What, where, whether

-The role of working memory and inhibition in foraging performance

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Abstract

Foraging is establishing itself as a powerful way of studying visual search in humans. Cognitive abilities related to foraging and visual search in general include feature search ability, feature integration ability, metacognition and executive functions (EF’s) such as working memory (WM), inhibition and attentional flexibility. While the role of some of these abilities in visual search has been established, little is known about the relationship between EF-subcomponents and foraging. The primary goal of the current study was to determine to what degree two facets of working memory, object-based and location-based WM, play a role in foraging performance. A second goal was to clarify the role of inhibition in foraging, not least to verify whether it would remain insignificant as seen in previous studies. Eighteen individuals aged between 21 and 33 (M = 24.4, SD = 2.7) were tested on a foraging task along with three tasks measuring object-based WM, location-based WM and inhibition, respectively. The results indicate that object-based WM and location-based WM jointly account for a considerable proportion of variance in foraging performance. The role of each of the WM components differs depending on the foraging condition and variables in question. As seen in previous research, inhibition does not seem to contribute to foraging performance. The implications of these results are discussed.
Þakkir

Okkur langar að þakka Ingu Maríu Ólafsdóttur kærlega fyrir ánægjulegt samstarf, handleiðslu og góð ráð. Einnig viljum við þakka Tómasi Kristjánssyni fyrir tæknilega aðstoð og hjálp við heimildhöfnum. Árna Kristjánssyni þökkum við fyrir gagnlegar athugasemdir og leiðbeiningar við vinnslu þessa verkefnis.
# Table of contents

Abstract ................................................................................................................................. 2
Cognitive Abilities Underlying Foraging ................................................................. 6
Executive Functions ........................................................................................................ 7
Working Memory ........................................................................................................... 8
Inhibition ......................................................................................................................... 9
The Current Study ........................................................................................................... 10
Method ................................................................................................................................ 11
  Participants ................................................................................................................... 11
  Foraging Task ............................................................................................................... 11
  Executive Functioning Tasks ...................................................................................... 12
  Procedure ..................................................................................................................... 13
Data Analysis .................................................................................................................. 14
Results .............................................................................................................................. 16
  Foraging Task: Descriptive Statistics ...................................................................... 16
  Executive Functions Tasks: Descriptive Statistics ................................................. 16
  Foraging and Executive Functions: Pearson Correlations .................................. 17
  Foraging and executive functions: Linear regressions ........................................... 21
Discussion ....................................................................................................................... 25
Conclusions .................................................................................................................... 28
References ....................................................................................................................... 29
Foraging studies have a long tradition in animal research, where a common research area involves behaviors that maximize predators’ energy intake with as little energy spending as possible (Bond, 1983; Dawkins, 1971). These studies have suggested that when food is easily found, predators switch randomly between different kinds of prey, but when food items are hard to find, limited attentional capacity of animals forces them to change their hunting behavior and focus on one type of prey at a time, even if that means ignoring equally available sources of energy in their proximity (Dukas, 2002). Foraging is also establishing itself as a powerful way of studying visual search in humans, possibly more so than common single-search tasks.

Árni. Kristjánsson, Jóhannesson, and Thornton (2014) introduced a new foraging iPad-task aimed at providing a better understanding of how human visual search is conducted when foraging for multiple targets of different categories. The task has proven itself successful in demonstrating that human visual foraging follows predictable patterns reflecting task difficulty and limitations in attention, much like what has been observed in animal foraging. When targets are defined by a single feature, discriminating them from distractors requires little attentional load. In this condition, participants most often switch rapidly and with ease between target categories, without it effecting the amount of time it takes to complete the task. However, during conjunction foraging where targets are defined by a conjunction of features, discriminating targets from distractors requires high attentional load. In this search condition, participants usually search exhaustively for one target category before switching over to the other target category (Árni. Kristjánsson et al., 2014).

Ólafsdóttir, Kristjánsson, Gestsdóttir, Jóhannesson, and Kristjánsson (2016) used the same foraging task to examine foraging ability of children aged 4-7 years, along with measures of self-regulation and verbal working memory. Their results showed that foraging patterns of children differ from those seen in adults. The children have greater difficulty foraging for two target types, not only during conjunction foraging but also during feature foraging where targets are defined by a single feature. These age-related differences in foraging are not seen on traditional single-target visual search tasks (Ólafsdóttir et al., 2016).
Cognitive Abilities Underlying Foraging

Cognitive abilities related to foraging and visual search in general include feature search ability, which seems to develop in infancy and remain stable throughout life (Miller, Haynes, & Weiss, 1985; Trick & Enns, 1998); feature integration ability, the binding of visual features of objects into a comprehensive whole, which seems to develop later than feature search ability and is affected by aging (Trick & Enns, 1998); metacognition, which can be defined as an individual’s insight into his or her own cognitive processes, along with an understanding of the capabilities and limitations there of (Miller et al., 1985) and executive functions (EF’s), such as working memory (WM), inhibition and attentional flexibility (Hommel, Li, & Li, 2004; Ólafsdóttir, Gestsdóttir, & Kristjánsson, submitted).

Feature search ability can be systematically manipulated. For example, consistency of visual features has been proven to increase search efficiency. This effect, the enhancement of visual processing with repeated presentation of the same target features, has been called Priming-of-Popout (PoP) (Brascamp, Blake, & Kristjánsson, 2011; Lamy, Antebi, Aviani, & Carmel, 2008). In a neurological examination of the frontal cortex of macaque monkeys, Bichot and Schall (2002) found that the repetition of target feature from one trial to another enhanced visual processing of the target, as reflected by faster eye-movements and more accuracy. Árni Kristjánsson and Driver (2008) found the same effect in humans. When features of both target and distractors were held constant, reaction times were much shorter than when these varied from one display to another.

Feature integration ability is involved in visual search where targets are defined by more than one feature. Research suggests that feature integration is performed in a similar way by children and adults, but that search efficiency is age-related (Ólafsdóttir et al., 2016; Trick & Enns, 1998; Woods et al., 2013). Trick and Enns (1998) examined changes in visual search over the life-span, finding that young children showed less ability for conjunction search than young adults and elderly, possibly reflecting less efficient feature integration capacity. Merrill and Lookadoo (2004) suggested that the ability to restrict visual search to relevant conjunctions of features might increase with age, explaining some of the age-related improvements seen in conjunction search.
Executive Functions

Executive functions have received substantial attention in recent years. While the exact number of proposed components of EF vary between researchers, most regard working memory, inhibition and attentional flexibility as its major constituents (Best, Miller, & Jones, 2009; Ólafsdóttir et al., submitted). EF’s have been studied in relation to cognitive, emotional, behavioral and social self-regulation, where it seems to play a role in various contexts (Best et al., 2009). For example, Bell, Wolfe, and Friedman (2007) found that performance on WM and inhibition tasks could be predicted by children’s self-reports of activation control, as measured by the ability to perform an action in spite of being motivated to avoid it. Another study revealed that inhibition in adolescence could be predicted by ability to resist temptation in pre-school (Eigsti et al., 2006). Likewise, it has been found that limitations in inhibition may contribute to risk-taking behaviors in adolescence (Steinberg, 2007). EF’s have also been studied with regard to school performance. Research suggests that verbal and non-verbal WM can predict performance in English, mathematics and science among children in middle school (Jarvis & Gathercole, 2003; St Clair-Thompson & Gathercole, 2006). Protopapas, Archonti, and Skaloumbakas (2007) linked deficits in EF’s to increased symptoms of dyslexia, resulting in exaggerated difficulties in reading, whereas Hooper, Swartz, Wakely, de Kruif, and Montgomery (2002) found some evidence of links between limitations in attentional flexibility (set-shifting) and poor writing abilities. Researchers have concluded that EF’s may play an important role in the development of reading-writing connections (Altemeier, Jones, Abbott, & Berninger, 2006).

While some results have suggested that the EF’s play a role in visual search performance, others have not. Woods et al. (2013) found that as children grow older, they become better equipped to organize visual search, resulting in more accurate localization of conjunction targets. In that way, the ability to plan (an EF-component) was found to affect conjunction search significantly. Ólafsdóttir et al. (2016) found that two EF-components, self-regulation and verbal working memory, were related to faster and more efficient foraging in children. On the other hand, Jóhannesson, Kristjánsson, and Thornton (2017) found no significant relationships between foraging patterns and either working memory or inhibition.
Working Memory

Of particular interest in the current study is the first EF-component mentioned earlier, namely working memory. WM can be described as a cognitive workspace where a limited amount of information can be stored and manipulated for short periods of time (Best et al., 2009; Hasher & Zacks, 1988). Multiple experiments and neuropsychological findings have provided support for division of working memory into separate object and location (spatial) subcomponents of visual WM, with independent storage, maintenance and manipulation processes (Baddeley, 1996; Baddeley, Sala, & Spinnler, 1991; Klauer & Zhao, 2004; see also Repovs & Baddeley, 2006). There has been considerable debate in the literature over the nature of WM. While some claim that it can only maintain one active search template at a time (Olivers, Peters, Houtkamp, & Roelfsema, 2011; van Moorselaar, Theeuwes, & Olivers, 2014), others have suggested that more than one templates can be active at any given time (Beck, Hollingworth, & Luck, 2012; Grubert & Eimer, 2015; T. Kristjánsson & Kristjánsson, 2017). The former view can be characterized as a single-template account of WM, the latter a load account (T. Kristjánsson & Kristjánsson, 2017).

WM plays an important role in visual search and foraging. For example, it allows individuals to remember previously searched areas and helps to steer spatial attention (Best et al., 2009). Limitations in WM can cause difficulties in planning and carrying out effective visual search (Woods et al., 2013). Luria and Vogel (2011) demonstrated that the degree to which WM is involved in visual search can be predicted by individual differences in WM capacity. Interestingly, they found that higher WM capacity was related to less involvement of WM in visual search. Han and Kim (2004) examined the effect of the administration of irrelevant WM tasks during visual search. According to their results, simply maintaining information in WM does not compromise the speed of visual search, whereas active manipulation of information slows the search process down, resulting in less efficient search.

Less clear is which subcomponent of WM is the most important for foraging ability (Ólafsdóttir et al., 2016). Is foraging performance best explained with a particular facet of WM? To date, little if anything is known about this matter. Foraging in humans is in and of itself a relatively new field of inquiry, and its relationship with WM remains a worthy subject of research. Because of how little is known about this relationship, only speculation can serve as support for particular hypotheses. Foraging is a type of visual search, so general theories on visual search may be used to predict possible outcomes and explain relationships. An early
theory of visual search is Treisman’s Feature Integration Theory (FIT) (Treisman & Gelade, 1980), which suggests that during a pre-attentive stage, single features of objects are registered across the visual field in a fast, automatic manner (parallel search). Later on, at an attentive stage, these features must be combined or integrated in a more effortful way into a comprehensive whole so that objects characterized by a conjunction of features can be identified (serial search). In this theory, emphasis is on the objects themselves and their nature. If WM’s role in foraging was to be predicted by FIT, one could assume that object-based WM would account for more variance in foraging performance than location-based WM - at least in conjunction search, where binding of features would take place. An alternative, more fluid account of visual search is provided by Wolfe’s Guided Search Theory (GST) (Wolfe, Cave, & Franzel, 1989). According to his theory, attention is guided by parallel top-down processes to perform a serial search of the visual field. Like Treisman’s theory, GST distinguishes between a pre-attentive stage, where search is parallel and spread over the visual field, and attentive stage, where search is serial and more area restricted (Wolfe, 1994). Yet another model of visual search is seen in Posner’s Visual Orienting Theory (VOT), which emphasizes the area-restricted nature of the attentional spotlight (Trick & Enns, 1998). According to this theory, attention is focused on a particular area of the visual field at any given time, allowing for processing of visual information from that area. In order to be able to process other areas, attention has to be moved voluntarily from one place to another in a serial sequence. The theory provides a biological analogy to support its case, namely - that the attentional spotlight can be mentally focused on an area in the same way that the fovea of the eye is physically oriented to a specific region to allow for accurate perception of objects within that area. In the latter two theories, Wolfe’s GST and Posners’s VOT, area and location gain weight as influencing factors in visual search. If one were to account for WM in foraging from that standpoint, the prediction might be that location-based WM would play a greater role in foraging performance than object-based WM.

**Inhibition**

Another prominent component of EF is inhibition, defined as the ability to inhibit a primed or predominant response. Garon, Bryson, and Smith (2008) distinguished simple inhibition from complex inhibition based on whether WM is needed in the inhibition process. Simple inhibition only requires participants to inhibit a response, imposing minimal strain on
WM. Complex inhibition on the other hand requires not only inhibition of a response but also the production of an alternative response, thereby demanding the active use of WM. Treisman and Sato (1990) suggested one way of how inhibition might be involved in visual search. In one of a series of experiments, they found that search was slower when the number of types of distractors increased. To account for this, they speculated that feature-based inhibition of distractor features took place, and that as the number of features to ignore increased with more distractors, inhibition of these became less efficient. Jóhannesson et al. (2017) studied the relation between foraging patterns and inhibition. They found that inhibitory control was not a reliable predictor of differences in foraging patterns. Ólafsdóttir et al. (submitted) tested 11-12 year old children on the same foraging task as previously mentioned along with a measure of inhibition. In line with the experiment conducted by Jóhannesson et al. (2017), no connection was found between inhibition and foraging performance. However, in both these studies a complex inhibition task was used where participants had to remember an arbitrary rule, inhibit a prepotent response and produce an incompatible alternative response (Ólafsdóttir et al., submitted). What then remains unclear is whether the results would be the same if simple inhibition was measured. With that kind of measurement, it would be possible to provide further support for whether the role of inhibition role in foraging performance really is insignificant or non-observable.

**The Current Study**

The goal of the current research was to cast light on the role of executive functions in foraging by using the iPad task originally developed by Árni. Kristjánsson et al. (2014). Of main interest was working memory, where the aim was to determine the contribution of two of its subcomponents to foraging performance, that is - object-based working memory and location-based working memory. A second goal was to determine the role of inhibition in foraging, where the aim was to clarify whether it remained non-observable, as found in Ólafsdóttir et al. (submitted) and Jóhannesson et al. (2017).
Method

Participants
A total of 21 students (7 male and 2 left handed) from the psychology department of the University of Iceland participated in the study. Three participants had to be eliminated due to colour blindness. The final sample therefore consisted of 18 individuals, aged between 21 and 33 ($M = 24.4$, $SD = 2.7$). All reported normal or corrected to normal vision and gave oral consent. All aspects of the experiment were reviewed and approved by the Icelandic bioethics committee.

Foraging Task

Equipment. The stimuli were displayed on an iPad 2 with screen dimensions of 20 x 15 cm and effective resolution of 1024 x 768 pixels. The iPad was placed on a table in front of participants in landscape mode and viewing distance was approximately 50 cm. Stimulus presentation and response collection were carried out with a custom iPad application written in Swift using Xcode.

Stimuli. iDot, a foraging task originally developed by Árni. Kristjánsson et al. (2014), was administered (see Fig.1). Each trial started with 40 stimuli displayed on the screen. Half of them were targets and half were distractors. During feature foraging, for half the participants the targets were green and red discs while yellow and blue discs served as distractors. For the other half of participants, the colours were reversed. During conjunction foraging, for half the participants the targets were red discs and green squares while the distractors were green discs and red squares. This was reversed for the other half of participants. The diameter of targets and distractors was 20 pixels (approximately $0.61^\circ$ at a 50 cm viewing distance). The items were randomly distributed on a non-visible 10 x 8 grid that was offset from the edge of the screen by 150 x 100 pixels. The viewing area therefore occupied 15 x 12 cm (approximately $17.1 \times 13.7^\circ$). The position of individual items within the grid was jittered by adding a random vertical and horizontal offset while the gaps between columns and rows ensured that items never approached or occluded each other. Therefore the overall spatial layout and the location of targets and distractors was randomly generated for each trial.
Executive Functioning Tasks

**Equipment.** The tasks were displayed on an 17.3" laptop computer screen with an effective resolution of 1600 x 900 pixels. The computer was placed on a table in front of participants, and the viewing distance was about 50 cm. Task presentation and response collection were carried out with the Amsterdam Neuropsychological Tasks (ANT) program (De Sonneville, 1999).

**Stimuli.** Three tasks from the ANT-program were administered: Go-NoGo, measuring simple inhibition of predominant response; Memory Search 2D Stimuli, measuring working memory and manipulation of memory load, and Spatial-temporal-span; measuring visuospatial working memory.

**Go-NoGo.** In this task, the stimulus was a square appearing at the center of the screen. There were two types of stimuli, and only one was presented at a time. The Go stimulus had a notch at the bottom, whereas the NoGo stimulus was a solid square. In this study, the proportions of Go and NoGo items were biased at a proportion of 75% to 25%.

**Memory Search 2D Stimuli.** In this task, four shapes of different colours appeared at the center of the screen, all at the same time, in a 2*2 matrix. In Part one, the target stimulus was one coloured shape (red circle), whereas in part two the targets were three coloured shapes (blue triangle, green square and a yellow cross).
**Spatial-temporal-span.** In this task, the stimulus was a large grey square containing nine smaller squares, defined with a bright green edge, in a 3*3 matrix. Several of the smaller squares were illuminated in a particular order. As the task progressed, the number of the illuminated squares increased.

**Procedure**

The order of the tasks - iDot, measuring foraging and ANT, measuring executive functions, was counterbalanced. In the ANT-part, the alignment of the tasks was counterbalanced with the exception that STS was always administered first or last. This was for convenience sake since participants had to use a computer mouse to complete it.

**Foraging task.** The participants were seated by a table with the iPad placed in landscape mode on the table in front of them. Half the participants started with the foraging search and the other half with the conjunction search. The participants were randomly assigned to their specific colour condition for both the feature and the conjunction search task. In both conditions, participants were instructed to use the index finger of their dominant hand to tap the targets while avoiding tapping the distractors. If participants hit a distractor, the trial ended and did not count towards the requirement of completing ten trials for both feature and conjunction search. When participants had tapped all the targets on each trial, the completion time for the trial appeared on the screen. When participants were ready for the next trial, they could tap anywhere on the screen to continue.

**Go-NoGo.** Two stimuli, the Go and the NoGo stimuli, were presented to participants on the computer screen as a part of the instructions. Participants were asked to take a good look at the stimuli shown. They were told that if the Go-stimulus (shown on the left - a box defined by a notch at the bottom) appeared on the screen, they were to respond by pressing an answer key (Alt-Gr for right handed participants, Ctrl for left handed). If the NoGo-stimulus appeared (shown to the right - a box without the notch) they were told not to respond, but to wait for the next stimuli to appear. After a practice trial, the task commenced. It consisted of 74 trials.

**Memory Search 2D Stimuli.** In part one, participants were presented with the target stimulus (a red circle) as a part of the instructions. They were told that at each given time during the task, four shapes in different colours would appear simultaneously on the screen. If the target was present among those four shapes, participants were told to respond "yes" (Alt-
Gr for right handed participants, Ctrl for left handed). If not, they should respond "no" (Ctrl for right handed participants, Alt-Gr for left handed). After a practice session, the task began. Part one consisted of 48 trials. In part two, participants were told that the task was now more difficult as the target stimuli would be three (blue triangle, green square and a yellow cross). As before, participants were asked to respond "yes" if any of the three targets were present among the four shapes presented each time, but "no" if none was present. After a practice session - and a refreshing of memory of the three target stimuli when needed - the task started. Part two also consisted of 48 trials.

**Spatial-temporal-span.** Participants were shown a big square containing nine smaller squares. The researcher started a demonstration trial by pressing the space-key, after which an auditory signal indicated the beginning of stimulus presentation. Subsequently, several of the small squares lit up in a particular order. A cursor appeared on the screen, allowing the researcher to demonstrate how one was to use a computer mouse to press the small squares that illuminated *in the opposite order* to the one that had been shown. Each new trial was initiated by pressing the space-key, and each time an auditory signal would indicate the start of a new trial. After a practice trial, the task began. It consisted of 16 trials, with the exception that if participants made two consecutive errors at the same difficulty level, the task was automatically stopped.

**Data Analysis**

In the foraging task, the first tap on each trial, errors, taps on areas between targets and reaction times more than three standard deviations from the mean RT’s were filtered out from data analysis. The dependent variables in both foraging conditions (feature and conjunction) were number of runs and switch cost (as in Ólafsdóttir et al., submitted; see also Á. Kristjánsson et al., 2014). A run was defined as a repeated tapping of the same target category one or more times, preceded and followed by tapping a different target category or no tap, as in the beginning of a trial (Árni. Kristjánsson et al., 2014). The number of runs was inversely proportional to how often a participant switched between target types within a given trial. In other words, the fewer the switches, the longer the runs and the lower the number of runs. Each trial consisted of two types of stimuli (20 targets and 20 distractors, a total of 40). The minimum number of runs in each trial was therefore two, which occurred when a participant exhaustively foraged for one target category and finished tapping on all targets of that type,
before turning to the other target category. In that case, run length was 20 taps. Similarly, the maximum number of runs in each trial was 40, which occurred when a participant switched between categories after every tap. In that case, run length was one tap. Switch cost was defined as the time it took to switch between target categories. In order to measure it, inter-target time (ITT) had to be calculated. ITT denotes the time between taps on two targets. In both foraging conditions, mean switch cost was calculated for each participant by subtracting the mean ITT of taps on the same target type as in the previous selection from the mean ITT of the first tap after switching to a new target category from the preceding tap (as in Árni. Kristjánsson et al., 2014). The mean number of runs and the mean switch cost for each participant in both conditions served as the final dependent variables (Ólafsdóttir et al., submitted; Ólafsdóttir et al., 2016).

In the executive functions tasks, dependent variables were reaction time, correctly recalled items in incorrect order, and inhibition of a predominant response. In order to measure object-based working memory, the MS2D-task was used. Mean reaction time of hits and correct rejections were added for both parts of MS2D to estimate mean overall RT. Subsequently, this mean RT from part 1 was subtracted the mean RT of part 2. The results constituted a new variable reflecting the difference in performance of the two parts, where a higher score reflected poorer object-based working memory. This can be considered a direct measurement of the capacity of object-based working memory (as in Brunnekreef et al., 2007). To measure location-based working memory, the STS-task was used. The number of correctly identified items in the correct order was subtracted from the number of correctly identified items. In this way, a variable was computed that could estimate location-based working memory directly. The new variable reflected location-based working memory in the way that a higher score reflected poorer ability (as in Schuitema et al., 2013). To measure simple inhibition, the GNG-task was used. A new variable was computed from the ratio of false alarms and total number of trials, reflecting the capability to inhibit a predominant response. False alarms were used instead of misses because in the GNG-tasks, misses were zero for all participants.

Despite some departures from theoretical assumptions, the relationship between foraging and the EF-components was assessed with Pearson correlations, simple linear and multiple linear regressions.
Results

Foraging Task: Descriptive Statistics

**Number of runs.** The mean number of runs for participants during feature foraging was 8.94 whereas during conjunction foraging the mean was 5.51 runs (see Table 1). A paired $t$-test was used to determine if this difference was significant. That turned out to be the case, $t(17) = 5.372, p < .001$. The mean difference was 3.43 runs (95% CI = 2.09; 4.78). The distribution of the number of runs in feature foraging was approximately symmetric, whereas in conjunction foraging it was strongly positively skewed.

**Switch cost.** The mean switch cost in the feature condition (34.02 ms) was much lower than in the conjunction condition (238.41 ms). A paired $t$-test showed that the difference between conditions was significant, $t(17) = 5.74, p < .001$. The mean difference was 204.39 ms (95% CI = 129.31; 279.47). The distribution of switch costs was strongly positively skewed in both feature and conjunction foraging.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of runs feature</td>
<td>8.94</td>
<td>2.04</td>
</tr>
<tr>
<td>No. of runs conjunction</td>
<td>5.51</td>
<td>2.55</td>
</tr>
<tr>
<td>Switch cost feature</td>
<td>34.02</td>
<td>10.48</td>
</tr>
<tr>
<td>Switch cost conjunction</td>
<td>238.41</td>
<td>38.75</td>
</tr>
</tbody>
</table>

Executive Functions Tasks: Descriptive Statistics

**Object-based working memory.** Object-based WM was estimated with differences in reaction times in the two parts of MS2D. The difference had a mean of 2658.72 ms (see table 2.), and its distribution was slightly negatively skewed.

**Location-based working memory.** Location-based WM was measured with correctly recalled items in incorrect order in STS. Correctly recalled items in the incorrect order had a mean of 10.06 items, with the distribution heavily negatively skewed.

**Inhibition.** Inhibition was measured with the ratio of false alarms to the total number of trials in GNG. This ratio had a mean of .012 (SD=.013) and its distribution was negatively skewed.
**Table 2. Means and standard deviations for object-based working memory, location-based working memory and inhibition**

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Object-based working memory</td>
<td>2658.722</td>
<td>792.323</td>
</tr>
<tr>
<td>Location-based working memory</td>
<td>10.056</td>
<td>7.384</td>
</tr>
<tr>
<td>Inhibition</td>
<td>.012</td>
<td>.013</td>
</tr>
</tbody>
</table>

**Foraging and Executive Functions: Pearson Correlations**

To explore connections between foraging ability and executive functions, a series of Pearson correlations ($r$) were calculated.

**Object-based working memory.** Table 3 shows a clear connection between object-based WM and the foraging variables. The results indicate that higher scores on object-based WM (reflecting poorer performance) were associated with lower number of runs in both foraging conditions. Likewise, a higher score on object-based WM correlated with larger switch costs in both conditions. All correlation coefficients for object-based WM proved to be significant (all $p < .050$).

**Location-based working memory.** Connections between location-based WM and foraging were slightly less pronounced, with one exception (mean switch cost conjunction, see table 3). The correlation between location-based WM and the number of runs in conjunction foraging was marginally significant ($p = .059$), where a higher score on location-based WM (again, reflecting poorer performance) was associated with fewer runs during conjunction search. A strong correlation was seen between location-based WM and switch cost in conjunction foraging, in that higher scores on location-based WM meant larger switch costs.

**Inhibition.** In accordance with previous research on the role of inhibition in foraging (Ólafsdóttir et al., submitted), simple inhibition didn’t seem to correlate with the number of runs or switch cost in either foraging condition (all $p > .05$).
Table 3. Correlations between executive functions and foraging variables

<table>
<thead>
<tr>
<th></th>
<th>Mean no. of runs feature foraging</th>
<th>Mean no. of runs conjunction foraging</th>
<th>Mean switch cost feature foraging</th>
<th>Mean switch cost conjunction foraging</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inhibition</td>
<td>.197</td>
<td>.163</td>
<td>-.038</td>
<td>-.072</td>
</tr>
<tr>
<td>Object-based working memory</td>
<td>-.474*</td>
<td>-.570*</td>
<td>.500*</td>
<td>.512*</td>
</tr>
<tr>
<td>Location-based working memory</td>
<td>-.427</td>
<td>-.453</td>
<td>.379</td>
<td>.746**</td>
</tr>
</tbody>
</table>

*p < .050; **p < .010

Figures 2 and 3 show scatterplots for WM-components and their correlations with number of runs and switch cost during both feature and conjunction foraging. Figure 2 shows that the variance in run number was larger for conjunction than feature foraging. Scores for object and location-based WM tasks were negatively correlated to the number of runs in both foraging conditions. Figure 3 reveals that the variance of switch cost was greater in conjunction foraging than in feature foraging, where it was limited. Scores on object and location-based WM tasks were moderately positively related to switch cost in feature foraging, whereas this relationship is more pronounced for conjunction foraging.
**Feature foraging**

![Plot](image)

**Conjunction foraging**

![Plot](image)

**Figure 2.** A scatterplot showing the correlation between Z-scores of object-based WM (green squares) and location-based WM (red circles) and the mean number of runs in feature and conjunction foraging. The green line shows the best fit for the correlation between mean number of runs and object-based WM, the red line shows the best fit for the correlation between mean number of runs and location-based WM. Note: Z-scores are used to due to differences in scales of measurements between object-based and location-based working memory.
Figure 3. Scatterplot showing the correlation between Z-scores of object-based WM (green squares) and location-based WM (red circles) and the mean switch cost in feature and conjunction foraging. The green line shows the best fit for the correlation between mean switch cost and object-based WM, the red line shows the best fit for the correlation between mean switch cost and location-based WM. Note: Z-scores are used due to differences in scales of measurements between object-based and location-based working memory.
Foraging and executive functions: Linear regressions

In order to cast further light on the relationship between the variables, simple and multiple linear regressions were executed. The primary goal was to determine whether either of two types of WM, object-based or location-based, had a greater contribution to foraging performance.

Table 4 shows the parameter estimated for simple linear regressions for object- and location-based WM and the four dependent variables (number of runs and switch cost in both feature- and conjunction foraging). The influence of object-based WM on the number of runs during feature foraging was significant, as well as during conjunction foraging. The effect of location-based WM on the number of runs in conjunction foraging was marginally significant. The influence of object-based WM on switch costs during feature foraging was significant. Object-based WM and location-based WM both had significant predictive value for switch cost during conjunction foraging.

Table 4. Simple linear regressions - object and location-based working memory’s influence on number of runs and switch cost in feature and conjunction foraging

<table>
<thead>
<tr>
<th></th>
<th>B</th>
<th>SE B</th>
<th>Beta</th>
<th>Sig</th>
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<tr>
<td><strong>Mean no. runs</strong></td>
<td></td>
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<tr>
<td><strong>feature</strong></td>
<td></td>
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<td>Object-based</td>
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<td>Location-based</td>
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<tr>
<td>working memory</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mean no. runs</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>conjunction</strong></td>
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<tr>
<td>Object-based</td>
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<tr>
<td>Location-based</td>
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<td>.077</td>
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<tr>
<td>Switch cost feature</td>
<td>Object-based working memory</td>
<td>.028</td>
<td>.012</td>
<td>.500</td>
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<tr>
<td>-------------------------------------</td>
<td>-----------------------------</td>
<td>------</td>
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<td>------</td>
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<tr>
<td>Location-based working memory</td>
<td>2.279</td>
<td>1.393</td>
<td>.379</td>
<td>.121</td>
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</table>

<table>
<thead>
<tr>
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<th>Object-based working memory</th>
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<th>.045</th>
<th>.512</th>
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<td>16.603</td>
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<td>.746</td>
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Table 5 first shows results for multiple linear regressions where both WM-components serve as predictive variables for number of runs. First in the table is a model where the mean number of runs in the feature foraging condition serves as a dependent variable. The model is not significant (see Note 1 in Table 5). Object-based WM may account for slightly more variance in the number of runs than location-based WM, but this cannot be determined with certainty from the data. Next in table 5 is a model where the dependent variable is the mean number of runs in the conjunction foraging condition. The model is significant, and object-based WM seems to account for more variance in number of runs than location-based WM (see Note 2 in Table 5).
Table 5. Multiple linear regression - object and location-based working memory’s influence on the number of runs for feature and conjunction foraging

<table>
<thead>
<tr>
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<th>B</th>
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<th>Sig</th>
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<tbody>
<tr>
<td><strong>Feature</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Object-based working memory</td>
<td>-.001</td>
<td>.001</td>
<td>-.353</td>
<td>.173</td>
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<tr>
<td>Location-based working memory</td>
<td>-.074</td>
<td>.068</td>
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<td><strong>Conjunction</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Object-based working memory</td>
<td>-.001</td>
<td>.001</td>
<td>-.459</td>
<td>.065</td>
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<td>Location-based working memory</td>
<td>-.084</td>
<td>.079</td>
<td>-.243</td>
<td>.307</td>
</tr>
</tbody>
</table>

Note 1. Feature: \( R^2 = .281; F = 2.926; \text{Sig} = .085 \)

Note 2. Conjunction: \( R^2 = .372; F = 4.436; \text{Sig} = .031 \)

Table 6 shows models where switch costs serve as the dependent variable. The first part of the table shows switch cost during feature foraging as the dependent variable. The model is not significant (see Note 3 in Table 6). Keeping that in mind, object-based WM may account for a slightly larger proportion of the variance in switch costs than location-based WM.

In the latter part of the table, switch cost during conjunction foraging is the dependent variable. The model is significant, but this time, the predictive power seems to be stronger for location-based WM (see Note 4 in Table 6). The predictive power of location-based working memory remains significant when object-based WM is controlled for.
Table 6. Multiple linear regression - object and location-based working memory’s influence on switch cost in feature and conjunction foraging

<table>
<thead>
<tr>
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<th>SE B</th>
<th>Beta</th>
<th>Sig</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Feature</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Object-based working memory</td>
<td>.023</td>
<td>.014</td>
<td>.414</td>
<td>.114</td>
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<tr>
<td>Location-based working memory</td>
<td>1.141</td>
<td>1.484</td>
<td>.190</td>
<td>.454</td>
</tr>
<tr>
<td><strong>Conjunction</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Object-based working memory</td>
<td>.045</td>
<td>.038</td>
<td>.216</td>
<td>.260</td>
</tr>
<tr>
<td>Location-based working memory</td>
<td>14.401</td>
<td>4.121</td>
<td>.647</td>
<td>.003</td>
</tr>
</tbody>
</table>

Note 3. Feature: $R^2 = .279; F = 2.896; \text{Sig} = .086$

Note 4. Conjunction: $R^2 = .593; F = 10.938; \text{Sig} = .001$

What stands out after having looked at these results is that generally, object-based WM seems to have a stronger effect on foraging ability than location-based WM. However, the relationship changes when it comes to switch cost during conjunction foraging. There, location-based WM accounts for considerably more variance than object-based WM.
Discussion

The primary goal of the current study was to determine whether either of two facets of working memory, object-based and location-based WM, contributed more to foraging performance. A second goal was to determine the role of inhibition in foraging to verify whether it would remain insignificant as seen in previous studies.

Our participants showed similar foraging patterns to those found in prior research (Jóhannesson et al., 2017; Árni. Kristjánsson et al., 2014; Ólafsdóttir et al., 2016). The number of runs was lower during conjunction foraging than during feature foraging and switch costs were much larger during conjunction than feature foraging. These differences between feature and conjunction foraging patterns are thought to reflect increased task difficulty in conjunction foraging and limited attentional resources.

As for foraging and individual WM-components, our results showed a clear relationship between object-based working memory and all foraging variables. Firstly, poorer object-based WM predicted lower number of runs. Secondly, poorer object-based WM was connected with greater switch costs. When looking at location-based working memory and its interaction with foraging performance, one strong relationship appeared, which is that poorer location-based WM was connected to greater switch costs during conjunction foraging. Although not clear, there seemed to be some connection between location-based working memory and the number of runs during both conditions (conjunction foraging in particular), but this was less pronounced. On the whole, object-based WM seemed to account for more variance in dependent variables, the exception being switch costs during conjunction foraging where location-based WM has substantially more predictive value than object-based WM.

When foraging was examined taking both working memory components into account, some of the individual relationships described above vanished while others remained intact. Together, object-based and location-based WM managed to account for a considerable amount of the variation in the number of runs during conjunction foraging ($R^2 = 0.372$), and object-based WM remained a marginally significant predictor when location-based WM was controlled for. Together, the WM-components accounted for a substantial amount of the variation in switch costs during conjunction foraging ($R^2 = 0.593$), and location-based WM remained a highly significant predictor when object-based WM was controlled for. Overall, WM-components therefore seemed to better predict performance during conjunction foraging than feature foraging.
The lack of significance of individual regression coefficients in the multiple linear regression, as compared to those seen when object-based WM and location-based WM are used separately to predict dependent variables, points to an overlap in the predictive ability of working memory components. Simple linear regression reveal that object-based WM can account for the variance of the dependent variables during both conditions, while location-based WM only taps into switch costs during conjunction foraging. Taking both WM-components into account in the multiple linear regression, the dependent variables for feature foraging can no longer be predicted. We speculate that the reason for this is that during feature foraging when targets are defined by a single feature, object-based working memory allows participants to keep both target categories active and switch between them with ease. In a manner of speaking, object-based WM may “suffice” when search requires only minimal effort. If location-based WM has a limited role in feature search, it may “cancel out” the predictive power that object-based WM seems to have in and of itself. This might explain why, when location-based WM is taken into the equation along with object-based WM, results are insignificant.

As stated above, multiple linear regressions indicate that WM-components seem to better predict performance for conjunction foraging than feature foraging. This might be because during conjunction foraging where targets are defined by two features, search becomes more effortful and requires more cognitive resources. There, as opposed to feature foraging, location-based WM may “kick in”. Both simple and multiple regressions (Pearson correlations for that matter as well) support strong connection between location-based WM and switch cost in conjunction foraging. This is for instance reflected in the fact that $R^2$ for simple linear regression, with location-based WM as the only predictor for switch cost, is only slightly lower than when both WM-components are taken into account, suggesting that object-based WM adds little to the prediction of switch cost during conjunction foraging. This relationship between location-based WM and switch cost during conjunction foraging seems to be the strongest relationship that appears among all possible combinations of variables. Location-based WM’s role in conjunction foraging is fairly easy to account for, as seen above. The reason for its role being more pronounced for switch cost than number of runs might be that it helps participants maintain a clear overview of the visual field and previously foraged areas, thereby allowing them to conduct a well organized search.
The greater contribution of object-based WM seen in the simple linear regressions generally supports Treisman’s Feature Integration theory. FIT places emphasis on the features of objects, or the objects themselves (the “what” in visual search). As mentioned earlier, FIT might therefore predict that object-based WM would account for more variance in foraging performance than location-based WM. Support for Posner’s Visual Orienting Theory can be found when switch cost in conjunction foraging is examined, both in simple and multiple linear regression’s. There, location-based WM has more predictive value than object-based WM. In Posner’s theory, emphasis is on the area-restricted nature of visual search, or the localization of objects (the “where” in visual search). If one were to predict the role of WM in foraging from that standpoint, location-based WM would play a greater role in foraging performance than object-based WM. Therefore, depending on the context, both theories can offer some prediction and explanation for the role of the different facets of WM in foraging performance.

No connection was found between inhibition and foraging performance, which is in line with the results of Ólafsdóttir et al. (2016) and Jóhannesson et al. (2017). This pattern was found even though we used a task that measured simple inhibition, requiring only the withholding of a prepotent response, thereby ensuring no confounding between inhibition and working memory. Based on these results, our conclusion is that inhibition’s role during foraging is small, or can even be ruled out.

The role of working memory in visual foraging could be studied much further. For example, it would be interesting to establish whether its effects are not on foraging strategies themselves, but on the execution and effectiveness of these strategies. That seems to be the case when comparing foraging patterns of individuals of different ages (Ólafsdóttir et al., submitted; Ólafsdóttir et al., 2016). Similarly, while working memory seems to contribute to foraging efficiency, there is evidence that it does not affect foraging patterns (Jóhannesson et al., 2017). If this is true, it underscores the notion that working memory affects visual search in a marked way, but mainly by enhancing performance through better administration of search strategies.

The non-observable role of inhibition in foraging is quite puzzling. One might think that inhibition would be an important factor. For example, it is easy to come to the conclusion that inhibition might contribute to the efficiency of search by “blocking out” distractors (more specifically, inhibiting processing of irrelevant information) and preventing the revisiting of
areas in the visual field that have already been searched (Bichot & Schall, 2002; Lamy et al., 2008; Treisman & Sato, 1990). One explanation for the absence of inhibition’s impact in this study could be the age of participants. Research suggests that young children rely to a greater extent on inhibition for self-regulation than older ones (Best et al., 2009), so if younger individuals or children had been tested here, there is a possibility that a connection between inhibition and foraging performance would have emerged. However, Ólafsdóttir et al. (submitted) did test young children, and found no relationship between foraging ability and inhibition (although it is worth noting that they measured complex inhibition unlike the current research were simple inhibition was estimated).

With a larger and more varied sample one might be able to further clarify the role of WM-components in foraging performance. It might even be worthwhile to test the role of inhibition yet again, perhaps with a more sensitive task than used here or a number of different tasks. Due to the modest sample size and narrow age range, the results might be somewhat unrepresentative of the connection between foraging and executive functions “in general”. This relationship might indeed change throughout life. A developmental perspective could prove to be informative in that context.

Conclusions

Working memory seems to play a considerable role in executing effective visual search. Even though the predictive power of each of the WM-components may not always be pronounced, together, object-based WM and location-based WM manage to account for a considerable amount of variation in foraging performance, especially during conjunction foraging. Further research could cast light on finer nuances in the relationship between executive functions and foraging.
References


