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SOURCES OF VARIATION IN SEARCH AND FORAGING: A THEORETICAL PERSPECTIVE

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ABSTRACT

Search – the problem of exploring a space of alternatives in order to identify target goals – is a fundamental behaviour for many species. Although its foundation lies in foraging, most studies of human search behaviour have been directed towards understanding the attentional mechanisms that underlie the efficient visual exploration of two-dimensional scenes. With this review, we aim to characterise how search behaviour can be explained across a wide range of contexts, environments, spatial scales, and populations, both typical and atypical. We first consider the generality of search processes across psychological domains. We then review studies of interspecies differences in search. Finally, we explore in detail the individual and contextual variables that affect visual search and related behaviours in established experimental psychology paradigms. Despite the heterogeneity of the findings discussed, we identify that variations in control processes, along with the ability to regulate behaviour as a function of the structure of search space and the sampling processes adopted, to be central to explanations of variations in search behaviour. We propose a tentative theoretical model aimed at integrating these notions and close by exploring questions that remain unaddressed.

SEARCH, FORAGING, AND THIS REVIEW

Search can be defined as the exploration of multiple alternatives to identify a goal. One of the most fundamental instantiations of a search problem is foraging, the process by which myriad species explore their surroundings for sustenance. A focus on foraging has a wide appeal for psychologists, as well as behavioural ecologists, because of its intuitive relationship with individual fitness and adaptation. Accordingly, a variety of psychological processes and paradigms have been claimed to be grounded in foraging. Nonetheless, the methods and assumptions of behavioural ecology and psychology often differ – whereas behavioural ecology is not normally concerned with the internal mechanisms responsible for foraging choices (Laland & Brown, 2011), psychological perspectives aim to characterise the mental abilities and cognitive processes that underpin efficient or successful foraging behaviours. Moreover, research within the two fields has generally been carried out in isolation and a cross-fertilisation of the fields would, therefore, be both desirable and valuable.

In the following discussion we present a review of studies that are of relevance to a psychological account of human search behaviour, and particularly one that emphasises the contribution of cognitive processing. In keeping with the topic of the Special Issue within which this review resides, we aim also to highlight some of the factors that account for variation in search behaviour. Those factors range from core evolutionary pressures that may have differentially shaped search behaviours in humans and closely-related animal species, to transient state-dependent differences in search associated with, say, stress or emotion. In light of this breadth, we will cover a variety of issues that span modern psychology, including evolution, development, neuropsychology, neuroscience, and genetics. The review is, by no means, intended to be exhaustive - indeed, this would scarcely be possible within an entire volume, such is the fecundity of the canon. Our scope is, however, somewhat restricted by the fact that respective topics of foraging and search span concepts and research areas that are very different. For example, foraging can incorporate a vast range of activities that include the handling and processing of food (Parker and Gibson, 1979; Whiten et al., 1996), as well as the clicking of buttons to make decisions about which side of a computer screen provides more dots of a given colour (Mobbs et al. 2013). Search on the other hand encompasses activities that include searching for a seen item after it disappeared from view, as in Piagetian object permanence tasks (see Bower, 1974), or spatial memory for individual locations in an environment such a search for a submerged platform in a water maze (Morris, 1981), as well as algorithms in cognitive science and AI (e.g. Stennings et al., 1987).

In this review we focus mostly on studies that have addressed problems requiring search amongst a large set of alternatives, as most often happens in foraging, where an organism needs to explore different locations (such as those of fruiting trees) by physically moving within a large scale environment or visually scanning an array of items to identify a target (such as a ripe berry in a bush). This includes situations were subjects need to retrieve multiple items from amongst a set of locations, as would normally happen when foraging for non-mobile resources in a naturalistic, semi-naturalistic, or simulated foraging tasks (see Alleva et al., 1995). It also encompasses the problem of visual search, where participants need to identify a target amongst a large set of distracter items. This latter paradigm has been widely investigated in experimental psychology, and will be discussed in some detail. As we shall see, the problems of foraging and search sometime converge and require similar solutions. Indeed, the relationship between the two terms is sometimes taken for granted, and they are often used interchangeably. Nonetheless, the similarity of the psychological processes required to forage in large spaces, and those required to perform a computer-based visual search task, can be questioned (Gilchrist, North & Hood, 2001), and we will include discussion of studies that have explicitly compared the two.

Our aim here is to characterise the extent to which search and foraging activities might be considered to be subtended by similar psychological processes. By showing how these behaviours vary, depending on individual, contextual, and methodological differences, we hope to get closer to a comprehensive and contemporary characterisation of abilities that may form an evolutionary basis for human mental operations. Our narrative begins with discussion of factors that have been shown to influence foraging, or foraging-like behaviours, across different species in naturalistic and laboratory research. We then move on to contributions provided by more simplified laboratory assays of search-related behaviour, covering both ‘traditional’ examinations of visual exploration as well as more applied examples of performance in real-world tasks in humans. Finally, we cover contributions from studies that have specifically attempted to address the commonality between visual search and larger-scale equivalents. We close by offering some general thoughts on these behaviours and discuss how cognitive control, in particular, might represent a domain general mechanism that can account for both the great differences between contexts, populations, and species, as well as the commonalities we see across them.

THE GENERALITY OF SEARCH

In order to survive, almost all species on Earth need to forage efficiently. Early vertebrates were mobile predators who, in order to survive and thrive, expended the energy required by swimming movements to obtain food (see: Murray et al. 2017). As such, it can be assumed that the basic principles for obtaining sufficient energy from food outweigh the energetic costs of moving around to collect it. Moreover, this basic relationship must be present in most mobile animal species.

Walking in the search landscape: Does it require cognition?

Although this Special Issue focuses on the psychological underpinnings of search, we cannot take for granted that efficient foraging necessarily requires any sophisticated mental ability. In fact, there are effective search patterns that can sustain foraging efficiency with only minimal cognitive requirements, or none at all. Search patterns are often characterised as “walks”, as they can be described as a sequence of steps, and populations of steps can be generated according to rules that range from the deterministic to the probabilistic. A deterministic walk is one that provides a unique solution to a specific search problem. Two examples of this would be a walk solving the travelling salesman problem, by finding the shortest route connecting a fixed set of locations, or one that follows the rule of always moving to the closest visible target (for examples of both see: Cramer and Gallistel, 1997). Psychological processes could also determine fixed sequences of steps, such as when an organism follows a previously learned route to a location, or when search is piloted by a perceived visual cue (for discussion see: Viswanathan, da Luz, Raposo & Stanley, 2011).

Foraging walks can resemble random patterns such as Brownian movements similar to those of inanimate molecules suspended in a liquid. Other walks used in search and foraging have different probability distributions (Viswanathan et al., 2011), and one of the most frequently-modelled iterations is the Lévy walk. Lévy walks are movement patterns where the direction of consecutive steps is chosen randomly but the length of movement is governed by a formula (a power law) that produces several short movements followed by occasional longer movements (for a detailed description see: Pyke, 2015). A schematic illustration of different types of walks and search patterns is provided in Figure 1.

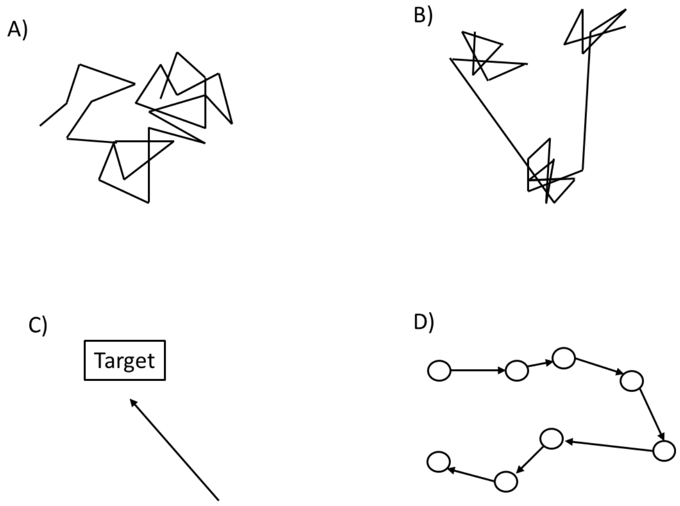


Figure 1 Schematic representation of different types of “walks” and foraging patterns: A) Random Brownian walk; B) Lévy walk; C) search “piloted” by a visible target; D) Deterministic walk following the rule: always move to the closest visible pattern.

A large variety of organisms appear to apply these principles to their foraging paths, including invertebrates such as insects, amoebae (Levandowsky, White & Schuster, 1997) and jellyfish (Hays et al. 2012), as well as mammals with large and complex brains such as monkeys (Ramos-Fernández et al., 2004). Even humans, likely the most cognitively complex of all organisms, have been described as using Lévy walks when foraging. For example, Raichlen et al., (2014) asked Hazda people of northern Tanzania, who follow a hunting-gathering lifestyle, to wear global positioning system (GPS) receivers whilst on foraging trips over a period of several days. Data were collected on males and females from different camps, who foraged on different resources, and their movements were compared to those predicted by different distributions of random walks. A significantly higher proportion of turning patterns during foraging bouts conformed to Lévy walks, compared to those consistent with other types of random walks. As similar results were found amongst people from different camps, it was suggested that these patterns had a high generality and were not generated by specific geographic characteristics of the foraging area, specific types of prey, or local cultural factors. Thus, it was suggested that, despite the fact that people could use memory and other cognitive skills to constrain their movements, their foraging paths were still satisfactorily explained by a general rule that pertains to a wide variety of organisms that do not possess high-level cognitive skills (Raichlen et al., 2014; Viswanathan et al., 2011).

Other instances of Lévy walks in humans have been reported in the forensic psychology literature. For example, patterns of burglaries have been claimed to conform to Lévy characteristics (Johnson, 2014), suggesting a very high generality for random search patterns that do not need to be guided by cognitive processes. The broad applicability of the Lévy walk approach across species is, however, controversial and its adaptive value has been questioned (Reynolds, 2015). Conflicting results have also been reported, especially among non-human primates. For example, it has been suggested that monkeys' foraging patterns sometimes conform to even more basic types of random walks, such as Brownian movements (Sueur, 2011). That said, primate search patterns are generally reported to be influenced by the shape of the environment, the distribution and configuration of resources (Menzel, 1973; Menzel, 1996; De Lillo, Visalberghi & Aversano, 1997; De Lillo, Aversano, Tuci & Visalberghi, 1998), and spatial memory (MacDonald & Wilkie, 1990; Janmaat, Ban & Boesch, 2013), and we next consider the origins of cognitive skills that may be deployed to support efficient foraging.

Exploration and exploitation: Out and about, and in our mind

Walks are influenced by a factor that is inherent to most formulations of foraging and search problems, and that is the relative costs and benefits associated with exploration and exploitation. This refers to the decision that an organism needs to make (deliberately or automatically) between either remaining in the same location (or its vicinity) to exploit resources to be found there, or moving away to explore other areas of a foraging space that might yield more resources than those still available locally. It has been claimed that, in this general formulation, the trade-off between exploitation and exploration has a very high generality (Hills et al., 2015). Indeed, any problem space that can be subdivided in sub-goals could, in principle, be conceptualised in terms of completing one of the sub-goals (exploitation) or moving to another sub-goal within the problem space (exploration). Convincing arguments have been put forward for this characterisation across a variety of problems, including, mate selection, internal semantic memory search (Hills et al., 2015) and the description of criminal behaviour (Johnson, 2014). Visual search, too, has been conceptualised in terms of time spent locally to analyse the visual characteristics of a target before gaze or attention is moved away from it to search for another candidate target within the display set for analysis (Hills et al., 2015).

Charnov's (1976) marginal value theorem (MVT) provided a highly influential framework to understand how optimal foraging behaviour might be underpinned by decision making along the exploration/exploitation axis. More specifically, the MVT allowed behavioural ecologists to make predictions about the foraging patterns of a variety of organisms in a range of different habitats where resources are arranged in patches. The MVT is probably the most prominent optimality model used to describe how an individual should behave in order to forage optimally among patchily distributed resources. Empty areas of space, where no food can be found between patches, make travelling energetically costly for the forager. The MVT model predicts that an optimal forager should keep searching within each patch or, in other words, should keep exploiting it, if the rate of return of food items (or rewards, more generally) is above the average return rate computed for the entire foraging space. By contrast, the forager should leave each patch when the rate of return of food items or rewards falls below the average return rate for the entire foraging space. Assuming that organisms strive to forage optimally, this model allows predictions to be made about how long they will stay in a patch before leaving it (give-up time) depending on the specific distance between patches, and how rich in food resources they are.

The broader generality of this principle was demonstrated by Hills, Jones and Todd (2012), who investigated the extent to which the MVT could be applied even to internal memory scan in humans. Participants were required to generate the names of as many animals as they could within three minutes, and the semantic proximity between each exemplar was then analysed. Not only did participants show a tendency to switch between categories (e.g. “water animals”, “African animals”) when the currently-sampled category began to be depleted, but the point of switching was accurately characterised by the MVT. Moreover, the individuals that made switching decisions conforming to the MVT were also those that retrieved more animals in total. These results point to a striking similarity between processes based on spatial search in an external environment and internal search in semantic memory. Moreover, such demonstrations show that mental representations conform to structural principles and, in this case, are not randomly deposited in a singular store but, instead, are hierarchically and categorically organised (Rosch et al., 1976).

Similar findings have been reported for both semantic and spatially-defined geographical categories (e.g. Patten et al., 2020), leading to a general theory that human cognitive operations have their evolutionary roots in spatially-distributed subsistence foraging. This was elaborated in a study by Hills, Todd and Goldstone (2010) that examined the priming of search behaviours across cognitive domains. Participants were initially assessed on a lexical search task, where they were required to find words (i.e. anagrams) among sets of letters. The foraging conceptualisation was that each letter set constituted a patch. The participants then undertook a spatial task that required them to search an array of pixels to find the ones that yielded a reward (i.e. pixels that turned green when visited).

Critically participants were assigned to one of two condition in this second task. In one condition, rewards were clumped in patches, which encouraged participants to keep searching in local areas before moving away. In the alternative condition, resources were more diffusely distributed amongst the array of pixels, which encouraged participants to avoid spending time in the same restricted area and, instead, move more across the array. Finally, participants performed the lexical search task a second time, and it was observed that those who had experienced the spatial search in a patchy space spent significantly more time in each patch of letters in the lexical search task (also see: Hills, Todd and Goldstone, 2008). This priming of search strategies from the spatial to the lexical search task was taken to indicate that central executive processes can be characterised as domain general search strategies. Throughout search, executive attentional processes would be tuned towards either exploration of exploitation of the environment. Importantly, the task must require some level of tuning as a consequence of the unpredictability of outcomes, as well as self-regulation by the organism for biasing search towards more exploration or exploitation across domains. In fact, in experiments where the information about where to forage was made explicit, and did not require search, the priming did not occur (Hills, Todd and Goldstone 2010). On the basis of these and similar results it has been proposed that the origin of human high level attentional processes may be based on dopaminergic systems that originated in animals, even before the invertebrate/vertebrate evolutionary split (e.g. Floresco, Seamans, & Phillips, 1996; Kischka et al., 1996).

Foraging and brain evolution: Are primates special and does diet matter?

Notwithstanding the generality of search processes, and their neural substrates, across species and problem domains, a strong argument for specificity has been proposed. The position states that the especial requirements of foraging for ephemeral fruit resources in a forest environment directly led to the emergence of large brains in primates and humans (Milton, 1981a, b; 1993; De Casien, Williams, & Higham 2017). This foraging hypothesis of brain evolution is, in fact, one of the primary theories put forward for the emergence of intelligence in primates (for a discussion see: Dunbar & Shultz, 2017). It stems from pioneering studies by Milton (1981a, b) showing an inverse relationship between gut length and brain size in primate species with a specialised frugivorous (spider monkeys) or folivorous (howler monkeys) diet. Folivorous primates evolved an elaborate digestive system that enables them to process toxins and extract nutrients from foliage, despite its low energy content. Since foliage is widely and constantly available in space and time, it is thought that there is no need for advanced cognitive processes to govern search at specific locations, and at particular points in time. By contrast, primates with a prevalently frugivorous diet have comparatively larger brains and shorter intestines. Fruit is easy to digest but it is an ephemeral resource that rapidly appears, ripens, and rots on specific fruiting trees in a forest environment (Milton, 1981; 1993). In some tropical rainforests the probability of randomly encountering a tree that is fruiting at a particular point in time can range from 1 in 10 to 1 in 1000 (Chapman et al., 2004; Janmaat et al., 2012). In these conditions, random walks could not lead to efficient searches for ripe fruit (Janmaat, Chapman, Meijer, & Zuberbuhler, 2012). It has, therefore, been argued that efficient fruit foraging requires higher level cognitive skills to memorise the location of fruiting trees, individuate the best routes connecting them (Milton, 1993) and predict their patterns of fruiting (Janmaat, 2013a, b). Such requirements would have triggered brain expansion in frugivorous primates and humans, since we share the same lineage (Milton, 1993). More speculatively, further species-specific brain developments in humans may have been due to climate changes that induced fruit shortage and resulted in the need to process less digestible plant products and obtain meat. In turn, this would have required technological and social advancements such as tool manufacture and use, cooperative hunting, and cooking (see: Milton, 1993; Aiello & Wheeler, 1995). Despite being overshadowed by other evolutionary hypotheses of the evolution of large brains and intelligence in primates (for a review see: Dunbar & Shultz, 2017), the foraging hypothesis has recently received further support based on more affluent and comprehensive sets of anatomical data (De Casien, Williams, & Higham 2017).

Aside from evolutionary arguments, ethological studies strongly suggest the deployment of very sophisticated cognitive skills in foraging primates. For example, observational studies of non-human primates foraging in the wild suggest that search in mangabey monkeys (Janmaat, Chapman, Meijer, & Zuberbuhler, 2012) and chimpanzees (Janmaat, Ban & Boesch, 2013a) is guided by a knowledge of the synchrony with which different fruiting trees produce fruit. This type of strategy had previously been suggested in studies where Japanese macaques were artificially fed particular types of fruit. When the animals were subsequently let free to forage in semi-natural settings, they were not only more likely to select trees of the same species as those that they had previously been fed, but also trees that had happened to fruit synchronously with those trees in that first environment (Menzel 1991). Again, this was taken as evidence for foraging choices based on knowledge of the botanical characteristic of the trees in the home range of the monkeys and their pattern of fruiting synchrony. Other studies, conducted in the wild, also indicate remarkable long term memory skills and the ability to predict what fruit can be found on specific trees across seasons (Janmaat et al., 2013b). This complements earlier evidence of the ability to plan optimal routes among foraging sites in chimpanzees (Menzel 1973) and vervet monkeys (Cramer and Gallistel, 1996).

Together, these results are consistent with the notion that non-human primates use advanced search skills when foraging for fruit, and conform to the foraging hypothesis of brain expansion in primates. As such, they do not sit comfortably with the notion that random walks are sufficient to explain the intricacies of foraging behaviour in primates. Useful advances in this field would be made by systematic experimental psychology studies aimed at testing specific cognitive competences in different primate species, relating these competencies to their diet, and comparing them directly to equivalent skills in humans. For historical, practical, or ethical reasons, most psychological studies have been focused on a limited set of primate species and, among them, those with a prevalently folivorous diet are rare. Although such an investigation would not be easy to conduct, and doubtlessly complicated by the need to take into account variations in the social organisation of species as well as seasonal variations in their diet, expanding our existing knowledge of primate cognition in relation to species-specific diet would be an important endeavour for future comparative cognition research.

Variations across species and the structure of the search space

For the time being, observational data on non-human primates foraging in the wild encourage the conclusion that primates deploy advanced mental abilities when foraging. This, paired with the preceding discussion points, suggests that it should be possible to identify some differences between primate and non-primate species in the mental abilities deployed in foraging and search. However, in naturalistic studies of foraging, the uncontrollable geographical characteristic of the habitat of the animals can make it difficult to compare different species, as well as the results of separate studies. In addition, group and individual search behaviours can be difficult to determine because many animals travel in groups (for a range of studies of group movements in primate and non-primate species, see Boinsky and Garber 2000) making statistical inferences difficult. Despite these challenges, some comparative considerations can be made on the basis of results from studies that have used similar simulated foraging environments and testing procedures with primate and non-primate species (De Lillo et al., 1997; 1998). In these simulated foraging environments it is possible to control for and manipulate the structure of the configuration of locations that animals need to explore and determine the effects of such manipulations across species.

De Lillo et al. (1997) investigated search efficiency in capuchin monkeys – a species amongst those with the highest encephalization index and a gut system similar to that of humans (Martin et al., 1985; Aiello & Wheeler, 1995). In multiple trials, monkeys were allowed to freely search a set of 9 containers (each baited with a peanut), collecting the rewards by walking (upside down) on the wiremesh from which the containers were suspended with short chains. A suspended array like this allowed for the containers to be returned to their original position after inspection, so that no permanent cues were left of previous visits. Search efficiency was defined as the total number of times that containers were visited, before all peanuts were collected. In this task an optimal search would consist in retrieving the rewards in 9 visits, one for each container, without any wasteful revisits of previously explored locations. Monkeys' search efficiency was examined in a within subjects A-B-A design, comparing conditions that featured either a diffuse matrix of containers or a patchy configuration, where containers were arranged as spatial clusters of 3 containers each (see Figure 2). The spacing between containers within each clustered set was half the length of the shorter distance between containers in each cluster. Monkeys received 60 trials with the matrix configuration, used as a baseline condition, followed by 60 trials with the patchy configuration and, finally, 60 trials in a control condition with the matrix configuration. Monkeys searched significantly more efficiently in the clustered configuration than in either the baseline or the control condition featuring the matrix. Moreover, this improvement could not be easily explained by an interaction between a bias to perform a given type of random walk (e.g. a Lévy walk) and the geometrical arrangement on containers. Rather, the improvement seemed to be due to self-regulation occurring with practice, over the course of the task. In fact, trend analyses showed that in the clustered configuration only, the number of redundant moves to visited locations decreased linearly across blocks of trials. Moreover, the number of superfluous revisits was negatively correlated with the tendency to search each cluster exhaustively before moving away from it. Finally, most errors consisted in revisiting containers upon re-entering clusters that were left only partially visited.

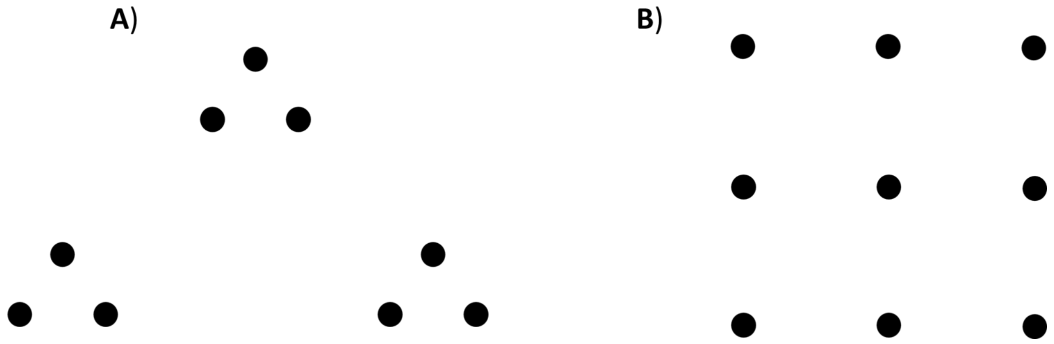


Figure 2 Configurations of the search space as used by De Lillo et al 1997: A) clusters; B) matrix. See text for explanations.

This pattern of results is consistent with the hypothesis that monkeys take advantage of clustered search spaces by hierarchically coding locations as they explore them so that, once a cluster is exhaustively explored, the animal could simply remember the location of entire clusters (and avoid going back to that region of space) rather than keeping track of each individual visited container. On occasions when the monkey fails to do so, re-entries into partially-explored clusters are likely to produce errors as the location of visited containers therein is no longer in memory. This hierarchical organisation could result in a reduction of the memory load required to keep track of the locations visited, which eventually translates to better search performance.

Subsequent studies tested different species using a similar experimental set-up, adapted for the ergonomic requirements and body size of the species under investigation. Taken together, the results of these studies point to a trend in the ability to benefit from clustered search spaces that parallels the taxonomic distance of the species tested from humans (and would also parallel the relative expansion of the frontal cortex of the species involved: Fuster, 2008; Passingham and Smaers, 2014). In fact, neither of two rodent species – mice (Valsecchi et al., 2001) and rats (Foti et al., 2007; De Lillo, 2012; 2019) – displayed more efficient searches in clustered sets compared to diffuse matrices of locations. Moreover, neither mice nor rats performed systematic searches that explored each set exhaustively before moving onto the next. They did not develop this search strategy in spite of repeated testing and the opportunity to self-regulate (however, it must be noted that rodents only received 30 trials for each of the conditions). By contrast preschool children (4 and 5 years old), tested in a task made as similar as possible to that presented to the monkeys, were performing systematically within a few trials (De Lillo, 2012). Children were required to search artificial “flowers” in order to collect plastic ladybirds hidden therein. The “flowers” were containers mounted on a stand, the height of which could be adjusted so that each individual child could only assess the presence of a ladybird by exploring the “flower” with their hand raised above eye-level. Children were more efficient at searching clustered arrays compared to matrices, and they displayed a strong tendency for exploring each cluster exhaustively before moving to another cluster. A similar study was conducted on the tree shrew (Bartolomucci et al 2001), a species that can be considered at the edge of the primate order, as it is sometimes classified as a primate and sometimes as part of its own separate order (Wilson and Reeder 2005). Search efficiency in this species also failed to benefit from a clustered search space when tested with a paradigm akin to that used with mice (Valsecchi et al 2001). However, tree shrews reportedly searched the clustered set more systematically than mice (Bartolomucci et al 2001). Adult humans tested in an immersive reality version of the task, using a procedure similar to that of children, showed a nearly optimal search performance in the clustered search space, accompanied by search patterns where clusters were exhaustively and systematically explored (De Lillo, Kirby and James, 2014). However, adult humans were also as proficient with searching the matrix and developed systematic searches there too (e.g. performing consecutive visits to targets within the same row or column). This general pattern of findings suggests that primates display a higher level of search performance and organisation when foraging in a clustered set, compared to non-primate species. Also, there seem to be a positive relationship between search performance and search organisation, possibly mediated by a reduction of the memory load necessary to keep track of the locations visited when systematic searches are performed in a clustered set. Amongst primates, this relationship seems to be particularly strong in humans.

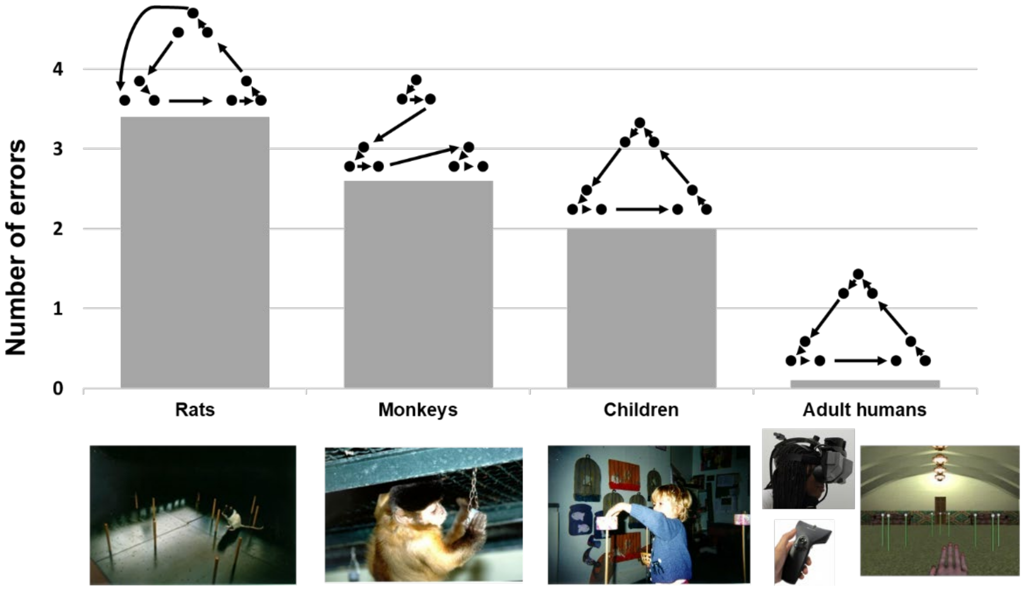


Figure 3 Number of errors consisting in revisiting a container already explored and typical search patterns shown by rats, monkeys, children and adult humans (tested with Virtual Reality) in a clustered search, as described by De Lillo (2012; 2019) and De Lillo, Kirby and James (2014). The search pattern shown is the optimal search path (i.e. one of the observed search paths where the 9 containers were explored with 9 moves only) which showed the strongest correlation with all optimal search paths shows by the same species. Errors are averaged across all trials, whether they featured an optimal search or not. When searching optimally, only primates typically use systematic searches where each cluster is exhaustively explored before moving on to the next. Among primates, humans develop very systematic search patterns where a fixed direction of travel is used.

Although the studies described above focus specifically on clustered search spaces, this not the only type of configuration of goals where primates spontaneously deploy systematic searches. In fact other studies show that capuchin monkeys adjust their searches to effectively explore sets arranged as a circle or as a line as well (De Lillo et al., 1998). Search spaces arranged as circular and linear configurations are of particular interest as they afford being explored systematically by searching adjacent targets along a given direction of travel. This is a strategy that would result in minimal distance travelled to explore the set and, at the same time, ensure effective tracking of locations visited in a foraging bout with a minimal memory demand. In fact, systematic explorations of such sets could work as notational systems (Karmiloff-Smith, 1992), and the position of the searcher at any particular point in time during search would indicate unambiguously which locations have been visited already (those left behind) and which ones are still to be explored (De Lillo et al., 1998). Capuchin monkeys can efficiently search linear arrays. Moreover, they show evidence of further regulating their search behaviour, even when their searches are optimal in terms of rewards collected. Thus, by practicing searching a linear array, capuchin monkeys gradually reduce the number of revisits of previously explored locations. Moreover, the monkeys keep regulating their search patterns even when they no longer make wasteful revisits of locations from which a reward has already been collected (De Lillo et al., 1998). For example, when they are able to collect nine rewards from nine containers, with the optimal number of nine total visits using an irregular search pattern, the monkeys can continue to modify their behaviour upon further exposure to the task until they eventually develop a systematic search pattern (i.e. starting from one end of the array and progressing to the other end by searching adjacent containers along one travel direction) (De Lillo et al., 1998; De Lillo 2012). This is illustrated in Figure 4.

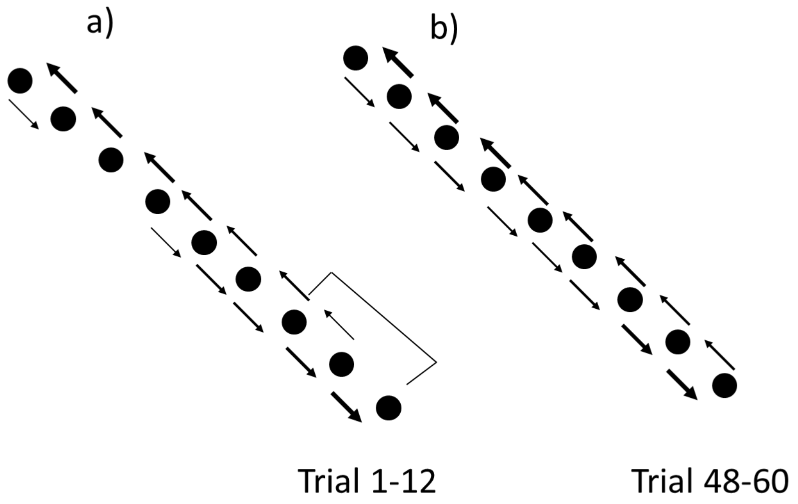


Figure 4 Search pattern of a capuchin monkey searching a linear array of containers to forage for peanuts as described in De Lillo, et al. (2018). The monkeys were given 60 trials, each requiring to retrieve peanuts from each of the 9 containers. The thickness of the arrows indicate the frequency of given transitions when the monkey moved from one container the next in the first (a) and the last (b) set of 12 trials. Although some trials featured optimal searches consisting in visiting all the containers in 9 moves only, the monkey kept regulating her behaviour until the search path featured a linear exploration from one end to the other of the linear array. Such searches can act as notational systems and reduce the working memory load imposed by keeping track of locations already explored. See text for explanation.

Adult humans have not been tested with a single line. However, as mentioned above, when left fee to search a square matrix of targets, they systematically explore each row or column from end to end, selecting adjacent targets in consecutive steps (De Lillo et al., 2014). The fact that they are prone to deploy systematic searches in arrays with a multiple lines, such as a square matrix, suggests that they would do so also in simpler arrays featuring one line only.

Search patterns in structured mazes

To our knowledge, there are few studies available that would enable a thorough evaluation of variations amongst non-primate species in the way that they explore square matrices of locations. However other paradigms, which have some elements in common with the circular and linear arrangements of search targets, provide some information about search behaviour in other *taxa*. Perhaps the most well-known example of such paradigms is the radial maze, which has been widely used to investigate search behaviour in rats and mice. It consists of a central platform from which a number of arms (usually 8 to 12) depart in a radial fashion. In some common preparations, all arms are baited and the animals are left free to explore the arms to retrieve food. Re-entries into arms already visited in a trial are considered working memory errors (Olton and Samuelson, 1976). Several studies with the radial maze report a tendency of rats to develop algorithmic search patterns, consisting of consecutive visits to spatially adjacent arms at specific angles in relation to each other (e.g. Dubreil et al., 2003; Foreman, 1985). Unfortunately, patterning in the radial maze has often been considered a mere confound by researchers interested in the assessment of spatial span in rodents, and procedures have been developed to discourage such search patterns rather than investigating them in their own right (Dubreil et al., 2003). As a consequence, not much information is available on how systematic search patterns emerge in rodents, how consistently they are used and their psychological determinants. Some studies have shown that algorithmic search in rats does not imply that the animals do not encode spatial information about explored arms (Foreman, 1985). Other studies have directly addressed the important issue of the extent to which rats benefit from search organisation in the radial maze when it is modified in ways that could afford hierarchical coding on the basis of the spatial relationship between the arms of the maze (Roberts, 1979; Shenk, Contant and Grobety, 1990).

Roberts (1979), for example, provided evidence for very accurate retention of arms visited by rats in a hierarchical radial maze, which featured secondary arms departing from primary arms. This structure afforded hierarchical searches where secondary alleys are exhaustively explored before moving to another primary alley. With task practice, rats in this condition develop principled search patterns leading to a very accurate retention of the alleys visited in each single trial (Roberts, 1979), providing evidence for the spontaneous emergence of spatial chunking in rats. However, the construction of the hierarchical maze (i.e. the apparatus was elevated and secondary alleys were separated by solid barriers) might facilitate rats’ behavioural chunking by preventing the animals from migrating directly from one secondary alley to another departing from a different primary alley. In fact, when this constraint is removed, other evidence for spatial chunking in rodents does not seem to be conclusive. For example, rats perform worse in radial mazes that afford chunking on the basis of the angular relationship between the arms, compared to performance in standard radial mazes of a comparable number of arms (Shenk, Contant and Grobety, 1990). However, the interpretation of these results is complicated by the fact that when different angular relationships were tested, search efficiency improved with some specific angular relationships, and deteriorated with others (see also: Shenk, Grobety, Lavenex and Lipp, 1995). Taken together with results showing the lack of systematic searching of clustered sets in rats and mice tested in the studies reviewed above (Foti et al., 2007; Valsecchi et al., 2001), the results of these radial maze studies suggest that rodents do not always flexibly regulate their behaviour to benefit from the structural properties afforded by the search space. Indeed, when trying to assess the relationship between the use of search strategies and performance, on the basis of an information theory analysis, Brown and Cook (1986) did not find a positive correlation between search performance and the use of response biases in rats’ choices in the radial maze.

Beyond rodents, avian species tested in search arrays analogous to the ones described thus far do not seem to show evidence of regulating their behaviour to conform to the structure of the search space either. For example, pigeons do not display patterns of search as systematic as those displayed by monkeys when foraging in arrays of feeders arranged in a linear (Spetch and Edwards, 1986) or in a circular fashion (Zentall, Stirn & Jackson-Smith, 1990). However, the studies reviewed here suggest that in primates, and in humans in particular, there is a strong association between search organisation and search efficiency, seemingly mediated by a more effective coding of displays arranged in either spatial clusters or a linear array which, when searched in systematic fashion, allows efficient tracking of the locations explored with minimal demand on memory. These studies are important as they enable us to observe spontaneous behaviour when agents are left free to select their serial pattern of exploration of the search space. This enables the detection of forms of behavioural self-regulation during the execution of the task. Nonetheless, freedom to organise search means that any relationship between search efficiency and search organisation can only be inferred from correlations. As such, the underlying cognitive factors often remain elusive. In the next section we will review how serial recall studies can provide some complementary information on the relationship between serial spatial organisation and memory reduction in the interrogation of a large set of spatial locations.

Travelling distance and memory load in serial recall

We have seen that, when left free to search a relatively large set of locations, primates (but, seemingly, not non-primate species) develop systematic exploration patterns, when the structure of the environment allows them to do so. We referred to the emergence of organised search as a form of self-regulation, since participants are not required to learn such patterns and do so spontaneously and gradually. An important question, therefore, concerns the kind of currency that is used for self-regulation – that is, the precise factors that are being maximised and minimised. Optimality models emphasise the role of distance travelled or time spent foraging (two measures that are closely related and often used interchangeably) as the observable currency that animals tend to minimise (instead of caloric consumption, which would be much more difficult to sample). Memory load, that efficient coding or strategy use could help to reduce, is also a currency that could be used for self-regulation in search (De Lillo et al., 1997; 1998; De Lillo, 2012). The respective role of travelling distance and memory load is, however, often confounded. This is because strategies that minimise travelling distance are also those that could reduce memory load (e.g. exploring clusters systematically would allow chunking and hierarchical coding but would also produce shorter routes throughout the set). In turn, using longer routes to explore a set of locations can lead to increased search time, which, itself, could result in a higher rate of forgetting for previously-explored locations. In the context of working memory studies, it has been shown that this is the case for serial spatial information and, typically, longer paths connecting a set of locations are more difficult to recall (Parmentier et al., 2005).

To advance our understanding of the psychological bases of search and foraging behaviour, it is important to address two related research questions. One is to verify that there is a causal relationship between systematic search patterns and memory for locations. The second is to examine the possibility of separating the effects of travelling distance from the effects of other cognitive factors in search efficiency. It is likely that this would be difficult to do using free search tasks. However, some attempts have been made at partitioning the effects of distance travelled and other factors on memory load with serial recall tasks. These tasks are often implemented using small-scale arrays, which afford a bird's eye view of the configuration of items, such as touch screens (De Lillo & Lesk, 2011; De Lillo et al., 2016). Such experiments tend to require participants to repeat back sequences of observed movements (e.g. icons flashing in sequence at different locations) as in a traditional spatial span task or Corsi test (e.g. Baddeley, 2003; Berch, Krikorian & Huha, 1998). The same kind of task has also been implemented in larger navigational spaces, using immersive virtual reality (VR). This mimics more naturalistic situations, where subjects do not have a bird's eye view of their environment and where travelling distance could be weighted more heavily (De Lillo et al., 2014, 2016). This navigational version of a serial recall task required people to follow a path amongst a set of vertical poles in an immersive VR environment. Each pole was surmounted by a white sphere and, at the beginning of a trial, one sphere turned red. Participants were required to approach the red sphere by navigating in the environment and then select it with a virtual hand, using a trigger on a manual controller. Once selected, the sphere resumed its white colour and, simultaneously, a different sphere turned red, which the participant had to approach and select. This happened until a "walk" comprising nine of these steps was performed. At this point, the participant was taken back to their starting position and asked to repeat the sequence by moving within the virtual space to select the poles, now all surmounted by white spheres, in the same order. With this task, it was possible to manipulate the spacing of the search locations to create conditions featuring clustered sequences of steps (those exploring the set by exhaustively visiting all the spheres in each cluster in turn) that had a longer path-length than non-clustered sequences (requiring moving to different cluster at each step). Regardless of task version (i.e. touch screen or VR), participants always made more memory errors in non-clustered sequences, even when they had a shorter path-length than clustered sequences (De Lillo et al., 2014). These results provide experimental confirmation that, for humans, there is a clear relationship between systematic serial visits to locations and the ability to remember them, supporting similar findings from small-scale spatial span tasks (De Lillo, 2004; De Lillo & Lesk, 2011). Additionally, they suggest that, for humans, the distance travelled is not the main factor that allows the reduction of memory load in this type of tasks. Rather, using a path that is compatible with the hierarchical coding of a patchy environment is more effective than using a shorter one (De Lillo et al., 2014; De Lillo et al., 2016). Detailed analyses of response times when patch size and number of parches is manipulated confirm the hierarchical nature of representations of these arrays in serial recall (De Lillo & Lesk, 2011).

Similar conclusions regarding the relative importance of path length can be derived in relation to the organisation of serial patterns used to explore square matrices of locations. The results of experiments where different sequence characteristics were manipulated, such as their path length and their conformity to a linear organisation (e.g. sequences with or without consecutive steps within the same row or column), show that linear organisation explains a larger portion of variance in recall than path length in humans (De Lillo et al., 2016).

Serial recall studies are extremely difficult to implement with animals and, as such, comparative data that would enable to evaluate the extent to which similar patterns are observed in other species are almost non-existent. Nonetheless, in one study humans and baboons were tested in a spatial span task, similar the tasks described above, where the path-length of sequences as well as their linear organisation was manipulated (Fagot and De Lillo, 2011). The results revealed that whilst human memory was affected by the linear organisation of the sequence but not by path-length, the opposite pattern was observed in baboons, whose memory was affected by path-length rather than linear organisation. These results suggest that monkeys may not have the same propensity as humans to detect the configurational property of a search space (in this case linear) and plan a sequence of steps so as to track their position in space in the most cognitively economic way. Rather, they may regulate search patterns striving to achieve shorter paths. This could be motivated by the reduction of either energetic costs or memory load induced by shortening search time (or, indeed, both).

Can attention to global structure explain interspecies variations in search?

In the study by Fagot and De Lillo (2011) the serial recall tasks were presented on a computer monitor. Thus, they featured a bird's eye view of the item display. Under these conditions, it is possible that the differences observed between humans and monkeys are due to interspecies variations in the ability to attend to the configuration described by the spatio-temporal sequence that they had to recall. This would be in line with numerous studies that indicate a strong bias in monkeys to attend to local elements within visual configurations, in sharp contrast with the well-known bias towards the detection of global aspects of hierarchical compounds (stimuli where local shapes or letters are spatially arranged to form global shapes or letters) observed in humans (Navon, 1977; Kimchi, 1991; see, however, cultural differences in global/local processing as discussed below e.g.: Caparos, et al., 2012). Comparative studies of visual search for hierarchical stimuli in humans and baboons report that only in monkeys was there an increase in response time as a function of set-size (an indication of attentional engagement) and that the slope of this increase was significantly steeper when search for global configurations was required (Deruelle & Fagot, 1998). These results were taken as an indication that the processing of global configurations is attentionally demanding in baboons but not in humans. Further studies with capuchin monkeys clarified that in monkeys, and in humans, control processes modulate the allocation of attention to local details or to global configurations (De Lillo, Spinozzi, Palumbo & Giustino, 2011). In fact, in a matching to sample task with hierarchical stimuli, it was possible to induce monkeys to reverse their spontaneous attention bias towards the analysis of local elements of the stimuli by presenting them with a high proportion of trials that required attending their global spatial arrangement and thus inducing an attention set for that level of stimulus processing (De Lillo et al., 2011).

It is possible that variations in attentional control processes that enable the flexible organisation of serial search as a function of the structure of the environment (so that working memory load is minimised) may explain some of the interspecies differences discussed above. fMRI studies conducted in humans indicate that such processes are associated with the activity in the prefrontal cortex (dorso-lateral and ventro-medial). The prefrontal cortex (which is traditionally associated with working memory) is, somehow paradoxically, more active when people have to reproduce sequences that conform to a linear structure (consecutive items within the same column or row of a matrix of locations), and that are easier to recall than unorganised sequences (Bor et al., 2003). Moreover, the fact that, in humans, these beneficial effects of serial organisation emerge and outweigh those of path-length in immersive virtual reality navigational spaces suggests that, at least in our species, any effect of these factors transcends visual perception (De Lillo et al, 2014; 2016). It is possible that processes mediated by frontal functions enable the flexibility of humans to rapidly regulate their behaviour to conform to the best data-reducing strategies for a given set of locations to explore. Other primates seem also to be able to do so but require repeated task exposure to self-regulate. Also self-regulation in monkeys could be mediated by an attempt to minimise path-length, possibly for its beneficial effects on memory. Other species considered above may have a more limited ability to regulate behaviour as a function of the search space. This may be explained by their lack of neocortex (as in birds) and by the fact that the presence of an analogue of the primate prefrontal cortex in rodents is still highly controversial (Güntürkün & Bugnyar, 2016; Uylings, Henk, Groenewegen, & Kolb, 2003).

Foraging across the lifespan

Within-species differences in foraging behaviour associated with age lie at the root of some evolutionary accounts of human development, and extended juvenility in humans has been directly linked to the emergence of complex cognitive operations that are necessary to undertake efficient and controlled search (Bock, 2004; Kaplan, Lancaster, Hill, & Hurtado, 2000). Thorough examination of foraging-like search in children has indeed revealed an emergence of systematic behaviours, associated with age, which supports such a conceptualisation. For example, preschool children tested in search tasks requiring the exploration of sets of containers arranged in a circular configuration (considered analogous to that of the arms of a radial maze), show an increase an algorithmic responding with age. Algorithmic responding refers to the systematic exploration of adjacent arms, one after the other in a clockwise or counter clockwise direction (Dubreuil et al., 2003). Across preschool ages, four year old children are more systematic than two year olds. Interestingly, when human adults and children over 4 years of age are prevented from using algorithmic responding, their search performance deteriorates more than that of two year olds (Aadland, Beatty and Maki, 1985; Foreman, Arber and Savage, 1984). This suggests a shift in development from the use of working memory to the use of strategic search to keep track of locations visited and avoidance of wasteful selection of previously explored locations. This has, however, been shown to interact with the effort required to search (see: Smith, Gilchrist, & Hood, 2005).

Other studies also suggest a link between age and the ability to use the structure of search space to search efficiently. For example, Uttal and colleagues (2001) asked children to locate reward stickers hidden under saucers, within a search space of 27 saucers arranged according to meaningful configuration (e.g. the shape of a dog). Children were shown the rewarded locations on maps and had to find them within the array of saucers. In one experimental condition lines were added in the map, connecting locations in a way that emphasised the meaningful shape of the configuration. Five year olds, but not 3 and 4 year olds, benefitted from the presence of such lines to the maps of the search space. This suggests that the ability to benefit from structural properties of the search space is subject to cognitive development.

Across the adult portion of the lifespan, however, changes in behaviour seem to pertain less to the use of environmental structure, and more to the trade-off between exploration and exploitation. The first, and perhaps most intuitive hypothesis to explain this trend, relates to the fact that exploring the environment in order to identify the most profitable food sources would be most adaptive in juveniles, rather than in individuals approaching the end of the their life cycle and, therefore, when future investments are unlikely to pay off (e.g. Eliassen et al., 2007). The second is that specific cognitive decline in the abilities supporting exploration results in the change of the ratio between exploration and exploitation in old age (Duzel et al., 2010). Studies have converged in showing that the tendency to search persistently within resource patches (exploitation) rather than changing patches (exploration) does tend to increase across the human lifespan. This tendency emerged, for instance, when young participants (in their twenties) were compared with older individuals (in their seventies) using computerised tasks simulating fishing. Participants were required to decide when they wanted to switch between fishing ponds, and older adults showed a tendency to stay in each pond for longer (Mata et al., 2009). Similar computerised tasks requiring participants (aged between 18 and 57 years) to search for treasure chests hidden in different domes revealed a correlation between the time spent in each dome and the age of participants (Louâpre, van Alphen & Pierre, 2010). A study (Schulz, Wu, Ruggeri, & Meder, 2019) comparing children of different age groups and adults in tasks requiring search amongst tiles within a matrix to reveal numeric rewards (eventually linked to monetary prizes) showed an increase in exploration between children and adults (9-11 years vs. 19-55 years), albeit not between the two ages tested in children (9-11 years vs. 7-9 years).

Despite the relatively robust evidence for changes in the ratio of exploration and exploitation with age, it would be important for future psychological investigations to determine its relationship with underlying cognitive abilities. Modelling approaches suggest that children select options characterised by a higher level of uncertainty, although they do not use generalisations of the outcome of previous searches to inform future searches as well as adults do. However, the cognitive underpinnings of these shifts still needs to be clarified (Schulz et al., 2019), and empirical insights are scant. The shift towards greater exploitation later in life has been examined by associating the tendency to explore with scores on other psychometric measures, but clear-cut differences in cognition that parallel the decrease in exploration in older people have not emerged consistently. For example Mata et al., (2013) did not find a relationship between the tendency to switch patches and individual differences in either fluid intelligence (taken as measure of underlying cognitive skills) or subjective value assigned to future explorations (taken as evidence for the perceived reduced benefits of exploration and related to the adaptive hypothesis mentioned above) in older adults.

Although more speculative, some evolutionary arguments provide insight into how changes in exploration/exploitation during the adult lifespan may be explained by both adaptive changes and cognitive decline. Within this framework, it has been proposed that the emergence of Alzheimer's disease (AD) could be related to different requirements of exploitation and exploration in foraging, and could also be considered in relation the expensive brain hypothesis of primate brain evolution. Reser (2009) notes that the cellular and metabolic changes that cause cognitive ageing, and eventually AD, start to occur relatively early in the lifespan. These changes mostly affect working memory, but leave procedural and semantic memory relatively spared. Reser (2009) argues that these changes are part of an adaptive metabolism reducing program (through tangle formation and cell loss). Whereas fluid skills and working memory would be necessary for detecting and learning environmental regularities, they would become less useful once these regularities have been learned later in the lifespan. At that stage, metabolically expensive brain processes would become a liability and thus mechanisms that reduce them may have been selected for. Those mechanisms did not have the capacity to become maladaptive when the human lifespan was shorter, but with increased modern life expectancies they lead to dementia. Naturally, these ideas may be difficult to test empirically, although they are not inconsistent with the age-related data discussed above. Moreover, they are also consistent with data showing an AD impairment in the ability to switch between sub-categories in semantic memory in a verbal fluency task (Raoux, Amieva et al. 2008). As such, a fundamental relationship is again drawn between human cognition and foraging in our ancestral environment.

VISUAL SEARCH AND BEYOND

Thus far, our discussion has focused mostly on relatively naturalistic assays of large-scale foraging, or foraging-like behaviour in semi-naturalistic and laboratory environments. This has been in order to draw a clear comparison between humans and non-human animals, and to ground our understanding of search behaviour in an evolutionarily-relevant context. However, the very great majority of our scientific knowledge of human search comes from decidedly (and intentionally) artificial assays of visual discrimination within small-scale displays. This has resulted in something of a chasm between fields, where our understanding of human foraging has perhaps lagged behind a more general characterisation of 'search' that is often assumed to subsume all exploratory tasks or contexts. Moreover, it is also arguable that the classic task from which this knowledge has sprung was not necessarily designed to characterise search behaviour in and of itself. Despite this idiosyncratic pedigree, however, laboratory studies of visual search have not only provided a constrained and controlled context within which we can carefully study very discrete components of function, but they also represent a fundamental platform from which scientists have been able to address a great variety of factors that play a role in exploratory behaviour. Of course, whether we can then comfortably tally such insights with those gleaned from more naturalistic contexts, or from other species, is a reassuringly complicated question.

The visual search paradigm

The visual search task has been a mainstay of human experimental psychology for over fifty years now. Its popularity as an empirical paradigm lies in its adaptability to a wide variety of perceptual and attentional questions, providing a platform to measure functions that range from basic stimulus detection and discrimination through to complex and high-cost image inspections by trained experts (for a superlative ‘retrospective’ of visual search see: Eckstein, 2011). The canonical version of the task requires participants to detect the presence (or absence) or a visually-defined target embedded within an array of non-target ‘distractor’ items. Manipulations of the size of the search array, the location and number of targets, and the similarities between target and distractor, then provide the standard tools to devise parametric assays of one’s function of choice.

Some of the earliest instantiations of the task were described by Neisser (1964), who investigated search time as a function of the relationship between targets and distractors, and by Estes and Taylor (1964), who varied set size to measure the limits of accurate detection and identification of briefly-presented information. However, the paradigm is perhaps most commonly associated with development of the Feature Integration Theory of attentional selection (Treisman & Gleade, 1980) and subsequent examinations, refinements, and refutations thereof (e.g. Bundesen, Habekost, & Kyllingsbaek, 2005; Duncan & Humphreys, 1990; Wolfe, 2007). This vein of research has given us some of the most enduring concepts of visual search, such as the apparent ease with which a visually distinctive item can be segmented from its distractors, irrespective of their number (e.g. single-feature or *simple* search), and the contrastingly effortful act of serially inspecting individual items in search of a target that shares perceptual features with its foils (conjunction or *difficult* search). Indeed, so compelling are these demonstrations that they have become lore in cognitive psychology, and are generally taken to represent fundamental features of human search behaviour. This is not only in spite of the fact that alternative theories have since been specified to re-describe these phenomena and their underpinnings, but it is also seemingly regardless of the exact underlying functions that the tasks were devised to measure in the first place.

This heterogeneity stems from the fact that search is a multifactorial construct, relying upon a synthesis of perceptual, attentional, control, and decision-making processes. As a mainstay of experimental psychology the visual search task has, therefore, been used to address such a broad range of factors that it is no mean feat to consider the field in its totality, let alone to expect a synthesis of empirical findings to result in a clear and comprehensive account of human search behaviour. Wolfe (2010), for example, observes that the very great majority of our understanding comes from observations of search operations that unfold within 1000ms, mostly representing a range of simple perceptually-based decisions made in laboratory contexts. Of course, this contrasts with the foraging-based search behaviours that we have already discussed in human and non-human animal species. Similarly, many naturalistic human search behaviours extend over multiple seconds, and that is before one looks beyond a purely ocular route to factor-in the body movements that may be required to bring potential targets into view. This, therefore, is the context within which the next phase of our discussion unfolds.

We will now consider some of the factors that have been shown to contribute to variability in visual search performance. Some of these sources of variation will be contextual in nature, and are based on the demands of the search task itself. Other sources of variation are in the characteristics of the individual performing the search, whether they are stable (such as one's working memory capacity) or related to a current states (such as one's present level of anxiety). Many of these observations are founded in the visual search task and are, therefore, associated with the aforementioned caveats. However, we will also address research that has formally addressed the domain-generality of search behaviour by observing behaviours in more naturalistic contexts.

Learning about the search space

The majority of tasks devised to assess search behaviour apply experimental controls in the same way as any other empirical assay of psychological process. Central to those controls is the notion of randomisation – i.e. in order to avoid extraneous confounds, trial order is randomised, as is the exact location of items in an array. Naturally, this will depend on the precise nature of the task, and the function being assessed, but scientists usually aim to remove any likelihood that participants might learn something about the experimental manipulations that then confounds the data collected. So, for example, the formative theoretical findings in the field (e.g. Duncan & Humphreys, 1989; Treisman & Gelade, 1980; Wolfe, Cave & Franzel, 1989) are based on the perceptual properties of targets and distractors, rather than any spatial or temporal characteristics. As such, whilst a participant might become a little more efficient at searching a display over time, one would not expect their data to reflect the influence of learning in any way.

However, we have seen that learning about the world is a fundamental influence on foraging-like search behaviour across many species, and other variants of the visual search task have been developed to specifically assess how search-relevant information might be accrued and exploited over the course of an experiment. For example, if the spatial location of the target is specified so that it is more likely to appear on one side of the array than the other, then participants begin to bias their search to that side, resulting in longer search times for items on the opposite side. This sensitivity to spatial statistics is known as probability cueing (e.g. Geng & Behrmann, 2002; 2005), and can be distinguished from the exploitation of sequential spatial dependencies that is observed when targets occupy the exact same location within a small number of trials (i.e. repetition priming: Kristjánsson & Campana, 2010; Walthew & Gilchrist, 2006). A similar learning effect is observed in the case of contextual cueing (Chun & Jiang, 1998), where an identical array is occasionally repeated over the course of many trials. Over time, participants become faster at reporting target features that are within these familiar contexts, even up to a week after initial exposure (Chun & Jiang, 2003).

What is striking about the cueing effects described here is that they seem to be implicit, in that participants do not report awareness of the manipulations when probed after the experiments. This has led theorists to suggest that they may not necessarily be top-down in origin. For example, Geng & Behrmann (2002) posit that the spatial probability cueing effect they observed lies at the level of the superior colliculus, and that sensitivity to environmental statistics is exerted in the facilitation of saccadic eye movements into the cued portion of the visual field. Naturally, characterising learning at the oculomotor level is difficult to reconcile with regional cueing by probability that occurs in human subsistence foraging (e.g. Kelly, 1995), or in the longer-term planning of foraging activities according to fruiting seasons, and this is a consideration that we will return to later. However, it is worthy of note that cueing effects are not always observed in visual search studies that have manipulated display statistics, which may be indicative of individual differences in either sensitivity to particular types of information, or in the cognitive strategies that searchers adopt when exploring visual displays.

Differences in search strategy

Lleras and von Mühlenen (2004) conducted a study where the experimental conditions of Chun and Jiang's (1998) study were faithfully recreated. However, they failed to observe the expected contextual cueing effect, suggesting that participants' attention was not being guided by repeated displays. Closer inspection of data revealed variability across individuals, with some participants consistently exhibiting the predicted positive cueing effect, some exhibiting no reliable cueing by repetition, and others consistently exhibiting a negative cueing effect (i.e. disadvantaging repeated displays). Post-experiment interviews confirmed that participants applied different strategies to the search task, with some taking an active strategy (i.e. performing a controlled and ordered search) and others adopting a passive strategy (i.e. allowing the target to 'appear' to them) – these latter participants were the ones that exhibited a positive contextual cueing effect. In a follow-up experiment, participants were specifically instructed to adopt one strategy or the other whilst searching. This confirmed their preceding observations, with 'passive' participants being twice as likely to exhibit the contextual cueing effect. As such, it seems that although an individual might be sensitive to salient information present in the display (in this case, on a spatio-temporal basis), the strategy they apply to searching may dictate whether or not they are able to make use of that information to improve performance.

Although this might seem to fly in the face of the associations between cognitive control and efficient foraging behaviours covered earlier, the effects of adopting a particular search strategy in this context can be understood further if one considers its oculomotor correlates. Watson et al. (2010) recorded eye movements during search, before which participants had been instructed to adopt either an active or a passive strategy. Commensurate with the data of Lleras and von Mühlenen (2004), behavioural data revealed a generally positive effect of a passive strategy on search efficiency – participants in this group demonstrated faster response times and shallower increases in latency with display size, compared to active searchers, although they also had a tendency to make more response errors. Eye movement data showed that passive search strategies were associated with a longer duration of the initial fixation, a smaller number of overall fixations, and a reduced likelihood of making any further fixations once the target had been apprehended. These data suggest that the effect of strategy on search efficiency lies not in the cognitive processing of visual information once it has been sampled, but in the sampling process itself. Active and passive strategies can, therefore, be (respectively) considered in terms of 'looking' and 'seeing', where the former strategy relies on a controlled and relatively effortful exploration of the visual scene, whereas the latter allows automatic processes to prioritise the allocation of attention. The notion that active looking depends upon executive processes has been supported by the demonstration that participants undertaking a concurrent task that occupied executive function became more efficient searchers (Smilek et al., 2006). We will return to this issue, and how it might apply differently to visual search and foraging, later in this review.

The properties of an individual observer's eye movements during visual exploration certainly seem to be consistent across different types of task (e.g. Castelhano & Henderson, 2008). It therefore seems useful to question whether inter-individual differences in search strategy represent stable characteristics, especially since they have the potential to exert a fundamental effect on behaviour. To address this question, Boot, Becic, and Kramer (2009) conducted a study where participants were required to perform a variety of search tasks. Two of those tasks would ideally favour a strategy with controlled focal attention to the target (i.e. an effortful search for a T amongst Ls, and a change blindness task using natural scenes), and two would not (i.e. a simple search for a tilted line amongst uniform distractors, and a dynamic dot detection task). They found that participants adopted a stable scanning strategy across all tasks – i.e. whilst they made fewer saccades in the simpler tasks, participants consistently adopted the same strategy, even when it led to slower and less accurate performance. To examine whether awareness of performance may exert an influence, Boot et al. (2009) administered the same battery of tasks but with both trial-level feedback and a monetary incentive to modify performance. Under these circumstances, participants did dynamically modify their strategies according to the demands of the task, so that they could optimise their performance. This, therefore, suggests that individuals may default to a particular strategy but are able to adopt alternative approaches to searching a scene when prompted by situational factors. This is supported by reports that default search strategies interact with the type of perceptual organisation encouraged by stimuli (Hogeboom & van Leeuwen, 1997).

The impact of experience

The origin of individual difference in search strategy might be traceable to differences in the neural structures underlying saccade generation, much like impairments of eye movement control in ageing (e.g. Butler, Zacks, & Henderson, 1999) or atypical development (e.g. Nigg et al., 2002). A similar link has, however, yet to be identified for typical search, although there does seem to be a role for personal experience in people's exploratory behaviour, suggesting that individual differences in strategy might emerge as a result of particular activities or situations that we typically engage in. Some of these differences appear to stem from behaviours that specifically tax our visual, motor, or cognitive systems, and perhaps more so than one might expect to happen in the natural world. So, for example, fruitful avenues of research have revealed how observers visually inspect natural scenes differently in relation to their expertise in, say, competitive sport (e.g. Abernethy & Russel, 1987; Ward, Williams, & Bennett, 2002; Williams & Davids, 1998) or when driving road vehicles (e.g. Chapman & Underwood, 1998; Crundall, Underwood, and Chapman, 1998; Underwood, Crundall, and Chapman, 1997).

Expertise-related differences in visual behaviours are considered to be associated with knowledge acquired about the particular context, and also with the associated cognitive load of performing the task in a dynamic context. However, there have been observations of experience in one domain seeming to incur general effects on search behaviour in other, more abstract, contexts. Castel, Pratt, and Drummond (2005), for instance, report effects of video game experience on search efficiency in a standard artificial laboratory search task. For their experienced group, they recruited people who played action-based video games at least four times a week, for a minimum of an hour a day, and had been doing so for at least six months. The comparison group played for less than one hour a month, and most had no experience at all. Participants were required to search for a target letter (b or d) within distractor letters – in an 'easy' search (see: Wolfe, 2007) the distractor letters were uniform (k), and in a 'hard' search they were variable (p, y, g, j, l, and h). The experienced group were faster to identify target letters in both conditions, and the researchers suggest that this might reflect a stronger stimulus-response mapping since experienced gamers are more used to making rapid responses to onscreen visual events. These findings support assertions (e.g. Green & Bavelier, 2003) that gaming experience is associated with more adept management of executive resources, as well as other demonstrations of additional spatial cognitive benefits (for a review see: Spence & Feng, 2010).

There are, however, caveats for between-group comparisons such as these, including questions about appropriate baseline measures (Boot, Blakely, & Simons, 2011). Moreover, although the effects of gaming appear to extend to search contexts that are not game-related, they still result from a comparison between experts and non-experts (e.g. the experienced group may be somewhat self-selecting, since people with poor visuospatial abilities might not gravitate towards playing video games). A more fundamental difference between groups has been observed in cross-cultural research, where variance in search performance appears not to be associated with expertise, per se, but with one's cultural experiences. Numerous studies of visual cognitive abilities have focused on thinking styles, where analytic thinking (commonly found in individualist cultures) has been thought to support a bias to local detail, whereas holistic thinking (associated with collectivist cultures) promotes a attention to the global structure of a scene. For example, Kuwabara and Smith (2012) found that American children were faster to locate objects in cluttered natural scenes than their Japanese counterparts, and Masuda and Nisbett (2006) found that American participants were faster to identify local changes to a scene (e.g. the colour of a vehicle) whereas East Asian participants were faster to identify contextual changes (e.g. the location of structural features). Such differences have also been observed at the oculomotor level, as in a study by Alotaibi, Underwood, and Smith (2017) that compared British and Saudi (respectively, individualist and collectivist cultures) in a comparative visual search task (i.e. participants were required to report the difference between two natural scenes, where one scene contained a small manipulation). They found that Saudi participants took longer to identify the target manipulation, and made more fixations before and after the target had been fixated, supporting an association between individualist culture and analytic perceptual style in the British participants.

The mechanisms underlying such a link are, however, unclear, and a recent reconceptualization of cross-cultural effects has implicated the physical environments associated with individualist and collectivist cultures, rather than the socio-political tenets of their societies. Linnell and Caparos (2020) review work conducted with the Himba (a remote society in Namibia, with a collectivist social structure) and have identified urbanisation as a large influencing factor on our attentional systems. For example, traditional Himba have been shown to demonstrate focused (i.e. analytic) spatial attention, whereas those that have relocated to a nearby urban settlement become defocused and more global in their engagement (Linnell, Caparos, de Fockert, & Davidoff, 2013). It has been posited that the clutter associated with urban environments promotes a more defocused perceptual strategy, and that urban environments in collectivist cultures tend to contain a greater proportion of high spatial frequency detail. Moreover, however, Linnell and Caparos (2020) suggest that arousal may mediate attentional state, and that higher levels of arousal associated with urban living (associated with behavioural demands) promote more exploratory (i.e. less focused) behaviour. This is thought to be linked to the locus coeruleus norepinephrine system (see: Aston-Jones & Cohen, 2005), which might perhaps provide us with that elusive neural basis for difference in search strategy. That said, it is unclear whether these empirical insights have yet included specific examinations of search behaviour itself. Interestingly, Shinar, McDowell, Rackoff, and Rockwell (1978) reported that field dependence (i.e. the relative tendency to favour local or global information) related both to laboratory visual search performance, and to performance in a driving task, which suggests a promising interrelation between factors that we will return to a little later when considering search performance in atypical populations.

Training search behaviours

Differential effects of individual experience upon search strategy and attentional allocation indicate the malleability of exploratory behaviour, and demonstrate that greater familiarity with a task or context might lead to more efficient behaviour. It is, therefore, no surprise that people have sought to develop specific interventions to improve search strategy, especially for individuals performing roles that rely upon efficient and accurate performance. A recent review by Kramer, Porfido, and Mitroff (2019) highlights the professional circumstances that require operatives to search small-scale and large-scale environments, in relation to the nature of the target (whether it is predictable, or can take variable forms), the nature of the environment (again, whether it is predictable or variable), and the technological changes in their field (whether there are frequent or infrequent changes to the apparatus supporting their role) (see Table 1). So, for example, a radiologist might be trained to detect known abnormalities within a very stable environment, whereas a checkpoint security operative is required to detect a wide variety of potential targets, and in variable situations. Both of these roles might be supported by rapidly-changing technological solutions (e.g. in scanning or image segmentation), whereas a pest controller is less likely to experience change to the facilities underpinning their task.

Table 1 Example professions that rely upon visual search abilities, along with estimations of variability in targets, search environment, and supporting technology (redrawn from Kramer et al., 2019).

Search Profession	**Examples**	**Target nature**	**Environment**	**Technology changes**
Checkpoint Security	Aviation, Border crossings, Building entrances	Highly variable	Variable	Frequent
Border Protection and Safety	Border crossing monitoring, Coast Guard search and rescue	Highly variable	Highly variable	Frequent
Medical Imaging	Radiology, Cytology, Pathology	Stable and Known	Stable	Frequent

Military searches	Checkpoints, Room clearing	Highly variable	Highly variable	Frequent
Product Inspection	Manufacturing plants, Product quality control check	Stable and Known	Stable	Frequent
Physical Inspection	Aircraft integrity	Stable and Known	Stable	Infrequent
Pest Control	Termite Inspection	Stable and Known	Stable	Infrequent
Lifeguarding	Pool/beach monitoring	Variable	Variable	Infrequent
Archaeology	Fossil discovery	Stable and Known	Variable	Infrequent

The training of search behaviour can be considered something that is approached either directly (i.e. one targets search strategy itself) or indirectly (i.e. improvements are a consequence of specific task-based training). These approaches are reviewed by Kramer et al. (2019), who identify three taxa of training format. The first, referred to as *knobology*, refers to specific training in the technology that supports search behaviour – this might be, for example, the X-ray apparatus used by aviation baggage screening staff. The benefit of this approach is that one can achieve a high level of performance with a relatively short amount of training, although it is unlikely to survive any changes to the context. The second training protocol, *object identification*, aims to provide the appropriate templates to expedite search, whether they are relatively constrained (e.g. malignant lesions in mammography) or unconstrained (e.g. offensive or contraband items in baggage screening). Similarly, this approach can have notable effects on search efficiency, although they are specific to the objects that are trained. Finally, *search strategy* is most often trained for situations where both target and context are unconstrained, such as safety inspection or lifeguard duty. Naturally, the payoff for strategy training is the most valuable, although it is the most complicated approach and presents with the most equivocal outcomes. Search strategy can be trained in a number of ways, such as identifying probable target locations, specifying a particular order of locations to fixate, or providing traces of an expert's search path to learn from. There is, however, no accepted gold standard of success, and whilst some protocols have been shown to reliably improve target localisation and target verification (both being important but separable components of search), others often find a trade-off between the two (e.g. the effort required to undertake a controlled search adversely affects decision making about target items).

Identification of the specific effects of training upon search behaviour provides an insight in the components of search that can be modulated by targeted intervention. For instance, a systematic review of eye tracking research in radiology, performed by Van der Gijp et al. (2017), presents different oculomotor features of search and shows how they seem to relate to diagnostic performance. Experts are generally found to spend less time inspecting images than novices, and this is associated with faster time to make the first fixation, a smaller number of overall fixations, and a greater number of fixations (of a longer duration) on areas of interest. These factors tended to interact with the nature of the task, so expertise is associated with shorter fixation durations on detection only tasks, and longer durations on detection and identification tasks, suggesting that attentional strategies are more sensitive to the matter in hand for trained individuals. Expert search patterns also seem to differ depending on both the task and context, so whilst inspection of a wrist and hand X-ray might follow a radial pattern of focal inspections, examination of a chest X-ray is characterised by more diffuse scanning, before focus on specific areas of interest. This strategic interplay between local and global levels is not seen in novices to the same degree, and whilst training of novices has been shown to improve the systematicity of search paths, and the coverage of the image, diagnostic performance is unaffected (Kok et al., 2016). This reinforces the existence of a complex interaction between knowledge and search.

Once again, it is worthwhile noting that these illustrations of the effects of training upon search are confined to specific real-world contexts. As such, it is interesting to consider whether training in an applied search context might transfer to more generic tasks. This was examined by Biggs and Mitroff (2014), who compared professional airport security officers to untrained participants in an effortful laboratory search task. Participants were required to detect the presence or absence of one or two T shapes, amongst distractor items formed of two orthogonal lines. Both targets and distractors were presented at different levels of perceptual salience (i.e. along a grey scale) on a grey cloud-like background. Contrary to what one might expect, professional searchers took longer to complete their searches than untrained participants, suggesting that effects of expertise on search time are indeed context-specific (for an example from orthodontics, see: Jackson, Clark, & Mitroff, 2013). Longer searches in experts were associated with a higher level of search diligence, with professionals being less likely to discontinue a search after having found the first target. This group were also just as likely to detect a low salience target first as they were a high salience target, suggesting that a more global search strategy preceded an analytic focus on target locations. These findings confirm those that that have been observed in real-world search contexts, and also suggest that effective search strategy (i.e. global to local) is not necessarily domain-specific.

Effects of functional strengths on search behaviours

Just as search can be modulated by training, it seems that natural differences in some domains can advantage search ability, without the strategic interference of curious scientists. An interaction of this kind is that between search and working memory capacity. This particular focus has its roots in the more general question of whether efficient visual search requires the involvement of memory to keep track of the locations that have been inspected. A low-level candidate was identified in the form of *inhibition of return* (see: Taylor & Klein, 1998), a mechanism that is thought to tag recently-visited items so that they are less likely to be re-inspected in the short-term. In contrast, it has been argued that visual search does not require this kind of memory, as exemplified by Horowitz and Wolfe’s (1998) demonstration that search within dynamic arrays (where targets and distractors changed location every 110ms) was no harder than within static arrays (for more on this particular debate see: Gilchrist & Harvey, 2000; Kristjánsson, 2000; Peterson et al., 2001). Links have also been drawn between search efficiency and higher-level working memory. For example, whilst Woodman, Vogel, & Luck (2001) reported that concurrent visual working memory load did not affect search slopes (i.e. the relationship between search time and set size), there was a consistent slowing of search time. Further exploration of dual task performance revealed reciprocal impairments of both efficiency and accuracy when search was performed at the same time as a spatial memory task (Woodman & Luck, 2004), and a slowing of search time that was proportional to spatial memory load (Emrich et al., 2010). It, therefore, seems that some components of search behaviour share common mechanisms with visuospatial working memory, and that the limited capacity of the latter might have implications for situations that tax both systems (see also: Emrich et al., 2009; Han & Kim, 2004; Luria & Vogel, 2011).

Working memory may not only contribute to keeping temporary records of inspected locations during a search – it has also been implicated in the maintenance of attentional templates, which describe the perceptual properties that distinguish targets from distractors. Such a role has been highlighted in studies that demonstrate interference between the specific contents of visual working memory and search efficiency. For example, Olivers, Meijer, and Theeuwes (2006) presented participants with a visual stimulus to be remembered (such as a particular shade of a colour), which was immediately followed by a search task. The search array was monochromatic, except for an irrelevant coloured distractor, and the interference produced by the distractor was always greatest when it shared the particular shade currently being held in memory. The same effects were not observed for items that were easier to encode in a verbal form (i.e. distinct colour names), supporting the argument that visual working memory and visual attention share common contents (see also: Bundesen et al., 2005; Olivers, 2009; Soto, Humphreys, & Heinke, 2006). Elegant electrophysiological evidence for this mechanism in action was provided by Carlisle, Arita, Pardo, and Woodman (2011), who illustrated the relationship between contralateral delay activity (CDA: an established event-related potential that correlates with object maintenance in visual working memory) and different types of search task. CDA was observed during search when participants were required to maintain a different template each trial, and not when the same template was required for all trials. Moreover, a drop in the amplitude of CDA in the latter task revealed the moment at which search became automated for participants. CDA was also shown to double in amplitude when participants were required to maintain two target templates at once, thus revealing a direct analogue for visual attentional load.

Given such an interrelation, it stands to reason that individuals with superior working memory abilities might exhibit certain benefits for search, especially since differences in working memory capacity (WMC) are thought to reflect variability in attentional control (Kane et al., 2001). This has, indeed, been evidenced in a number of studies, although the interactions between systems are perhaps a little more complex than immediately imagined. Whilst Kane et al. (2006) found no significant correlations between WMC (as measured by the complex span task) and search efficiency across a number of tasks, Poole and Kane (2009) found an advantage for higher WMC participants in tasks that required them to perform a restricted search amongst a subset of items, whilst ignoring items in other locations. This implicates a role for WMC in search that fundamentally requires top-down attentional control (in this case, a restricted attentional focus), rather than the prototypical visual search task. This is supported by Sobel et al. (2007), who found no relationship between WMC and stimulus-driven (i.e. bottom-up) search, but steeper search slopes for low WMC participants in search that required top-down suppression of bottom-up salience.

Findings such as these indicate that cognitive strengths might lend a hand to certain search tasks, thus providing a benefit to those individuals that possess them. In the case of WMC, we can see that the benefit is for specific forms of search task, and that the activity is, nevertheless, effortful (i.e. irrespective of WMC, increased load is associated with decrements to performance). In contrast, there might be some differences between individuals that incidentally benefit search, rather than necessarily sharing similar mechanisms. This has been explored for people with synaesthesia, a heterogeneous phenomenon that, for some individuals, combines sensory input from one modality with properties of another modality. So, for example, one person may consistently experience individual letters of the alphabet in particular colours (grapheme-colour synaesthesia), and another may experience certain sounds as tactile sensations on their body (auditory-tactile synaesthesia). The potential for this to affect functional components of perception was suggested by Ramachandran and Hubbard (2001) in their case report of two grapheme-colour synaesthetes who displayed a perceptual advantage that seemed indicative of their phenomenological experiences. Participants were presented with an array of achromatic graphemes for a brief period, where identical letters were arranged in a geometric form, on a random background of alternative letters. Whilst controls detected and reported the embedded shape with 59% accuracy, the participants with synaesthesia performed at 81%, suggesting that their idiosyncratic experiences of colour may have provided an additional cue that enabled faster grouping and pop-out of the global form. A relationship between synaesthesia and search efficiency was more specifically reported by Palmeri et al. (2002), who found that a synaesthetic individual produced shallower slopes in effortful search (in this case, for achromatic digits) than controls, which was directly related to target digits that were phenomenologically paired with a particular colour.

As enticing as these results appear, however, follow-up investigations have proved to be more equivocal. Rothen and Meier (2009), for example, were unable to replicate Ramachandran and Hubbard’s (2001) findings in a group study. Ward et al. (2010) refined the general account, on the basis that it should not be possible to experience synaesthetic colouration of an achromatic grapheme without first having sufficiently processed the letter itself in order for its associated colour to be experienced. Accordingly, they found no evidence for pop-out of embedded figures, but a superiority for synaesthetes that depended on the proportion of items that they reported as being perceived coloured, on a trial-by-trial basis. This suggests that phenomenological colour does not group and segment displays on a pre-attentive basis, but requires focal attention to provide a benefit to synaesthetes, and only at that particular locus. This account was supported by Rich & Karstoft (2013), who incorporated a set size manipulation and found no evidence for pre-attentive pop out in synaesthetes. They did, however, replicate the finding that synaethetes were more accurate in reporting the embedded figure, and suggested that colour might be used strategically as an additional cue, thus providing faster grouping. As such, it appears that synaesthesia can offer some advantages to individuals, but perhaps as a higher-level cue.

Synaesthesia is a relatively rare phenomenon, and it is not generally associated with overt functional strengths or weaknesses in other functions. In contrast, there have been demonstrations of superiority in the visual search performance of people with autism, which is striking in the context of a condition that is associated with relative impairments in a number of domains, including social communication (American Psychiatric Association, 2013), Theory of Mind (Baron-Cohen, 1989), and executive tasks such as planning and inhibition (Ozonoff et al., 1991). There are, however, numerous demonstrations of relative strengths across a variety of visuospatial tasks (for reviews see: Behrmann, Thomas, and Humphreys, 2006; Dakin & Frith, 2005; Simmons et al., 2009) that have, in turn, inspired theories of autism that are based on functional superiorities (Enhanced Perceptual Functioning: Mottron et al., 2013) or biases (Weak Central Coherence: Happé & Booth, 2008) in the visual perceptual domain (c.f. Smith & Milne, 2017). An autistic advantage in search performance was first implicated in the findings of Shah and Frith (1983), who reported that children with autism were reliably faster on the Embedded Figures Test (which requires localisation of a simple geometric shape embedded within a more complex image) than typically developing participants. This was more formally addressed in the context of visual search by Plaisted, O'Riordan, and Baron-Cohen (1998), who found that children with autism were faster to detect targets in an effortful conjunction search than typically developing controls. This result has been confirmed with more appropriately-matched control participants (O'Riordan, Plaisted, Driver, & Baron-Cohen, 2001), with more perceptually complex search items (Jarrold, Gilchrist, & Bender, 2005), and in adult participants (O'Riordan, 2004).

Empirical findings, therefore, provide a generally consistent picture of superior performance in autism for target detection in the context of effortful serial search. The basis of this advantage, however, is perhaps a little less formalised at present. Plaisted et al. (1998) suggested that people with autism possess enhanced perceptual discrimination (see also: Joseph et al., 2009), an account that shares conceptual features with the Enhanced Perceptual Functioning theory of autism (Mottron et al., 2013). However, the theory itself does not elaborate on the processes that support search behaviour per se, nor do alternative theories of perceptual differences in autism (Happé & Booth, 2008; Pellicano & Burr, 2012). Moreover, an examination of performance on search and psychophysical discrimination tasks (Brock, Xu, & Brooks, 2011) reported no correlation in adults with high levels of autistic traits (despite superior search performance compared to adults with low traits). This has led other theorists to propose more attentionally-based accounts – for example Kaldy, Giserman, Carter, & Blaser (2016) argue that the tendency to over-focus on tasks, at the cost of task disengagement, might support efficient search behaviour, whilst also incurring some relative difficulties in other domains.

Deficits in search behaviour

Visuospatial behaviours in autism have attracted a lot of theoretical interest because they reflect the presence of particular strengths in the context of a condition that is otherwise typified by relative impairment (at least in the context of formal diagnosis: American Psychiatric Association, 2013). This is, however, singularly unusual in the study of search behaviour in atypical populations, and exploratory behaviour is usually used as an assay of functional deficit associated with particular neurological, genetic, or psychiatric conditions. For example, Wilkinson & McIlvane (2013) compared children with autism and children with Down syndrome (matched on both verbal and performance IQ) on a search task that required them to locate a previously-presented object within a four-by-four array of different objects. In one condition, objects that shared the same colour were clustered into quadrants, and in another all objects were randomly distributed within the array. Both groups displayed search time and accuracy benefits for the clustered condition, although children with Down syndrome were significantly slower and less accurate than their autistic counterparts in both conditions. These findings support the account of a relative superiority for search in autism, and also demonstrate a benefit for searching organised arrays that applies across populations. However, in the absence of a control group, or more detailed measures, it is difficult to identify the functional differences that might describe the two populations.

A more detailed assay of search behaviour in developmental disorders was reported by Scerif et al. (2004), who compared performance in toddlers with Williams syndrome and toddlers with Fragile X syndrome – like Down syndrome (but unlike our current knowledge of autism), these are conditions with a clearly-identifiable and clinically-diagnosable genetic basis. Participants performed a multi-target search upon a touchscreen, and were required to activate only the large circles, amongst an array of circles of differing size, to locate their hidden quarry (i.e. monsters that revealed themselves upon touching of the circle). On some measures, participants from each of these populations were found to perform similarly to controls, exhibiting similar search speeds and paths. However, there were some specific indices of impairment that dissociated the two groups. Participants with Williams syndrome confused targets with distractors more than any other group, making more false alarms especially when display sizes were large and when distractors were more similar to targets. In contrast, participants with Fragile X syndrome made many more reactivations of targets, even though the monsters that had previously been discovered remained visible. These findings therefore point towards clear differences in search behaviour that help to identify the correlates of particular genetic profiles. In the case of Williams syndrome, participants demonstrated difficulties distinguishing targets and distractors that tally with other reports of differences in perceptual judgement (e.g. Porter & Coltheart, 2006). On the other hand, participants with Fragile X syndrome exhibited a higher-level executive deficit of inhibiting perseverative responses, which corresponds with other reports of atypical attentional control (e.g. Wilding, Cornish, & Munir, 2002). Importantly, both of the profiles are also commensurate with adult functioning in these respective conditions.

Studying search behaviour in developmental conditions provides an insight into cognitive systems that have developed atypically from the outset, whether one is studying children or adults (Karmiloff-Smith, 1998). This contrasts somewhat with the more frequent application of search tasks as a means to understand the impact of atypical circumstances on a system that is, up until a given point, presumed to function typically. A clear example of this is in the case of neurological damage that results from, say cerebrovascular accident or head injury. In this context, search tasks can provide insights into the abilities that have been impaired and also afford the construction of theories that account for functional substrates of behaviour in intact and damaged brains. A good case in point is in the examination of search in patients with hemispatial neglect, which can be broadly defined as an impairment in responding to stimuli on one side of space (usually the left, following damage to right-hemisphere structures). Eglin, Robertson and Knight (1989), found that neglect patients searched both feature and conjunction displays in a serial manner, and behaviour was equivalent when stimuli were restricted to either the left or right side of the display. However, when stimuli appeared on both sides there was a clear laterality effect – detection of targets in the intact side was unaffected by distractors in the neglected side, whereas detection of targets in the neglected side was slowed by the presence of distractors on the intact side. This was more pronounced for demanding search arrays, as well as when there was a larger set size in the intact field. Such findings suggest not only a disruption of parallel (or efficient) search across the visual field in neglect, but also a deficit in shifting attention into the neglected field in the presence of competing objects in the intact field (c.f. Grabowecky, Robertson, & Treisman, 1993).

This relationship between attentional deficit and visual exploration was refined by Behrmann, Watt, Black, and Barton (1997), who recorded patients' eye movements whilst they searched for all instances of a target letter within a large random array of different letters. Searches were found to begin in the intact field, on the basis of initial fixations. There were significantly fewer fixations in the neglected side of the array, and they were also of a shorter duration than fixations in the intact field.

The data supported the notion of an attentional gradient, with exploration being less likely to be directed to regions further into the neglected field, along with a subjective shift of the midline into the intact field. Moreover, they demonstrate the additional insights that eye movements can provide in neuropsychological analyses. Accordingly, very similar methods and stimuli were also employed by Rösler et al. (2000) to address atypical search behaviour in Alzheimer's disease. They found a greater number of fixations in the patient group, compared to older adult and young adult controls, and also observed that fixations were of a much longer duration. These findings are indicative of an attentional deficit in the disease that may affect disengagement from one item, or initiation of an attentional shift to another. The authors also explore the idea that impaired perceptual decision making processes, along with a reduction in the size of the Useful Field of View (i.e. the amount of surrounding information perceived during a fixation: Duchek et al., 1997) may account for the lengthening of fixation durations and a general disorganisation of search strategy (see also: Tales et al., 2004).

Impairments such as these have also been observed in neuropsychiatric conditions with more circumscribed neurological or behavioural features. Fuller et al. (2006) found that schizophrenia was associated with greater search slopes than those observed in controls, both proportionally and in absolute terms, with average search times being up to 88% larger. A subsequent report from the same group (Gold et al., 2007) identified a relatively typical profile of efficiency for simple search, but significantly greater slopes in search requiring top-down control, suggesting unimpaired implementation of selection but a particular impairment of attentional control. Like neglect, this may also be exacerbated by a reduced Useful Field of View, since Elahipanah, Christensen, and Reingold (2010) found search efficiency to be inversely proportional to the eccentricity of the target. Relative difficulties with effortful search are mirrored in studies of individuals with depression, and Hammar, Lund, & Hugdahl (2003) report increased search times for conjunction targets, relative to control participants, in the presence of comparable performance in single feature search. Similar findings have been reported in patients with late life depression (Potter, Madden, Costello, & Steffens, 2013), consolidating a general impression that search impairments in clinical or neuropsychological cohorts are most likely to be apparent in effortful contexts that require greater attentional control. That said, it is noteworthy that Parkinson's disease (PD) appears to be associated with relative impairments of single feature search, compared to conjunction search, which might indicate a more low-level deficit of basic saliency processing, perhaps related to dopaminergic abnormalities (Mannan, Hodgson, Husain, Kennard, 2008).

Studies with patients with PD can also help highlight important relationships between eye movements and working memory performance. Hodgson et al (2018) recorded eye movements in people with PD and in controls during the execution of a variation of a working memory task. Participants were required to search for reward tokens among identical square icons presented in different spatial locations on a monitor. The icons represented boxes where tokens could be found and collected by mouse-clicking them (i.e. when a box was mouse-clicked, the content was revealed). Participants were instructed that only one token could be present at any time in the search space and, importantly, that boxes that had contained a reward could not be rewarded again in subsequent displays (searches) until all rewards were found. Thus, participants needed to keep track of where rewards were found in previous searches to avoid within search errors (WSE), and also to avoid revisiting previously rewarded locations in new searches to avoid between search errors (BSE). Results revealed a correlation in control participants between fixations to locations which had previously been found to contain a reward in a simple version of the task (with fewer locations to search) and the ability to avoid BSE in a more difficult version of the task (with more locations to search). The same correlation was absent in patients with PD, who also showed more WSE as well as BSE compared to controls in the difficult version of the task. The overall pattern of results was taken to indicate the following: first, that eye movements can be used a strategy for refreshing fading memories of items that have to be held in working memory across searches; and, second, that differences in strategy, more than working memory differences, may explain variations between PD and controls. By contrast differences in WM may be more likely to explain individual differences among control participants.

State-dependent differences in search

Variability in search associated with neurological, genetic, or psychiatric atypicality might be considered a relatively stable characteristic of a population. Indeed, Potter et al. (2013) found that inefficiencies in conjunction searches persisted even after other clinical symptoms of late life depression had declined. There are, however, relatively acute state-dependent changes to typical search performance that affect many individuals. These changes can correspond to perturbations in affect, although they might also be related to the psychoactive properties of ingested substances.

The relationship between effortful search and clinical levels of depression seems intuitively predictive of a more general relationship between affective states and cognitive operations that require greater control. In the context of typical healthy individuals, relevant research seems to have mostly focused on the effects of stress on search performance – this resides within a more general scientific interest in cognitive function under pressured circumstances, and search is often used as a visuospatial measure to test the predictions of theories that posit specific relationships between anxiety and processing resources (e.g. Eysenck & Calvo, 1992). Laborde, Lautenbach, and Allen (2015) induced stress in participants (by informing them that their performance would be competitively judged and published publicly) and required them to search a 10 x 10 grid of numbers so that they could then click on as many consecutive examples as possible within a two-minute period. Stress was associated with poorer performance, although this was unrelated to concurrent measures of heart rate variability. Stress induction procedures have also been found to result in inefficient anticipatory search behaviour in soccer players monitoring sporting footage (Vater, Roca, & Williams, 2016), and a greater number of fixations in table tennis players during competition (Williams, Vickers, Rodrigues, & Hillis, 2000). Although heterogeneous in their methods and focus, studies in this area, therefore, provide a general illustration of the deleterious effects of stress.

The perception of threat, or feelings of panic, have also been shown to affect search efficiency although, rather than showing a decrement in performance, participants can instead demonstrate benefits to their search behaviour. Becker (2009) required participants to detect the presence or absence of a house, amongst pictorial stimuli arranged in a circle. Preceding each array was an emotional face at fixation (fearful, happy, or neutral), and participants were found to be selectively more efficient in the threat-related trials, regardless of the fact that the object of their search was itself neutral. This benefit seems to align with other demonstrations that threat-related stimuli are often detected more efficiently than other items. For example, Eastwood, Smilek, and Merikle (2001) found that search for negatively-valenced faces produced shallower slopes than search for positive faces (an effect that was abolished when stimuli were inverted). Similarly, Öhman, Flykt, and Esteves (2001) found that participants were significantly faster at locating threat-related stimuli (e.g. a snake) within an array of non-threatening distractors (e.g. flowers) than they were at locating non-threatening targets within an array of threatening distractors. Results such as these have been interpreted in the context of an early-warning system, mediated by the amygdala, that preattentively evaluates stimuli for instances of threat and rapidly directs attention to items that sound the alarm (see: LeDoux, 2000). These findings are, however, not without controversy, and more recent studies have sought to clarify a variety of factors, including the contribution of low-level image salience to some observed effects, and whether apparent pop-out of emotional stimuli is actually better described as an incremental serial process (for examples of review articles see: Brosch, Pourtois, & Sander, 2010; Van Bockstaele et al., 2014).

Exogenous effects on behaviour can also come in the form of psychoactive substances ingested by individuals. In small amounts, the effects appear to be negligible – for example, Lamers and Ramaekers (2001) report that neither low doses of alcohol nor marijuana affected visual exploration of scenes during a real-world driving test, and a combination of both substances only reduced the occurrence of search behaviours by 3%. In a laboratory setting, however, Abroms & Fillmore (2004) found that both lower and higher doses of alcohol reduced the duration of inhibition of return effects, suggesting that ingestion of the substance has identifiable effects on mechanisms that might affect search efficiency. This contrasts with the effects of d-amphetamine, which appears to extend the duration of inhibition of return, thus showing a potential to enhance efficiency (Fillmore, Rush, & Abroms, 2005). Other benefits have been reported after the more workaday ingestion of caffeine, with a report by Lorist, Snel, Kok, & Mulder (1996) finding evidence for enhancement of search times in low load (2 item) displays, but no enhancement for higher load (4 item) displays. Caffeine has also been found to improve performance in cancellation search tasks (Marsden & Leach, 2000), although this was nullified by concurrent ingestion of alcohol (which, alone, was found to impair performance). In addition, MDMA ingestion in an in-field (the field being a nightclub) study of individuals taking Ecstacy, revealed deleterious effects of the substance on both simple and effortful searches performed using a hand-held device (Parrott & Lasky, 1998).

Revisiting differences across the lifespan

Many sources of variability covered thus far might be considered to differentiate *between* individuals (i.e. one may or may not work in airport security, have Alzheimer's disease, or drink coffee). However, if we successfully negotiate the average human lifespan then there are effects of development and ageing that operate *within* the individual. We have already discussed some of these differences in the context of foraging, with especial reference to the use of environmental structure and the trade-off between exploration and exploitation. However, studies of visual search across the lifespan have focused more specifically on related changes in the control of attention. The initial stages of this journey have received less attention than the later stages, but studies of visual search behaviours in infancy and childhood tend to reveal some basic distinctions that we observe in adults. Gerhardstein and Rovee-Collier (2002) trained infants and young children aged between 1-3 years to touch a screen when they had located an image resembling a popular children's character, embedded in an array of distractor characters – distractors differed either by a single feature or a conjunction of features. Search profiles of all participants resembled those that we would expect from adults, with flat search time slopes for single feature searches, and slopes that rose in proportion to increased display sizes in conjunction searches. That said, there appears to be a clear developmental trajectory for conjunction search, with reports that children's search slopes are steeper than those of adults (Thompson & Massaro, 1989; Trick & Enns, 1998). These findings are taken as evidence for a maturation of attentional control mechanisms, with the emergence of adult-like shifting and engagement at 7 years, and adult-like disengagement at 9 years (Lété & Ducrot, 2013).

The validity of using traditional visual search tasks to test children was called in to question by Brennan et al. (2017), who found adult-like conjunction slopes in children when they were searching for a stimulus that they were more motivated to find. To further address the potential impact of task engagement, de Liaño, Quirós-Godoy, Pérez-Hernández, and Wolfe (2020) employed a more game-like search paradigm, where children were required to search for a pre-specified target item (a piece of 'treasure') by activating it on a touchscreen. Participants searched for different items on each trial, within different set sizes, and the task finished when they had found all of the stolen treasure, thus adding a competitive element to the endeavour. Compared to young adults, 4 year old children were less accurate (i.e. being more likely to report a target absent when it was, in fact, present), slower (i.e. a higher intercept), and less efficient (i.e. a steeper search time x display size slope). When data were normalised to represent distance from 'ideal' adult-like performance, participants were found to reach peak accuracy at about 9 years, but slope and intercept were not equivalent until around 14 years. These data support the view that effortful search is underpinned by different executive mechanisms, which mature at different rates.

Just as search behaviour develops in children until it reaches adult-like levels, there are concomitant decrements in performance that are associated with older-adulthood, as evidenced by studies that have explicitly recruited 'lifespan' cohorts that straddle these age groups (e.g. Hommel, Li, and Li, 2004; Trick and Enns, 1998). Such reports have illustrated a relatively U-shaped pattern of performance, although the rise and fall of search efficiency does not necessarily appear to be a result of mirror-like variability in behaviour for young and old. Hommel et al. (2004), for example, found that older adults were generally more cautious, with extended search times on target absent trials, and were also more adversely affected by larger display sizes, with smaller target-present to target-absent slope ratios (1:1.5) that were indicative of them not actively scanning all locations. Foster, Behrmann, and Stuss (1995) report similar findings, with a clear differentiation between comparable performance between younger and older adults on single-features searches, and a clear older-adult decrement in conjunction search. In particular, they highlight greater variability in performance across trials, and poorer performance for more eccentric targets. Together, these findings make a similar argument for robust feature extraction processes that are protected from ageing, but age-related impairment in more demanding tasks that require attentional control.

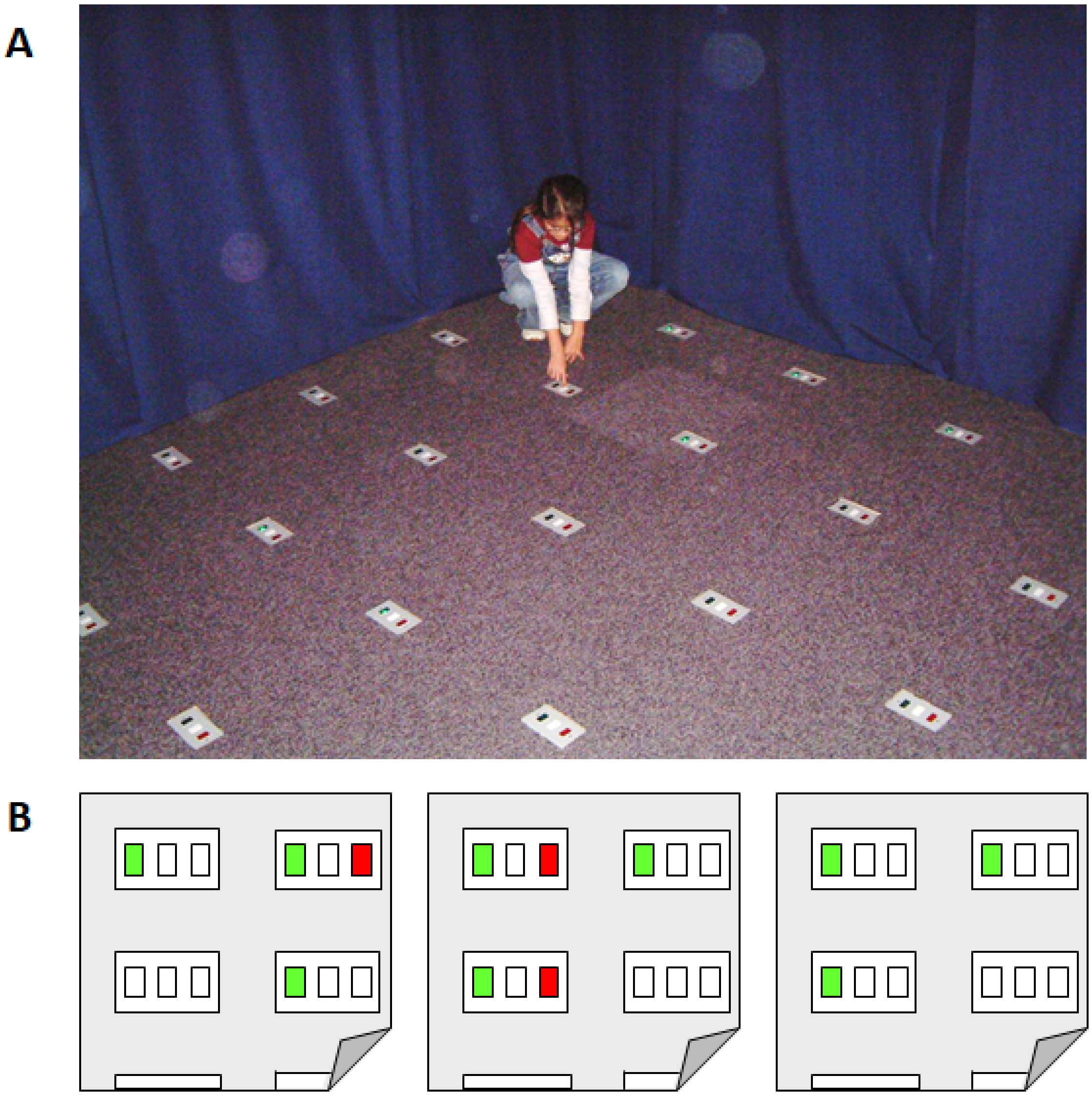
The picture is, however, not necessarily one of inexorable impairment. Clancy and Hoyer (1994), for example, found that medical technologists did not exhibit age-related decline in search for items within their area of expertise (i.e. bacterial morphology), although they did with standard search for letter stimuli. These data therefore suggest that experience can attenuate the effects of age, and that those effects might not be uniformly deleterious to all search contexts. Interestingly, this mirrors the aforementioned argument proposed by Reser (2009), which postulated an adaptive basis for cognitive decline on the mitigating presence of crystallised knowledge, which becomes dysfunctional only with extended modern lifespans. There is also evidence for a strategic processing shift in older adulthood that might be applied to maintain a good level of functioning. Allen and Payne (2012) compared younger and older adult performance on a preview search task, where a subset of distractors was presented before the rest of the array – this manipulation is generally found to benefit performance, enabling participants to ignore the previewed stimuli and only search the remaining subset (Watson and Humphreys, 1997). The authors report comparable behavioural performance between groups, but little overlap in its neural correlates, with a greater involvement of frontal structures in the older adults. They argue that this indicates a compensatory mechanism applied by older adults, with a recruitment of working memory resources being necessary to maintain a similar level of performance to younger participants. Observations such as these serve to highlight that whilst behavioural properties of search may fail to distinguish between individuals or tasks, the processes underling it, or the instantiation thereof, may be somewhat different.

Linking visual search to foraging

The visual search task has long been considered to represent a simple and controlled context from which we can test predictions about search behaviour in general (Wolfe, 1994). Naturally, this thinking lies at the root of most laboratory assays of psychological function, and is evident not only in the introductory preambles to many discussions of the subject (i.e. we are seeking to understand the everyday processes that facilitate finding faces in crowds and lost house keys), but also in explicit arguments that *visual* search mechanisms are equivalent to those employed in larger-scale contexts (e.g. inhibition of return as a “foraging facilitator”: Klein & MacInnes, 1999). Associated with a recent update to the Guided Search theory that emphasises foraging-like properties of visual search (Wolfe Wolfe, Cain, Ehinger, & Drew, 2015), a strand of studies has explicitly sought to draw direct parallels between two-dimensional search in the laboratory and core properties of subsistence foraging that were discussed in earlier sections of this review. For example, Wolfe (2013) had participants complete a 'berry picking' task, where they used a mouse to navigate between different patches and then click on individual stimuli to harvest as many as possible within ten minutes (feedback was provided as to whether each berry was good or bad, and points were awarded accordingly). Across a number of different manipulations, Marginal Value Theorem provided a very good description of exploitation/exploration decisions – i.e. exploitation occurred until the instantaneous rate of return reached the average rate of return, whereupon participants moved to a new patch. Only when visual cues were degraded, or when the quality of berries was more variable, did MVT cease to account for behaviour. Similar 'foraging search hybrid' studies have enriched the account, revealing similar behaviour when participants search satellite images for specific buildings (Ehinger & Wolfe, 2016) along with a clear role for target value (Wolfe, Cain, & Alaoui-Soce, 2018), where increased value is associated with increased likelihood of exploration decisions, in pursuit of high-value targets, and a greater degree of individual difference in search strategy.

This line of research has made an important contribution to the creation of some parity when comparing visual search to foraging, especially with regards to factors such as the value of targets and their distribution. There have, however, been relatively few direct comparisons between two-dimensional visual search and search in other spatial contexts, such as large-scale three-dimensional environments. Indeed, one might consider such comparison the missing link between the cross-species comparisons discussed earlier in this article and more traditional laboratory studies of human search behaviour. Perhaps the first attempt to assess whether the hallmarks of visual search might be present in a fully-motile foraging-like task was that reported by Gilchrist, North & Hood (2001), who laid out a 3m x 3m array of locations for participants to physically search. The array comprised a variable number of 35mm film canisters, and on 50% of trials a marble was contained within one of them. This required participants to visit each search location and shake the canister, in order to discern the presence or absence of the target. The authors found that there was a target-present to target-absent slope ratio of 1:2, supporting a serial self-terminating interpretation of search behaviour, akin to the sort that typifies visual search for a conjunction target. They did, however, find that reinspection rates were lower than those that have been observed in eye tracking studies of difficult visual search, and argued that the increased effort required to search the array likely resulted in greater role for memory (i.e. tagging visited locations) and the adoption of search strategy.

A more direct comparison between visual search and foraging-like search was reported by Smith, Hood, and Gilchrist (2008), who used a novel electronic apparatus to display search arrays on the floor of a 4m x 4m laboratory. Participants completed a simple feature-present search (distractors were green lights and the target was green and red), a more difficult feature-absent search (distractors were green and red lights and the target was green), and a foraging-like search where all locations were green and the target location was revealed upon physical inspection (Figure 5). A target was present in all conditions, and participants were required to walk to it and activate an adjacent switch (except for the foraging condition, where they activated every illuminated location until finding the target). The ‘visual search’ conditions mirrored what one would expect to see in a 2D equivalent on a monitor, with a flat function for simple search and a sloped relationship between search time and array size for difficult search. The foraging condition yielded much longer search times, rising with display size, and there were very few reinspections. Such findings are, perhaps, not particularly surprising, but they extend the properties of visually-guided search to large-scale 3D space, and draw a distinction between that and the non-visually-guided search that might form a component of naturalistic foraging behaviour.



Feature present: red target amongst green distractors

Feature absent: green target amongst red and green distractors

Foraging: possible locations are green; target red when activated

Figure 5 Illustration of the laboratory space described by Smith et al. (2008) (A), and the different search conditions specified by illumination of a subset of search locations. (B).

As we have seen in ethological studies, however, real-world foraging behaviour relies on more than simply inspecting a collection of locations until a target is acquired. There may be visual cues that guide behaviour (although they might not be stable over time), one might not be able to perceive all potential locations from a single vantage point, search itself might unfold over a relatively long period of time, and the entire endeavour may be informed by past experiences of success and failure. Attempting to draw parity is, therefore, quite the puzzle, although some studies have begun to address simple components. For instance, the impact of spatial statistics gleaned from previous searches has been addressed in the context of large-scale probability cueing. Smith, Hood, and Gilchrist (2010) found that participants were sensitive to a cue that favoured one side of a large-scale search array on the laboratory floor, indicating that visual search and foraging-like search might both be informed by statistical learning. However, when the starting position for the search was manipulated so that participants approached the array from one end of the mid-sagittal axis or the other then participants did not learn about the contingency. Whilst this suggests that probability cueing may not inform all forms of foraging-like search, especially that which does not begin each foray from the exact same viewpoint, subsequent research from Jiang, Won, Swallow, and Mussack, (2014) found that visual apprehension of a target (a coin) within a large-scale naturalistic environment (an outdoor section of University campus) was supported by environmentally-based probability cueing, irrespective of the participant’s location. These differences perhaps highlight the impact of task and testing environment on the conclusions we are likely to draw. The same might be said for conclusions about individual differences, since Pellicano et al. (2011) found that a replication of Smith et al.’s (2010) probability cueing paradigm did not reveal the predicted search strengths in children with autism, but instead demonstrated the presence of unsystematic and suboptimal search paths, and a greater likelihood of reinspections (compared to typically developing children).

With these caveats in mind, it may be most appropriate to throw off the shackles of traditional search tasks altogether and embrace something a little more ecologically valid when it comes to assessing exploratory behaviour in different spaces. That ecological validity might perhaps come in two forms – i.e. closer to the evolutionary bases of search behaviour, or closer to our present-day experiences. An example of the former comes from studies reported by De Lillo and colleagues (De Lillo, Kirby, & James, 2014; De Lillo, Kirby, & Poole, 2016) that have studied the impact of environmental structure on search strategy and spatial memory. These were discussed in an earlier section, and provide a paradigm that affords direct comparisons between individuals, contexts, and even species. An example of an ecologically valid approach that is relevant to contemporary real-world search comes from Foulsham, Chapman, Nasiopoulos, & Kingstone (2014) who used mobile eye tracking apparatus to record real-world search for a named pigeon hole in a University mail room. They varied both bottom-up saliency of the target (a surround to distinguish the target pigeon hole) and top-down strategy (informing participants of the additional visual cue), and found that target conspicuity alone had little effect on search efficiency, although top-down knowledge of target appearance greatly reduced search time and effort. Both of these demonstrations again reveal that whilst behaviours might vary greatly between search behaviours in different spaces, they might still be subject to similar influences, and controlled in similar ways (see also: Kerster, Rhodes, & Kello, 2016).

CONCLUSIONS AND REMAINING QUESTIONS

This review has covered a disarmingly vast range of issues that span the evolution of the human mind, from foraging in our frugivorous primate ancestors to the inspection of medical images in oncologists. Such breadth can be attractive in some contexts, but the scientist is naturally suspicious of accounts that claim to find commonality across disparate contexts. Here, however, it is fully appropriate that we draw from such a deep well, since the literature does indeed abound with some grand claims about human search behaviour and its relation to psychological function. Indeed, some of the theories we have touched upon argue that demands associated with foraging in the ancestral environment have formed the very basis of human cognitive development (Kaplan et al., 2000), cognitive control (Hills et al., 2010), and cognitive decline (Reser, 2009). Perhaps at a more constrained level, psychologists characterising visual search have made arguments for the presence of domain-general processes that are shared with search in other contexts, including foraging (e.g. Klein & MacInnes, 1999; Wolfe, 1994). In this review, we have considered the examination of variability as key to making some headway in these questions, and it is certainly apparent that a consideration of differences in search behaviour (across species, tasks, and contexts) has revealed a strikingly similar set of factors.

We began this review with some key concepts derived from behavioural ecology to highlight the generality of search processes, across species and domains. These include a variety of random walks, and models, which allegedly do not require memory or cognitive control. We then reviewed studies highlighting the role of cognitive control in foraging decisions conforming to the MVT and the arguments that have been put forward for identifying the origin of these control processes in dopaminergic systems that are present in all metazoan organisms (vertebrate and invertebrates). Research was then described that shows the emergence of clear differences between humans, other primates and rodents in tasks where the spatial structure of the search space was systematically manipulated. On the basis of the studies considered, we emphasised the need to consider behavioural variations in search occurring when the structure of the environment and the serial paths taken to explore it are varied. When this is not done, one could be led to the false conclusion that the cognitive mechanisms underpinning search are the same across phyla, or that we can fully understand search and foraging processes without reference to the psychological processes that mediate them.

The primate prefrontal cortex is rich in dopaminergic fibres that may well be homologous to more archaic dopaminergic systems. As we have seen, much empirical research and theoretical reasoning has converged on the role of dopaminergic systems in helping organisms decide when to switch from exploitation to exploration, and it is been shown that the human prefrontal cortex plays a key role in this type of decision making (Kolling et al, 2012). However, we argue that another pivotal role of advanced prefrontal functions is to help us apprehend the structure of the environment and organise effective search patterns through it. The interplay between these two key aspects of foraging (i.e. when to switch between exploration and exploitation search modes, and how to organise search as a function of the structure of the search space) can help us characterise variations in search behaviour and the cognitive factors underpinning them. We have seen that cognitive development in children leads to enhanced ability to benefit from the structure of the environment that needs to be searched. Functionally these abilities may be related to the need early in life to learn the structure of one's own habitat and devise strategies to best exploit it. This ability may also be related to the ability to detect global properties of visual patterns, which also seems to develop well into adolescence. By contrast, changes later in life seem to relate more to the switch towards more exploitative strategies. The extent to which this is due to a decline in the abilities that sustain effective exploration still remains to be investigated in detail.

In contrast to cross-species assays of foraging behaviour, our overview of behavioural difference in the visual search literature revealed a great many potential sources of variability in exploration. Whilst some of these factors were similar to those identified in foraging, such as change across the lifespan or the exploitation of structural properties of the search space, others seem a world away. For example, we addressed how specific training might improve search performance, as well as how more general differences in (ostensibly unrelated) life experiences might also affect behaviour. We have also seen that search might differ between individuals on the basis of functional atypicalities (e.g. clinical, developmental, and neuropsychological conditions), as well as within individuals on the basis of psychological or psychopharmacological state. The variety of concepts, their general specificity to humans, and the restriction of these insights to two-dimensional monitor-based search for a unique target, might lead one to question how relevant they might be to the general conclusions that we are drawing here. However, it seems that control of search might be the factor that unites many of these illustrations of variability in visual search, as well as in spatial search and foraging. As with assays of foraging, it is the emergence and decline of controlled processes that typifies lifespan changes in visual search. Moreover differences in visual search behaviour that associated with atypical development and pathological ageing generally seem to converge on difficulty with tasks that require more effort and greater control.

A core question is, therefore, whether these additional insights enable us to characterise the concept of control within search with any greater specificity. Earlier in this review, we focused on the general positive relationship between the volume of prefrontal cortices and the level of executive function. That said, executive control is notoriously difficult to define, since the term has historically been used in a variety of ways (see: Posner & DiGirolamo, 1998). One can take a representative model, such as that of Norman and Shallice (1986), and apply it to search and foraging behaviour. So, for example, contention scheduling can use appropriate schemata to coordinate simple or well-learned search behaviours, which remain active until the target is achieved or resources from multiple locations have been collected (two facets of the same problem of having to efficiently explore the search space). In contrast, when the search context is novel, complex, or competitive, executive control is affected through the supervisory attentional system, which has access to an overview of the situation and the goals of the individual, and assists through inhibiting some schemata and further activating others.

This type of explanation is not always adopted by scientists that study visual search, who tend to favour a lower-level of description – for example, we have seen that superiority in effortful searches that are associated with autism have been attributed to enhanced perceptual discrimination (i.e. differences in the function and connectivity of primary visual cortex) rather than attentional control (see: Mottron et al., 2013; Plaisted et al., 1998). However, other accounts of visual search behaviour formally include the concepts of bottom-up and top-down guidance, which one might readily map on to the respective operation of contention scheduling and the supervisory attentional system. Moreover, models of visual search behaviour such as Guided Search (Wolfe et al., 1989) describe guidance in effortful conjunction search in terms of the excitation of target features and the inhibition of non-target features, which is also reminiscent of the Norman and Shallice (1986) account of executive control. As such, it might indeed be possible to apply a domain-general mechanism to the multifarious ways in which search can unfold over physical and conceptual space. Nonetheless, it is becoming increasingly evident that the simple dichotomy between top-down and bottom-up attention does not adequately characterise the subtlety of the involvement of cognitive control in visual search. Rather, the role of reward and selection history contributes, with goal directed activity and stimulus salience, to the formation of the priority map that eventually guides visual search (Awh, Belopolsky & Theeuwes, 2012; Theeuwes & Failing, 2020). Similarly, the conceptualisation of search in the variety of contexts outlined here, requires movement beyond a strict dichotomy of attentional control contraposed to the rigid use of fixed exploration sequences or schemas. The intervening role of regulatory processes that can take place over series of trials and foraging bouts would, therefore, need to be added to a model. Thus, relatively automatic sequencing can derive from attentional processes that pick-up structural properties of the search space and use them strategically, or can be formed more gradually by self-regulatory processes that use energetic and/or cognitive costs as a currencies for regulation. The way in which we envisage the interplay of these factors in the control of search is schematically illustrated in Figure 6 and will be elaborated further below in this discussion.

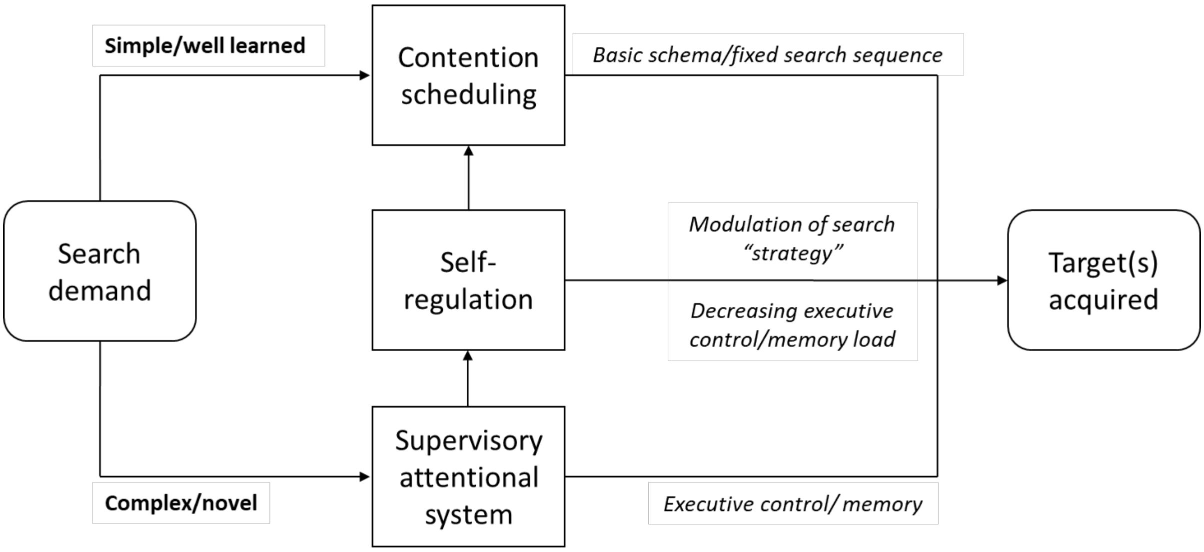


Figure 6 Schematic illustration of the psychological determinants of search as discussed in this article. See text for explanations.

Our final discussion would not be complete without considering the role of memory in the control of search, and in the maintenance or updating of search strategy, which has been a clear feature across a number of different components of search and foraging covered here. In the short term, working memory is generally thought to actively maintain perceptual templates during search, and so it is interlinked in fundamental ways to visual attention. It can also be required to keep track of locations visited in each foraging bout. In the long-term, memory is necessary to support learning about spatial or temporal regularities of the search space, and this might be required for a single bout of searching or something that informs multiple bouts over much longer periods (e.g. in the case of fruiting patterns). Certain structural properties of the search array can be strategically exploited to alleviate the load associated with actively maintaining information, and we have seen that only primates develop a tendency to exhaustively search each patch in clumped arrays before moving onto the next patch. Moreover, only humans seem to systematically make use of rows and columns within matrix-like structures. These differences in the regulation of search not only point to differences in environmental pressures that have shaped search behaviour in different species, but also to a difference in the way that search decisions are actively controlled in order to maximise efficiency. Those decisions may be made on the basis of a given currency (e.g. a trade-off between effort – which, as we argued above, could be either physical or mental - and reward) but they are also associated with the evolution of the frontal lobes in primates. Interestingly, individual differences in human working memory capacity do not seem to affect the features of search that rely on basic visual attention – instead, variation is apparent in tasks that require the active suppression of perceptual features in favour of top-down information. This suggests that working memory not only serves to maintain search templates or to keep track of previously visited locations, but also to facilitate the cognitive control mechanisms that account for the higher-level organisation of search.

Naturally, as with any review of this nature, there are numerous aspects of search behaviour that we have not covered here, and some of these were alluded to at the beginning of this paper. So, for example, we have not discussed search in the context of spatial memory studies (including water maze studies with animals, and human analogues thereof). Nor have we covered developmental assays of search within the Piagetian tradition, where children make inferences regarding where to search for objects following multiple displacements. Both examples have made fundamental contributions to our subject, although they tend to require the exploration of a restricted set of locations for a single solution (e.g. a submerged platform, or an object), rather than optimisation of resource gathering where multiple locations can yield rewards. We have also not covered studies that relate diet and foraging behaviour to hippocampal volume, which might provide useful parallels between search and navigation. In the context of visual search, there are many additional phenomena that could form the basis of variability in behaviour, including perceptual components of search within natural scenes (Hollingworth, 2006) and changes in performance associated with search for multiple targets (e.g. target shedding: Bandara, Grant, Hirshfield & Velipasalar, 2020). All of these omissions, intentional or otherwise, only further illustrate the breadth and depth of the problem before us, and the many potential theoretical furrows that remain to be ploughed.

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