3.95, p = .068$, and $F(1, 17) = 3.50, p = .079$ respectively.

Twenty Trials. Across 20 trials, the mean number of never rewarded locations selected was 10.62 ($SD = 1.32$) for 5-7 year old children, 7.60 ($SD = 3.36$) for 8-9 year olds, and 5.46 ($SD = 3.38$) for children aged 10-11 years old. The means are shown in Figure 6.5.

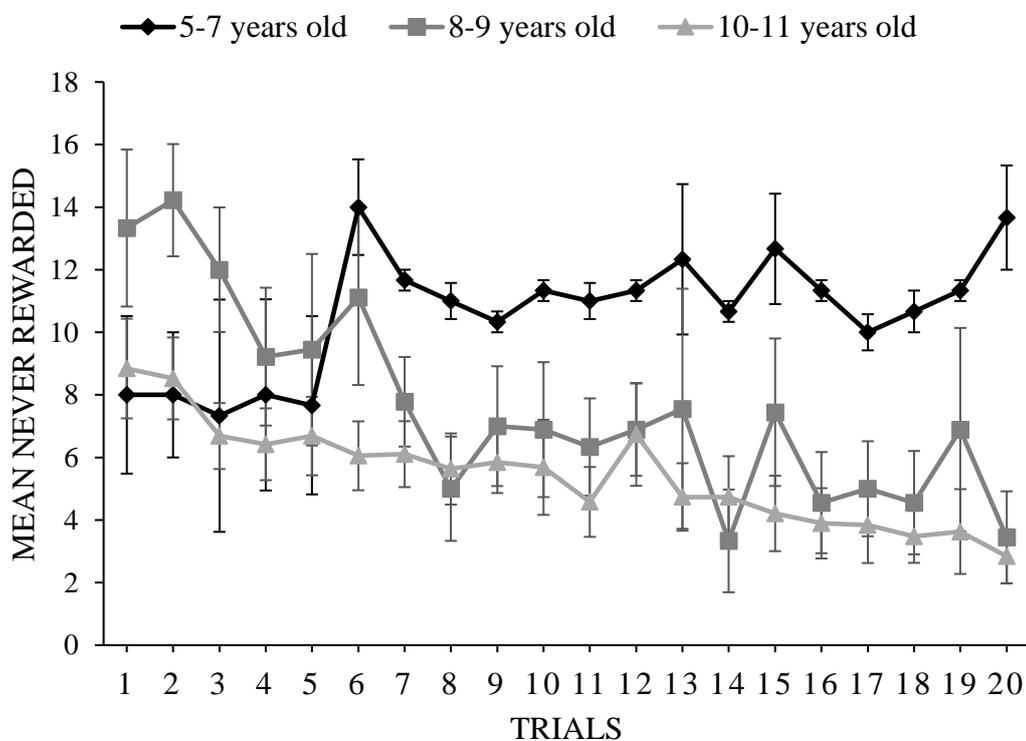


Figure 6. 5 The mean number of never rewarded locations selected shown across 20 trials for each age group, with ± 1 SE bars.

The results of a 20 (Trials) x 3 (Age) x 2 (Sex) ANOVA revealed a marginally significant main effect of Age, $F(2, 25) = 3.29, p = .054$, with independent samples t-tests indicating that 5-7 year old children made significantly more visits to locations that never yielded a reward than 10-11 year old children, $t(20) = 2.57, p < .05$. There was no significant effect of Trials, $F(8.44, 211.02) = 1.75, p = .086$, Sex, $F(1, 25) = .01, p = .920$, nor any significant interactions, minimum $F(16.88, 211.02) = 1.55, p = .082$.

A further ANOVA indicated that the performance of 8-9 and 10-11 year old children showed a significant linear decline across the trials, $F(1, 8) = 10.35, p < .05$, and $F(1, 18) = 11.19, p < .01$ respectively. This was non-significant for children aged 5-7 years old, $F(1, 2) = 2.54, p = .252$.

Working Memory.

Eight Trials. For the number of visits made to circles previously selected within a trial, the mean number made by 5-7 year olds was 4.93 ($SD = 4.87$), 13.80 ($SD = 13.68$) for 8-9 year olds, and 5.05 ($SD = 5.55$) for 10-11 year old children. The mean number of revisits are shown across trials in Figure 6.6.

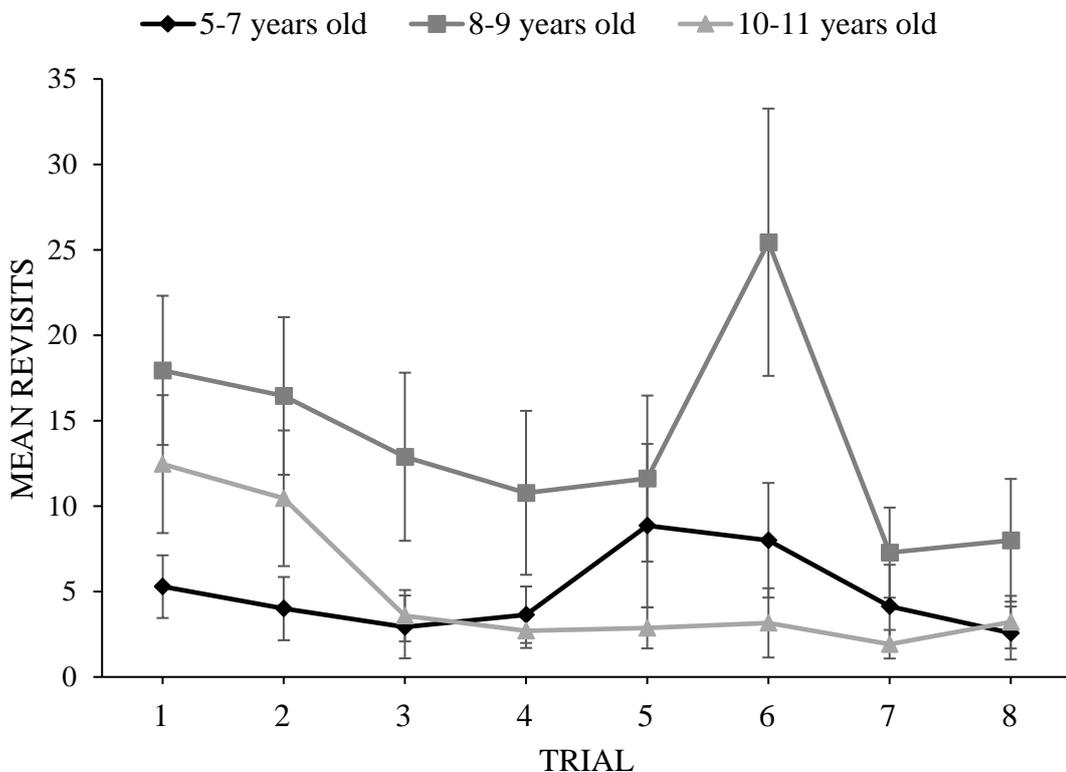


Figure 6. 6 The mean number of revisits made across the first 8 trials for each age group, with ± 1 SE bars.

An 8 (Trials) x 3 (Age) x 2 (Sex) ANOVA was carried out which showed significant effects of Trials, $F(5.17, 258.62) = 3.53, p < .01$, Age, $F(2, 50) = 10.06, p < .001$, and an interaction of Trials x Age, $F(10.35, 258.62) = 2.02, p < .05$. Independent samples t-tests showed that 8-9 year old children made significantly more revisits than children aged 5-7 years old in trials 1 and 2, minimum $t(22.17) = -2.67, p < .05$, and more than 10-11 year olds in trial 6 only, $t(19.30) = 2.76, p < .05$. There were no significant differences between 5-7 and 10-11 year old children in the number of revisits made, minimum $t(31.14) = -1.62, p = .116$. The ANOVA also indicated a significant effect of Sex, $F(1, 50) = 7.80, p < .01$, and a significant interaction of Age x Sex, $F(2, 50) = 5.32, p < .01$. Independent samples t-tests indicated that within the 8-9 year old age group, female children ($M = 23.59$) made significantly more revisits than males ($M = 7.57$), $t(16) = 2.91, p < .05$, which is shown in Figure 6.7. Additionally, females aged 8-9 years old made significantly more revisits than both 5-7 year old females ($M = 6.94$) and 10-11 year old females ($M = 5.13$), $t(9) = -2.29, p < .05$, and $t(19) = 4.72, p < .001$ respectively.

A further ANOVA indicated that only children aged 10-11 years old showed a significant linear decline in the number of revisits made across the trials, $F(1, 23) = 6.57, p < .05$. This was non-significant for children aged 5-7 years old, $F(1, 13) = .01, p = .929$, and 8-9 years old, $F(1, 17) = 2.55, p = .129$.

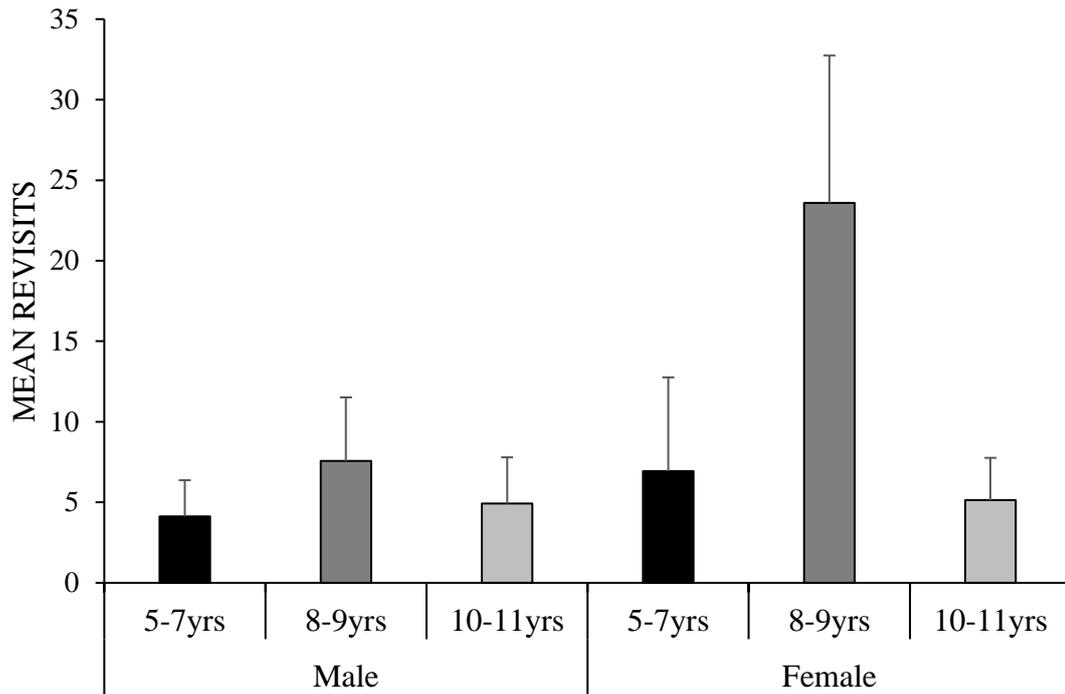


Figure 6. 7 The mean number of revisits made by each sex and each age group, across the first 8 trials, with +1 SE bars.

Twenty Trials. The mean number of revisits made by 5-7 year old children across the 20 trials was 2.22 ($SD = .65$), 6.36 ($SD = 3.77$) for 8-9 year olds, and 3.46 ($SD = 2.38$) for 10-11 year old children. This is shown in Figure 6.8.

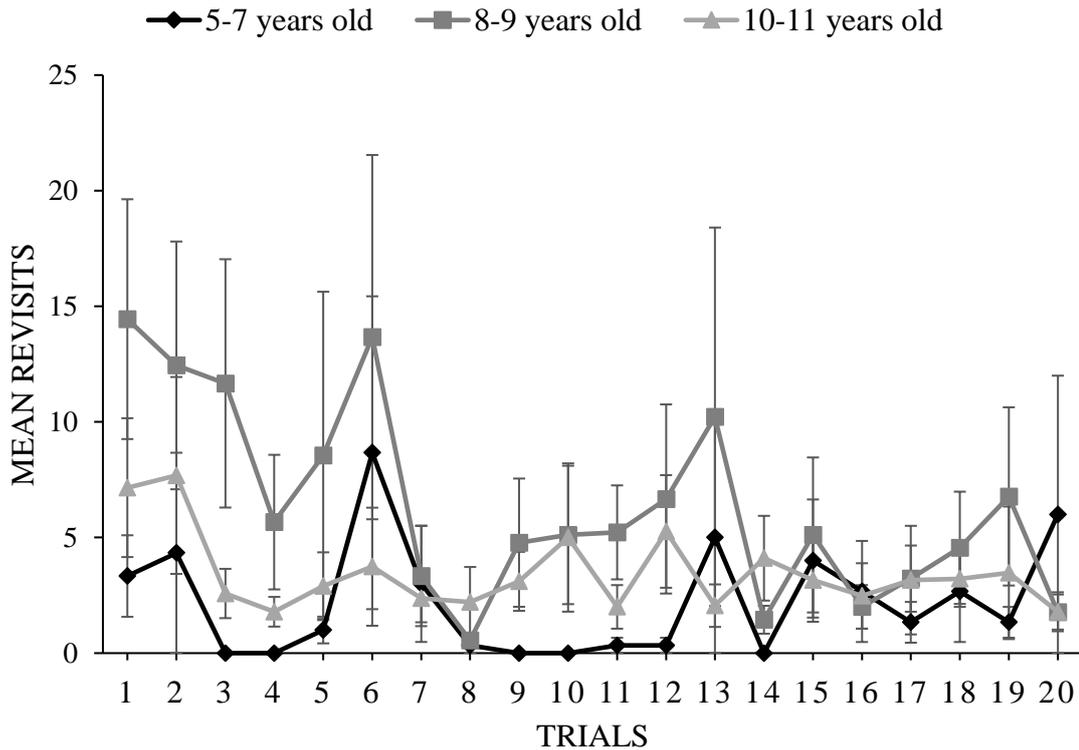


Figure 6. 8 The mean number of revisits made by each age group, shown across 20 trials, with ± 1 SE bars.

A further 20 (Trials) x 3 (Age) x 2 (Sex) ANOVA was carried out which revealed a significant main effect of Age, $F(2, 25) = 7.01, p < .01$. Independent samples t-tests indicated that 8-9 year old children made significantly more revisits overall than 5-7 year olds, $t(9.20) = -3.16, p < .05$, but did not make significantly more than 10-11 year olds despite a trend, $t(11.13) = 2.12, p = .058$. There was no significant difference in number of revisits made by 5-7 and 10-11 year old children, $t(12.96) = -1.88, p = .083$. The ANOVA revealed no significant effect of Trials, $F(7.87, 196.80) = 1.13, p = .343$, Sex, $F(1, 25) = 1.14, p = .296$, nor any interactions, minimum $F(2, 25) = 2.73, p = .085$.

A further ANOVA across the trials showed no significant linear component for each 5-7 year old children, $F(1, 2) = .01, p = .919$, 8-9 year olds, $F(1, 8) = 2.24, p = .173$, nor 10-11 year olds, $F(1, 18) = .95, p = .343$.

6.3 Discussion

In a touchscreen task derived from naturalistic foraging situations, children became more efficient foragers across the trials. Children were able to complete a higher number of trials within the time limit the older they were, suggesting that children show a developmental trend in search efficiency as they age. Across the first eight trials, the findings indicated that 8-9 year old children were initially less efficient and made more selections until a trial was completed than 5-7 and 10-11 year old children. The youngest and the intermediate age group also made more LTM errors than the oldest group, suggesting that older children became more efficient in avoiding locations that never yielded a reward than their younger counterparts. However, the findings also indicated that 8-9 year old children made the largest number of WM errors, and showed a tendency to make a greater number of revisits than children of the other age groups. Across 20 trials, a developmental trend persisted, and findings also indicated that 10-11 year old children showed a linear decline in the number of selections and never rewarded locations visited, whilst 8-9 year old children's performance also showed this trend. The performance of 5-7 year old children did not appear to improve across the trials. Differences between 8-9 year old children and the oldest age group were not significant, however in terms of WM, 8-9 year old children continued to make more WM errors than the youngest age group.

6.3.1 A Developmental Trend in Structure Detection?

The number of selections made and the number of never rewarded locations selected across 20 trials was used to infer pattern detection, to assess children's understanding of which 'species' – or colours – were rewarded. Children aged 10-11 and 8-9 years old showed a significant improvement across the trials, compared to the children of the youngest age group whose performance appeared to deteriorate as the trials progressed. These results suggested that as a child's age increased, fewer trials were needed to learn that within a trial, particular 'species' were rewarded, and that two species were always rewarded. In accordance with the current findings, Imbo et al. (2009) concluded that older children further benefited from using the structure of the task in comparison to younger children. As such, the finding that older children were better able to detect patterns within the task than children of the younger age groups, suggests that within a task which taps cognitive functions related to the DLPFC, an

ability to detect patterns within stimuli appears to develop across childhood, consistent with previous findings (Diamond, 2002; Kwon et al. 2002).

6.3.2 Development of Foraging Efficiency

The foraging task outlined appears to be a useful paradigm within which to assess a number of cognitive competences across children of different ages. The findings suggest that overall foraging efficiency measured by an ability to learn which locations were profitable and which locations to avoid, improves with age, which is in accordance with previous findings which show a developmental trend in cognition (Williams et al. 1999; Bedard et al. 2002; Frye et al 1995; Zelazo et al. 1996). Initially, the youngest age group appeared to perform well, before performance deteriorated across 20 trials and developmental trends were present for these measures. The deterioration across these measures may reflect poorer LTM skills in young children, who may be less able to retain information relating to which locations should be avoided. However, an alternative explanation may be that young children have poorer attention skills, which have been shown to become more efficient as children age and to also show developmental improvements (Hagen & Hale, 1973), thus whilst efforts were made to make the task interesting for young children, boredom effects may have occurred as the trials progressed. In turn, this may have had an effect on their overall efficiency and LTM ability.

However, the finding that 8-9 year old children showed poorer WM performance than the youngest age group, does not appear to be consistent with previous findings which have shown an increase in WM capacity with age (Farrell Pagulayan et al. 2006; Orsini et al. 1987; Luciana & Nelson, 1998; Hamilton et al. 2003; Gavens & Barrouillet, 2004; Bayliss et al. 2005). It is unclear why children of this age committed a higher number of WM errors, however it is cause for further investigation. Additionally, there is cause to further assess the foraging competences children show. Younger children in particular may have struggled with the large number of locations to-be-searched, and future research could consider presenting the display set gradually, by using an incremental procedure. In this way, it may more accurately determine whether children show clear developmental trends across the relevant cognitive competences involved in efficient foraging behaviour.

6.3.3 Sex Differences in Children's Search

Across the first eight trials, a significant effect of sex was found across all measures of this task, with males making fewer selections until the completion of a trial, fewer visits to locations that never yielded a reward, and fewer revisits than females. In particular, females aged 8-9 years old were found to make more WM errors than males of the same age, and females of the other age groups. These differences only occurred during the outset of trials however, and this sex difference diminished across 20 trials.

The finding that males outperformed females within this search task is in accordance with previous findings (Silverman et al. 2000; Moffat et al. 1998; Sandstrom et al. 1998; Merrill, Yang, Roskos & Steele, 2016). The current findings support the notion that sex differences are seen amongst children as well as in adults, and occur early on in development (Spetch & Parent, 2006; Levine, Huttenlocher, Taylor & Langrock, 1999). However, it remains unclear as to why females within the intermediate age group tested performed worse than both the younger and older children within this task, and further investigation would be beneficial. Additionally, in contrast to the current findings, McGuinness and Morley (1991) found sex differences amongst children on a three-dimensional search task but did not find the same differences when the task was given in two-dimensions. The results of this chapter showed a male advantage in a two-dimensional foraging task, which lends further support to the claim that this task is a useful and informative method to measure the cognitive skills required for efficient foraging.

6.3.4 Conclusions

Overall, these findings support evolutionary developmental theories which suggest that the long developmental period humans experience is an adaptive function which aids high-level cognition (Bjorklund & Pelligrini, 2000; Geary & Bjorklund, 2000; Bjorklund & Bering, 2002). An effect of age was seen across the measures of this foraging task, showing a developmental trend particularly in the development of LTM and in the detection of which locations to avoid. The results of this chapter suggest that the cognitive competences involved in foraging behaviour and the search for multiple food items become more advanced as children age, consistent with the idea that across evolutionary history, these skills were more beneficial to older children (Surovell, 2000). As such, the findings support the notion that childhood is an important and adaptive function of the lifespan where important cognitive developments occur.

The results of this chapter furthered the findings of the previous two chapters, investigating the development of cognitive competences in humans, and provided further evidence to suggest that this foraging paradigm is a valuable method with which to assess the cognitive skills thought to have evolved from foraging behaviour. This paradigm was derived from situations non-human primates face today, though studies with humans only allow inferences about human behaviour. The touchscreen task developed provided a valuable and suitable method with which to assess non-human primates within an experimental paradigm, which the final experimental chapter implemented.

Chapter 7: Foraging efficiency and Detection of Structure in Baboons, *Papio papio*

7.1 Introduction

Humans show a proficiency for detecting and monitoring temporal structure. The touchscreen foraging task developed afforded the successful assessment of both an ageing and a developmental population, investigating the high level cognitive skills required for efficient foraging. In the current chapter, this task further afforded the assessment of a non-human primate species, *Papio papio*, to provide a direct comparison between humans and primates, and to provide insights into when this proficiency to detect structure may have evolved along the primate lineage.

The assessment of humans within the foraging task described in the previous chapters, whilst derived from studies of non-human primates foraging in natural habitats, only allows inferences to be made about human behaviour and cognition. A direct comparison between species tested using the same task would allow inferences to be made regarding the evolution of cognitive skills relevant to efficient foraging. The development of the touchscreen task provided a valuable opportunity to test a group of baboons which were touchscreen trained and housed at a research centre in Aix, Marseille, within this foraging paradigm which the initial VR task did not afford.

7.1.1 Baboon Lineage and Ecology

Whilst studies of primates with which humans share common ancestry is undoubtedly valuable, Jolly (2001) notes that ancestral baboons shared the same sub-Saharan environments as ancestral hominins unlike forest-dwelling apes, and therefore conditions which may have impacted human evolution would have also had a parallel effect on baboon species.

Baboons, *Papio papio*, belong to the family *Cercopithecidae*, which consists of two subfamilies; *Cercopithecinae*, to which baboons belong, and *Colobinae*, consisting of folivorous colobus monkeys. A baboons diet is typically omnivorous which allows them to exploit a range of ecological niches, including savannahs, woodland savannahs, forests, and mountainous environments (Napier & Napier, 1967; 1985). The divergence of baboons from leaf-eating colobines suggests that their ancestors may not have been primarily folivorous, and they may have benefited from subsidising their diet with fruits when available. The divergence of the two subfamilies is thought to have occurred at a similar time to that when early hominins were diverging from a common ancestor with

chimpanzees, and perhaps within very similar habitats across Africa (Gilbert et al. 2010; Jolly, 2001; Zinner et al. 2009). Therefore, it has been suggested that studying baboons and other primates within this clade analogously, can provide interesting and useful insights into human evolution to assess the similarities and differences that have evolved independently of shared ancestry (Jolly, 2001). As such, the study of baboons allows for a unique and useful investigation of human evolution.

7.1.2 Baboon Cognition

Diet is thought to play a large role in the evolution of higher cognitive skills across primate species (Fleagle, 2013), including humans, and frugivorous primates in particular are thought to have evolved high level cognition due to the requirements of foraging on ephemeral resources (Milton, 1981a; 1993). Baboons show complex cognitive abilities, including analogical reasoning skills (Flemming, Thompson & Fagot, 2013; Fagot & Parron, 2010; Fagot, Wasserman & Young, 2001), and a considerable LTM capacity (Fagot & Cook, 2006). Wild chacma baboons have been observed making meaningful goal-directed movements towards resources suggesting that they acquire spatial knowledge of locations in their environment (Noser & Byrne, 2007a). They have also been found to change their routes towards these resources which further suggests that baboons build mental representations of their environment (Noser & Byrne, 2007b). Studies assessing mangabey monkeys, a species of the Papionini tribe to which baboons belong, have suggested that they rely on spatial memory to find trees that are most likely to yield fruit (Janmaat et al. 2006; Olupot et al. 1997). Janmaat et al.'s (2006) findings suggested that the monkeys directed their searches to trees that were fruiting, and that they distinguished between trees that had and had not been recently depleted. Whilst baboons are primarily omnivorous, they may also possess the cognitive skills required to forage on ephemeral resources, as closely related mangabeys show.

7.1.3 Foraging Efficiency of Baboons and Humans

The current study aimed to directly compare the cognitive skills required for efficient foraging in humans and baboons. Efficient foraging is supported by LTM, WM, and an ability to detect temporal patterns of food availability, and therefore an ability to detect structure during search. Whilst previous studies have observed and studied mangabey monkeys (Janmaat et al. 2006; Olupot et al. 1997) and chimpanzees

(Janmaat et al. 2013a; 2013b; Ban et al. 2014) in their use of temporal fruit availability patterns during foraging bouts, this has not been investigated in baboons, and has not yet been experimentally assessed with a non-human primate species. An investigation of foraging efficiency and use of high-level cognitive skills within an experimental foraging task derived from naturalistic observations, would assess where similarities and differences lie between humans and baboons. Additionally, the assessment of whether baboons who are not primarily frugivorous show a tendency to detect fruiting patterns, may provide insights into primate cognition and the hypothesis that frugivorous primates have evolved specific cognitive abilities due to the ecological conditions of seasonal forests.

7.2 Experiment 10

This experiment presented baboons with a modified version of the touchscreen task initially described for Experiment 8. The display the baboons were presented with consisted of fewer locations to-be-searched, though retained the same foraging paradigm and temporal patterning. The group of baboons were housed in a large, outdoor enclosure with voluntary access to testing booths which each contained a touchscreen monitor. This provided an ideal set-up with which to assess a non-human primate species with the touchscreen task developed. The facilities allowed access to water and the testing apparatus when desired, and food was provided daily, regardless of the amount of time spent completing the task. Testing adhered to ethical standards and received approval from the relevant ethical committee at the CNRS Primate Centre.

7.2.1 Methods

Subjects. Data was collected from four baboons (B1, B2, B3, and B4) housed at the CNRS Primate Centre in Rousset-sur-Arc, Université d'Aix, Marseille. The baboons were male, with a mean age of 9.46 years old ($SD = .69$).

Apparatus and Environment. The research facility comprised of a large outdoor enclosure (700m²) with a series of 10 automatic learning touch screens, which individuals used voluntarily to participate in the research and gain food rewards (see Fagot & Paleressompouille, 2009). Baboons could access the test boxes through their enclosure, and each testing booth allowed baboons to enter individually. Each booth contained an LCD touchscreen monitor (19 inches), with arm ports for the baboons to

touch the screen. The arm ports contained antennae to identify the subject, as each baboon was microchipped. This allowed the experimental program to resume the point of testing where the baboon left previously. When a correct response was given, a dispensing machine rewarded the subjects with grains of dry wheat.

The experiment presented 25 locations to-be-searched, which was the maximum number of locations that could be displayed on screen as subjects used the palm of their hands to select locations instead of their finger. As described for Experiments 8 and 9, the task presented coloured circles. Five different colours were used, four of which (blue, green, red and orange) were potentially rewarded in a given trial, whilst purple circles never yielded a reward. The circles were presented on the touchscreen, with a white background.

Design and Procedure. Each trial represented a foraging bout, and in any given trial two tree species, or colours, yielded food rewards. Once a circle was touched by the subject, a click sound was played if that location did not yield a reward, or the dispenser was activated and a food reward was dispensed to the subject if a rewarded circle was selected. In a given trial, if a rewarded circle was revisited and the reward had previously been taken, only a click sound was played. The trial was terminated once all food rewards had been found, and a blank screen was shown for 5 seconds before a new trial began. There was no explicit penalty for selecting an unrewarded circle, but implicitly the task delayed reward and required more effort for the same amount of reward, if unrewarded circles were selected.

Due to the number of subjects, a repeated measures design was used and all subjects completed test trials of two conditions which solely manipulated the predictability of the food availability across trials; predictable and unpredictable. The predictable pattern followed the same temporal patterning as described for Experiment 8, which featured two concurrent patterns of a SA between red and orange circles, and a DA between green and blue circles. This temporal pattern was repeated across the trials for the predictable condition. In the unpredictable condition, the same pairs of colours were rewarded. In this condition, one DA colour (blue or green) and one SA colour (red or orange) were always rewarded together. However, the order in which these would be rewarded could not be predicted across the trials. In both conditions, purple circles never yielded a reward.

The task initially appeared to be difficult for the baboons to complete, thus an incremental procedure was introduced. This procedure included training trials with 7 and 14 locations respectively, featuring the predictable temporal pattern, and test trials with 25 locations featuring both predictable and unpredictable patterns. All testing was administered in blocks of 100 trials. The 7-location array included two blue circles, two green circles, and one each of red, orange, and purple circles. In any given trial, there were three rewards to be found. Subjects completed 10 blocks before the number of locations in the array was increased to 14 locations. The 14-location array included four blue circles, four green circles, and two each of red, orange, and purple circles. Here, in a given trial, there were 6 rewards to be found. Subjects B1, B2 and B4 completed 10 blocks, whilst B3 only completed 54 trials of the first block. However, B3 continued to complete the trials with 25 locations. The 25-location array was presented as a 5 x 5 matrix, with six blue circles, six green circles, five purple circles, and four each of red and orange circles. Within each trial, 10 circles each yielded a reward. Subjects B1, B3, and B4 completed 6 blocks within the unpredictable condition first, and then completed 6 blocks within the predictable condition. B2 also completed 12 blocks of test trials, but completed the predictable trials first followed by the unpredictable trials. The location arrays are illustrated in Figure 7.1.

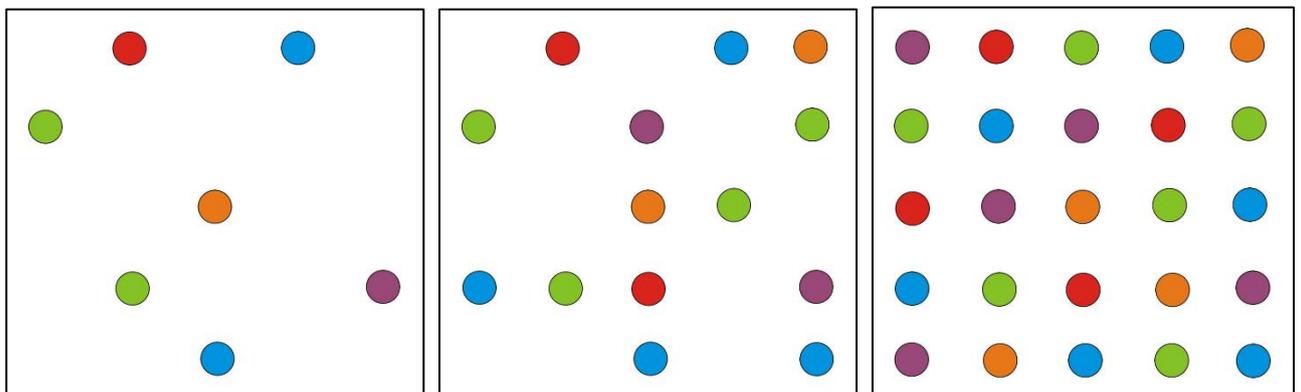


Figure 7. 1 The incremental training procedure, with 7-, 14-, and 25-location arrays.

Measures. An overall measure of foraging efficiency calculated the number of selections made until a trial was completed, and LTM was assessed by calculating the number of selections made to locations which never yielded a reward. WM was assessed by calculating the number of revisits made within a trial. To determine whether

subjects detected the temporal patterns of reward availability, the proportion of correct first choices made within both the SA and DA were also calculated, as described for the experiment presented in Chapter 5.

7.2.2 Results

Overall Foraging Efficiency.

Training Trials. Across the training trials, the mean number of selections subjects made in the 7-location array was 11.08 ($SD = 2.05$), and 32.25 ($SD = 8.51$) in the 14-location array. The means for each block of trials are shown in Figure 7.2.

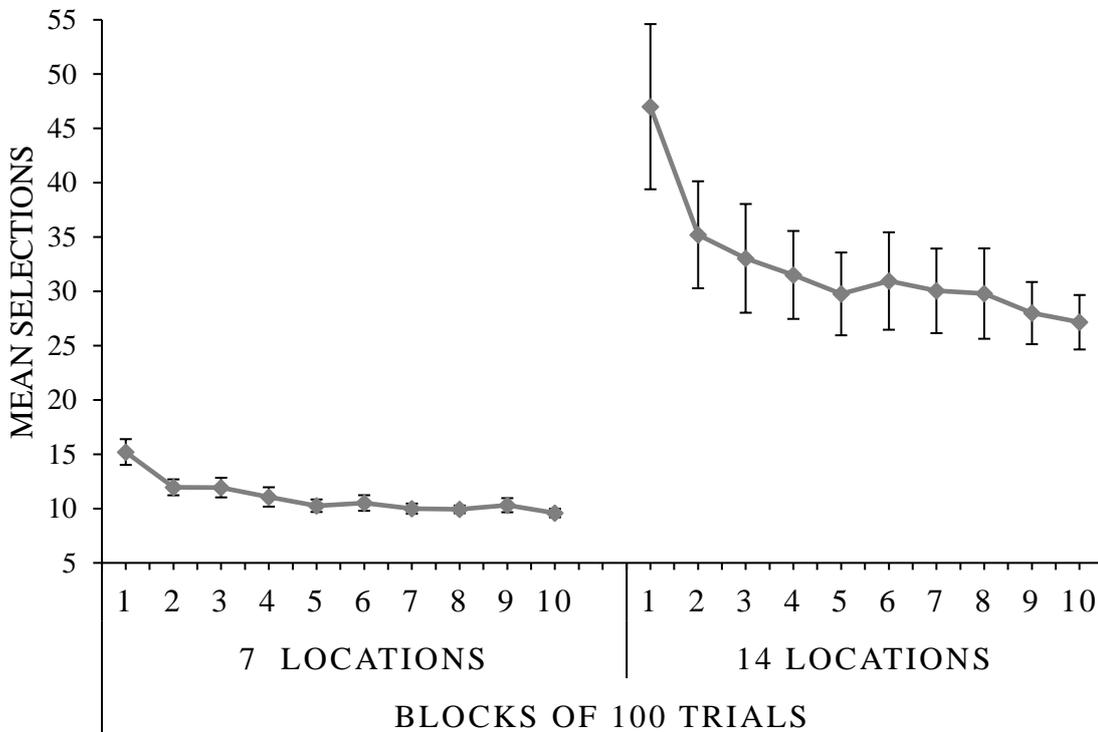


Figure 7. 2 The mean number of selections to the completion of a trial across blocks of 100 training trials, with ± 1 SE bars.

Test Trials. In the 25-location array, the mean number of selections made by subjects in the unpredictable condition was 63.50 ($SD = 14.41$), and 59.61 ($SD = 8.55$) in the predictable condition. The mean number of selections for each subject and the order in which subjects completed the trials, are shown below in Figure 7.3.

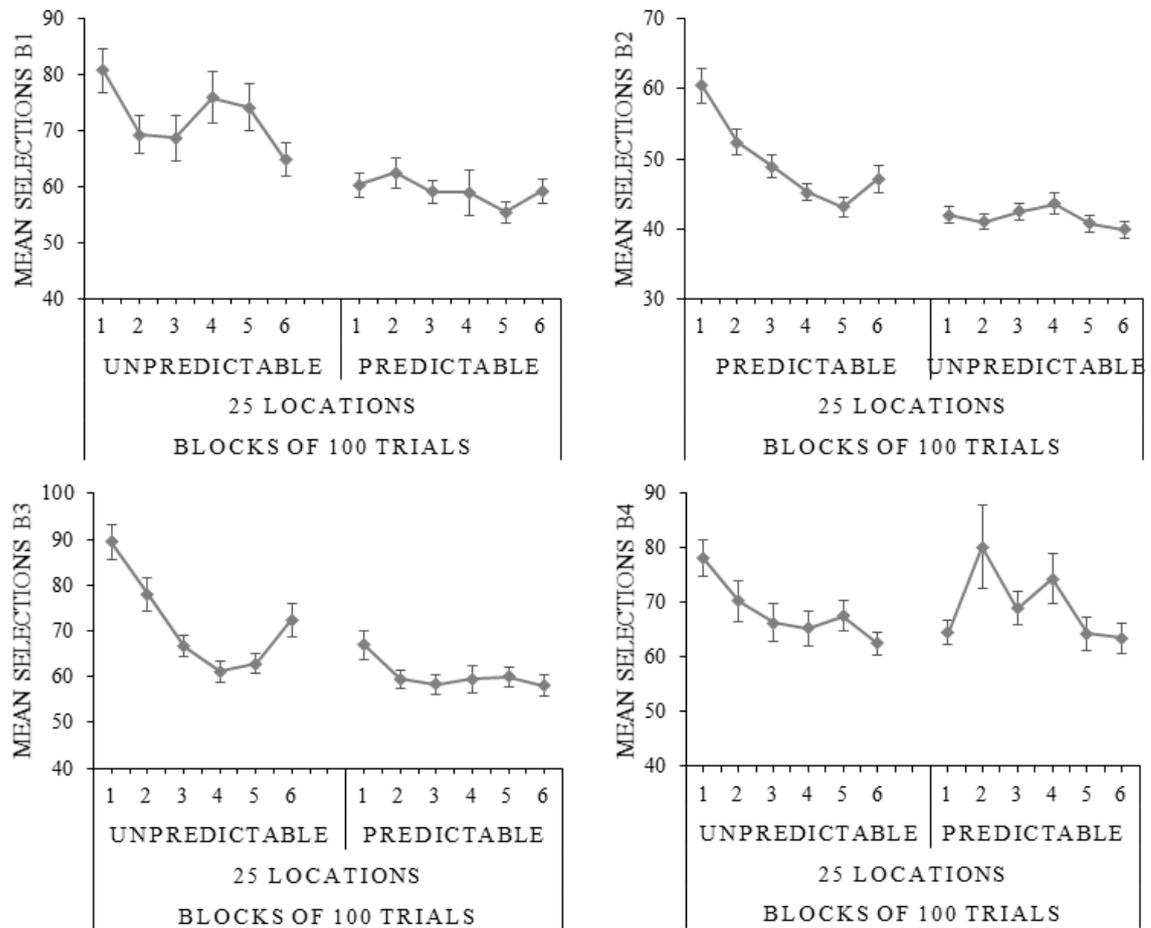


Figure 7. 3 The mean number of selections to the completion of a trial made by each subject, in the 25-location array, with ± 1 SE bars.

To test for differences between the predictable and unpredictable conditions, a 6 (Blocks) x 2 (Condition) ANOVA was run. A significant effect of Blocks was found, $F(5, 15) = 6.02, p < .01$. There was no significant effect of Condition, nor an interaction of Blocks x Condition, suggesting that as expected, in both conditions subjects made a similar number of selections. There was a significant linear component for Blocks, $F(1, 3) = 39.40, p < .01$, which in accordance with Figure 7.3, suggests that this was due to the number of selections decreasing as the trials progressed.

Long Term Memory.

Training Trials. Considering the mean number of never rewarded circles selected, subjects visited few purple circles overall. The mean number of purple circles selected in the 7-location array was .17 ($SD = .03$), and .56 ($SD = .37$) in the 14-location

array. Figure 7.4 below shows a decrease in the number of never rewarded locations visited, however, the overall number of purple circles visited remained low.

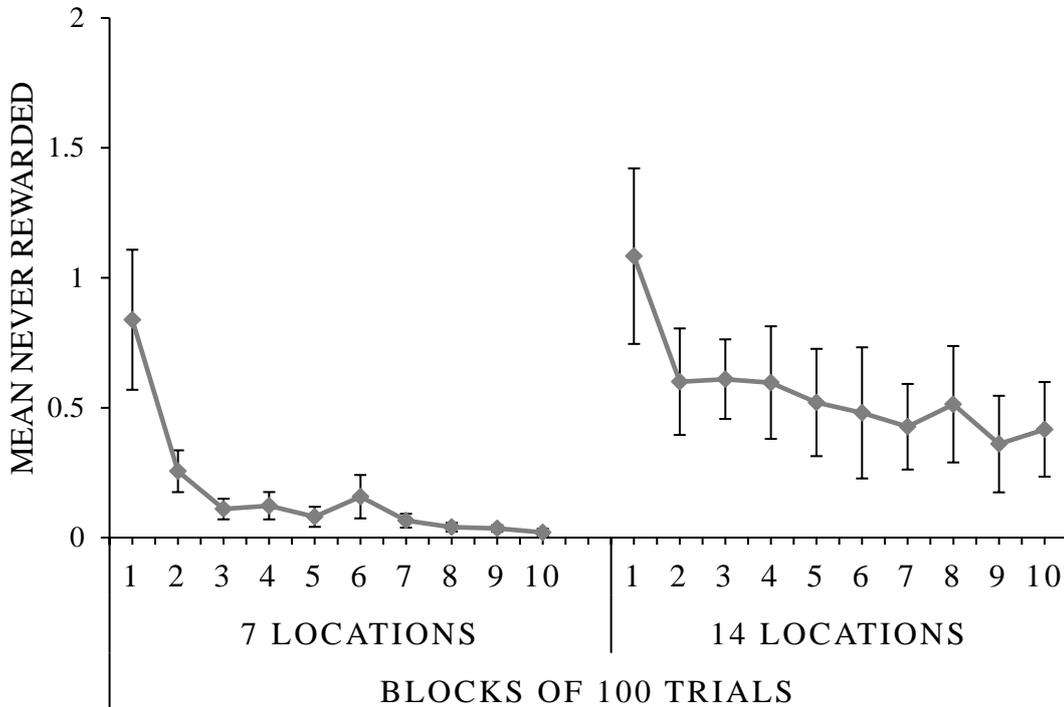


Figure 7. 4 The mean number of never rewarded locations selected across blocks of 100 training trials, with ± 1 SE bars.

Test Trials. In the 25-location array, subjects made a mean number of 2.67 ($SD = 1.63$) visits to never rewarded locations in the unpredictable trials, and 2.45 ($SD = 1.27$) visits in the predictable trials. The mean number of purple circles selected and the order in which subjects experienced each condition, are shown below in Figure 7.5.

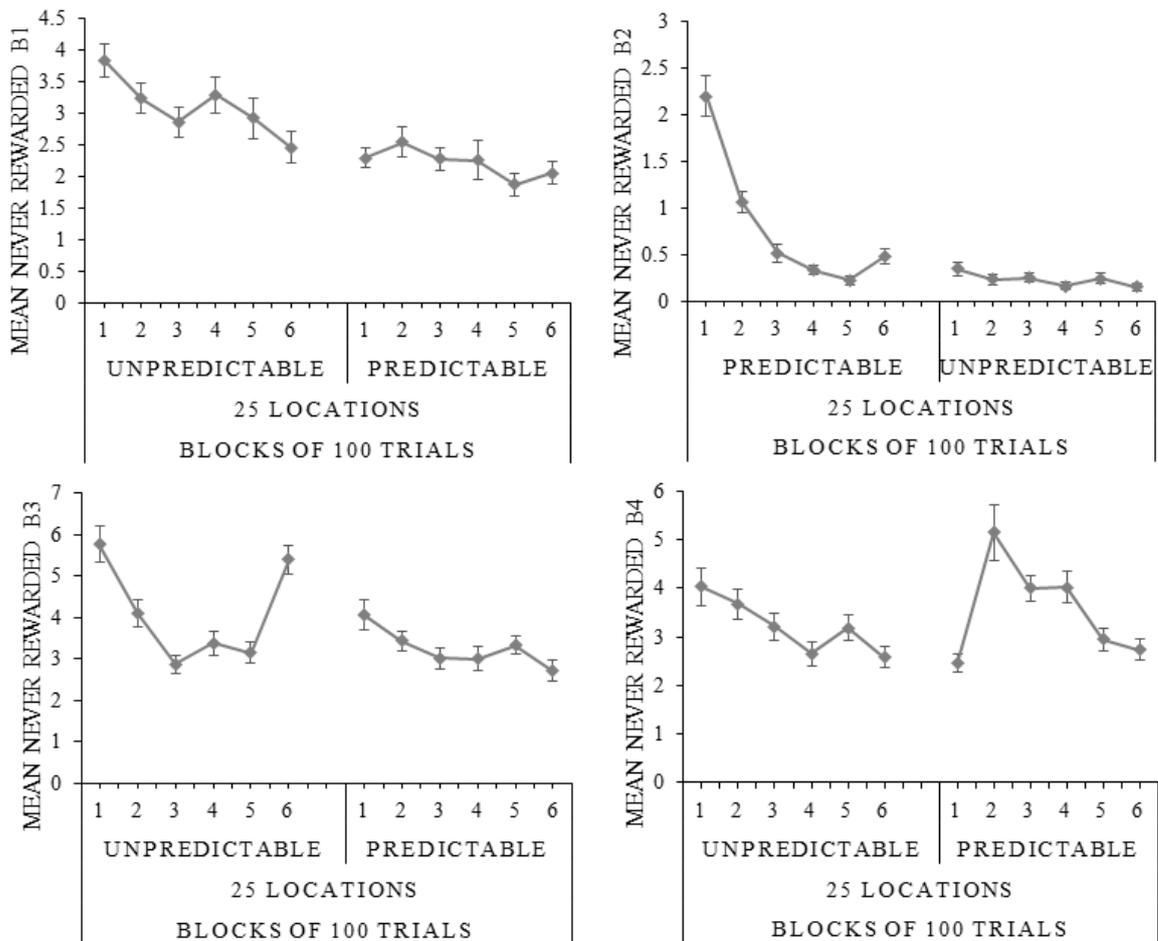


Figure 7. 5 The mean number of never rewarded circles selected by each subject, in the 25-location array, with ± 1 SE bars.

A further 6 (Blocks) x 2 (Condition) ANOVA was carried out to assess differences in the number of never rewarded circles visited between the predictable and unpredictable conditions. There was no significant effect of Blocks, Condition, nor a significant interaction between the two factors. However, the trend analysis indicated that across the test trials, there was a significant linear relationship for Blocks, $F(1, 3) = 211.03$, $p < .01$, which in accordance with Figure 7.5, indicates that the number of never rewarded locations selected decreased across the trials.

To assess whether baboons avoided locations which never yielded rewards significantly more than chance level, one-sample t-tests were run. For the 7-, 14-, and 25-location arrays, there was a 1/7, 2/14, and 5/25 chance respectively that a purple circle would be selected, therefore the mean number of selections for each array was compared to the test values of 1, 2, and 5. The results showed that subjects made

significantly less selections to never rewarded circles than expected by chance in the 7-location array, $t(3) = -8.94, p < .01$, the 14-location array, $t(2) = -6.02, p < .05$, and the 25-location array, $t(3) = -3.41, p < .05$.

Working Memory.

Training Trials. The mean number of revisits subjects made in the 7-location array was 5.71 ($SD = 1.96$), and in the 14-location array subjects made an average of 20.73 ($SD = 8.23$) revisits. This is shown in Figure 7.6 for the training arrays.

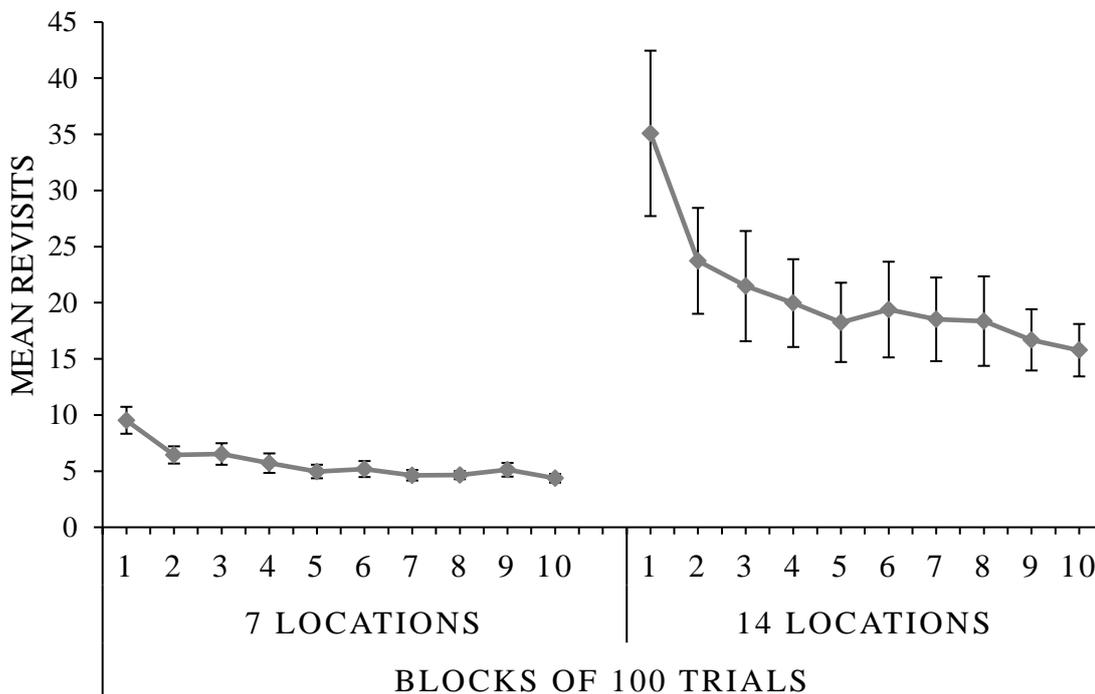


Figure 7. 6 The mean number of revisits made across blocks of 100 training trials, with ± 1 SE bars.

Test Trials. In the 25-location array, the mean number of revisits made was 42.85 ($SD = 13.49$) in the unpredictable condition, and 38.95 ($SD = 7.94$) in the predictable trials. The means for each subject and the order in which they completed the trials are shown below in Figure 7.7.

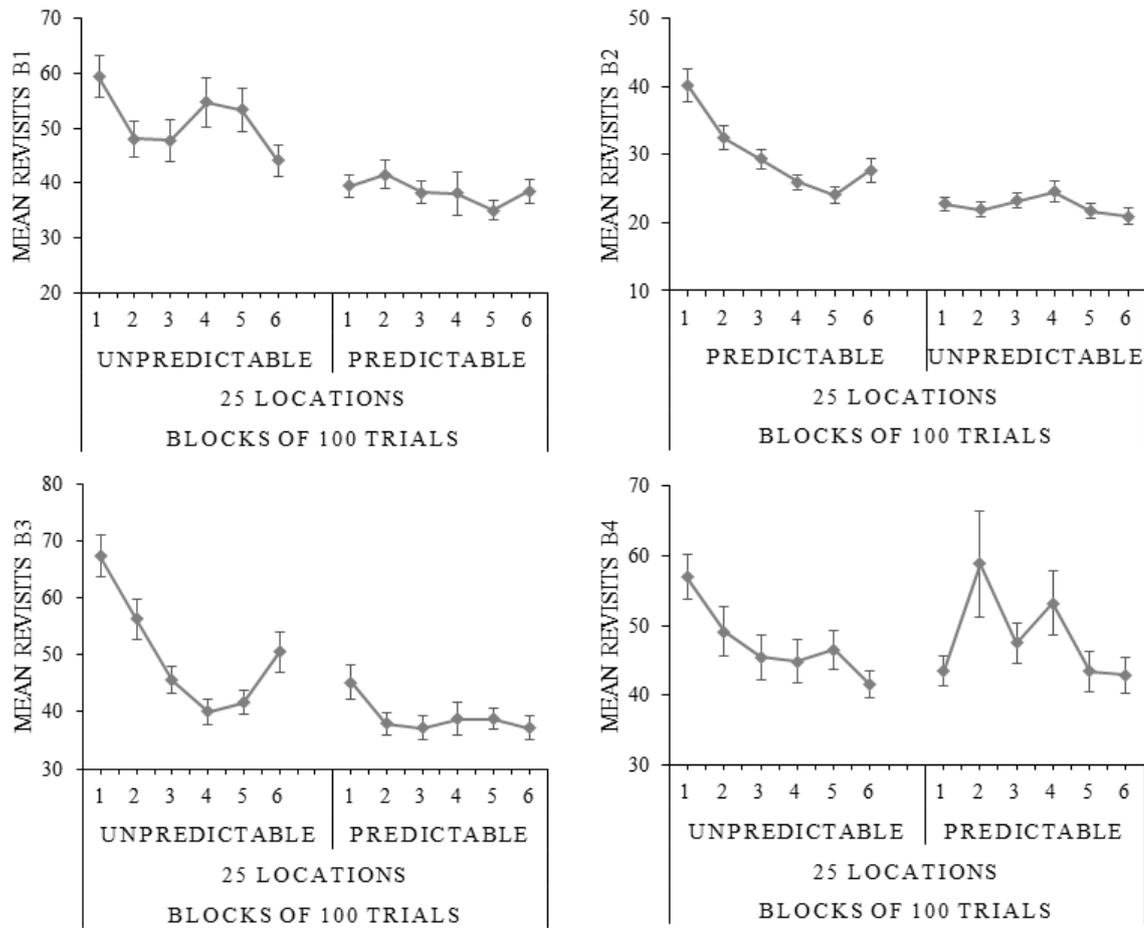


Figure 7.7 The mean number of revisits made by each subject, in the 25-location array, with ± 1 SE bars.

To assess the number of revisits made across the two test conditions, a 6 (Blocks) x 2 (Condition) ANOVA was run. A significant effect of Blocks was found, $F(5, 15) = 5.84, p < .01$. There was no significant effect of Condition, nor an interaction of Blocks x Condition, indicating that as expected, performance in both conditions was similar. The trend analysis results for Blocks showed a significant linear component, $F(1, 3) = 35.95, p < .01$, which taken concurrently with an inspection of Figure 7.7, indicates that the mean number of revisits decreased overall as the trials progressed.

Detection of Temporal Patterns.

Single Alternation: Training Trials. The proportion of correct first choices made within the SA pattern was calculated to assess whether subjects were directing their searches to a rewarded colour. For the 7-location array, the proportion of correct

first choices of the SA was .50 ($SD = .04$), and .51 ($SD = .05$) in the 14-location array. Across all trials, the proportion of correct first choices remained around chance level of .5 (Figure 7.8).

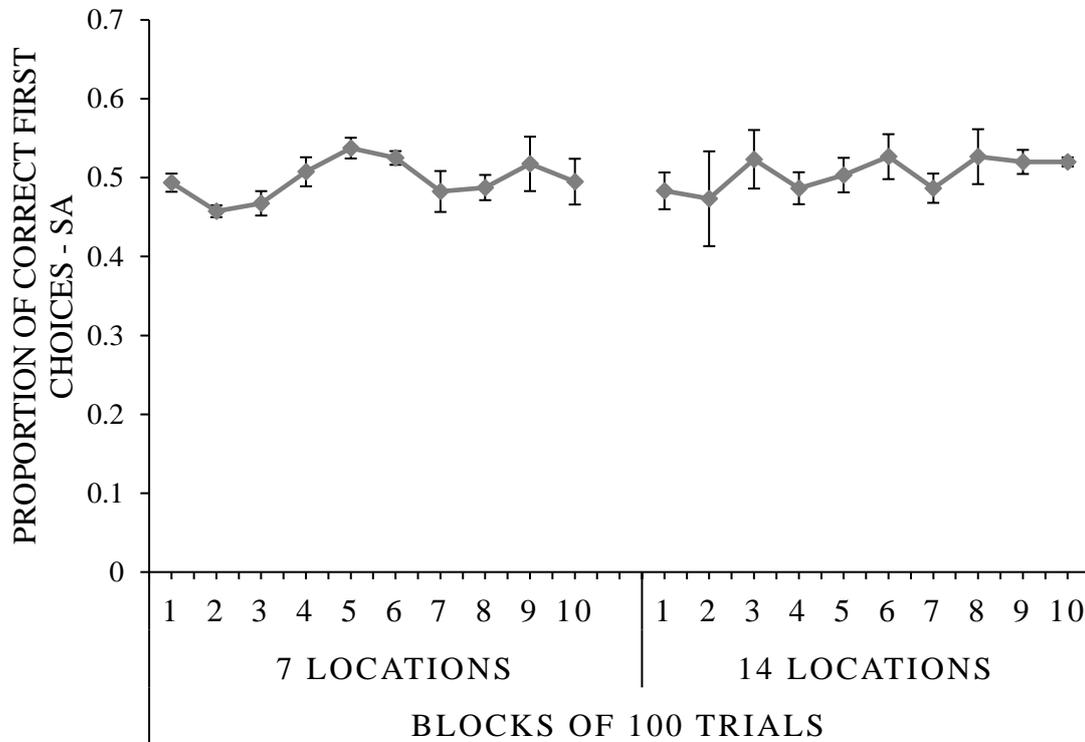


Figure 7. 8 The proportion of correct first choices made in the single alternation pattern across blocks of 100 training trials, with ± 1 SE bars.

Single Alternation: Test Trials. In the 25-location array, the proportion of correct first choices of the SA was .50 ($SD = .05$) in the unpredictable trials, and .50 ($SD = .04$) in the predictable trials, suggesting that subjects performed similarly in both conditions. The means for each subject and the order they completed each condition are shown below in Figure 7.9.

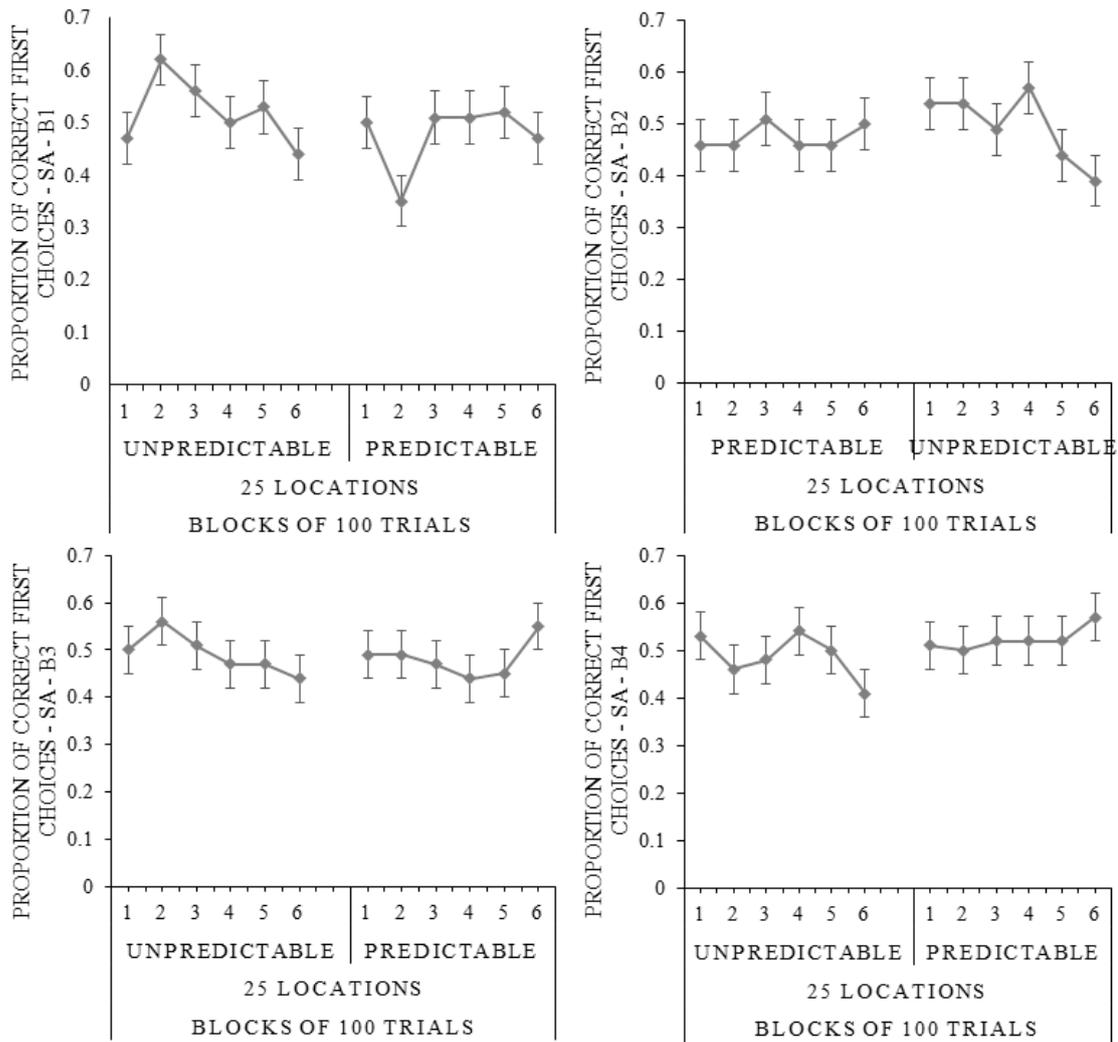


Figure 7. 9 The proportion of correct first choices of the single alternation pattern for each subject in the 25-location array, with ± 1 SE bars.

To assess ability to detect the SA in the 25-location array, a 6 (Blocks) x 2 (Condition) ANOVA was carried out. A significant interaction of Blocks x Condition was found, $F(5, 15) = 4.23, p < .05$, with post hoc paired-sample t-tests indicating that in block 6, subjects performed significantly better in the predictable condition compared to the unpredictable condition, $t(3) = 3.81, p < .05$. However, there was no significant effect of Condition, nor Blocks. There was no significant linear component for Blocks, suggesting that performance remained relatively constant across the trials.

To compare performance against chance level across each array size, one-sample t-tests were used. As subjects appeared to avoid locations which never yielded a reward, subjects had a 3/6, 6/12, and a 10/20 chance to select a rewarded location on

their first choice of the SA in the 7-, 14-, and 25-location arrays respectively. One-sample t-tests used a test statistic therefore of .5. The results indicated that subjects did not perform significantly better than chance level. As this pattern must be learnt across the trials, the last block of predictable trials was analysed separately. However, this was also non-significantly different from chance level, suggesting that baboons did not detect the temporal pattern or use this information to guide search.

Double Alternation: Training Trials. The proportion of correct first choices within the DA made by subjects in the 7-location array was .51 ($SD = .04$), and .50 ($SD = .04$) in the 14-location array. The means are illustrated in Figure 7.10.

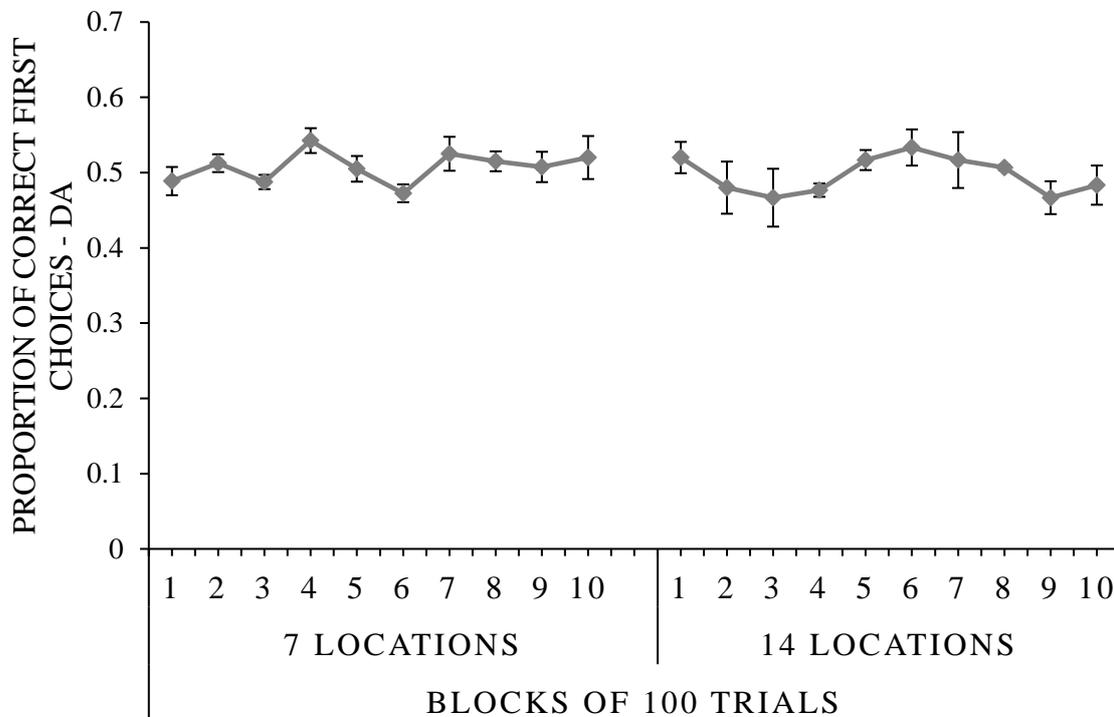


Figure 7. 10 The proportion of correct first choices of the double alternation pattern across blocks of 100 training trials, with ± 1 SE bars.

Double Alternation: Test Trials. In the 25-location array, the proportion of correct first choices of the DA was .50 ($SD = .04$) in the unpredictable test trials, and .50

($SD = .04$) in the predictable condition, suggesting that subjects performed similarly across all trials. The means are shown below in Figure 7.11 for each subject.

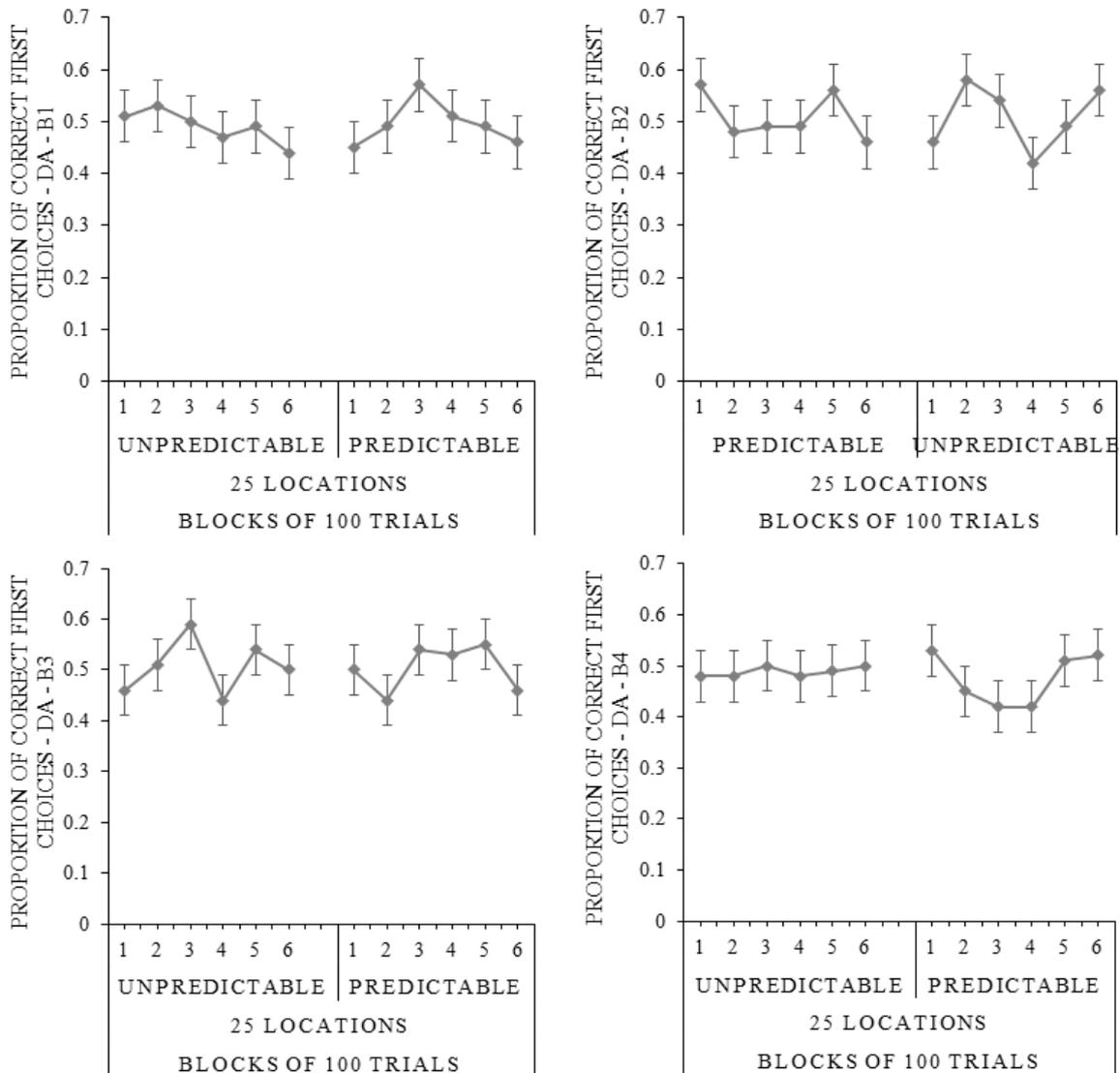


Figure 7. 11 The proportion of correct first choices made in the double alternation pattern, for each subject in the 25-location array, with ± 1 SE bars.

A further 6 (Blocks) x 2 (Condition) ANOVA was run to assess learning of the DA. Results showed that there were no significant effects of Blocks, Condition, nor an interaction between the two factors. The trend analysis for this measure showed no significant linear component for Blocks, again suggesting that performance was similar across the trials.

One-sample t-tests to assess whether subjects were above chance at directing their first choice to a rewarded circle in the DA pattern were carried out. The test statistic of .5 was used, as subjects had a 2/4, 4/8, and a 6/12 chance to select a rewarded location of the DA on their first choice in the 7-, 14-, and 25-location arrays respectively. Results again found that subjects did not perform significantly better than chance level across the blocks, and within the last block of the predictable trials, further suggesting that subjects did not detect or use structured temporal information.

Analysis of Runs. The design of the experiment enabled subjects to leave the testing stations at will, and therefore the baboons could terminate testing mid-trial or mid-block. To ensure the accuracy of the findings, the longest run of trials each subject completed without leaving the testing box (range = 49-65 trials) was analysed for the predictable trials. Analysing the last 8 trials of the longest runs, a one-sample t-test comparing the proportion of correct first choices subjects made of the SA and DA temporal patterns confirmed that subjects did not perform significantly above chance level.

7.2.3 Discussion

The foraging efficiency of baboons improved across trials. The number of selections, revisits, and selections of never rewarded locations showed a significant decline across trials of the 25-location array, and therefore an improvement as the trials progressed. The findings indicated that baboons were particularly proficient at avoiding locations which were never profitable, and were significantly less likely to select a location that never yielded a reward than chance level would predict. This was the case across the three array sizes (7, 14, and 25), suggesting that baboon LTM was very efficient across the trials. However, baboons showed a tendency to make a large number of selections until the completion of a trial, and a large number of revisits overall. Despite this, the finding that the number of errors made decreased across the trials, indicates that baboons learned to forage more efficiently as the experiment progressed.

However, in this experimental foraging task, baboons did not appear to use differential search strategies when food availability could be predicted compared to when this was unpredictable. The proportion of correct first choices that baboons made to circles of the SA and to circles of the DA were not significantly different than expected by chance, indicating that baboons did not selectively direct their first choice

at the outset of a trial to a rewarded location. This appears to be an important difference in baboon and human cognition.

7.3 Experiment 11

In Experiment 10, baboons searched within a smaller array than that which humans experienced in the experiment described for Experiment 8. It is possible that fewer locations to-be-searched may result in a lower incentive to use a structured search strategy. Within larger arrays or spaces, for an efficient search individuals must be more selective about the locations they choose to visit. It may be the case that there was not enough incentive to learn cognitively demanding temporal patterns when a search of all locations did not produce a high cost. Additionally, baboons experienced a repeated measures design whereas humans completed trials of only one condition. Experiencing unpredictable trials initially may have had an effect on baboon performance in subsequent predictable trials, as they may have anticipated that all trials were unpredictable. To directly compare human and baboon performance, Experiment 11 therefore tested humans within the same 5 x 5 array that baboons were presented with to assess whether this ability to detect temporal patterns across trials persists.

7.3.1 Methods

Participants. Nine participants (6 female and 3 male) from the university took part for either course credit or were paid a small fee for their time. Participants were aged between 18 and 28 years old ($M = 21.22$, $SD = 3.27$).

Apparatus and Environment. The same touchscreen task as described for Experiment 1 was presented to participants, displaying the same array, coloured circles, and temporal patterns. The task was modified for human use, in accordance with the touchscreen task described in the two previous chapters. When a circle was touched, a click sound was played and the circle disappeared for 0.5 seconds to reveal an apple underneath the circle if a rewarded location was selected, or no image if an unrewarded circle was selected.

Design and Procedure. The training trials were not required here and only the 25-location array was presented. In accordance with Experiment 1, a repeated measures design was used. Participants completed 100 trials each of the predictable and

unpredictable conditions, whilst the order they experienced these conditions alternated between participants. Participants were instructed to find the hidden apples, and were given a short break between conditions, or when required. Each trial terminated once all virtual rewards had been found, and a black screen was presented asking the participant to press the space bar to continue.

Measures. The same measures as described for Experiment 10 were analysed here, and results were analysed first to assess human performance, before being compared with the first 100 trials (block 1) baboons completed of both the predictable and unpredictable conditions.

7.3.2 Results

Overall Foraging Efficiency.

Humans. The mean number of selections made by participants in the predictable condition was 12.65 ($SD = 4.06$), and 12.92 ($SD = 4.74$) in the unpredictable condition. The means are shown below in Figure 7.12.

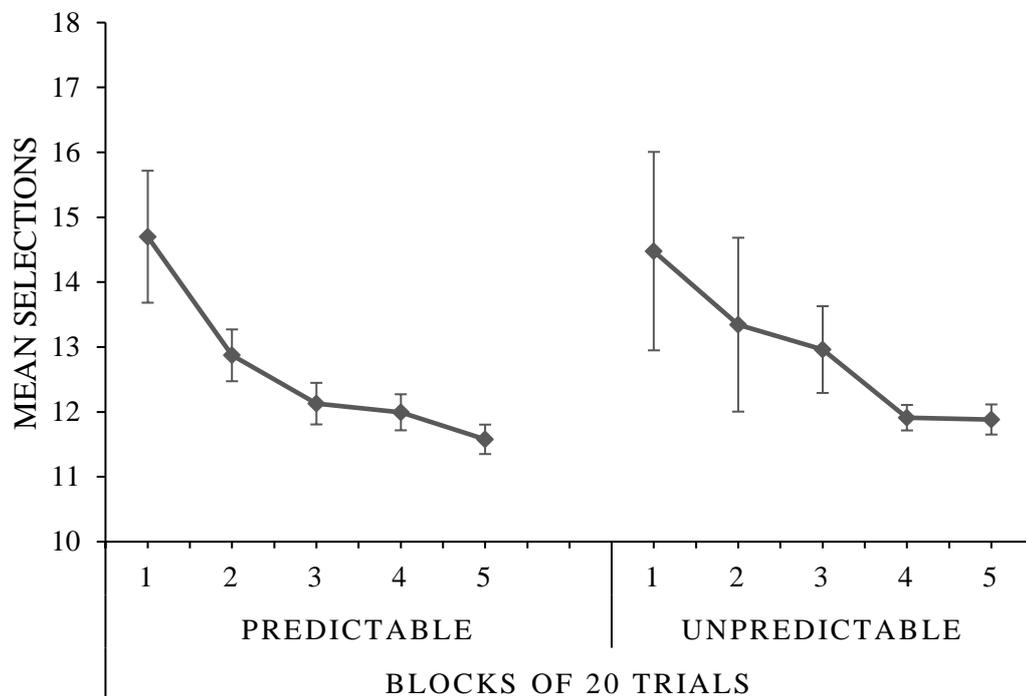


Figure 7. 12 The mean number of selections to the completion of a trial for human participants across the predictable and unpredictable conditions, with ± 1 SE bars.

A 5 (Blocks) x 2 (Condition) ANOVA was carried out which showed a significant effect of Blocks, $F(1.48, 11.81) = 10.99, p < .01$. No significant effect of Condition was found, nor a significant interaction of Blocks x Condition. A significant linear component was found for Blocks, $F(1, 8) = 12.77, p < .01$, which taken concurrently with Figure 7.12, indicates that participants became more efficient across the trials.

Species Comparison. To compare the performance of humans and baboons, the mean number of selections made by both species across 100 trials of each condition are shown below in Figure 7.13.

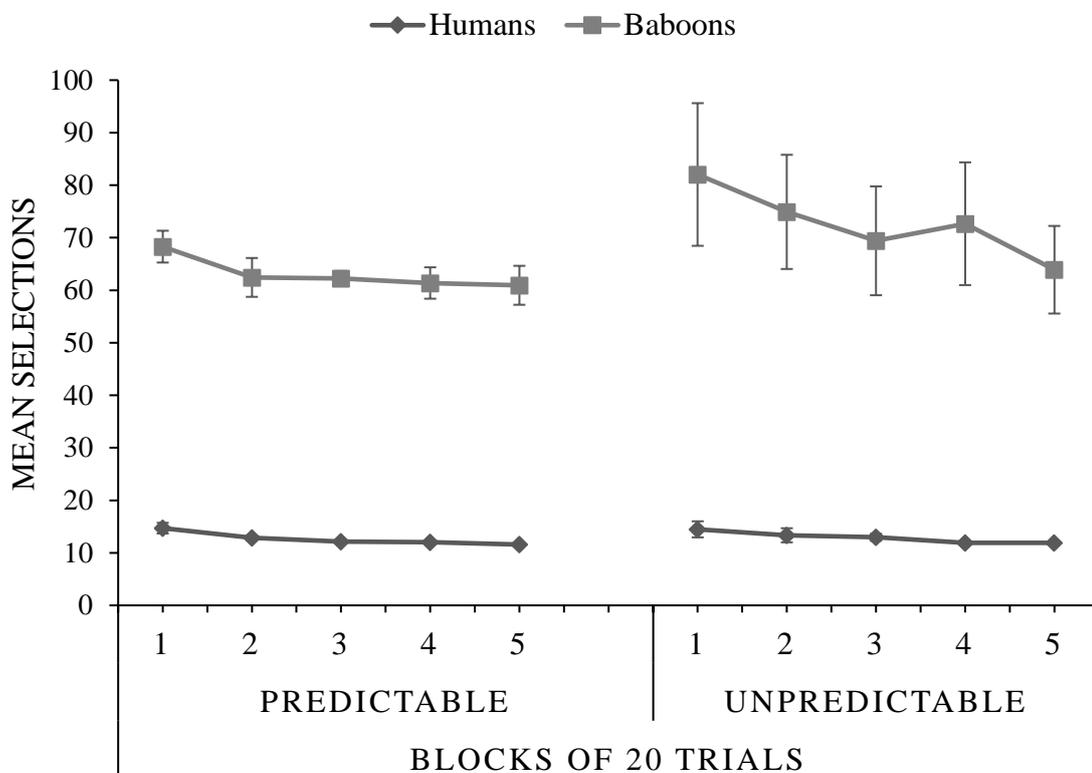


Figure 7. 13 The mean number of selections made by humans and baboons across the predictable and unpredictable conditions, with ± 1 SE bars.

To assess differences between species, a 5 (Blocks) x 2 (Condition) x 2 (Species) ANOVA was run. There was a significant effect of Blocks, $F(1.58, 17.34) = 15.32, p < .001$, and a significant interaction of Blocks x Species, $F(1.58, 17.34) = 6.03, p < .05$. A significant main effect of Species was also found, $F(1, 11) = 224.62, p$

< .001. Post hoc independent samples t-tests confirmed that in all 10 blocks, baboons made significantly more selections until the completion of a trial than humans, minimum $t(3.08) = 4.94, p < .05$. There was no significant effect of Condition, nor an interaction of Condition x Species, indicating that individuals of each species group made a similar number of selections in both the predictable and unpredictable trials. To compare the rate of learning between species, linear regression slopes were calculated for each condition for each species. An independent samples t-test analysed the slopes. There was a significant difference in slopes during the unpredictable trials, $t(11) = -3.50, p < .01$, with baboons showing a steeper slope than humans, however there was no significant difference between the slopes of learning when comparing the predictable trials. As the unpredictable trials were experienced first by most of the baboons, this could be explained by the large number of selections made by baboons which showed a sharper decrease across the trials in comparison to human performance.

Long Term Memory.

Humans. In the predictable trials, participants made an average of .34 ($SD = .97$) selections to never rewarded circles, and .34 ($SD = 1.12$) selections to these circles in the unpredictable trials. Figure 7.14 below shows that humans selected relatively few circles that never yielded a reward.

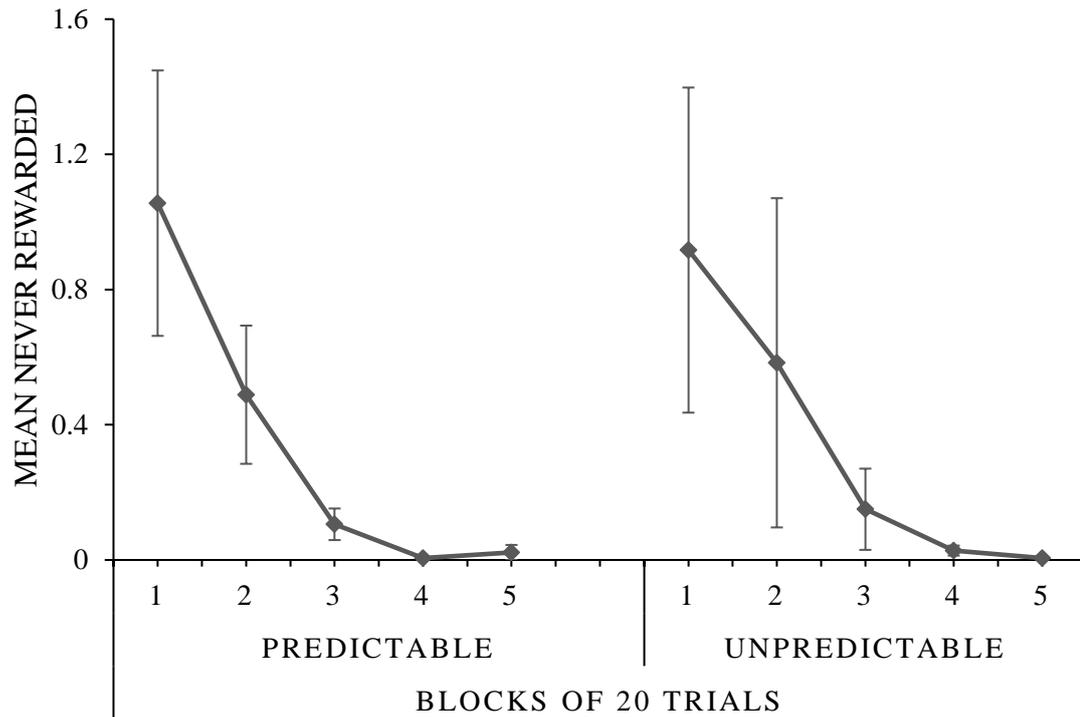


Figure 7. 14 The mean number of never rewarded locations selected by humans, shown for each predictability condition, with ± 1 SE bars.

A 5 (Blocks) x 2 (Condition) ANOVA was carried out which showed a significant effect of Blocks, $F(1.35, 10.76) = 12.99, p < .01$. There was no significant effect of Condition, nor an interaction of Blocks x Condition. A significant linear component was found for this measure, $F(1, 8) = 15.69, p < .01$, which in conjunction with Figure 7.14, indicates that participants showed a decline across the trials in the number of locations selected that never yielded a reward.

Species Comparison. Comparing the performance of humans and baboons, the mean number of never rewarded locations selected by both species are shown in Figure 7.15.

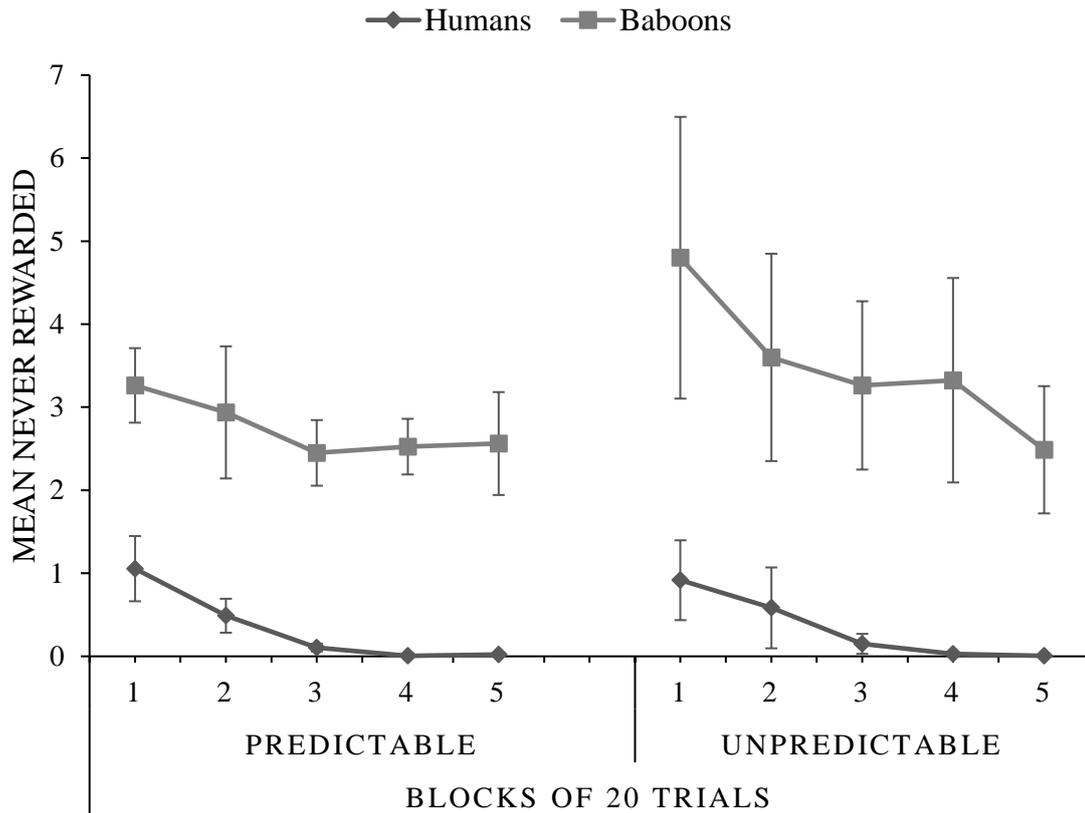


Figure 7. 15 The mean number of never rewarded locations selected by humans and baboons, shown for both the predictable and unpredictable conditions, with ± 1 SE bars.

A further ANOVA, 5 (Blocks) x 2 (Condition) x 2 (Species), indicated a significant effect of Blocks, $F(1.80, 19.84) = 18.58, p < .001$. A significant main effect of Species was also found, $F(1, 11) = 32.25, p < .001$, with independent samples t-tests indicating that baboons made significantly more visits to never rewarded circles than humans, $t(3.10) = 3.71, p < .05$. All other effects and interactions were non-significant. To compare the rate of learning between species, an independent samples t-test compared the linear regression slopes of each condition for each species, which showed no significant differences. For both the predictable and unpredictable conditions, both species learned which locations to avoid at a similar rate.

Working Memory.

Humans. Participants made an average of .93 ($SD = 2.51$) revisits to locations previously searched within the same trial in the predictable condition, compared to .78 ($SD = 2.63$) revisits made in the unpredictable condition. The means are shown in Figure 7.16.

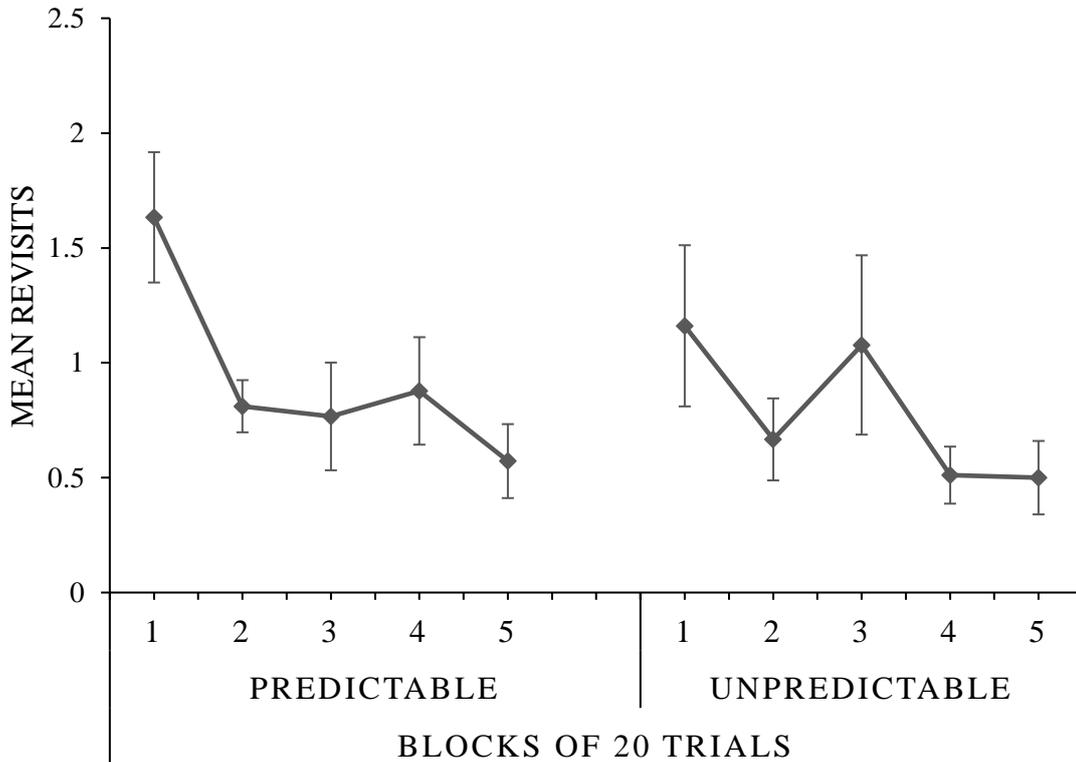


Figure 7. 16 The mean number of revisits made by human participants across each condition, with ± 1 SE bars.

The results of a 5 (Blocks) x 2 (Condition) ANOVA showed a significant effect of Blocks, $F(1.97, 15.75) = 6.21, p < .05$. Confirming that participants performed similarly in both conditions, there was no significant effect of Condition, nor an interaction of Blocks x Condition. A significant linear component was found for Blocks, $F(1, 8) = 18.80, p < .01$. This, in accordance with Figure 7.16, indicates that participants made fewer revisits as the trials progressed.

Species Comparison. To compare the performance of humans and baboons, the means across each block of trials for both species are shown in Figure 7.17.

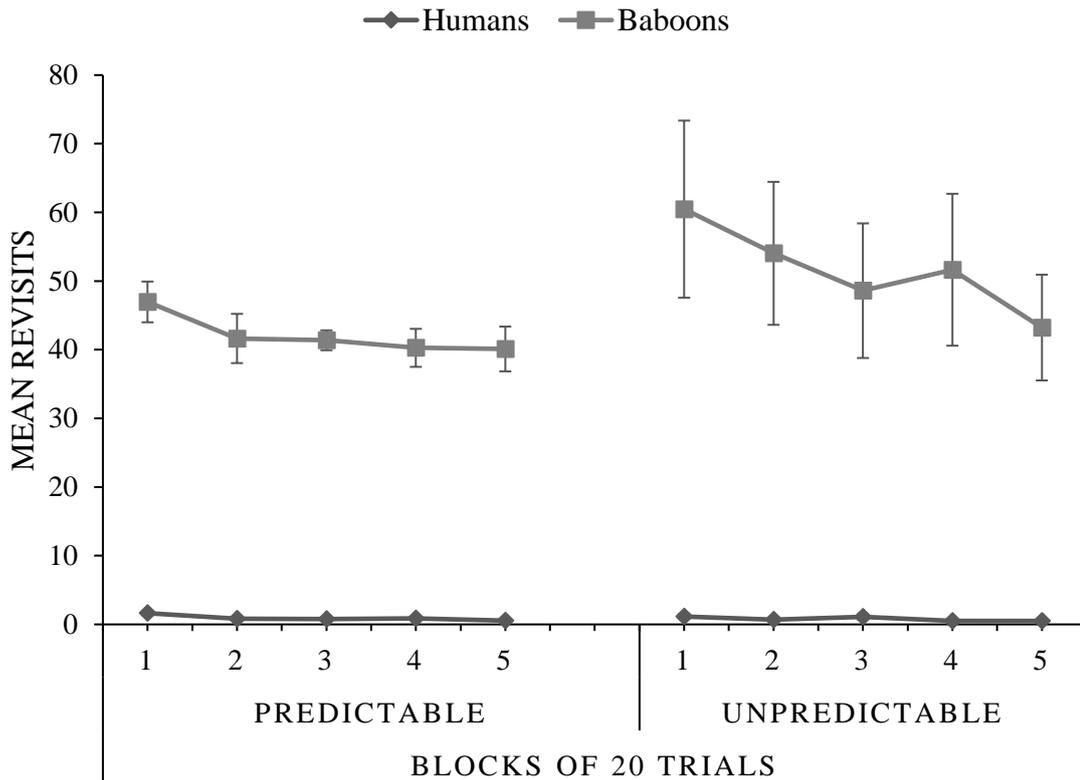


Figure 7. 17 The mean number of revisits made by humans and baboons across the predictable and unpredictable conditions, with ± 1 SE bars.

A further 5 (Blocks) x 2 (Condition) x 2 (Species) ANOVA was carried out. A significant effect of Blocks, $F(1.36, 14.91) = 11.87, p < .01$, a significant interaction of Blocks x Species, $F(1.36, 14.91) = 9.09, p < .01$, and a significant main effect of Species, $F(1, 11) = 186.41, p < .001$, was found. Independent samples t-tests again indicated that baboons performed significantly worse, and made more revisits than humans across all blocks of trials, minimum $t(3.00) = 4.60, p < .05$. There was no effect of Condition, nor an interaction of Condition x Species, indicating that performance was similar across both predictability conditions. To compare the linear regression slopes in the rate of learning between species, an independent samples t-test revealed a significant difference in the unpredictable condition only, $t(3.02) = -3.44, p < .05$. Baboons showed a steeper slope across these trials. The order in which baboons completed the conditions, may explain the steeper decline in the unpredictable trials compared to humans.

Detection of Temporal Patterns.

Single Alternation: Humans. Participants made an average of .62 ($SD = .49$) correct first choices of the SA in the predictable condition, and .50 ($SD = .50$) correct first choices in the unpredictable condition. The proportions of correct first choices made by humans for this temporal pattern are shown in Figure 7.18.

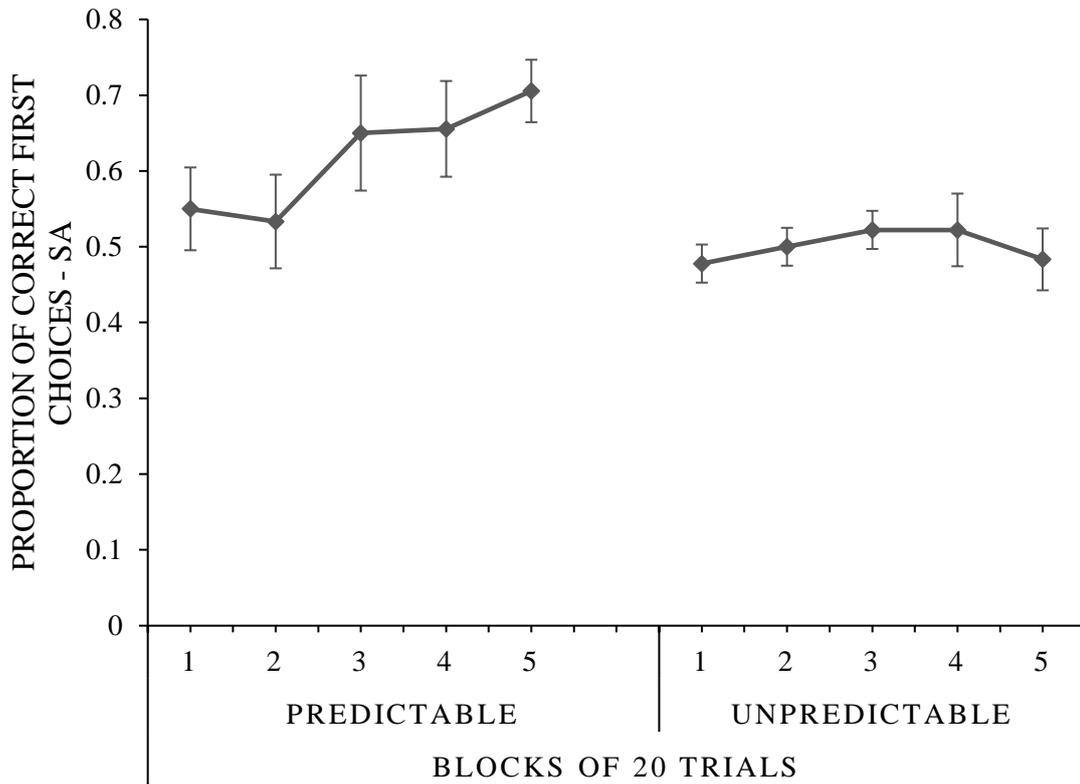


Figure 7. 18 The proportion of correct first choices of the single alternation pattern made by humans, across the two conditions, with ± 1 SE bars.

To first of all assess whether humans detected the SA temporal pattern, a 5 (Blocks) x 2 (Condition) ANOVA was carried out. There was a significant effect of Condition, $F(1, 8) = 6.41, p < .05$, with a paired samples t-test showing that humans made significantly more correct first choices of the SA in the predictable trials than the unpredictable trials, $t(8) = 2.53, p < .05$. There was no significant effect of Blocks, nor an interaction between the two factors. With chance level set at .5 to assess whether participants initially selected a rewarded location, one sample t-tests confirmed that participants made significantly more correct first choices in the predictable trials than

chance level, $t(8) = 2.79, p < .05$, whilst performance was not significantly different to chance level in the unpredictable trials.

Single Alternation: Species Comparison. The proportion of correct first choices of the SA pattern are shown below in Figure 7.19, for both humans and baboons.

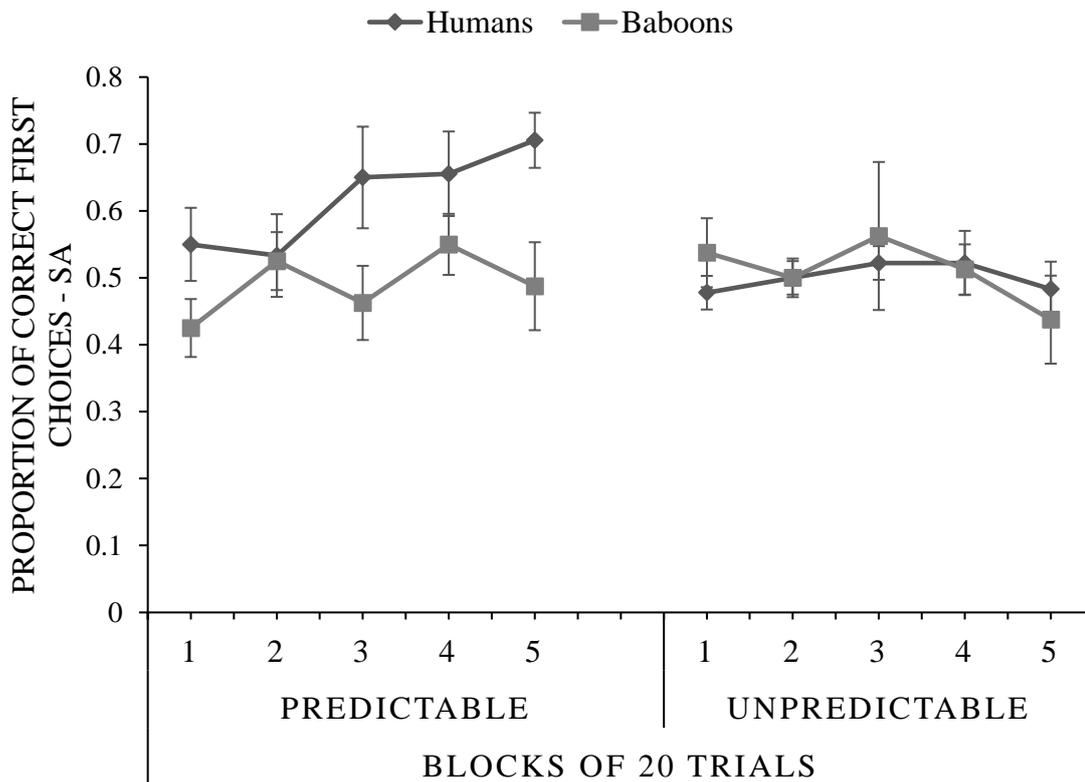


Figure 7. 19 The proportion of correct first choices of the single alternation pattern made by humans and baboons, with ± 1 SE bars.

A further 5 (Blocks) x 2 (Condition) x 2 (Species) ANOVA was carried out. There was no significant effects of Blocks, Condition, or Species, nor any significant interactions between the factors. However, as the temporal pattern must be learnt across trials, it is likely that this pattern was not detected until the end of the predictable trials, and therefore any differences between species in their ability to detect this may not be apparent across all trials. A one-way ANOVA was run which indicated that in the last block of predictable trials, humans made significantly more correct first choices than baboons, $F(1, 11) = 8.32, p < .05$. Performance was not significantly different in the last block of unpredictable trials. Using linear regression slopes, an independent

samples t-test comparing the slopes between species did not find statistically significant differences across either the predictable or unpredictable trials.

Double Alternation: Humans. Participants appeared to perform similarly in the predictable ($M = .52, SD = .50$) and the unpredictable trials ($M = .51, SD = .50$), when considering the proportion of correct first choices made in the DA pattern. This is shown in Figure 2.20, across both conditions.

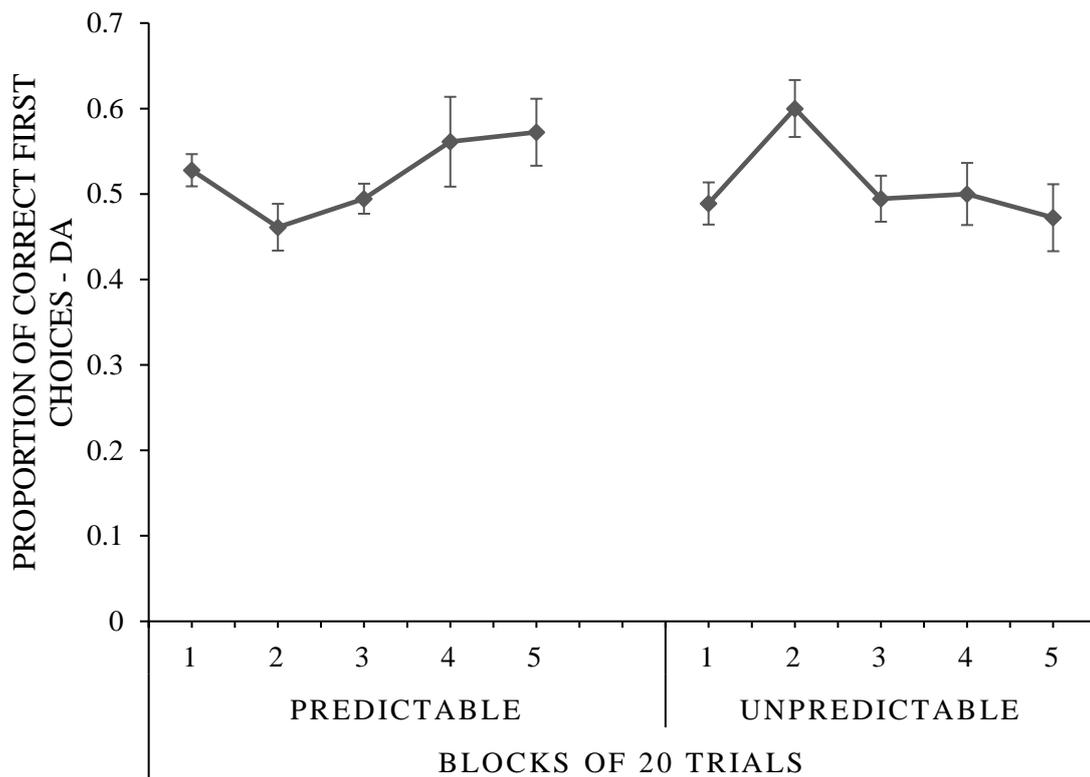


Figure 7. 20 The proportion of correct first choices made by humans in the double alternation pattern, for both conditions, with ± 1 SE bars.

To assess whether humans learnt the DA temporal pattern, a 5 (Blocks) x 2 (Condition) ANOVA was carried out. Findings showed a significant interaction of Blocks x Condition, $F(4, 32) = 4.21, p < .01$, with paired sample t-tests indicating that within Block 2, performance was higher in the unpredictable condition than the predictable trials, $t(8) = -2.96, p < .05$. However, there was no significant effect of Blocks nor Condition. One sample t-tests, with chance level set at .5, indicated that

performance was not significantly higher than chance would predict. This was also the case when comparing the last block of predictable trials against chance level.

Double Alternation: Species Comparison. Comparing the performance of both humans and baboons on this measure, the proportion of correct first choices made by both species within the DA is shown in Figure 2.21 below.

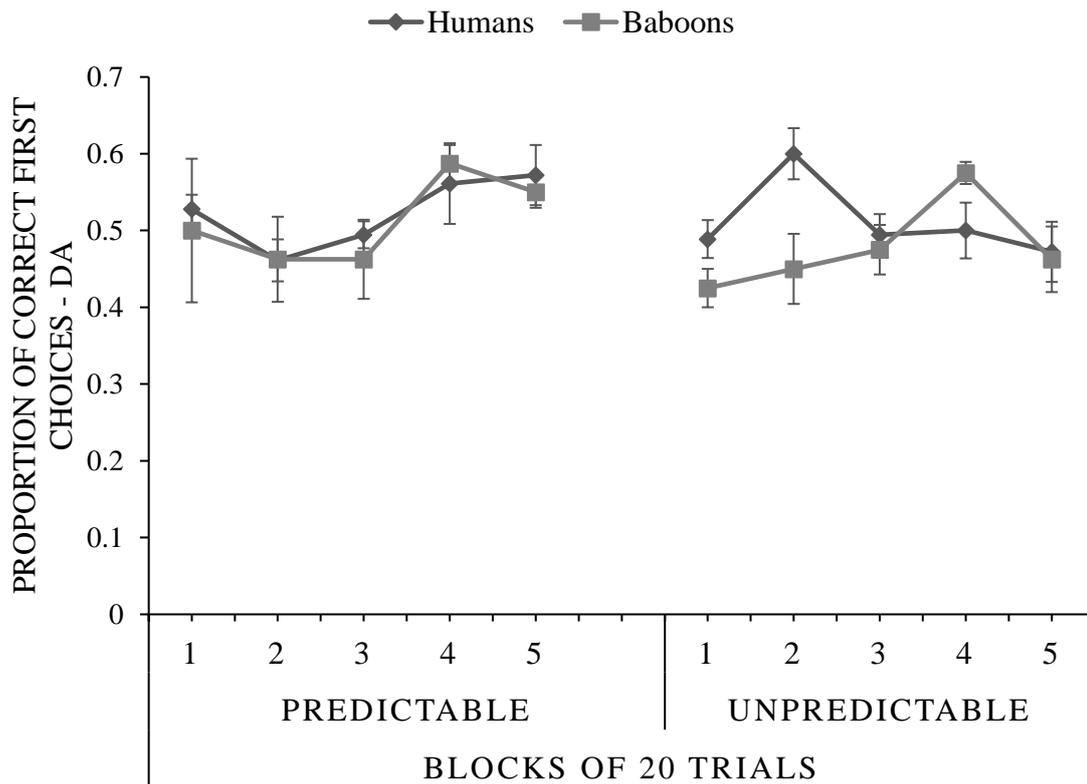


Figure 7. 21 The proportion of correct first choices of the double alternation pattern made by humans and baboons, with ± 1 SE bars.

A 5 (Blocks) x 2 (Condition) x 2 (Species) ANOVA was carried out, which showed no significant effects nor interactions between the factors. A comparison between species in the last block of the predictable condition using a one-way ANOVA also showed no significant differences. A further independent samples t-test comparing the linear regression slopes confirmed that both humans and baboons showed a similar rate of learning, and revealed no significant differences between the slopes.

7.3.3 Discussion

Humans were efficient at searching the array, and quickly learned which ‘species’ yielded rewards. Baboons made significantly more visits to never rewarded locations than human participants, however both species made relatively few visits to these locations overall, indicating that all subjects were proficient in learning which locations were always unprofitable. The comparison further showed that baboons made significantly more selections and revisits during a trial than humans, across all blocks of each condition, suggesting that inter-species differences exist in overall foraging efficiency and WM ability.

The results also indicated that humans detected the SA temporal pattern across trials and used this information to direct their first choice at the outset of a trial to a rewarded location. By the last block of trials, humans made significantly more correct first choices of the SA pattern than baboons who appeared to continue to perform at chance level. However, no significant effect was found for the DA pattern, suggesting that humans were unable to detect the second temporal pattern in this array of locations, and showed a similar level of performance as baboons. This disparity in the findings of this experiment compared to the findings reported in Chapters 4 and 5 which found that humans detected both patterns of reward availability, could be explained by the smaller search array presented which may provide a lower incentive for restrictive search. For baboons, it could also be the case that this task did not provide enough incentive to restrict searches and to detect the temporal patterning of reward availability. However, baboons did largely restrict their search to locations of rewarded or potentially rewarded colours and tended to avoid purple circles which never yielded a reward, therefore a lack of motivation does not fully explain this finding.

7.4 General Discussion

Baboons became more efficient in their search and showed an improvement in overall search efficiency, LTM, and WM ability. However, baboons did not reach the level of efficiency over three thousand trials, as that shown by humans in Experiment 11. Baboons appeared unable to detect the temporal patterns of food availability across the trials, or at the very least did not use this information to direct their first choice on future trials to a location that was most likely to be yielding a reward. These findings suggest that an ability to detect structure during search may be an important cognitive difference between humans and baboons.

7.4.1 Baboon Cognition

The findings of this chapter highlight the value of this foraging task, as it afforded a comparative assessment of high-level cognitive skills which is less achievable with VR. The proficiency shown by baboons in LTM is consistent with previous findings which have shown a large LTM capacity in this species (Fagot & Cook, 2006), with the current findings suggesting that baboons are particularly efficient at learning and remembering across the experiment which locations are never profitable. Baboons in the current task did not appear to benefit from temporal structure however, suggesting that this ability to detect structure may be an important inter-species difference. Consistent with this finding, Noser and Byrne's (2010) results suggested that planning abilities of baboons appeared limited, whilst in a Corsi-type task, Fagot and De Lillo (2011) suggested that an ability to detect and use spatial structure may be a notable difference between humans and baboons. However, the design of the current task allowed baboons to terminate testing mid-trial if they left the testing station, which then led to that individual starting mid-trial when they re-entered the box. This may have prevented baboons from detecting temporal structure, as unlike the task with humans, testing was intermittently paused. Nevertheless, further analyses were not indicative of a tendency to detect the temporal patterns, even when runs of trials where no breaks were taken were analysed. Baboons may have employed a win-stay-lose-shift search strategy which would not require any patterns across trials to be learnt (see Nowak & Sigmund, 1993), which is a successful search strategy to use particularly in uncertain circumstances (Posch, 1997).

7.4.2 Detection of Temporal Structure

The finding that baboons did not benefit from temporal structure appears to be consistent with Milton's (1981; 1993) hypothesis which proposed that frugivorous species evolved sophisticated cognitive abilities, due to the requirements of foraging on ephemeral resources. As baboons are typically omnivorous (Napier & Napier, 1967; 1985) and evolved within ancestral savannah environments (Jolly, 2001), baboons may not possess the cognitive skills required for foraging on ephemeral resources within a forest environment. Baboons did not show the same ability to detect when food will be available in this task as frugivorous primates show in their natural habitats (Janmaat et al. 2006; 2012; 2013a). A study by Wahungu (1998) directly compared the foraging

behaviour of baboons and frugivorous mangabey monkeys. When fruits were scarce, baboons followed a foraging strategy which exploited open woodlands, whilst frugivorous mangabeys continued to forage within the forest. When fruits become more abundant, baboons switched their foraging strategy and moved into the forest to find fruit. This supports the notion that baboons may not have evolved the cognitive competences required for foraging on ephemeral resources, or that baboons may have lost these abilities across evolutionary time as their ability to digest a more varied diet evolved. In light of the present results, it can be suggested that the cognitive skills required to detect and learn the seasonality of ephemeral resources may have evolved in hominins before the move to a savannah environment, where our ancestors are thought to have inhabited a woodland environment (White et al. 2009). The persistence of these cognitive abilities in humans today despite a shift to a more omnivorous diet, suggests that an ability to detect structure during foraging played a large and significant role in human survival.

7.4.3 Conclusions

The foraging task presented allowed the exploration of similarities in human and baboon cognition, and to consider where differences lie. The present results are consistent with the notion that diet was an important factor in the evolution of high level cognitive skills, and suggest that important differences in the use of structure exist between humans and baboon species. Nevertheless, the findings here leave open avenues for further research with non-human primates. To further investigate the hypothesis that diet triggered the emergence of larger brains and sophisticated cognitive skills in primates (Milton, 1981; 1993), implementing this experimental foraging paradigm with predominantly folivorous and frugivorous primates would allow further insights into the evolution of primate cognition.

Chapter 8: General Discussion

8.1 Detecting Structure

The search for structure is prevalent amongst humans. Finding patterns in stimuli allows us to reduce the amount of information to be processed and prevents an overload of information. The evolution of superior pattern processing in humans is thought to be due to the expansion of the cerebral cortex, and is also often seen across non-human primates (Mattson, 2014). Whilst the patterns and similarities between incidents we experience can be misinterpreted, an evolutionary biology model suggests that this is an evolutionarily adaptive approach if this ability to recognise patterns results in a large fitness benefit (Foster & Kokko, 2009). Chater (1996; 1999; Chater & Vitanyi, 2003) proposed that this propensity to find patterns in stimuli, is often found by identifying the one that offers the simplest explanation. Pothos and Chater (2002) found that humans spontaneously organised stimuli into categories based on the simplest choice, whilst Iyengar and Kamenica (2007) found that when participants faced a larger number of choices they showed a preference for the simplest and easily-understandable options. Humans appear to show a preference for the simplest route through an environment (De Lillo, 2012), which can also be considered as those which follow the structure of the search array. Recall accuracy has been found to be higher when sequences to-be-recalled followed the structure of the array, thus when subsequent locations in a sequence were within the same row, column or diagonal line (Bor et al. 2003). Further studies provided evidence to suggest that humans benefit from the structure of spatial arrays when locations also represent a patchy foraging space. Recall accuracy was improved when locations were arranged as clusters on-screen and subsequent locations within a sequence to-be-recalled were within the same cluster before switching to the next cluster of locations (De Lillo, 2004; De Lillo & Lesk, 2010). This tendency to benefit from spatial structure was also found when participants searched arrays of locations arranged as either clusters or matrices within VR environments (De Lillo & James, 2012), further supporting the notion that humans base search on structure and simplicity principles.

8.2 Experimental Chapters

This thesis aimed to further characterise this propensity to detect and use patterns within spatial search, in particular by assessing ability to use structure; a

concept fundamentally related to simplicity. To understand foraging and search behaviour, many models including optimal foraging theory (Charnov, 1976) use energy and travel distance to explain how individuals regulate behaviour. A desire to reduce cognitive load and travelling distance both result in choosing the route or pattern that is the shortest, or the simplest, therefore these two principles can easily become entangled within the literature. To consider cognition comparatively, the methodologies used aimed to assess humans within paradigms designed for use with non-human species, or derived from studies observing primates in natural foraging situations. Whilst it is indeed important to design experiments to test animal cognition in a meaningful way for individual species, for comparison with humans it is equally important, yet often overlooked, to test humans within these paradigms also. The initial experiment presented allowed us to distinguish between the motivating principles of search and to further investigate and characterise the use and benefits of structure in spatial memory. This ability to find and benefit from structure in stimuli was considered throughout in relation to being a specific evolutionary adaptation to reduce memory load in humans, whilst this thesis also considered results in relation to non-human findings. Both the physical structure of a search environment and the conceptual structure of information to be held in memory were assessed in this series of VR and touchscreen-based search tasks.

Chapter 2: The Role of Distance Travelled. A motivation to reduce cognitive load and travelling distance is often considered one of the same within spatial and visual search paradigms. To address this confound, the initial experiment employed ISSR within a VR environment (see De Lillo & James, 2012). Participants were required to follow a particular route through a series of locations before recalling the sequence, where sequences to-be-recalled were either structured, which required participants to make subsequent visits to locations which were in the same cluster, row, or column before moving to the next, or were unstructured, which violated this rule and subsequent visits to locations involved switching clusters, rows, or columns. Bor et al.'s (2003) findings indicated that the DLPFC, an area of the brain thought to be specific to WM capability, showed increased activation when structured sequences were shown to participants, suggesting that the DLPFC is associated with high-level cognitive functions involved in the search for structure. Assessing humans within spatial arrays initially designed for use with capuchin monkeys (De Lillo et al. 1997), this VR

experiment allowed the manipulation of cognitive load and travelling distance which is otherwise impossible within an observational or free-search study, to disentangle these two motivations behind search.

The results showed that despite a further travelling distance, recall accuracy was higher when sequences to-be-recalled followed a structured trajectory through a large search space, compared to when sequences followed an unstructured path through a small search space. This experiment was the first to distinguish between search efficiency explanations based on cognitive economy and travelling distance, with this finding suggesting that humans are motivated by a desire to reduce cognitive load over decreasing travelling distance. In accordance with previous research (Bor et al. 2003; De Lillo, 2004; De Lillo & James, 2012), the presentation of spatial information which followed the structure of the search array, resulted in more accurate recall suggesting that memory load was eased.

In an exhaustive search task, capuchin monkeys were found to spontaneously visit each location within a cluster before moving to the next (De Lillo et al. 1997), and appeared to develop linear search strategies across the trials (De Lillo et al. 1998), suggesting that non-human primates also possess a proficiency for a higher order ability to detect and use structure. However, only ISSR allows the manipulation of the paths to be followed through the search space to experimentally assess the relationship between structured search and accuracy. An on-screen ISSR task found that baboons did not benefit from structured sequences unlike humans (Fagot & De Lillo, 2011). Whilst baboons do not appear to show a tendency to exploit spatial structure, it is unclear whether capuchin monkeys and other primarily frugivorous species would show similar tendencies to humans within an ISSR task, which is cause for further investigation.

Whilst the findings of this experiment showed that humans benefit to a greater degree from the structure of pathways despite a longer travelling distance, this could also reflect a desire for participants to avoid becoming lost in smaller environments where pathways to-be-followed are unstructured which would result in further time and energy spent searching locations already depleted. In this way, findings can be seen to be consistent with an optimal foraging strategy (Charnov, 1976) as participants aimed to minimise the costs of future revisits, expending additional energy. Overall, this tendency for humans to benefit from the structure of sequences to-be-recalled, despite a further distance to-be-travelled, strongly suggests that the benefits of reducing memory

load during search outweighs the costs of a further travelling distance and is an important motivating factor of search.

Chapter 3: Chunking within Spatial Working Memory. The initial experimental chapter highlighted the benefit of spatial structure during search by humans to promote cognitive economy, however data-reducing strategies in the form of chunking have also been claimed to be used by rats (Dallal & Meck, 1990; Macuda & Roberts, 1995). Chunking is an efficient search strategy in humans (Miller, 1956), however the tasks used to assess this differ from the chunking paradigm used with rats. Rats appeared to reduce memory load by visiting arms within a radial maze which contain all of a preferred food type first, before visiting arms containing another food type, and finally arms containing the least preferred food. However, searching for food within a search space is an ecologically different task from those used to assess verbal chunking in humans (Cohen et al. 2003), thus this set of experiments assessed humans within this search condition.

Locations within this task were arranged as a matrix which hid virtual foods, and findings indicated that participants spontaneously showed a strong tendency to use the structure of the search space to learn where the food rewards were located, as opposed to using the type of food found at each location to aid memory. When asked to use a chunking by food type strategy, participants learned where each food type was located, which suggested that humans are also efficient at learning to use this strategy during search. Humans also spontaneously and efficiently used the structure of the search space when searching within a radial maze, and searched for foods by visiting adjacent or opposite arms of the maze. These findings highlighted the importance of assessing humans within paradigms designed to assess animal cognition, to ascertain where similarities and differences lie. In contrast to rat behaviour, humans did not appear to use the items found at each location to guide search when given the opportunity to do so, which is an important distinction to make between rodent and human cognition. In the present set of experiments, the preferred search strategy was to search using the structure of the search space which could also be explained by a proximity-based strategy, though further research is required to disentangle these two principles.

It is possible that humans did not have a real food incentive to chunk preferred items together unlike rats who may follow an optimal strategy to exploit patches with the most profitable items first (Charnov, 1976; Cohen et al. 2003). Memory for where

the preferred food type is may indirectly result in an organised and efficient search pattern, whilst humans in contrast appear to choose the simplest search strategy which follows spatial structure. How humans would choose to search for real food items within a radial maze is perhaps an idea for future research. However, it is clear that humans do not spontaneously use a chunking by food type strategy as a method to ease memory load within a hidden food paradigm in a VR search space. It can be suggested that humans, and perhaps non-human primates, may encode structure differently from non-primates, and it is possible that this proficiency to detect structure is related to the emergence of higher order cognition in primate species.

Chapter 4: Detection of Temporal Structure in Search. Due to the cognitive differences expressed within Chapter 3 between rats and humans, the experiments outlined in Chapter 4 aimed to address specific adaptations that may pertain only to primates in their ability to detect and use structure in search. Frugivorous foraging behaviour for ephemeral and patchily-distributed fruits is thought to have triggered high-level cognitive skills and cerebral expansion in primates (Milton, 1981a). The cerebral expansion seen within the primate order is particularly apparent in the frontal lobes (Semendeferi, Lu, Schenker & Damasio, 2002) which contain the DLPFC - an area found to be related to WM and an ability to benefit from structure in humans (Bor et al. 2003) – and may also pertain to non-human primates. The selective pressures of foraging for ephemeral resources may have impacted human evolution, and whilst we cannot be sure of the exact conditions our hominin ancestors faced, evidence suggests that hominins evolved within forest environments prior to a savannah (White et al. 2009). This suggests that early hominids evolved within similar environments as those experienced by chimpanzees today, making chimpanzee foraging a useful basis on which to assess human cognitive skills. Recent studies observing primates suggest that they are able to predict which locations will be most profitable to travel to (Janmaat et al. 2013a; Janmaat et al. 2012), and suggest that chimpanzees use flexible Euclidean maps to direct their searches (Normand & Boesch, 2009). However, these studies are observational, and many environmental factors may influence foraging behaviour. Associative learning theories would make different predictions to explain foraging behaviour, as it may be the case that individuals use visual cues to guide search, such as the colour of ripe fruit, and acquisition of spatial information is not necessary for this. It

is thought that if a particular salient cue is attended to, then an individual is less likely to attend to an equally predictive though less salient second cue, producing an overshadowing effect (Mackintosh, 1971; 1976).

This set of experiments required participants to search for hidden apples within a large matrix of locations. Two experiments indicated that participants were highly efficient at detecting which locations yielded rewards, and avoiding unrewarded and previously visited locations. Participants spontaneously directed their searches towards those locations that were most likely to be yielding fruit at the start of a given trial. Participants were able to efficiently do this when one temporal pattern of food availability was presented across the trials, and also when the complexity of this temporal patterning increased. The finding that humans show a strong propensity for detecting and monitoring temporal patterns, is consistent with the behaviour shown by non-human primates (Janmaat, Ban & Boesch, 2013a; Janmaat, Ban & Boesch, 2013b; Janmaat et al. 2012). Within this task however, there is very little incentive for participants to do this, as a win-stay lose-shift strategy would not be expensive in terms of time and effort. The finding that humans show this tendency to use temporal structure to direct search is compatible with the notion that humans, and perhaps primates, have evolved a specific adaptation due to selective pressures of foraging on patchy and ephemeral resources, to detect structure in stimuli to minimise effort expended during search.

Experimentally disentangling the visual and spatial cues available in this foraging task, showed that humans did acquire spatial knowledge of food rewards when visual cues were removed. The removal of the visual cue of colour had a detrimental effect on performance compared to the performance by participants who only had spatial cues available from the outset. Typically, tasks assessing associative learning principles, including overshadowing, use tasks that require a single response per trial (Mackintosh, 1971; 1976; Prados, 2011; Kosaki et al. 2013), whilst the findings here showed for the first time that overshadowing occurs within a foraging paradigm requiring the search for multiple items. Additionally, these findings suggest that whilst visual cues were relied on to an extent when they were available to use, humans were able to find the hidden rewards using only spatial cues. Removal of cues from a naturalistic forest environment is impossible to do, however this result supports the notion that it is possible that within these environments, non-human primates who forage throughout their home range daily, do acquire spatial knowledge to some extent

of their environment. It is possible that searches are guided by visual cues such as the colour of ripe fruit, though these results do not rule out the notion that primates build mental spatial representations, which further research with primates using this foraging paradigm would help to determine.

Chapter 5: Effects of Ageing in the Detection of Temporal Structure. The set of experiments outlined in Chapter 4 provided an ecologically valid, and suitable experimental paradigm to assess multiple cognitive competences within a foraging situation. This task afforded the unique opportunity to assess the effect of ageing on a number of cognitive skills within a task derived from naturalistic situations. In older adults, many studies suggest that memory and cognitive performance declines (van Hooren et al. 2007; Hills et al. 2013; see Bishop et al. 2010, for a review) which is also found within spatial memory and foraging tasks (Moffat et al. 2001; Mata et al. 2009; Zancada-Menendez et al. 2015). Park et al. (2002) found a linear decline for tasks including the use of WM, LTM, and speed of processing, which are abilities specifically pertinent to foraging behaviour. Specifically, age-related differences have been found to be specific to tasks dependent on the DLPFC (MacPherson et al. 2002), suggesting that tasks investigating ability to detect structure may be a valuable method to assess ageing. Phillips et al. (2006) additionally stated that to more accurately assess human ageing, ecologically valid and naturalistic tasks must be used. However, a task based upon search for items within a supermarket may not tap the relevant cognitive skills required within a forest environment, where hominin cognition is thought to have initially evolved (Milton, 1981a; White et al. 2009), suggesting that a foraging task is the most evolutionarily-relevant task to use.

In a touchscreen version of the task employed in Chapter 4, both young and older adults became more efficient foragers across the trials. However, older adults did not reach the same level of accuracy in detecting the temporal patterns of reward availability across the trials as younger adults, suggesting that cognitive abilities reliant on the DLPFC show a decline with age (MacPherson et al. 2002). The results also indicated that older adults had detected the temporal patterns and were using this information, albeit not to the same accuracy or at the same rate as younger adults. This suggests that whilst older adults showed a deficit in detecting and using structured temporal information, they did not show an inability to benefit from structure. Older

adults also appeared to be less efficient foragers across the trials and took significantly longer to learn which locations never yielded a reward and should be avoided than younger adults, however, the learning rates across the trials indicated that older adults did not perform significantly differently in terms of selections and revisits than younger adults. The results of this chapter indicated that within this ecologically valid task assessing the use of structure within search - an ability which is thought to rely on the DLPFC - effects of age are evident. To further this, research using fMRI would help advance our understanding of the role of the DLPFC during search, and how it is affected in ageing participants.

Chapter 6: Developmental Changes in Foraging Efficiency. As the results of the experiments described in Chapter 5 demonstrated that this foraging paradigm was sensitive to effects of ageing, Experiment 9 assessed whether this task would also detect differences between developmental age groups. Within evolutionary psychology, it is thought that cognitive mechanisms serve different advantages at different stages of development and maturity (Bjorklund & Bering, 2002). More specifically, research shows an increase in WM span performance as age increases (Farrell Pagulayan et al. 2006; Gavens & Barrouillet, 2004; Hamilton et al. 2003), and a developmental increase in ability to use rules (Frye et al. 1995; Zelazo et al. 1996; Siegler & Chen, 1998). In relation to pattern detection, Diamond (2002) suggested that cognitive functions related to the DLPFC show a continuous improvement into early adulthood, which suggests that an ability to detect and benefit from structure (see Bor et al. 2003) may also show a developmental trend. To investigate foraging efficiency further, primary school children aged 5-11 years old were assessed using the same foraging touchscreen task as administered in the experiment described in Chapter 5.

Children appeared to show a developmental trend in terms of overall efficiency and LTM. Children in the intermediate and oldest age groups showed a greater rate of improvement across the trials compared to children in the youngest age group, whose performance did not appear to improve across the trials. This improvement across the trials for the number of selections made and the number of never rewarded locations selected suggested that older children had started to learn that within a trial, particular colours, or 'species', were rewarded, and that two species were always rewarded, showing evidence of pattern detection. As an ability to detect and benefit from structure

is thought to be reliant on the DLPFC, this finding suggests that this area of the brain continues to develop across childhood, and perhaps into early adulthood. In relation to WM ability however, children of the intermediate age group appeared to make the greatest number of errors, which is in contrast with previous research showing a developmental trend in WM ability (Farrell Pagulayan et al. 2006; Gavens & Barrouillet, 2004; Hamilton et al. 2003). However, it should be acknowledged that the number of items to search was large and the temporal pattern was complex. An initial pilot study may have helped to improve the methodology implemented. For instance, increasing the number of locations presented by using an incremental procedure may give a more accurate understanding of where these cognitive competences necessary for efficient foraging may develop. Additionally, presenting a less complex single temporal pattern, also may provide a more accurate representation of temporal structure recognition in children. Overall, these findings are compatible with evolutionary developmental theories (see Bjorklund & Bering, 2002), as there was a clear effect of age across the measures. This suggests that cognitive competences develop and become more advanced as they age, which is consistent with the notion that the cognitive skills required for efficient foraging benefitted older children who were more likely to have experienced foraging pressures to a greater degree than younger children (Bjorklund & Bering, 2002). Further work assessing where efficient foraging competences develop in children using an incremental version of this paradigm would further our understanding of these cognitive skills; in particular, an ability to detect temporal structure.

Chapter 7: Detection of Temporal Structure in Baboons, *Papio papio*. The experiments described effectively demonstrate that the foraging task employed was a useful paradigm to assess foraging efficiency and detection of temporal structure. As this paradigm has proved valuable in the assessment of spatial cognitive competences across different populations, this task also afforded the assessment of a non-human primate species. Spatial tasks are primarily non-verbal, thus they are particularly useful to assess spatial ability across species using the same experimental task. However, findings from experiments with humans only allow inferences to be made about human cognition, and an experimental assessment of primate behaviour under these conditions was required to investigate the differences and similarities in primate cognition. The touchscreen task initially described in Chapter 5 allowed a unique opportunity to

experimentally assess the cognitive competences that this task affords with a group of touchscreen-trained baboons.

The findings indicated that baboons became more efficient foragers and made fewer selections, revisits, and visits to never rewarded locations as the task progressed. Baboons were particularly efficient at avoiding non-profitable locations, and quickly learned to avoid locations that never yielded a food reward. Further findings indicated that inter-species differences occurred with regard to an ability to detect temporal structure, as baboons did not appear to use temporal information to direct searches to profitable locations. In comparison with humans, both species made relatively few visits to never rewarded locations. Humans were able to detect the SA temporal pattern that was presented across the trials, and were more likely to direct their first choice on a trial to a rewarded location than baboons. This suggests that an ability to benefit from temporal structure may be an important difference between human and baboon cognition. However, it should be noted that baboons were able to leave their testing boxes at will, and it is therefore possible that baboons did not detect temporal patterns of food availability due to pausing the experiment regularly. Runs of trials were therefore analysed in which baboons did not leave the testing box, though these were not indicative of an ability to detect temporal structure.

These findings may be explained by the notion that baboons are not primarily frugivorous, and their diet is more opportunistic (Napier & Napier, 1967; 1985). Many baboon traits seen today may be due to their adaptations from living on a savannah (Whiten, Byrne, Barton, Waterman & Henzi, 1991), and so an ability to detect fruiting patterns would not have been as advantageous within this environment as it would be within a forest. Similarly, it is possible that as omnivorous and flexible foragers, an ability to detect patterns of food availability was redundant to baboon evolution, as other food sources were accessible and exploited. However, it should also be acknowledged that in this experiment, humans did not detect the DA temporal pattern, therefore we should be cautious stating that baboons may not be able to detect temporal structure. The temporal patterns presented were also complex, and it is unclear whether a single temporal pattern would have been detected and exploited. Further research investigating this cognitive competency in baboons would better our understanding of this issue, perhaps using a large-scale foraging search space which would require travel between food locations, and altering the temporal pattern presented. It is possible that an ability to detect structure in this way evolved later down the primate lineage, and was

advantageous for an early ancestor of chimpanzees and humans. Therefore, it would also be beneficial for future research in this domain to compare frugivorous and folivorous primates within this task to experimentally assess an ability to detect and benefit from structure. These results demonstrated a successful implementation of a sophisticated cognitive task with a non-human species, providing evidence for the first time that the foraging paradigm developed here can be successfully used comparatively.

8.3 Sex Differences

A further question this body of work aimed to investigate was the issue of sex differences in spatial memory and in ability to detect and use structure. Many studies investigating human spatial memory report sex differences, with males outperforming females in tasks using geographical and Euclidean information (Lawton, 1994; Saucier et al. 2002), dynamic spatial ability (Law et al. 1993), and mental rotation (Moffat et al. 1998), whilst females show a proficiency for object location (Voyer et al. 2007; Silverman et al. 2007; Buss, 2009). The predominant evolutionary theory to explain this difference in humans is the *hunter-gatherer hypothesis* (Silverman & Eals, 1992) based upon the division of labour that humans experienced throughout evolutionary history, with a more recent explanation proposing that a male advantage in spatial cognition occurs across species due to inter-male competition and sexual selection, in Ecuver-Dab and Robert's (2004) *twofold selection process*.

Within the ISSR task described in the first experimental chapter there was a robust sex difference, with males largely outperforming females. Male participants overall made more correct responses and recalled the path sequences more accurately than females, consistent with evolutionary theories of sex differences proposing that males evolved superior spatial memory skills. Despite a trend for a male advantage when locations were arranged in clusters, females did not perform significantly differently to males in these trials. This suggests that females may have a propensity for foraging within patchy environments, resulting in a more similar level of performance by both sexes. These findings are compatible with the notion that selective pressures for enhanced spatial abilities were present in males due to their hunting role during the EEA, whereas a females' role required search through small scale, patchy spaces, resulting in a more proximal search strategy (Silverman & Eals, 1992). These findings are also consistent with the view that superior spatial ability was shaped by male competition and sexual selection, whilst female spatial abilities favour a more proximal

strategy due to mothering constraints (Ecuyer-Dab & Robert, 2004). Concerning an ability to detect temporal structure, when two concurrent temporal patterns were presented, females in the partially predictable condition made more selections until the completion of a trial than males. However, this occurred only at the outset of the experiment, and suggests that females were initially impaired by the unpredictability of the temporal patterning to a greater extent than males, which also lends support to the notion of superior navigational skills in males. Once the visual cue of colour was removed, females also appeared to show a greater impairment, which supports previous research showing a greater reliance on landmarks in spatial tasks by females (Lawton, 1994; Saucier et al. 2002). However, male and female ability to detect temporal structure did not differ across the experiments, and all participants appeared to learn the temporal patterns significantly better than chance level. A clear effect of sex was also found when assessing children on this foraging task. Once again, a male advantage was found only at the outset of trials, where females overall made more selections, visits to never rewarded locations, and revisits than males. WM was particularly affected by sex, with analyses indicating that this difference lay within the intermediate age group, as females here made significantly more WM errors than males of this age group, and also more than females aged 5-7 and 10-11 years old. These findings suggest that sex differences also occur in a touchscreen-based foraging task which taps the cognitive requirements of foraging, yet does not require navigation through a search space. However, it remains unclear as to why female children aged 8-9 years old performed less accurately on this measure of WM. Further research assessing children of these age groups with a smaller array of locations to better assess ability to detect temporal patterns would aid understanding of whether sex differences persist when WM load is eased.

When investigating structure in the form of chunking, the results largely showed that males and females did not differ in their ability to search within this task, despite an intuitive relation to object location tasks in which females have been found to excel (see Silverman et al. 2007). The similarity in performance in this task may reflect a female proficiency for locating objects whilst also promoting male navigational skills. When assessing ageing in the foraging task described in Chapter 5, no effects of sex were found amongst both the young and older adult age groups. Previous research has found that older females outperform males on verbal memory tasks, though show no difference between males within other cognitive domains (van Hooren et al. 2007), thus

it may be the case that sex differences, in particular within non-verbal tasks, are less prevalent amongst an aging population.

8.4 Value of VR and Touchscreen Methodologies

The methodologies and designs used throughout these experiments are novel ways of investigating memory. The value of VR tasks is particularly apparent in spatial tasks where real-life large-scale spaces are often not experimentally practical. The tasks used in Chapters 2 and 3 were based on the notion of testing humans within animal paradigms where non-human species are required to move through a test environment. In this regard, VR is a particularly useful tool in which to replicate large scale environments previously used with non-human animals. Both these chapters emphasise the importance of this, assessing humans in tasks previously designed for capuchin monkeys (De Lillo et al. 1997) and rats (Dallal & Meck, 1990; Macuda & Roberts, 1995), to assess where true similarities and differences lie in behaviour and cognition across species. Similarly, VR allowed the development of a task based on observational studies of primates foraging within natural environments (Janmaat et al. 2012; Janmaat et al. 2013a; Janmaat et al. 2013b), allowing the assessment of humans within a task capturing the essential aspects of foraging for ephemeral resources. VR also allowed the manipulation of cues which can be impossible to separate in natural settings. The experiments described in Chapters 2 and 4 successfully disentangled factors which often become confounded within visuo-spatial tasks and observational studies, and which cannot be easily manipulated in naturalistic environments.

However, there are also advantages to using a touchscreen version, as it is easier to administer and the data collection rate is higher. This version of the task is quick to complete in comparison to VR and the risk of experiencing motion sickness is extinguished, which is important when assessing ageing and young population cohorts. Additionally, both versions of this task can be considered ecologically valid, as regardless of the medium used to present it, the task captured the essential skills required for foraging. From this, it is reasonable to use this ecologically valid paradigm to more accurately assess effects of ageing on these abilities, and to assess how these skills develop in children. The touchscreen version of this task also benefits from being an appropriate diagnostic tool, as it is a relatively simple task to complete and administer, and is a battery of tests within a single task. The findings described within Chapter 5 are indicative of healthy ageing, but any deficits in performance here could

reflect a deficit in memory on one or more of these cognitive measures. A further benefit to this methodology was the affordance of comparative assessment. The touchscreen task was undoubtedly valuable in the assessment of non-human primates, which allowed a direct comparison between humans and baboons in a task derived from naturalistic foraging situations and capturing the requirements of foraging for ephemeral resources.

VR and touchscreen comparison. The experiments presented in Chapters 4 and 5 used the same foraging paradigm and temporal patterns across trials, but were presented using different mediums. The task presented to participants in Chapter 4 employed a VR methodology, where participants walked through an environment and experienced changing viewpoints as they moved through the search space, whilst the task described in Chapter 5 used a 2D touchscreen, where all locations were shown in plan-view and could all be seen from a single viewpoint. This allowed a comparison between the performances of young adult participants completing a task tapping the same cognitive measures, but experiencing different viewpoints and navigational requirements. The findings here indicated that participants who completed the VR task made significantly fewer selections until the completion of a trial, fewer revisits to locations previously searched within a trial, and fewer visits to locations that were never rewarded than participants who completed the same task presented on a touchscreen. Those who used VR also made significantly more correct first choices of the SA, suggesting that overall, they were better able to detect this temporal pattern than those who used the touchscreen. There was however no significant difference when assessing detection of the DA, perhaps as this was a more difficult pattern to learn overall. Participants within both experiments became efficient foragers and improved across all measures, however, the findings support the conclusions of previous research (Boud et al. 1999; Smith et al. 2005) as the locations of rewards and when they would be available was more accurately learned within a VR environment than when participants searched within the 2D search space. However, this may be explained by the allowance of less costly mistakes in VR. Selecting an alternative location on a touchscreen is relatively quick and easy, unlike in a VR environment where a participant must spend extra time travelling to an alternative location if they select an unrewarded pole. In this regard, it is likely that participants make less mistakes when the cost of making them is higher (Gibson et al. 2000; Gilchrist et al. 2001). These results imply that VR may

afford a more accurate assessment of the memory competences involved in foraging, and allows for a more ecologically valid set-up.

Evaluation of methods. The cognitive skills necessary for an efficient search within VR environments are considered to more accurately reflect the skills required within real-life situations. Boud, Haniff, Baber, and Steiner (1999) found that engineering students who were shown assembly instructions in VR were better at product assembly than those who were shown 2D drawings, indicating that different cognitive competences are employed. Additionally, Smith et al. (2005) assessed search within large-scale search spaces, and found no effect of age unlike typical visuo-spatial search tasks performed as a 2D task on a computer screen, suggesting that differences may be alleviated in tasks which are carried out in navigational spaces where participants must use different competences to explore their environment. As foraging typically involves physically navigating through environments, the use of VR to assess memory in search and foraging situations therefore allowed a more accurate assessment of the competences involved. Considering this, previous research by Ruddle and Lessels (2006) has suggested that full body movement is crucial for an efficient search within a VR environment, stating that the visual detail presented to participants is less important than physical movement. However, this contrasts with research suggesting full immersion in a VR environment is not always required for successful results (Bowman & McMahan, 2007). Moreno and Mayer (2002) found that students who used a HMD to view and walk through a VR environment did not learn the task better than those who viewed the environment on screen and used a mouse to move through the space. The medium through which VR is viewed did not appear to play a significant role in performance, and in accordance with the findings of this thesis, suggests that the use of a HMD, 3D glasses, and presenting the environment on-screen only, would not affect performance in spatial tasks. The use of VR, regardless of full body movement, appears to be a valuable and effective way to measure cognitive skills. Similarly, the findings outlined within this thesis also highlight the effectiveness of 2D versions capturing the required cognitive competences for efficient foraging. Previous research has found that large-scale search retains some characteristics of screen-based visual search tasks but reduces the occurrence of revisits (Gilchrist et al. 2001; Smith et al. 2008). This was also found in the comparison above, as overall foraging efficiency, WM, LTM and detection of the SA temporal pattern was superior in VR. However, participants who

completed the task in VR did not detect the DA pattern to a higher degree than those who used the touchscreen. In both experiments, participants were able to learn this pattern better than chance level would predict, suggesting that on this measure of temporal pattern detection, VR and visual search are similarly effective.

Considering the limitations and difficulties faced throughout the experiments, VR can often have the undesired complication of motion sickness. In the experiments described, a number of participants reported feeling motion sick whilst using VR, which initially made data collection difficult and was thought to be due to a disparity of receiving rich visual information without physical body movement. This was a property lacking from the study, as physical movement with the HMD or 3D glasses was not possible due to testing room constraints. This was generally overcome by making participants aware of the symptoms, offering participants regular breaks, and using an on-screen version of the task without the HMD or 3D glasses. Whilst Ruddle and Lessels (2006) proposed that full body movement was necessary when using VR, it was clear from this body of work that participants who completed the foraging task in VR were efficient foragers and were proficient in detecting and exploiting the temporal patterns present. This was also the case, albeit to a lesser degree, by those who experienced the touchscreen version, supporting the notion that whilst VR and visual search tasks employ different cognitive competences, there are similarities which make both methods a useful and valuable tool to investigate foraging cognition.

8.5 Final Conclusions

The findings outlined in this thesis suggest that humans have a strong tendency to detect structure in search, whether it is using the physical structure of the search space, or finding structure and patterns in stimuli across time. Using the structure of items within a search space is an efficient strategy which eases memory load by allowing humans to more easily keep track of previous searches. A motivation to reduce cognitive above travelling costs was evident, with further findings indicating that humans naturally exploited the spatial arrangement of locations when given the opportunity to search arrays with hidden food types. This finding was consistent with the notion that primates differ in their ability to benefit from structure in comparison with non-primate species. Considering hominid evolution, early humans would have inhabited and foraged within patchy and variable forest environments that required specific cognitive skills to find food sources (Lovejoy, 1981; Milton, 1981a; White et

al. 2009). A cognitive ability to reduce the memory load experienced when searching multiple locations would have been beneficial, to more easily recall where food sources were located. By considering the evolutionary pressures related to the emergence of high-level cognition, the experimental foraging paradigm used allowed the comparison of a number of cognitive competences across a healthy ageing population, a developmental cohort of primary school children, and a group of non-human primates, highlighting where similarities and differences lie in comparison with young adults.

There are however, questions that are yet to be answered. The findings in relation to chunking by food type indicate that humans do not spontaneously use this strategy, however, it is not yet known how non-human primates would behave in this experimental situation. This would allow further comparison between species to assess the differences between human and non-human search strategies. The results of the final experiment showed that baboons did not detect, or at least, did not use temporal structure to predict food availability, though it is again unknown whether primarily frugivorous monkeys, or great apes, would detect these patterns. Further research in this area would show where higher order cognitive skills may have evolved throughout the primate lineage, by assessing whether frugivorous primate species who are thought to possess high-level skills due to foraging on ephemeral resources (Milton, 1981a; 1993), show a proficiency for the detection and use of structure in comparison to primarily folivorous primates. Previous research on frugivorous birds has indicated that they track fruit availability (Levey, 1988), thus it would also be important to consider an ability to detect structured temporal patterns across species, which may have occurred due to similar evolutionary pressures as those experienced by early anthropoids. These findings also have implications for the notion of mental maps (Tolman, 1948), and overshadowing theory (Mackintosh 1971; 1976), and further research considering the extent to which spatial memory is acquired or is overshadowed by visual or olfactory cues in primates and other species would further our understanding of this issue during foraging.

Findings also indicated that humans become less efficient foragers as they age, though further research in this domain would benefit from employing fMRI methods in conjunction with this task, to determine the role of the DLPFC in young and older adults in their ability to detect temporal structure. Considering the value of VR, testing ageing and developmental populations with egocentric viewpoints in VR or in real-life large-scale spaces would additionally be a valuable contribution to this area to further

assess the cognitive skills required during foraging in spatial environments. During egocentric foraging, the findings showed that humans did acquire spatial information, despite an effect of overshadowing by salient visual cues. However, the extent to which this occurs in a visual search foraging task with allocentric information, remains unclear and is cause for further investigation. Lastly, an ability to detect and benefit from temporal structure during foraging did not appear to be affected by sex. Interestingly, Baron-Cohen et al. (2003) proposed that males, and more specifically those on the autistic spectrum (Baron-Cohen, 2002) are particularly efficient at systemising; an ability to detect patterns in data. This suggests that being a systemiser is intuitively related to an ability to detect and exploit spatial and temporal structure during foraging, however the findings did not reflect a male advantage here. It would therefore be an interesting venture to investigate this notion further in the search and foraging paradigms outlined.

In conclusion, the propensity to detect and benefit from structure plays an important role in human cognition. Humans show a tendency to promote cognitive over energetic economy, and a strong proficiency to use both spatial and temporal structure in stimuli. These findings suggest that this competency and the associated cognitive abilities may be primarily human, though further research with non-human species both across the primate order and other animal species, would allow us to assess whether this proficiency is uniquely human. Whilst considering the evolutionary pressures under which higher order cognition may have evolved in primates, these findings also have implications for healthy ageing and development in humans. By assessing cognition within non-verbal spatial situations, the experimental paradigms afforded the consideration of the high-level cognitive skills required in these situations across species which additionally has important implications for comparative cognitive psychology. These findings therefore contribute to a range of important and novel topics within human cognition and leaves open new opportunities to investigate the benefits of structure in non-human spatial cognition.

Appendix

Appendix A: Ethical Approval for the VR Experiments

University of Leicester Ethics Review Sign Off Document



To: **Melissa Kirby**

Subject: Ethical Application Ref: **demonstrat-315e**

(Please quote this ref on all correspondence)

15/10/2012 09:23:21

Psychology

Project Title: **Systemising and Working Memory in virtual Reality Foraging**

Thank you for submitting your application which has been considered.

This study has been given ethical approval, subject to any conditions quoted in the attached notes.

Any significant departure from the programme of research as outlined in the application for research ethics approval (such as changes in methodological approach, large delays in commencement of research, additional forms of data collection or major expansions in sample size) must be reported to your Departmental Research Ethics Officer.

Approval is given on the understanding that the University Research Ethics Code of Practice and other research ethics guidelines and protocols will be compiled with

- <http://www2.le.ac.uk/institution/committees/research-ethics/code-of-practice>
- <http://www.le.ac.uk/safety/>

The following is a record of correspondence notes from your application **demonstrat-315e**. Please ensure that any proviso notes have been adhered to:-

Oct 13 2012 2:03PM Hi Heather, could you accept this application for me , please?
Thanks, Giorgio

Oct 15 2012 9:23AM Thank you for writing such a thorough application.
Well done!

--- END OF NOTES ---

Appendix B: Consent Form for Experiment 1, Chapter 2

Participant Consent Form

BACKGROUND INFORMATION

Title: Systemising and Spatial Working Memory in Virtual Reality Foraging

Researchers: Our names are Melissa Kirby and Dr Carlo De Lillo from the University of Leicester, School of Psychology.

Purpose of data collection: Doctoral research

Details of Participation: This study is a virtual reality foraging task which will last approximately 1 hour and 20 minutes, with a 10-15 minute break in between. During this break, you will be required to complete a short questionnaire. The virtual reality task requires you to wear a headset and to navigate around a set of poles using a hand held device. In each trial, you will be shown a sequence which requires you to move through the set of poles, and to then recall the sequence.

CONSENT STATEMENT

1. I understand that my participation is voluntary and that I may withdraw from the research at any time during testing without giving any reason.
2. I am aware of what my participation will involve.
3. My data are to be held confidentially and only Melissa Kirby and Carlo De Lillo will have access to them.
4. My data will be kept in a locked filing cabinet for a period of at least five years after the appearance of any associated publications. Any aggregate data (e.g. spreadsheets) will be kept in electronic form for up to one year after which time they will be deleted.
5. In accordance with the requirements of some scientific journals and organisations, my coded data may be shared with other competent researchers. My coded data may also be used in other related studies. My name and other identifying details will not be shared with anyone.
6. The overall findings may be submitted for publication in a scientific journal, or presented at scientific conferences.
7. I will be able to obtain general information about the results of this research by giving the researcher my email address.

I am giving my consent for data to be used for the outlined purposes of the present study.

All questions that I have about the research have been satisfactorily answered.

I agree to participate.

Participant's signature: _____

Participant's name (please print): _____

Date: _____

If you would like to receive a summary of the results by e-mail, when this is available, please provide your email address: _____

Please note that this form will be kept separately from your data

Appendix C: Consent Form for Experiments 2, 3 and 4, Chapter 3

Participant Consent Form

BACKGROUND INFORMATION

Title: Spatial Working Memory in Virtual Reality Foraging Environments

Researchers: Our names are Melissa Kirby and Dr Carlo De Lillo from the University of Leicester, School of Psychology.

Contact email address: mk217@le.ac.uk; cdl2@le.ac.uk

Purpose of data collection: Doctoral research

Details of Participation: This study is a virtual reality foraging task which will last approximately 1 hour, with a 10-15 minute break in between. During this break, you will be required to complete a short questionnaire. The virtual reality task requires you to wear a headset and to navigate around a set of poles to find the hidden foods, using a hand held device.

CONSENT STATEMENT

1. I understand that my participation is voluntary and that I may withdraw from the research at any time during testing without giving any reason.
2. I am aware of what my participation will involve.
3. My data are to be held confidentially and only Melissa Kirby and Carlo De Lillo will have access to them.
4. My data will be kept in a locked filing cabinet for a period of at least five years after the appearance of any associated publications. Any aggregate data (e.g. spreadsheets) will be kept in electronic form for up to one year after which time they will be deleted.
5. In accordance with the requirements of some scientific journals and organisations, my coded data may be shared with other competent researchers. My coded data may also be used in other related studies. My name and other identifying details will not be shared with anyone.
6. The overall findings may be submitted for publication in a scientific journal, or presented at scientific conferences.
7. I will be able to obtain general information about the results of this research by giving the researcher my email address.

I am giving my consent for data to be used for the outlined purposes of the present study

All questions that I have about the research have been satisfactorily answered.

I agree to participate.

Participant's signature: _____

Participant's name (please print): _____

Date: _____

If you would like to receive a summary of the results by e-mail, when this is available, please provide your email address: _____

Please note that this form will be kept separately from your data

Appendix D: Consent Form for Experiments 5, 6, and 7, Chapter 4

Participant Consent Form

BACKGROUND INFORMATION

Title: Spatial Working Memory in Virtual Reality Foraging Environments

Researchers: Our names are Melissa Kirby, and Dr Carlo De Lillo from the University of Leicester, School of Psychology.

Contact email address: mk217@le.ac.uk; cdl2@le.ac.uk

Purpose of data collection: Doctoral research

Details of Participation: This study is a virtual reality foraging task which will last approximately 1 hour 40 minutes, with a 5-10 minute break to complete a questionnaire. The virtual reality task requires you to wear 3D glasses and to navigate around a set of coloured poles, using a hand held device. The task requires you to select the poles to find the all the foods hidden within the array.

CONSENT STATEMENT

1. I understand that my participation is voluntary and that I may withdraw from the research at any time during testing without giving any reason.
2. I am aware of what my participation will involve.
3. My data are to be held confidentially and only Melissa Kirby and Carlo De Lillo will have access to them.
4. My data will be kept in a locked filing cabinet for a period of at least five years after the appearance of any associated publications. Any aggregate data (e.g. spreadsheets) will be kept in electronic form for up to one year after which time they will be deleted.
5. In accordance with the requirements of some scientific journals and organisations, my coded data may be shared with other competent researchers. My coded data may also be used in other related studies. My name and other identifying details will not be shared with anyone.
6. The overall findings may be submitted for publication in a scientific journal, or presented at scientific conferences.
7. I will be able to obtain general information about the results of this research by giving the researcher my email address.

I am giving my consent for data to be used for the outlined purposes of the present study

All questions that I have about the research have been satisfactorily answered.

I agree to participate.

Participant's signature: _____

Participant's name (please print): _____

Date: _____

If you would like to receive a summary of the results by e-mail, when this is available, please provide your email address: _____

Please note that this form will be kept separately from your data

Appendix E: Ethical Approval to Assess Ageing in Young and Older Adults

University of Leicester Ethics Review Sign Off Document



To: **Melissa Kirby**

Subject: Ethical Application Ref: **mk217-b668**

(Please quote this ref on all correspondence)

16/12/2014 10:59:46

Psychology

Project Title: **Spatial working memory foraging task - can humans learn complex synchronicity patterns, and is there an age related decline?**

Thank you for submitting your application which has been considered.

This study has been given ethical approval, subject to any conditions quoted in the attached notes.

Any significant departure from the programme of research as outlined in the application for research ethics approval (such as changes in methodological approach, large delays in commencement of research, additional forms of data collection or major expansions in sample size) must be reported to your Departmental Research Ethics Officer.

Approval is given on the understanding that the University Research Ethics Code of Practice and other research ethics guidelines and protocols will be compiled with

- <http://www2.le.ac.uk/institution/committees/research-ethics/code-of-practice>
- <http://www.le.ac.uk/safety/>

The following is a record of correspondence notes from your application **mk217-b668**. Please ensure that any proviso notes have been adhered to:-

Dec 15 2014 3:07PM As discussed on email, PREC have reviewed this application and have the following feedback:
PREC are in agreement that, in line with the BPS Code of Human Research Ethics, that the participants should be contacted if they score in a range which might indicate impairment. This contact could make it clear that the researcher is not clinically qualified and hence cannot interpret the MoCA and that they should contact their GP if they are concerned.
If you can make the associated amendments to the application form I will look over it as soon as I possibly can.
Best wishes,
Ruth

Dec 15 2014 9:17PM As discussed on email, I am happy in principle with the application now but I think that the consent form perhaps needs a bit more thought. When I said in my email that there should be a statement on the consent form outlining that they would be contacted if they scored within a certain range, I meant for this to be elaborated upon such that the consent that the participant was providing was fully informed i.e. it could outline what the test is assessing (if this is felt to be appropriate), what the scores could possibly indicate, and to ensure that the participants are happy for you to contact them should they score in a range that would indicate the possibility of mild cognitive impairment.

It would also be a good idea to consider the protocol relating to the contacting of the participant should their score indicate a mild cognitive impairment. How would you contact them? And what would you say to them?

I am officially on annual leave tomorrow but I will check my email to see whether you have referred the application back to me.

Best wishes,

Ruth

Dec 16 2014 10:59AM Hi Melissa,
Thanks for these amendments. I approve this application on the condition that participants are to be told verbally at the point of consent about the administration of the MoCA, what it measures, and that if their score indicates concern that they will be contacted. This needs to be explained fully to ensure that their consent is fully informed.
Good luck with the research.
Best wishes,
Ruth

--- END OF NOTES ---

Appendix F: Permission to use the MoCA Questionnaire

RE: MoCA - Permission to use. - Google Chrome

<https://email.le.ac.uk/owa/?ae=Item&a=Open&t=IPM.Note&id=RgAAAADQmbjFdXGkRadDHcBOo%2bqaBwCRWrPMaT5cRbDI>

Reply Reply All Forward

RE: MoCA - Permission to use.

MoCA [info@mocatetest.org]

To: Kirby, Melissa

Cc: 'Dr Ziad Nasreddine MD FRCP(C)' [ziad.nasreddine@cedra.ca]

03 December 2014 21:07

- You replied on 04/12/2014 18:59.

Hello Melissa,

Thank you for your interest in the MoCA®.

You are welcome to use the MoCA® Test as you described below with no further permission requirements.

No changes or adaptations to the MoCA® Test and instructions are permitted.

All the best,

Kathleen Gallant, MSOT
Occupational Therapist/Psychometrician
On behalf of Dr Ziad Nasreddine, Neurologist, MoCA® Copyright Owner
CEDRA: Center for Diagnosis and Research on Alzheimer's disease
4896 Taschereau Blvd, suite 250, Greenfield Park, J4V 2J2, Québec, Canada
Tel: 450-672-1931 ext: 285 Fax: 450-672-1443
kathleen.gallant@cedra.ca
www.mocatetest.org
www.cedra.ca

Appendix G: Consent Form for Older Adults in Experiment 8, Chapter 5

Participant Consent Form

BACKGROUND INFORMATION

Title: Spatial Working Memory in a Touchscreen Foraging Environment

Researchers: Our names are Melissa Kirby and Dr Carlo De Lillo from the University of Leicester, School of Psychology.

Contact email address: mk217@le.ac.uk; cdl2@le.ac.uk

Purpose of data collection: Doctoral research

Details of Participation: This is a touchscreen foraging task which will last approximately 1 hour. The task requires you to select locations on screen in order to find the hidden food items. There will also be a brief cognitive questionnaire (MoCA) to complete.

CONSENT STATEMENT

1. I understand that my participation is voluntary and that I may withdraw from the research at any time during testing without giving any reason.
2. I am aware of what my participation will involve.
3. My data are to be held confidentially and only Melissa Kirby and Carlo De Lillo will have access to them.
4. My data will be kept in a locked filing cabinet for a period of at least five years after the appearance of any associated publications. Any aggregate data (e.g. spreadsheets) will be kept in electronic form for up to two years.
5. In accordance with the requirements of some scientific journals and organisations, my coded data may be shared with other competent researchers. My coded data may also be used in other related studies. My name and other identifying details will not be shared with anyone.
6. The overall findings may be submitted for publication in a scientific journal, or presented at scientific conferences.
7. I will be able to obtain general information about the results of this research by giving the researcher my email address.
8. I understand that the MoCA is used to aid the testing of mild cognitive impairment and that this information is required for publication purposes should this study be published. If my MoCA result falls within a certain range, and should I need to be contacted, I agree to provide my phone number. I understand that this would only be a numerical result as the researchers are not qualified to interpret the results of this test.

I am giving my consent for data to be used for the outlined purposes of the present study

All questions that I have about the research have been satisfactorily answered.

I agree to participate.

Participant's signature: _____

Participant's name (please print): _____

Date: _____

Should you need to be contacted regarding the MoCA, please provide your phone number: _____

If you would like general information about the results of this research, please provide your

email address: _____

Please note that this form will be kept separately from your data

Appendix H: Consent Form for Young Adults in Experiment 8, Chapter 5

Participant Consent Form

BACKGROUND INFORMATION

Title: Spatial Working Memory Touchscreen Foraging Task

Researchers: Our names are Melissa Kirby and Dr Carlo De Lillo from the University of Leicester, School of Psychology.

Contact email address: mk217@le.ac.uk; cdl2@le.ac.uk

Purpose of data collection: Doctoral research

Details of Participation: This study is a touchscreen foraging task which will last approximately 30-40 minutes with short breaks between blocks of trials. You will also be required to complete a short questionnaire. The task requires to you select locations on the screen in order to find the hidden foods.

CONSENT STATEMENT

1. I understand that my participation is voluntary and that I may withdraw from the research at any time during testing without giving any reason.
2. I am aware of what my participation will involve.
3. My data are to be held confidentially and only Melissa Kirby and Carlo De Lillo will have access to them.
4. My data will be kept in a locked filing cabinet and stored electronically for a period of at least five years after the appearance of any associated publications.
5. In accordance with the requirements of some scientific journals and organisations, my coded data may be shared with other competent researchers. My coded data may also be used in other related studies. My name and other identifying details will not be shared with anyone.
6. The overall findings may be submitted for publication in a scientific journal, or presented at scientific conferences.
7. I will be able to obtain general information about the results of this research by giving the researcher my email address.

I am giving my consent for data to be used for the outlined purposes of the present study

All questions that I have about the research have been satisfactorily answered.

I agree to participate.

Participant's signature: _____

Participant's name (please print): _____

Date: _____

Please note that this form will be kept separately from your data

Appendix I: Ethical Approval to Assess Developmental Cognition in Children

RE: Melissa Kirby Ethics application - Google Chrome

<https://email.le.ac.uk/owa/?ae=Item&a=Open&t=IPM.Note&id=RgAAAADQmbjFdXGkRadDHcBOo%2bqaBv>

Reply Reply All Forward

RE: Melissa Kirby Ethics application

Gerdjikov, Todor V. (Dr.)

To: Kirby, Melissa

16 June 2015 15:54

- You replied on 16/06/2015 16:31.

Thanks Melissa,
I just approved this subject to (1) the DBS clearance coming through and (2) use of verbal assent with the children: ie in addition to getting the parents' permission you should verbally ask the children whether they would like to take part in the study. Sorry about the confusion with this application.
Cheers,
Todor

From: Kirby, Melissa
Sent: 16 June 2015 15:08
To: Gerdjikov, Todor V. (Dr.)
Subject: RE: Melissa Kirby Ethics application

Hi Todor,

RE: FW: Melissa Kirby Ethics application - Google Chrome

<https://email.le.ac.uk/owa/?ae=Item&a=Open&t=IPM.Note&id=RgAAAADQmbjFdXGkRadDHcBOo%2bqaBv>

Reply Reply All Forward

RE: FW: Melissa Kirby Ethics application

Kirby, Melissa

To: Fuggetta, Giorgio (Dr.)

Attachments: (2) [Download all attachments](#)
 image005.jpg (9 KB); image006.png (25 KB)

26 June 2015 09:17

From: Fuggetta, Giorgio (Dr.)
Sent: 26 June 2015 08:00
To: Kirby, Melissa
Subject: RE: FW: Melissa Kirby Ethics application

Hi Melissa,

Your ethics application has been approved.

Best
Giorgio

04/09/2015

Ethics Reference: 325-mk217-schoolofpsychology

TO:

Name of Researcher Applicant: Melissa Kirby

Department: Psychology

Research Project Title: Developmental changes in ability to detect spatio-temporal patterns in a foraging touchscreen task

Dear Melissa Kirby,

RE: Ethics review of Research Study application

The University Ethics Sub-Committee for Psychology has reviewed and discussed the above application.

1. Ethical opinion

The Sub-Committee grants ethical approval to the above research project on the basis described in the application form and supporting documentation, subject to the conditions specified below.

2. Summary of ethics review discussion

The Committee noted the following issues:

I approve this application

3. General conditions of the ethical approval

The ethics approval is subject to the following general conditions being met prior to the start of the project:

As the Principal Investigator, you are expected to deliver the research project in accordance with the University's policies and procedures, which includes the University's Research Code of Conduct and the University's Research Ethics Policy.

If relevant, management permission or approval (gate keeper role) must be obtained from host organisation prior to the start of the study at the site concerned.

4. Reporting requirements after ethical approval

You are expected to notify the Sub-Committee about:

- Significant amendments to the project
- Serious breaches of the protocol
- Annual progress reports

- Notifying the end of the study

5. Use of application information

Details from your ethics application will be stored on the University Ethics Online System. With your permission, the Sub-Committee may wish to use parts of the application in an anonymised format for training or sharing best practice. Please let me know if you do not want the application details to be used in this manner.

Best wishes for the success of this research project.

Yours sincerely,

Prof. Mark Lansdale

Chair

Appendix J: Consent Form Sent to Children's Parents in Experiment 9, Chapter 6

School of Psychology
University of Leicester
Henry Wellcome Building
Lancaster Road
Leicester, LE1 9HN
Email: mk217@le.ac.uk

Dear parent or guardian,

My name is Melissa Kirby and I am a PhD student at the University of Leicester. I would like to ask your consent for your child to take part in a short psychology experiment that I will be running at Rykneld Primary School during the week of 29th June 2015.

The experiment is a simple touchscreen search task which requires participants to select locations on a screen in order to find hidden apples. This should take approximately 15 minutes in total. I am investigating the search strategies that humans use under different conditions, and this particular study is derived from studies observing primate foraging. I am interested in the effect of ageing on this cognitive behaviour, and have already collected data using this task from university students and older adults. I am now aiming to investigate how this behaviour changes developmentally amongst children.

If you are happy for your child to take part in this study, please return the parental consent form by 26th June. Please note that as well as parental consent, your child will also be asked on the day if they are still happy to take part. All participants have the right to withdraw at any time.

If you have any questions or concerns, please do not hesitate to contact me.

Best wishes,

Melissa Kirby

PhD Student and Graduate Teaching Assistant.

Parental Consent Form

BACKGROUND INFORMATION

Title: Developmental changes in foraging cognition in a touchscreen task.

Researchers: My name is Melissa Kirby from the University of Leicester, School of Psychology, supervised by Dr Carlo De Lillo.

Purpose of data collection: Doctoral research.

Details of Participation: This is a touchscreen search task which will last approximately 15 minutes. The task itself will take 10 minutes, with 5 minutes for explaining the task to participants. The task consists of 36 coloured locations on screen, which need to be selected in order to find the hidden apples.

CONSENT STATEMENT

1. I understand that my child's participation is voluntary and that he/she may withdraw from the research at any time up until findings are submitted for publishing, without giving any reason.
2. I am aware of what my child's participation will involve.
3. My child's data is to be held confidentially and only Melissa Kirby and Dr Carlo De Lillo will have access to them.
4. My child's data will be kept for a period of at least five years after the appearance of any associated publications, after which time they will be deleted.
5. In accordance with the requirements of some scientific journals and organisations, my child's coded data may be shared with other competent researchers. The coded data may also be used in other related studies. My child's name and other identifying details will not be shared with anyone.
6. The overall findings may be submitted for publication in a scientific journal, or presented at scientific conferences.
7. I will be able to obtain general information about the results of this research by emailing Melissa Kirby at mk217@le.ac.uk.
8. I understand that I can contact the researcher/s at either mk217@le.ac.uk or cdl2@le.ac.uk if I have any questions about the research before my child takes part.

I am giving my consent for my child's data to be used for the outlined purposes of the present study.

All questions that I have about the research have been satisfactorily answered.

I agree for my child to participate.

Parent's signature: _____

Parent's name (please print) _____

Participant's name (please print): _____

Date: _____

This study was reviewed by the University of Leicester Psychology Research Ethics Committee (PREC). You may contact the Chair of PREC Dr. Ruth Hatcher at rmh12@le.ac.uk if you have any questions or concerns regarding the ethics of this project.

Please note that this form will be kept separately from the data

To be completed on day of testing:

Participant's name: _____

Age: _____

Appendix K: Consent Form for Experiment 11, Chapter 7

Participant Consent Form

BACKGROUND INFORMATION

Title: Spatial Working Memory Touchscreen Foraging Task

Researchers: Our names are Melissa Kirby and Dr Carlo De Lillo from the University of Leicester, School of Psychology.

Contact email address: mk217@le.ac.uk; cdl2@le.ac.uk

Purpose of data collection: Doctoral research

Details of Participation: This study is a touchscreen foraging task which will last approximately 1 hour. The task requires to you select locations on the screen in order to find the hidden foods.

CONSENT STATEMENT

1. I understand that my participation is voluntary and that I may withdraw from the research at any time during testing without giving any reason.
2. I am aware of what my participation will involve.
3. My data are to be held confidentially and only Melissa Kirby and Carlo De Lillo will have access to them.
4. My data will be kept in a locked filing cabinet and stored electronically for a period of at least five years after the appearance of any associated publications.
5. In accordance with the requirements of some scientific journals and organisations, my coded data may be shared with other competent researchers. My coded data may also be used in other related studies. My name and other identifying details will not be shared with anyone.
6. The overall findings may be submitted for publication in a scientific journal, or presented at scientific conferences.
7. I will be able to obtain general information about the results of this research by giving the researcher my email address.

I am giving my consent for data to be used for the outlined purposes of the present study

All questions that I have about the research have been satisfactorily answered.

I agree to participate.

Participant's signature: _____

Participant's name (please print): _____

Participant's age: _____ Gender: _____

Date: _____

Please note that this form will be kept separately from your data

References

- Aadland, J., Beatty, W. W. & Maki, R. H. (1985). Spatial memory of children and adults assessed in the radial maze. *Developmental Psychobiology*, *18*, 163-172.
- Alderman, N., Burgess, P. W., Knight, C. & Henman, C. (2003). Ecological validity of a simplified version of the multiple errands shopping test. *Journal of the International Neuropsychological Society*, *9*, 31-44.
- Anderson, D. P., Nordheim, E. V., Moermond, T. C., Gone Bi, Z. B. & Boesch, C. (2005). Factors influencing tree phenology in Taï National Park, Côte d'Ivoire. *Biotropica*, *37*, 631-640.
- Andrews-Hanna, J. R., Snyder, A. Z., Vincent, J. L., Lustig, C., Head, D., Raichle, M. E. & Buckner, R. L. (2007). Disruption of large-scale brain systems in advanced aging. *Neuron*, *56*, 924-935.
- Ardila, A. (2008). On the evolutionary origins of executive functions. *Brain and Cognition*, *68* (1), 92-99.
- Astur, R. S., Tropp, J., Sava, S., Constable, R. T. & Markus, E. J. (2004). Sex differences and correlations in a virtual Morris water task, a virtual radial arm maze, and mental rotation. *Behavioural Brain Research*, *151*, 103-115.
- Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*, 829-839.
- Baddeley, A. & Hitch, G. (1974). Working memory. *Psychology of Learning and Motivation*, *8*, 47-89.
- Balter, M. (2010). Did working memory spark creative culture? *Science*, *328*, 160-163.
- Ban, S. D., Boesch, C. & Janmaat, K. R. L. (2014). Tai chimpanzees anticipate revisiting high-valued fruit trees from further distances. *Animal Cognition*, *17*, 1353-1364.
- Barkley, R. A. (1991). The ecological validity of laboratory and analogue assessment methods of ADHD symptoms. *Journal of Abnormal Child Psychology*, *19*, 149-178.
- Baron-Cohen, S. (2002). The extreme male brain theory of autism. *Trends in Cognitive Sciences*, *6*, 248-254.
- Baron-Cohen, S., Richler, J., Bisarya, D., Gurunathan, N. & Wheelwright, S. (2003). The systemizing quotient: An investigation of adults with Asperger syndrome or high-functioning autism, and normal sex differences. *Philosophical Transactions of the Royal Society of London B*, *358*, 361-374.

- Bartolomucci, A., de Biurrun, G. & Fuchs, E. (2001). How tree shrews (*Tupaia belangeri*) perform in a searching task: Evidence for strategy use. *Journal of Comparative Psychology*, *115*, 344-350.
- Bashore, T. R., Wylie, S. A., Ridderinkhof, K. R. & Martinerie, J. M. (2014). Response-specific slowing in older age revealed through differential stimulus and response effects on P300 latency and reaction time. *Aging Neuropsychology and Cognition*, *21*, 633-673.
- Bayliss, D. M., Jarrold, C., Baddeley, A. D., Gunn, D. M. & Leigh, E. (2005). Mapping the developmental constraints on working memory span performance. *Developmental Psychology*, *41*, 579-597.
- Bedard, A-C., Nichols, S., Barbosa, J. A., Schachar, R., Logan, G. D. & Tannock, R. (2002). The development of selective inhibitory control across the life span. *Developmental Neuropsychology*, *21* (1), 93-111.
- Bernstein, C., Kacelnik, A. & Krebs, J. R. (1991). Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology*, *60*, 205-225.
- Betzig, L. (1989). Causes of conjugal dissolution: A cross-cultural study. *Current Anthropology*, *30*, 654-676.
- Bishop, N. A., Lu, T. & Yankner, B. A. (2010). Neural mechanisms of ageing and cognitive decline. *Nature*, *464*, 529-535.
- Bjorklund, D. F. & Bering, J. M. (2002). The evolved child: Applying evolutionary developmental psychology to modern schooling. *Learning and Individual Differences*, *12*, 1-27.
- Bjorklund, D. F. & Pellegrini, A. D. (2000). Child development and evolutionary psychology. *Child Development*, *71*, 1687-1708.
- Boakes, R. (2008). *From Darwin to behaviourism: Psychology and the minds of animals*. Cambridge: Cambridge University Press.
- Bogin, B. (1997). Evolutionary hypotheses for human childhood. *Yearbook of Physical Anthropology*, *40*, 63-89.
- Bor, D., Duncan, J., Wiseman, R. J. & Owen, A. M. (2003). Encoding strategies dissociate prefrontal activity from working memory demand. *Neuron*, *37*, 361-367.

- Boud, A. C., Haniff, D. J., Baber, C. & Steiner, S. J. (1999). Virtual reality and augmented reality as a training tool for assembly tasks. *IEEE Information Visualization Proceedings*, 32-36.
- Bowman, D. A. & McMahan, R. P. (2007). Virtual reality: How much immersion is enough? *IEEE Computer Society*, 40, 36-43.
- Breslin, P. A. S. (2013). An evolutionary perspective on food and human taste. *Current Biology*, 23, R409-R418.
- Brown, J. S. (1999). Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research*, 1, 49-71.
- Burgess, P. W., Alderman, N., Evans, J., Emslie, H. & Wilson, B. A. (1998). The ecological validity of tests of executive function. *Journal of the International Neuropsychological Society*, 4, 547-558.
- Burgess, P. W., Alderman, N., Forbes, C., Costello, A., Coates, L. M-A., Dawson, D. R., Anderson, N. D., Gilbert, S. J., Dumontheil, I. & Channon, S. (2006). The case for the development and use of 'ecologically valid' measures of executive function in experimental and clinical neuropsychology. *Journal of the International Neuropsychological Society*, 12, 194-209.
- Buss, D. M. (2009). *Evolutionary Psychology: The New Science of the Mind*, 3rd Ed. Boston: Pearson Education.
- Campbell, A. (1999). Staying alive: evolution, culture, and women's intrasexual aggression. *Behavioural and Brain Sciences*, 22, 203-252.
- Capitani, E., Laiacona, M. & Ciceri, E. (1991). Sex differences in spatial memory: A reanalysis of block tapping long-term memory according to the short-term memory level. *The Italian Journal of Neurological Sciences*, 12, 461-466.
- Cashdan, E., Marlowe, F. W., Crittenden, A., Porter, C. & Wood, B. M. (2012). Sex differences in spatial cognition among Hadza foragers. *Evolution and Human Behaviour*, 33, 274-284.
- Chamizo, V. D., Aznar-Casanova, J. A. & Artigas, A. A. (2003). Human overshadowing in a virtual pool: Simple guidance is a good competitor against locale learning. *Learning and Motivation*, 34, 262-281.
- Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K. & Zanne, A. E. (1999). Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*, 15, 189-211.

- Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9, 129-136.
- Chase, W. G. & Simon, H. A. (1973). Perception in chess. *Cognitive Psychology*, 4, 55-81.
- Chater, N. (1996). Reconciling simplicity and likelihood principles in perceptual organization. *Psychological Review*, 103, 566-581.
- Chater, N. (1999). The search for simplicity: A fundamental cognitive principle? *The Quarterly Journal of Experimental Psychology*, 52, 273-302.
- Chater, N. & Vitanyi, P. (2003). Simplicity: A unifying principle in cognitive science? *Trends in Cognitive Sciences*, 7, 19-22.
- Chivers, D. J. & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. *Journal of Morphology*, 166, 337-386.
- Cohen, B. H. (1963). Recall of categorized word lists. *Journal of Experimental Psychology*, 66, 227-234.
- Cohen, J., Pardy, S., Solway, H. & Graham, H. (2003). Chunking versus foraging search patterns in the hierarchically baited radial maze. *Animal Cognition*, 6, 93-104.
- Coolidge, F. L. & Wynn, T. (2001). Executive functions of the frontal lobes and the evolutionary ascendancy of Homo sapiens. *Cambridge Archaeological Journal*, 11, 255-260.
- Coolidge, F. L. & Wynn, T. (2005). Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeological Journal*, 15 (1), 5-26.
- Dallal, N. L. & Meck, W. H. (1990). Hierarchical structures: chunking by food type facilitates spatial memory. *Journal of Experimental Psychology: Animal Behaviour Processes*, 16 (1), 69-84.
- Darwin, C. R. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.
- Davidson, M. C., Amso, D., Anderson, L. C. & Diamond, A. (2006). Development of cognitive control and executive functions from 4 to 13 years: Evidence from manipulations of memory, inhibition, and task switching. *Neuropsychologia*, 44, 2037-2078.

- De Lillo, C. (2004). Imposing structure on a Corsi-type task: Evidence for hierarchical organisation based on spatial proximity in serial-spatial memory. *Brain and Cognition*, 55, 415-426.
- De Lillo, C. (2012). The use of spatial structure in working memory: A comparative standpoint. In D. McFarland, K. Stenning, & M. McGonigle-Chalmers (Eds.), *The Complex Mind: An Interdisciplinary Approach* (pp. 38-54). London: Palgrave MacMillan.
- De Lillo, C., Aversano, M., Tuci, E. & Visalberghi, E. (1998). Spatial constraints and regulatory functions in monkeys' (*Cebus apella*) search. *Journal of Comparative Psychology*, 112, 353-362.
- De Lillo, C. & James, F. C. (2012). Spatial working memory for clustered and linear configurations of sites in a virtual reality foraging task. *Cognitive Processing*, 13 (1), 243-246.
- De Lillo, C., Kirby, M. & James, F. C. (2013). Spatial working memory in immersive virtual reality foraging: Path organization, traveling distance and search efficiency in humans (*Homo sapiens*). *American Journal of Primatology*, 9999, 1-11.
- De Lillo, C. & Lesk, V. E. (2010). Spatial clustering and hierarchical coding in immediate serial recall. *European Journal of Cognitive Psychology*, 22, 216-246.
- De Lillo, C., Visalberghi, E. & Aversano, M. (1997). The organization of exhaustive searches in a patchy space by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 111, 82-90.
- Dempster, F. N. (1978). Memory span and short-term memory capacity: A developmental study. *Journal of Experimental Child Psychology*, 26, 419-431.
- Deruelle, C. & Fagot, J. (1997). Hemispheric lateralisation and global precedence effects in the processing of visual stimuli by humans and baboons (*Papio papio*). *Laterality: Asymmetries of Body, Brain and Cognition*, 2, 233-246.
- Deruelle, C. & Fagot, J. (1998). Visual search for global/local stimulus features in humans and baboons. *Psychonomic Bulletin and Review*, 5, 476-481.
- Diamond, A. (2002). Normal development of prefrontal cortex from birth to young adulthood: Cognitive functions, anatomy, and biochemistry. In D. Stuss and R. Knight (Eds.), *Principles of Frontal Lobe Function* (pp. 466-501). New York: Oxford University Press.

- Dominy, N. J., Garber, P. A., Bicca-Marques, J. C. & Azevedo-Lopes, M. A. de O. (2003). Do female tamarins use visual cues to detect fruit rewards more successfully than do males? *Animal Behaviour*, *66*, 829-837.
- Dunbar, R. I. M. & Schultz, S. (2007). Understanding primate brain evolution. *Philosophical Transactions of the Royal Society B*, *362*, 649-658.
- Eals, M. & Silverman, I. (1994). The hunter-gatherer theory of spatial sex-differences: Proximate factors mediating the female advantage in recall of object arrays. *Ethology and Sociobiology*, *15*, 95-105.
- Ecuyer-Dab, I. & Robert, M. (2004). Have sex differences in spatial ability evolved from male competition for mating and female concern for survival? *Cognition*, *91*, 221-257.
- Fagot, J. & Cook, R. G. (2006). Evidence for large long-term memory capacities in baboons and pigeons and its implications for learning and the evolution of cognition. *Proceedings of the National Academy of Sciences*, *103*, 17564-17567.
- Fagot, J. & De Lillo, C. (2011). A comparative study of working memory: Immediate serial spatial recall in baboons (*Papio papio*) and humans. *Neuropsychologia*, *49*, 3870-3880.
- Fagot, J. & Deruelle, C. (1997). Processing of global and local visual information and hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). *Journal of Experimental Psychology*, *23*, 429-442.
- Fagot, J. & Paleressompouille, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behaviour Research Methods*, *41*, 396-404.
- Fagot, J. & Parron, C. (2010). Relational matching in baboons (*Papio papio*) with reduced grouping requirements. *Journal of Experimental Psychology: Animal Behaviour Processes*, *36*, 184-193.
- Fagot, J., Wasserman, E. A. & Young, M. E. (2001). Discriminating the relation between relations: The role of entropy in abstract conceptualization by baboons (*Papio papio*) and humans (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behaviour Processes*, *27*, 316-328.
- Farrell Pagulayan, K., Busch, R. M., Medina, K. L., Bartok, J. A. & Krikorian, R. (2006). Developmental normative data for the Corsi block-tapping task. *Journal of Clinical and Experimental Neuropsychology*, *28*, 1043-1052.

- Fleagle, J. G. (2013). *Primate adaptation and evolution*, 3rd ed. London: Academic Press.
- Flemming, T. M., Thompson, R. K. R. & Fagot, J. (2013). Baboons, like humans, solve analogy by categorical abstraction of relations. *Animal Cognition*, *16*, 519-524.
- Foreman, K. B., Addison, O., Kim, H. S. & Dibble, L. E. (2011). Testing balance and fall risk in persons with Parkinson disease, an argument for ecologically valid testing. *Parkinsonism & Related Disorders*, *17*, 166-171.
- Foster, K. R. & Kokko, H. (2009). The evolution of superstitious and superstition-like behaviour. *Proceedings of the Royal Society B*, *276*, 31-37.
- Foti, F., Spirito, F., Mandolesi, L., Aversano, M. & Petrosini, L. (2007). Effects of spatial food distribution on search behaviour in rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, *121*, 290-299.
- Frayser, D. W. & Wolpoff, M. H. (1985). Sexual dimorphism. *Annual Review of Anthropology*, *14*, 429-473.
- Frye, D., Zelazo, P. D. & Palfai, T. (1995). Theory of mind and rule-based reasoning. *Cognitive Development*, *10*, 483-527.
- Gaulin, S. J. C. & FitzGerald, R. W. (1986). Sex differences in spatial ability: an evolutionary hypothesis and test. *The American Naturalist*, *127* (1), 74-88.
- Gaulin, S. J. C. & FitzGerald, R. W. (1989). Sexual selection for spatial-learning ability. *Animal Behaviour*, *37*, 322-331.
- Gavens, N. & Barrouillet, P. (2004). Delays of retention, processing efficiency, and attentional resources in working memory span development. *Journal of Memory and Language*, *51*, 644-657.
- Geary, D. C. (1995). Sexual selection and sex differences in spatial cognition. *Learning and Individual Differences*, *7*, 289-301.
- Geary, D. C. & Bjorklund, D. F. (2000). Evolutionary developmental psychology. *Child Development*, *71*, 57-65.
- Gibson, B. S., Li, L., Skow, E., Brown, K. & Cooke, L. (2000). Searching for one versus two identical targets: When visual search has a memory. *Psychological Science*, *11*, 324-327.
- Gilbert, C. C., Goble, E. D. & Hill, A. (2010). Miocene *Cercopithecoidea* from the Tugen Hills, Kenya. *Journal of Human Evolution*, *59*, 465-483.
- Gilchrist, I. D. & Harvey, M. (2000). Refixation frequency and memory mechanisms in visual search. *Current Biology*, *10*, 1209-1212.

- Gilchrist, I. D., North, A. & Hood, B. (2001). Is visual search really like foraging? *Perception*, 30, 1459-1464.
- Gobet, F. & Simon, H. (1998). Expert chess memory: Revisiting the chunking hypothesis. *Memory*, 6, 225-255.
- Golding, J. F. (2006). Motion sickness susceptibility. *Autonomic Neuroscience: Basic and Clinical*, 129, 67-76.
- Golledge, R. G. (1999). *Wayfinding behaviour: Cognitive mapping and other spatial processes* (Eds.). Baltimore: The John Hopkins University Press.
- Gresack, J. E. & Frick, K. M. (2003). Male mice exhibit better spatial working and reference memory than females in a water-escape radial arm maze task. *Brain Research*, 982, 98-107.
- Guérard, K. & Tremblay, S. (2012). The effect of path length and display size on memory for spatial information. *Experimental Psychology*, 59, 147-152.
- Guérard, K., Tremblay, S. & Saint-Aubin, J. (2009). The processing of spatial information in short-term memory: Insights from eye tracking the path length effect. *Acta Psychologica*, 132, 136-144.
- Hagen, J. W. & Hale, G. A. (1973). The development of attention in children. *ETS Research Report Series*, 1973 (1), 1-37.
- Hamilton, C. J., Coates, R. O. & Heffernan, T. (2003). What develops in visuo-spatial working memory development? *European Journal of Cognitive Psychology*, 15 (1), 43-69.
- Hamilton, W. D. & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, 218, 384-387.
- Harcourt-Smith, W. E. H. & Aiello, L. C. (2004). Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy*, 204, 403-416.
- Harvey, P. H., Clutton-Brock, T. H. & Mace, G. M. (1980). Brain size and ecology in small mammals and primates. *Proceedings of the National Academy of Sciences of the United States of America*, 77, 4387-4389.
- Hill, K. & Hurtado, A. M. (1996). *Ache life history: The ecology and demography of a foraging people*. New York: Aldine de Gruyter.
- Hills, T. T., Mata, R., Wilke, A. & Samanez-Larkin, G. R. (2013). Mechanisms of age-related decline in memory search across the adult life span. *Developmental Psychology*, 49, 2396-2404.

- Hubbell, S. P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, *203*, 1299-1309.
- Iachini, T., Sergi, I., Ruggiero, G. & Gnisci, A. (2005). Gender differences in object location memory in a real three-dimensional environment. *Brain and Cognition*, *59*, 52-59.
- Imbo, I., Szmalec, A. & Vandierendonck, A. (2009). The role of structure in age-related increases in visuo-spatial working memory span. *Psychologica Belgica*, *49*, 275-291.
- Ingram, D. K. (1988). Complex maze learning in rodents as a model of age-related memory impairment. *Neurobiology of Aging*, *9*, 475-485.
- Iyengar, S. S., & Kamenica, E. (2006). Choice overload and simplicity seeking. *University of Chicago Graduate School of Business Working Paper*, *87*, 1-27.
- Jacobs, L. F., Gaulin, S. J. C., Sherry, D. F. & Hoffman, G. E. (1990). Evolution of spatial cognition: Sex-specific patterns of spatial behaviour predict hippocampal size. *Proceedings of the National Academy of Science USA*, *87*, 6349-6352.
- Janmaat, K. R. L., Ban, S. D. & Boesch, C. (2013a). Tai chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes. *Animal Cognition*, *16*, 851-860.
- Janmaat, K. R. L., Ban, S. D. & Boesch, C. (2013b). Chimpanzees use long-term memory to monitor large fruit trees and remember feeding experiences across seasons. *Animal Behaviour*, *86*, 1183-1205.
- Janmaat, K. R. L., Byrne, R. W. & Zuberbuhler, K. (2006). Primates take weather into account when searching for fruit. *Current Biology*, *16*, 1232-1237.
- Janmaat, K. R. L., Chapman, C. A., Meijer, R. & Zuberbuhler, K. (2012). The use of fruiting synchrony by foraging mangabey monkeys: a 'simple tool' to find fruit. *Animal Cognition*, *15*, 83-96.
- Janson, C. H. (2007). Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition*, *10*, 341-356.
- Jolly, C. J. (2001). A proper study for mankind: Analogies from the Papionin monkeys and their implications for human evolution. *Yearbook of Physical Anthropology*, *44*, 177-204.
- Jones, K. E. & MacLarnon, A. M. (2004). Affording larger brains: Testing hypotheses of mammalian brain evolution on bats. *The American Naturalist*, *164* (1), E20-E31.

- Kappelman, J. (1996). The evolution of body mass and relative brain size in fossil hominids. *Journal of Human Evolution*, 30, 243-276.
- Kaufman, S. B. (2007). Sex differences in mental rotation and spatial visualization ability: Can they be accounted for by differences in working memory capacity? *Intelligence*, 35, 211-223.
- Klein, R. M. & MacInnes, W. J. (1999). Inhibition of return is a foraging facilitator in visual search. *Psychological Science*, 10, 346-352.
- Kohler, W. (1925a). *The mentality of apes*. New York: Harcourt Brace.
- Kohler, W. (1925b). Intelligence in apes. *Pedagogical Seminary and Journal of Genetic Psychology*, 32, 674-690.
- Kosaki, Y., Austen, J. M. & McGregor, A. (2013). Overshadowing of geometry learning by discrete landmarks in the water maze: Effects of relative salience and relative validity of competing cues. *Journal of Experimental Psychology: Animal Behaviour Processes*, 39, 126-139.
- Kwon, H., Reiss, A. L. & Menon, V. (2002). Neural basis of protracted developmental changes in visuo-spatial working memory. *Proceedings of the National Academy of Sciences*, 99, 13336-13341.
- Lacreuse, A. & Herndon, J. G. (2009). Nonhuman primate models of cognitive aging. In J. L. Bizon & A. Woods (Eds.), *Animal Models of Human Cognitive Aging* (pp. 1-30). US: Humana Press.
- Laiacona, M., Barbarotto, R. & Capitani, E. (2006). Human evolution and the brain representation of semantic knowledge: is there a role for sex differences? *Evolution & Human Behaviour*, 27, 158-168.
- Law, D. J., Pellegrino, J. W. & Hunt, E. B. (1993). Comparing the tortoise and the hare: gender differences and experience in dynamic spatial reasoning tasks. *Psychological Science*, 4 (1), 35-40.
- Lawton, C. A. (1994). Gender differences in way-finding strategies: relationship to spatial ability and spatial anxiety. *Sex Roles*, 30, 765-779.
- Lehning, M., Leplow, B., Friege, L., Herzog, A., Ferstl, R. & Mehdorn, M. (1998). Development of spatial memory and spatial orientation in pre-schoolers and primary school children. *British Journal of Psychology*, 89, 463-480.
- Levine, S. C., Huttenlocher, J., Taylor, A. & Langrock, A. (1999). Early sex differences in spatial skill. *Developmental Psychology*, 35, 940-949.

- Levy, L. J., Astur, R. S. & Frick, K. M. (2005). Men and women differ in object memory but not performance of a virtual radial maze. *Behavioural Neuroscience*, *119*, 853-862.
- Levey, D. J. (1988). Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs*, *58*, 251-269.
- Louchart, A., Wesselman, H., Blumenschine, R. J., Hlusko, L. J., Njau, J. K., Black, M. T., Asnake, M. & White, T. D. (2009). Taphonomic, avian, and small-vertebrate indicators of *Ardipithecus ramidus* habitat. *Science*, *326*, 66-66e4.
- Lovejoy, O. C. (1981). The origin of man. *Science*, *211*, 341-350.
- Luciana, M. & Nelson, C. A. (1998). The functional emergence of prefrontally-guided working memory systems in four- to eight-year-old children. *Neuropsychologia*, *36*, 273-293.
- MacArthur, R. H. & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*, 603-609.
- MacDonald, S. E., Pang, J. C. & Gibeault, S. (1994). Marmoset (*Callithrix jacchus jacchus*) spatial memory in a foraging task: win-stay versus win-shift strategies. *Journal of Comparative Psychology*, *108*, 328-334.
- MacPherson, S. E., Phillips, L. H. & Della Sala, S. (2002). Age, executive function, and social decision making: A dorsolateral prefrontal theory of cognitive aging. *Psychology and Aging*, *17*, 598-609.
- Macuda, T. & Roberts, W. A. (1995). Further evidence for hierarchical chunking in rat spatial memory. *Journal of Experimental Psychology: Animal Behaviour Processes*, *21* (1), 20-32.
- Mackintosh, N. J. (1971). An analysis of overshadowing and blocking. *Quarterly Journal of Experimental Psychology*, *23*, 118-125.
- Mackintosh, N. J. (1976). Overshadowing and stimulus intensity. *Animal Learning and Behaviour*, *4*, 186-192.
- Mata, R., Wilke, A. & Czienskowski, U. (2009). Cognitive aging and adaptive foraging behaviour. *Journal of Gerontology: Psychological Sciences*, 10.1093/geronb/gbp035.
- Mattson, M. P. (2014). Superior pattern processing is the essence of the evolved human brain. *Frontiers in Neuroscience*, *8*, 1-17.

- McBride, T., Arnold, S. E. & Gur, R. C. (1999). A comparative volumetric analysis of the prefrontal cortex in human and baboon MRI. *Brain, Behaviour & Evolution*, *54*, 159-166.
- McBurney, D. H., Gaulin, S. J. C., Devineni, T. & Adams, C. (1997). Superior spatial memory of women: Stronger evidence for the gathering hypothesis. *Evolution and Human Behaviour*, *18*, 165-174.
- McDaniel, M. A. & Einstein, G. O. (2011). The neuropsychology of prospective memory in normal aging: A componential approach. *Neuropsychologia*, *49*, 2147-2155.
- McGuinness, D. & Morley, C. (1991). Sex differences in the development of visuo-spatial ability in pre-school children. *Journal of Mental Imagery*, *15*, 143-150.
- Menzel, E. W. (1973). Chimpanzee spatial memory organization. *Science*, *182*, 943-945.
- Merrill, E. C., Yang, Y., Roskos, B. & Steele, S. (2016). Sex differences in using spatial and verbal abilities influence route learning performance in a virtual environment: A comparison on 6- to 12-year old boys and girls. *Frontiers in Psychology*, *7*: 258, doi: 10.3389/fpsyg.2016.00258.
- Metcalfe, N. B. & Monaghan, P. (2003). Growth versus lifespan: Perspectives from evolutionary ecology. *Experimental Gerontology*, *38*, 935-940.
- Milgram, N. W., Head, E., Weiner, E. & Thomas, E. (1994). Cognitive functions and aging in the dog: Acquisition of nonspatial visual tasks. *Behavioural Neuroscience*, *108*(1), 57-68.
- Miller, G. A. (1956). The magical number seven, plus or minus two: some limits on our capacity for processing information. *The Psychological Review*, *63*, 81-97.
- Milton, K. (1981a). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist*, *83*, 534-548.
- Milton, K. (1981b). Food choice and digestive strategies of two sympatric primate species. *The American Naturalist*, *117*, 496-505.
- Milton, K. (1993). Diet and primate evolution. *Scientific American*, *269*, 86-93.
- Milton, K. (2003). The critical role played by animal source foods in human (*Homo*) Evolution. *Journal of Nutrition*, *133*, 3886S-3892S.
- Moffat, S. D., Hampson, E. & Hatzipantelis, M. (1998). Navigation in a “virtual” maze: Sex differences and correlation with psychometric measures of spatial ability in humans. *Evolution and Human Behaviour*, *19*, 73-87.

- Moffat, S. D., Zonderman, A. B. & Resnick, S. M. (2001). Age differences in spatial memory in a virtual environment navigation task. *Neurobiology of Aging*, 22, 787-796.
- Myerson, J., Ferraro, F. R., Hale, S. & Lima, S. D. (1992). General slowing in semantic priming and word recognition. *Psychology and Aging*, 7, 257-270.
- Napier, J. R. (1972). *Primates and their adaptations*. London: Oxford University Press.
- Napier, J. R. (1976). *Primate locomotion*. London: Oxford University Press.
- Napier, J. R. & Napier, P. H. (1967). *A handbook of living primates: Morphology, ecology and behaviour of nonhuman primates*. London: Academic Press.
- Napier, J. R. & Napier, P. H. (1985). *The natural history of the primates*. London: Cambridge University Press.
- Nasreddine, Z. S., Phillips, N. A., Bedirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L. & Chertkow, H. (2005). The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, 53, 695-699.
- New, J., Krasnow, M. M., Truxaw, D. & Gaulin, S. J. (2007). Spatial adaptations for plant foraging: Women excel and calories count. *Proceedings of the Royal Society B*, 274, 2679-2684.
- Newman, M. C. & Kaszniak, A. W. (2000). Spatial memory and aging: Performance on a human analog of the Morris water maze. *Aging, Neuropsychology and Cognition*, 7, 86-93.
- Normand, E. & Boesch, C. (2009). Sophisticated Euclidean maps in forest chimpanzees. *Animal Behaviour*, 77, 1195-1201.
- Noser, R. & Byrne, R. W. (2007a). Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus*. *Animal Behaviour*, 73, 257-266.
- Noser, R. & Byrne, R. W. (2007b). Mental maps in chacma baboons (*Papio ursinus*): using inter-group encounters as a natural experiment. *Animal Cognition*, 10, 331-340.
- Noser, R. & Byrne, R. W. (2010). How do wild baboons (*Papio ursinus*) plan their routes? Travel among multiple high-quality food sources with inter-group competition. *Animal Cognition*, 13, 145-155.
- Nowak, M. & Sigmund, K. (1993). A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature*, 364, 56-58.

- Olton, D. S. & Samuelson, R. J. (1976). Remembrance of places passed: spatial memory in rats. *Journal of Experimental Psychology: Animal Behaviour Processes*, 2, 97-116.
- Olupot, W., Chapman, C. A., Waser, P. M. & Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology*, 43 (1), 65-78.
- Orsini, A., Chiacchio, L., Cinque, M., Cocchiaro, C., Schiappa, O. & Grossi, D. (1986). Effects of age, education and sex on two tests of immediate memory: A study of normal subjects from 20 to 99 years of age. *Perceptual and Motor Skills*, 63, 727-732.
- Orsini, A., Grossi, D., Capitani, E., Laiacona, M., Papagno, C. & Vallar, G. (1987). Verbal and spatial immediate memory span: Normative data from 1355 adults and 1112 children. *The Italian Journal of Neurological Sciences*, 8, 537-548.
- Pacheco-Cobos, L., Rosetti, M., Cuatianquiz, C. & Hudson, R. (2010). Sex differences in mushroom gathering: Men expend more energy to obtain equivalent benefits. *Evolution and Human Behaviour*, 31, 289-297.
- Palmer, J. (1995). Attention in visual search: Distinguishing four causes of a set-size effect. *Current Directions in Psychological Science*, 4, 118-123.
- Pammi, V. S. C., Miyapuram, K. P., Bapi, R. S. & Doya, K. (2004). Chunking phenomenon in complex sequential skill learning in humans. *Neural Information Processing*, 3316, 294-299.
- Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D. & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychology and Aging*, 17, 299-320.
- Parker, S. T. & McKinney, M. L. (1999). *Origins of intelligence: The evolution of cognitive development in monkeys, apes, and humans*. Baltimore: The Johns Hopkins University Press.
- Parmentier, F. B. R., Elford, G. & Maybery, M. (2005). Transitional information in spatial serial memory: Path characteristics affect recall performance. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 31, 412-427.
- Phillips, L. H., Henry, J. D. & Martin, M. (2008). Adult aging and prospective memory: The importance of ecological validity. In M. Kliegel, M. A. McDaniel & G. O. Einstein (Eds.), *Prospective Memory: Cognitive, Neuroscience, Developmental*,

- and Applied Perspectives* (pp. 161-185). New York: Lawrence Erlbaum Associates.
- Phillips, L. H., Kliegel, M. & Martin, M. (2006). Age and planning tasks: The influence of ecological validity. *International Journal of Aging and Human Development*, *62*, 175-184.
- Posch, M. (1997). Win stay-lose shift: An elementary learning rule for normal form games. *Santa Fe Institute*, *97*, 06-056e.
- Postma, A., Jager, G., Kessels, R. P. C., Koppeschaar, H. P. F. & van Honk, J. (2004). Sex differences for selective forms of spatial memory. *Brain and Cognition*, *54*, 24-34.
- Pothos, E. M. & Chater, N. (2002). A simplicity principle in unsupervised human categorization. *Cognitive Science*, *26*, 303-343.
- Prados, J. (2011). Blocking and overshadowing in human geometry learning. *Journal of Experimental Psychology: Animal Behaviour Processes*, *37* (1), 121-126.
- Premack, D. (2007). Human and animal cognition: Continuity and discontinuity. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 13861-13867.
- Price, P. W. (1996). *Biological evolution*. Fort Worth: Saunders College Publishing.
- Reader, S. M. & Laland, K. N. (2001). Primate innovation: Sex, age, and social rank differences. *International Journal of Primatology*, *22*, 787-805.
- Reader, S. M. & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 4436-4441.
- Read, D. W. (2008). Working memory: A cognitive limit to non-human primate recursive thinking prior to hominid evolution. *Evolutionary Psychology*, *6*, doi:10.1177/147470490800600413.
- Rendell, P. G. & Thomson, D. M. (1999). Aging and prospective memory: Differences between naturalistic and laboratory tasks. *Journal of Gerontology: Psychological Sciences*, *54B*, 256-269.
- Roitblat, H. L., Tham, W. & Golub, L. (1982). Performance of *Betta splendens* in a radial arm maze. *Animal Learning and Behaviour*, *10* (1), 108-114.
- Rozin, P. (1996). Towards a psychology of food and eating: From motivation to module to model to marker, morality, meaning, and metaphor. *Current Directions in Psychological Science*, *5* (1), 18-24.

- Ruddle, R. A. & Lessels, S. (2006). For efficient navigational search, humans require full physical movement but not a rich visual scene. *Psychological Science*, *17*, 460-465.
- Ruff, C. (1987). Sexual dimorphism in human lower limb bone structure: Relationship to subsistence strategy and sexual division of labour. *Journal of Human Evolution*, *16*, 391-416.
- Sandstrom, N. J., Kaufman, J. & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research*, *6*, 351-360.
- Sargis, E. J. (2004). New views on tree shrews: The role of Tupaiids in primate supraordinal relationships. *Evolutionary Anthropology*, *13*, 56-66.
- Saucier, D. M., Green, S. M., Leason, J., MacFadden, A., Bell, S. & Elias, L. J. (2002). Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behavioural Neuroscience*, *116*, 403-410.
- Semendeferi, K., Lu, A., Schenker, N. & Damasio, H. (2002). Humans and great apes share a large frontal cortex. *Nature Neuroscience*, *5*, 272-276.
- Servan-Schreiber, E. & Anderson, J. R. (1990). Learning artificial grammars with competitive chunking. *Journal of Experimental Psychology*, *16*, 592-608.
- Sharples, S., Cobb, S., Moody, A. & Wilson, J. R. (2008). Virtual reality induced symptoms and effects (VRISE): Comparison of head mounted display (HMD), desktop and projection display systems. *Displays*, *29*, 58-69.
- Shettleworth, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences*, *14*, 471-481.
- Siegler, R. S. & Chen, Z. (1998). Developmental differences in rule learning: A microgenetic analysis. *Cognitive Psychology*, *36*, 273-310.
- Silverman, I., Choi, J., Mackewn, A., Fisher, M., Moro, J. & Olshansky, E. (2000). Evolved mechanisms underlying wayfinding: Further studies on the hunter-gatherer theory of spatial sex differences. *Evolution and Human Behaviour*, *21*, 201-213.
- Silverman, I., Choi, J. & Peters, M. (2007). The hunter-gatherer theory of sex differences in spatial abilities: data from 40 countries. *Archives of Sexual Behaviour*, *36*, 261-268.

- Silverman, I. & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (pp. 531-549). New York: Oxford Press.
- Singh, D., Dixon, B. J., Jessop, T. S., Morgan, B. & Dixon, A. F. (2010). Cross-cultural consensus for waist-hip ratio and women's attractiveness. *Evolution and Human Behaviour*, *31*, 176-181.
- Sinopoli, K. J., Schachar, R. & Dennis, M. (2011). Reward improves cancellation and restraint inhibition across childhood and adolescence. *Developmental Psychology*, *47*, 1479-1489.
- Smirni, P., Villardita, C. & Zappalá, G. (1983a). Influence of different paths on spatial memory performance in the block-tapping test. *Journal of Clinical Neuropsychology*, *5*, 355-359.
- Smirni, P., Villardita, C. & Zappala, G. (1983b). Spatial memory span in adolescents: Cultural and sex differences. *Perceptual and Motor Skills*, *57*, 175-178.
- Smith, A. D., Gilchrist, I. D. & Hood, B. M. (2005). Children's search behaviour in large-scale space: Developmental components of exploration. *Perception*, *34*, 1221-1229.
- Smith, A. D., Hood, B. M. & Gilchrist, I. D. (2008). Visual search and foraging compared in a large-scale search task. *Cognitive Processes*, *9*, 121-126.
- Smyth, M. M. & Scholey, K. A. (1992). Characteristics of spatial memory span: Is there an analogy to the word length effect, based on movement time? *The Quarterly Journal of Experimental Psychology*, *47* (1), 91-117.
- Spetch, M. L. (1995). Overshadowing in landmark learning: Touch-screen studies with pigeons and humans. *Journal of Experimental Psychology: Animal Behaviour Processes*, *21*, 166-181.
- Spetch, M. L. & Parent, M. B. (2006). Age and sex differences in children's spatial search strategies. *Psychonomic Bulletin & Review*, *13*, 807-812.
- Spinozzi, G., De Lillo, C. & Truppa, V. (2003). Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *117* (1), 15-23.
- Stevens, J. R., Hallinan, E. V. & Hauser, M. D. (2005). The ecology and evolution of patience in two new world monkeys. *Biology Letters*, *1*, 223-226.

- Stevens, J. R., Rosati, A. G., Ross, K. R. & Hauser, M. D. (2005). Will travel for food: Spatial discounting in two new world monkeys. *Current Biology*, *15*, 1855-1860.
- Sumner, P. & Mollon, J. D. (2000). Chromaticity as a signal of ripeness in fruits taken by primates. *The Journal of Experimental Biology*, *203*, 1987-2000.
- Surovell, T. A. (2000). Early paleoindian women, children, mobility, and fertility. *American Antiquity*, *65*, 493-508.
- Teaford, M. F. & Ungar, P. S. (2000). Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 13506-13511.
- Terrace, H. S. (2001). Chunking and serially organized behaviour in pigeons, monkeys and humans. In R. G. Cook (Eds.), *Avian Visual Cognition* [Online]. Available at: www.pigeon.psy.tufts.edu/avc/terrace/
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *The Psychological Review: Monograph Supplements*, *2*, i-109.
- Tolman, E. C. (1948). Cognitive maps in rats and men. *The Psychological Review*, *55*, 189- 208.
- Tooby, J. & DeVore, I. (1987). The reconstruction of hominid behavioural evolution through strategic modelling. In W. G. Kinzey (Eds.), *The Evolution of Human Behaviour: Primate Models* (pp. 183-237). New York: State University of New York Press.
- Uttal, D. H., Gregg, V. H., Tan, L. S., Chamberlin, M. H. & Sines, A. (2001). Connecting the dots: Children's use of a systematic figure to facilitate mapping and search. *Developmental Psychology*, *37*, 338-350.
- Vadillo, M. A., Bárcena, R. & Matute, H. (2006). The internet as a research tool in the study of associative learning: An example from overshadowing. *Behavioural Processes*, *73*, 36-40.
- Valsecchi, P., Bartolomucci, A., Aversano, M. & Visalberghi, E. (2000). Learning to cope with two different food distributions: The performance of house mice (*Mus musculus domesticus*). *Journal of Comparative Psychology*, *114*, 272-280.
- van Hooren, S. A. H., Valentijn, A. M., Bosma, H., Ponds, R. W. H. M., van Boxtel, M. P. J. & Jolles, J. (2007). Cognitive functioning in healthy older adults aged 64-

- 81: A cohort study into the effects of age, sex, and education. *Aging, Neuropsychology, and Cognition*, 14, 40-54.
- van Schaik, C. P., Terborgh, J. W. & Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, 24, 353-377.
- Verhaeghen, P. & Salthouse, T. A. (1997). Meta-analysis of age-cognition relations in adulthood: Estimates of linear and nonlinear age effects and structural models. *Psychological Bulletin*, 122, 231-249.
- Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E. & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, 100, 3328-3342.
- Voeks, R. A. (2007). Are women reservoirs of traditional plant knowledge? Gender, ethnobotany and globalization in northeast Brazil. *Singapore Journal of Tropical Geography*, 28, 7-20.
- Voyer, D., Postma, A., Brake, B. & Imperato-McGinley, J. (2007). Gender differences in object location memory: A meta-analysis. *Psychonomic Bulletin and Review*, 14 (1), 23-38.
- Wahungu, G. M. (1998). Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus*. *African Journal of Ecology*, 36, 159-173.
- Watson, J. B. (1903). *Animal education: An experimental study on the physical development of the white rat, correlated with the growth of its nervous system*. Chicago: University of Chicago Press.
- White, T. D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C. O., Suwa, G. & Wolde-Gabriel, G. (2009). *Ardipithecus ramidus* and the paleobiology of early hominids. *Science*, 326, 75-86.
- Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G. & Henzi, S. P. (1991). Dietary and foraging strategies of baboons. *Philosophical Transactions of the Royal Society of London B*, 334, 187-197.
- Wiener, J. M. & Mallot, H. A. (2003). 'Fine-to-coarse' route planning and navigation in regionalized environments. *Spatial Cognition and Computation*, 3, 331-358.
- Williams, B. R., Ponesse, J. S., Schachar, R. J., Logan, G. D. & Tannock, R. (1999). Development of inhibitory control across the life span. *Developmental Psychology*, 35 (1), 205-213.

- Winterhalder, B. (1981). Optimal foraging strategies and hunter-gatherer research in anthropology: Theory and models. In B. Winterhalder, and E. Alden Smith (Eds.), *Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses* (pp 13-35). Chicago: University of Chicago Press.
- Wolfe, J. M. (2013). When is it time to move to the next raspberry bush? Foraging rules in human visual search. *Journal of Vision*, *13*, doi:10.1167/13.3.10.
- Yerkes, R. M. (1913). Comparative psychology: A question of definitions. *The Journal of Philosophy, Psychology and Scientific Methods*, *10*, 580-582.
- Yerkes, R. M. (1914). The study of human behaviour. *Science*, *39*, 625-633.
- Yoerg, S. I. & Kamil, A. C. (1982). Response strategies in the radial arm maze: Running around in circles. *Animal Learning and Behaviour*, *10*, 530-534.
- Yu, L., Tucci, V., Kishi, S. & Zhdanova, I. V. (2006). Cognitive aging in zebrafish. *PLoS ONE*, *1*(1): e14. doi: 10.1371/journal.pone.0000014.
- Zancada-Menendez, C., Sampedro-Piquero, P., Meneghetti, C., Labate, E., Begega, A. & Lopez, L. (2015). Age differences in path learning: The role of interference in updating spatial information. *Learning and Individual Differences*, *38*, 83-89.
- Zelazo, P. D., Frye, D. & Rapus, T. (1996). An age-related dissociation between knowing rules and using them. *Cognitive Development*, *11*, 37-63.
- Zinner, D., Groeneveld, L. F., Keller, C. & Roos, C. (2009). Mitochondrial phylogeography of baboons (*Papio* spp.) – Indication for introgressive hybridization? *BMC Evolutionary Biology*, *9*: 83, doi: 10.1186/1471-2148-9-83.
- Zuberbuhler, K. & Janmaat, K. R. L. (2010). Foraging cognition in non-human primates. In M. L. Platt and A. A. Ghazanfar (Eds.), *Primate Neuroethology* (pp 64-80). Oxford: Oxford University Press.