Are Foraging Patterns in Humans Related to Working Memory and Inhibitory Control?

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Abstract: In previous studies we have shown that human foraging patterns appear to be constrained by attention. However, we also noted clear individual differences in foraging ability, where some individuals can apparently keep more than one target template in mind during foraging. Here, we examine whether such individual differences relate to more general working memory capacity and/or the ability to inhibit a primed, or prepotent response. We had three main goals. First, to replicate general patterns of attention-constrained foraging. Second, to verify that some individuals appear immune to such constraints. Third, to investigate a possible link between individual foraging style and working memory abilities measured on a digit-span task and inhibitory control measured with a Stroop task. In sum, we replicated the finding that foraging differs greatly by whether foraging targets are defined by a single feature or a conjunction of features, but also again found that some observers show little differences in foraging between the two conditions, seemingly shifting with ease between search templates. In contrast, neither working memory nor Stroop performance were reliable predictors of these individual differences in foraging pattern. We discuss the implications of the findings for theories of visual attention.

Key words: foraging, working memory, inhibitory control, visual search, attention.

The sheer multitude of stimuli hitting our retinas at a given moment far exceeds the processing capacity of the visual system. Many findings show how strongly attention determines what we see (Mack & Rock, 1998; Most et al., 2001; Neisser & Becklen, 1975; Rensink, O'Regan, & Clark, 1997). A dominant paradigm for understanding how humans attend to important or conspicuous items in their visual field has been the visual search paradigm, where observers typically search for a single target among a variable number of distractors (Duncan & Humphreys, 1989; Á. Kristjánsson, 2015; Treisman & Gormican, 1988; Wolfe, 1998, 2016).

A largely separate literature has also developed on how animals forage for multiple targets (or typically multiple food sources; Bond, 1983; Dawkins, 1971; Langley, Riley, Bond, & Goel, 1996; Reid & Shettleworth, 1992). For many scenarios, such multiple target search (or foraging) is ecologically more valid for humans than single target search, since our goals tend not to be so narrow as to involve a single target type. However, this paradigm has only recently received sustained interest from investigators of human visual cognition (Cain, Vul, Clark, & Mitroff, 2012; Gilchrist, North, & Hood, 2001; Hills, Kalff, & Wiener, 2013; Á.

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Kristjánsson, Jóhannesson, & Thornton, 2014; Thornton & Horowitz, 2004; Wolfe, 2013).

Animals Forage in Runs

Many species tend to forage in "runs"—selecting food of the same type in sequences that are longer than could be expected by chance. Such run foraging has been thought to be mediated by internal templates or "search images" that control the way the animals sample the environment (Nakayama & Martini, 2011; Tinbergen, 1960). Tinbergen investigated the foraging behavior of birds, concluding that they "perform a highly selective sieving operation on the visual stimuli that reach their retina [and] can only use a limited number of different search images at the same time" (Tinbergen, 1960, pp. 332–333). This can cause the birds to focus exclusively on a single food source. This tendency is more pronounced when prey is "cryptic" or hard to detect, when they are likely to ignore other available sources of food (Dukas & Ellner, 1993). Note, however, that when food items are conspicuous, animals may switch quickly between available sources (e.g. choosing the closest food item), interleaving short runs of choices of different prey types.

The search image concept is supported by results such as those of Dawkins (1971), who found that chicks that could choose to eat two types of grain of differing colors chose to eat the same colored grain again and again, before switching to the other color and then picked that grain color for long "runs." These runs were longer than could be expected by chance. Reid and Shettleworth (1992) reported similar results, showing how pigeons chose more frequent color grains more often than would be expected by chance.

What ties this literature on animal foraging strongly to the visual search literature is that cognitive "top-down" processes are used to explain the findings (Nakayama, Maljkovic, & Kristjánsson, 2004). In the visual search literature, "visual working memory" representations (Awh & Jonides, 2001) are typically thought to guide the search, while the concept of "internal search images" is used in the animal foraging literature (Nakayama et al., 2004). While the language may differ somewhat, it is not clear that there is effectively a large difference between these concepts.

Recent Investigations of Human Foraging

Human foraging performance has lately received increased interest (Cain et al., 2012; Jóhannesson, Thornton, Smith, Chetverikov, & Kristjansson, 2016; Á. Kristjánsson et al., 2014; Smith, Hood, & Gilchrist, 2008; Wolfe, 2013). We recently introduced an iPad foraging task in which human observers have to tap 40 targets from two categories as quickly as possible from amongst 40 distractor items (Jóhannesson et al., 2016; Á. Kristjánsson et al., 2014). The targets disappeared once they were tapped. If participants tapped one of the distractor items, they received an error message and the trial ended.

When a single feature (color) sufficed to distinguish the targets from distractors (e.g. green and red targets among blue and yellow distractors), human observers switched easily between target types, a pattern consistent with animal foraging for conspicuous prey (e.g., Bond, 1983; Langley et al., 1996; Reid & Shettleworth, 1992). During a comparable conjunction-foraging task, the targets could only be distinguished from distractors on the basis of two features (in this case shape and color). This classic attentional manipulation (Treisman & Gelade, 1980) severely affected foraging strategies in a manner consistent with animals foraging for cryptic prey (Dawkins, 1971; Dukas, 2002; Dukas & Ellner, 1993). That is, the majority of participants completely altered their foraging style during conjunction-foraging, selecting the same target type in long runs, often until all targets of that type were finished, and only then beginning to select the other target type.

Overall, the pattern of results obtained with the iPad task suggested that there were similar constraints in foraging abilities for both humans and animals. However, importantly, a subset of participants (approximately 25%) seemed unaffected by the increased

attentional load imposed by the conjunction manipulation, and continued to switch frequently between target categories with little cost in either speed or accuracy. These participants—who we termed "super-foragers"—raised the interesting possibility that foraging ability may vary according to individual differences, perhaps reflecting differences in attentional capacity and/or working memory (WM) resources.

Current Goals

What might explain these differences in foraging patterns? Do the observers who can switch easily between target types during conjunction-foraging have any measurable characteristics that could be uncovered with other tasks?

We can speculate that for rapid and effective switching during conjunction-foraging, at least two capabilities are required. Good inhibition abilities will be needed to prevent participants from picking the same target as they just did, since observers have a very strong tendency to pick recently attended target types in traditional visual search (Brascamp, Blake, & Kristjánsson, 2011; Chetverikov & Kristjánsson, 2015). Such a prepotent (or primed, Á. Kristjánsson & Campana, 2010) tendency must be overcome, or inhibited for rapid switching. Furthermore, the two targets must be kept in mind—for example, as a visual WM representation (or perhaps a search image; Nakayama & Martini, 2011; Tinbergen, 1960). It is therefore likely that good WM abilities will also be useful for efficient foraging. It is of course possible that rapid switching of representations within WM could also accomplish this (as some theories of WM would require; see van Moorselaar, Theeuwes, & Olivers, 2014; Olivers, Peters, Houtkamp, & Roelfsema, 2011), although this seems a less likely possibility. In other words, given the nature of the foraging task, perhaps the "super-foragers" may have better inhibition skills, and/or larger WM capacity. Note that the "super" aspect of performance here relates specifically to the relatively rare ability to switch between target categories during conjunction-foraging, rather than to more general aspects of foraging efficiency, an issue we return to in the Discussion.

We tested 32 participants on three tasks designed to assess: (a) the mechanisms required for efficient foraging, measuring feature and conjunction-foraging performance; (b) WM capacity, using a backward digit span task (see Wilde, Strauss, & Tulsky, 2004); and (c) performance on the well-known Stroop (1935) task, which has been shown to be a good measure of inhibitory control.

We had three main goals. First, we wished to replicate the majority pattern of feature-conjunction-foraging seen in our previous paper. Second, we wanted to establish if any individuals showed evidence of "super-foraging" (as in Jóhannesson et al., 2016; Á. Kristjánsson et al., 2014). Third, we wished to relate foraging performance to the two cognitive measures, hoping to assess the degree to which efficient foraging is constrained by WM and inhibitory control.

Methods

Participants

A total of 16 participants (13 female) from the University of Malta community and 16 participants (10 females) from the University of Iceland community took part in the experiment on a voluntary basis. Mean age was 25 years (SD = 8 years, range 18–48 years). All were naïve about the purpose of the experiment and reported normal or corrected-to-normal vision.

Ethics

All aspects of the experiment were reviewed and approved by the respective ethics committees at the University of Malta and the University of Iceland and conformed to the ethical guidelines set out by the Declaration of Helsinki for testing human participants. All participants provided written, informed consent.

Equipment

We displayed the stimuli on an iPad 2 with a 20 × 15-cm screen and a resolution of 1024 × 768 pixels. The iPad was placed on a table in front of the participant in landscape mode, so that viewing distance was approximately 50 cm. Viewing distance was not precisely controlled, so we report size in both pixels and degrees visual angle. We prepared a custom iPad application written in objective-C using Xcode and Cocos2d libraries for stimulus presentation and response collection. When inferring about the statistical properties of the runs distributions (e.g. randomness and number of runs) we used the function runstest.m (from the Statistical and Machine Learning Toolbox in Matlab). In all other statistical analyses, we used the R statistical program (R Core Team, 2014) running in the RStudio environment (RStudio Team, 2015).

Stimuli and Measures

In the feature-foraging task, the targets were red and green disks while the distractors were yellow and blue disks. In the conjunction-foraging task, the targets were red squares and green disks and the distractors were green squares and red disks for half of the participants (in counterbalanced order) and for the other half, the targets were red disks and green squares while the distractors were green disks and red squares. There were 20 stimuli of each of the four types, drawn on a black background. The diameter of targets and distractors was 20 pixels, or approximately 0.46° visual angle. The display items were distributed randomly on the screen, placed on a non-visible 10 × 8 grid. The viewing area occupied 15 × 12 cm (approximately 17.1 × 13.7°). Item position within the grid was jittered by adding a random horizontal and vertical offset to create less uniform appearance. The position of each display item was randomly determined for each trial.

Stroop Task

The Stroop stimuli were printed on paper and positioned at a comfortable distance in front of the participant. To measure baseline performance, 50 (plus 10 for training) red, green, and blue rectangles were used. To induce Stroop interference, color names printed in another color ink (e.g. "red" was printed in blue or green) were used. The color names were in English, both in Malta and Iceland. For all conditions, participants were required to read the color of the ink in which the stimuli were printed as quickly as possible and this time was recorded with a stopwatch. The order in which the printed stimuli appeared in both conditions was random but the same for all participants. Stroop interference was computed as the difference between the color word condition minus the baseline condition.

WM Task, Digit Span

The WM task required participants to listen to and repeat—in reverse order—a series of digit strings of various lengths. Digit strings of five different lengths ranging from four to eight digits were read aloud—one by one—by the experimenter. There were four strings of each length for a maximum total of 20 trials. Four versions of the task were prepared and the digits in each string were initially randomly selected. Participants were randomly assigned to one of the four versions. The correct answer was checked by the experimenter as each digit string was repeated. If participants failed to correctly report four strings in a row, the task was terminated. Performance was measured by summing the lengths of the correctly reported digit strings.

Procedure

The experiment consisted of four tasks starting with either the Stroop or digit span tasks in counterbalanced order. The third task was always feature-foraging followed by conjunction-foraging. Testing was performed in a quiet room with normal illumination.

For the two foraging tasks, the iPad was placed in front of participants in landscape orientation. Participants were instructed to tap all targets as quickly as they could, while avoiding errors. If an error was made, feedback was given and a new trial started. Participants had to complete 10 correct feature-foraging trials and 10 correct conjunction-foraging trials, with brief training before the start of each block.

Table 1 Comparison between main dependent measures for Malta and Iceland

Task	Malta		Iceland		t-value	df	p-value
	Mean	*SD*	*Mean*	*SD*			
Runs, feature	13.3	4.0	15.3	3.9	1.45	29.9	.158
Runs, conjunction	3.9	2.6	4.6	4.1	0.57	25.4	.571
WM scores	43.0	23.8	59.7	28.5	1.79	29.1	.083
Stroop scores	7.5	4.3	7.5	6.4	0.01	26.3	.989

Data Analysis

Before combining the data, we compared the four main dependent measures (number of runs in each condition, Stroop interference, and digit span) between the countries and found no significant differences (all ps > .08, see Table 1). Our main dependent measure for the foraging tasks was the average number of runs. We define a run as "a succession of one or more types of symbols which are followed and preceded by a different symbol or no symbol at all" (Gibbons, 2003, p. 76; see Á. Kristjánsson et al., 2014). Based on our previous work, we expected that the number of runs would generally reduce during the conjunction condition, but that there might be consistent individual differences. Therefore, in the following, we divided the participants into two groups based on the number of runs during conjunction-foraging; in one group are those that were in the top quartile and in the other group are those in other quartiles. For consistency with our previous papers (Jóhannesson et al., 2016; Á. Kristjánsson et al., 2014) we termed those above the 75th percentile "super-foragers" (SF) and those below the 75th percentile "normal-foragers" (NF).

Subsequently, we compared the between-group performance on the WM and Stroop tasks using t-tests. Degrees of freedom were adjusted whenever unequal variances were detected (Levene's test). Furthermore, as the number of participants in the two foraging groups will always be unbalanced (given our definition), we also computed measures that looked for relationships between our measures of interest and the entire sample. Thus, we ran simple correlations between these measures and: (a) the number of runs during feature-foraging; (b) the number of runs during conjunction-foraging; and (c) the difference in the number of runs between feature- and conjunction-foraging. We also ran regression analyses that included the sample locations (Iceland vs. Malta) as an exploratory measure.

In addition to examining the number of runs, we also tested whether run behavior appeared to be random or constrained in any way. If observers can choose targets at will, foraging behavior is considered random, compared to if they stick to the same target type for long runs. Typically, foraging is random during feature-foraging and non-random during conjunction-foraging. Random foraging during conjunction conditions is another hallmark of SF behavior. We used the One-Sample Runs Test to determine if the foraging behavior was random or not, for each participant in both conditions. Bonferroni corrections were applied to control for multiple comparisons.

Finally, to more fully capture overall patterns of foraging, we also included measures of foraging speed (i.e. total time to complete a trial) and distance travelled. For this latter measure, we computed the Euclidean distance in pixels between each tap on a target, summing this across all 40 responses. For both time and distance, we compared the performance of each group across conditions.

Results

Feature- and Conjunction-Foraging

As can be seen in Figure 1, we replicate our previous results where most observers show large differences in foraging depending upon condition. Specifically, the number of runs is

high during feature-foraging (Figure 1, dotted line and open circles), suggesting frequent switches between target type, while during conjunction-foraging (Figure 1, solid line and filled circles) most observers foraged in fewer, longer runs, indicating that they selected the same target type repeatedly. A direct comparison between the number of runs in these two conditions showed that this overall pattern is significant (paired-

$t(31) = 12.47, p < .001$; Cohen's $d = 2.205$).

As in Á. Kristjánsson et al. (2014) and Jóhannesson et al. (2016), a few observers foraged using a larger than average number of runs during conjunction-foraging. These are our putative SFs (SF group, $n = 8$) and are indicated by the triangles in Figure 2.

The majority of foragers, our NFs (NF group, $n = 24$) are indicated by the dots. Figure 2A shows the relationship between number of runs in each condition for all the participants, suggesting that there is a positive correlation between the number of runs in the feature and the conjunction conditions. In Figure 2B, we show the difference between the relationship of number of runs in each condition for each group. The panel clearly shows that it is the SFs that mainly contributed to the

positive slope in Figure 2A. The average number of runs for the SF group during conjunction-foraging was 9.4 ($SD = 3.03$) while for the NF group it was 2.6 ($SD = 0.6$). This difference was significant, $t(7.2) = 6.6, p < .001$; Cohen's $d = 3.151$. The difference between the SF (*Mean* = 15.6 runs, $SD = 2.6$ runs) and NF group (*Mean* = 13.9 runs; $SD = 4.4$ runs) during feature-foraging was not significant, $t(20.4) = 1.29 \ p = .21$; Cohen's $d = 0.463$.

Table 2 summarizes the run behavior for each participant and also shows the pattern of random and non-random foraging across conditions. We note that although the number of runs clearly differs by condition according to group, the prevalence of random trials during conjunction-foraging is much less obvious. That is, even for our SF group, the majority of trials during conjunction-foraging appears to contain runs that are long enough to be classified as non-random. We have not seen this pattern in previous studies, and will return to this shortly. We also note that two participants (M11 & I15) hardly seemed to switch at all during either conjunction- or feature-foraging.

Figure 3 provides a summary of distance and time measures in the two conditions. Consistent with our previous findings, the distance
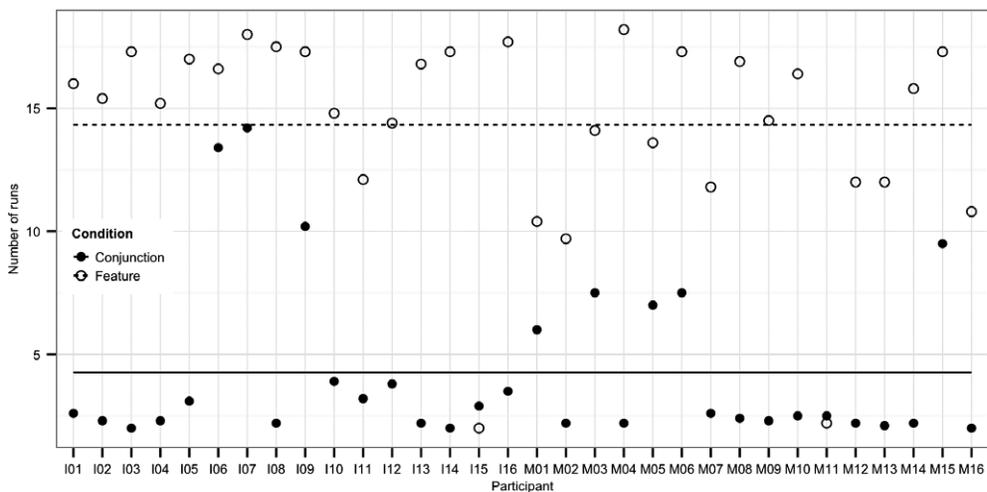
Figure 1 The figure shows the average number of runs for each participant in the feature and conjunction tasks. The dotted and solid horizontal lines represent the average number of runs in the feature and conjunction conditions, respectively.

traveled during conjunction-foraging (*Mean* = 6228 pixels; *SD* = 394 pixels) was significantly greater than during feature-foraging (*Mean* = 5056 pixels; *SD* = 508 pixels), $t(31) = 16.96$, $p < .001$; Cohen's $d = 2.998$. While there was only a difference of 135 pixels between foraging groups in the feature condition (*Mean*_SF = 4955 pixels; *SD* = 531 pixels; *Mean*_NF = 5090 pixels; *SD* = 508 pixels; $t(11.6) = 0.63$, $p = .54$; Cohen's $d = 0.259$), this increased to 370 pixels in the conjunction condition (*Mean*_SF = 5950 pixels; *SD* = 520 pixels; *Mean*_NF = 6320 pixels; *SD* = 303 pixels; $t(8.6) = 1.91$, $p = .09$; Cohen's $d = 0.87$). Although this latter difference did not reach significance, a glance at the effect size and at Figure 3B seems to suggest a clear trend for the majority of SF participants to gain a distance advantage, as we had found in our original study (Á. Kristjánsson et al., 2014).

Panels C and D of Figure 3 summarize completion time data. Participants were generally slower during conjunction-foraging ($M = 19.4$ s, $SD = 4.6$ s) than during feature-foraging ($M = 15.5$ s, $SD = 3.8$ s), as might be expected, $t(31) = 7.47$, $p < .001$; Cohen's $d = 1.32$. Group comparisons also revealed that in the conjunction condition, SFs (*Mean*_SF = 23.2 s; *SD* = 3.9 s) were on average 5 s slower than NFs (*Mean*_NF = 18.1 s; *SD* = 4.1 s), $t(12.6) = 3.2$, $p = .007$; Cohen's $d = 1.292$. There was no difference in completion times during feature-foraging (*Mean*_SF = 15.9 s, *SD* = 2.3 s; *Mean*_NF = 15.4 s, *SD* = 4.3 s), $t(22.8) = 0.39$ $p = .723$; Cohen's $d = 0.135$.

The consistent slowing for the SF group suggests that there is a cost associated with continuing to switch between target categories during conjunction-foraging. However, examination of Figure 3D indicates that while the SF group was consistently slower, there is considerable within-group variability and that the range of completion times overlaps with that of the NF group. This overlapping range of completion times was also observed in our original study.

WM Task

The digit span for the SF group (*Mean* = 54.6, *SD* = 25.9) did not differ from the NF group (*Mean* = 50.3, *SD* = 28.1), $t(12.9) = 0.405$, $p = .693$; Cohen's $d = 0.162$. Furthermore, as shown in Table 3, there was no significant correlation (all $ps > .2$) within the entire sample
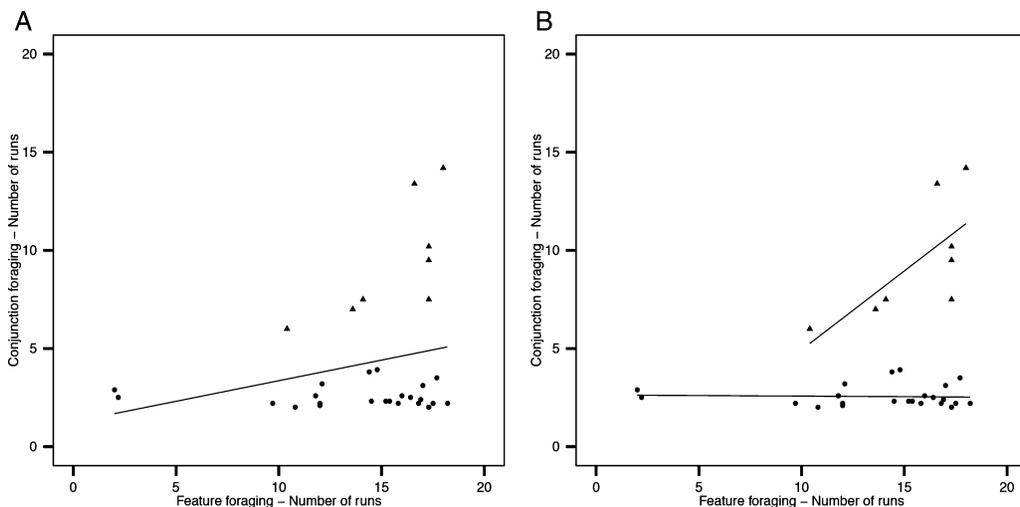
Figure 2 (A) The general relationship between foraging behavior in the feature and conjunction tasks. (B) The relationship between foraging in the feature and conjunction tasks for each group. The triangles represent the participants that were classified as super-foragers by our definition and the dots represent the normal-foragers.

Table 2 Summary of run behavior in the experiment for Malta (M) and Iceland (I)

Participant	Feature-foraging		Conjunction-foraging		Foraging group
	Mean runs	Non-random	*Mean* runs	Non-random	
M01	10.4	7	6.0	10	SF
M02	9.7	7	2.2	10	NF
M03	14.1	2	7.5	8	SF
M04	18.2	0	2.2	10	NF
M05	13.6	2	7.0	7	SF
M06	17.3	0	7.5	7	SF
M07	11.8	5	2.6	10	NF
M08	16.9	0	2.4	10	NF
M09	14.5	1	2.3	10	NF
M10	16.4	3	2.5	10	NF
M11	2.2	10	2.5	10	NF
M12	12.0	3	2.2	10	NF
M13	12.0	5	2.1	10	NF
M14	15.8	1	2.2	10	NF
M15	17.3	1	9.5	7	SF
M16	10.8	5	2.0	10	NF
I01	16.0	1	2.6	10	NF
I02	15.4	2	2.3	10	NF
I03	17.3	0	2.0	10	NF
I04	15.2	1	2.3	10	NF
I05	17.0	0	3.1	9	NF
I06	16.6	1	13.4	3	SF
I07	18.0	0	14.2	1	SF
I08	17.5	1	2.2	10	NF
I09	17.3	0	10.2	6	SF
I10	14.8	1	3.9	10	NF
I11	12.1	4	3.2	10	NF
I12	14.4	1	3.8	10	NF
I13	16.8	1	2.2	10	NF
I14	17.3	1	2.0	10	NF
I15	2.0	10	2.9	10	NF
I16	17.7	0	3.5	10	NF

Note. For each participant, we show the mean number of runs per trial in each condition, the number of trials classified as non-random (runs test, based on 10 trials), and whether individuals were classified as super (SF) or normal foragers (NF).

between the number of runs and digit span, either for conjunction- or feature-foraging (see Table 3).

Stroop Task

We found an overall Stroop interference effect (*Mean* = 7.5 s, *SD* = 5.4 s), one-sample-*t* (31) = 7.85, $p > .001$; Cohen's $d = 1.388$. The Stroop interference for the SF group (*Mean* = 6.7, *SD* = 5.8) was not different from that for the NF group (*Mean* = 7.8, *SD* = 5.4), $t(11.3) = 0.4677$, $p = .649$; Cohen's $d = 0.195$.

Finally, we examined whether there was any evidence of a relationship between run behavior and our individual difference measures across all participants. As Table 3 shows, none of the correlations approached significance.

Overall Relationship Between Number of Runs and Other Measures

Finally, we ran multiple regression separately for the feature and conjunction conditions. In these analyses, the number of runs was the dependent variable and the sample locations

Table 3 Correlation analyses for the whole dataset ($N = 32$)

Correlation between	r-value	t-value	df	p-value
Num runs feat vs. Stroop	−0.227	1.27	30	.212
Num runs conj vs. Stroop	−0.008	0.04	30	.965
Diff num runs vs. Stroop	−0.194	1.08	30	.287
Num runs feat vs. WM	0.135	0.74	30	.463
Num runs conj vs. WM	0.133	0.74	30	.467
Diff num runs vs. WM	0.020	0.11	30	.913

(Iceland vs. Malta), Stroop interference, and WM scores (digit span) were the predictor variables. Table 4 provides a summary of this analysis. Neither the model for the conjunction condition ($F(7, 24) = 0.73$, $p = .645$; adjusted $R^2 = −0.06$) nor that for the feature condition ($F(7, 24) = 1.64$, $p = .172$; adjusted $R^2 = 0.13$) were significant. As Table 4 shows, no predictor
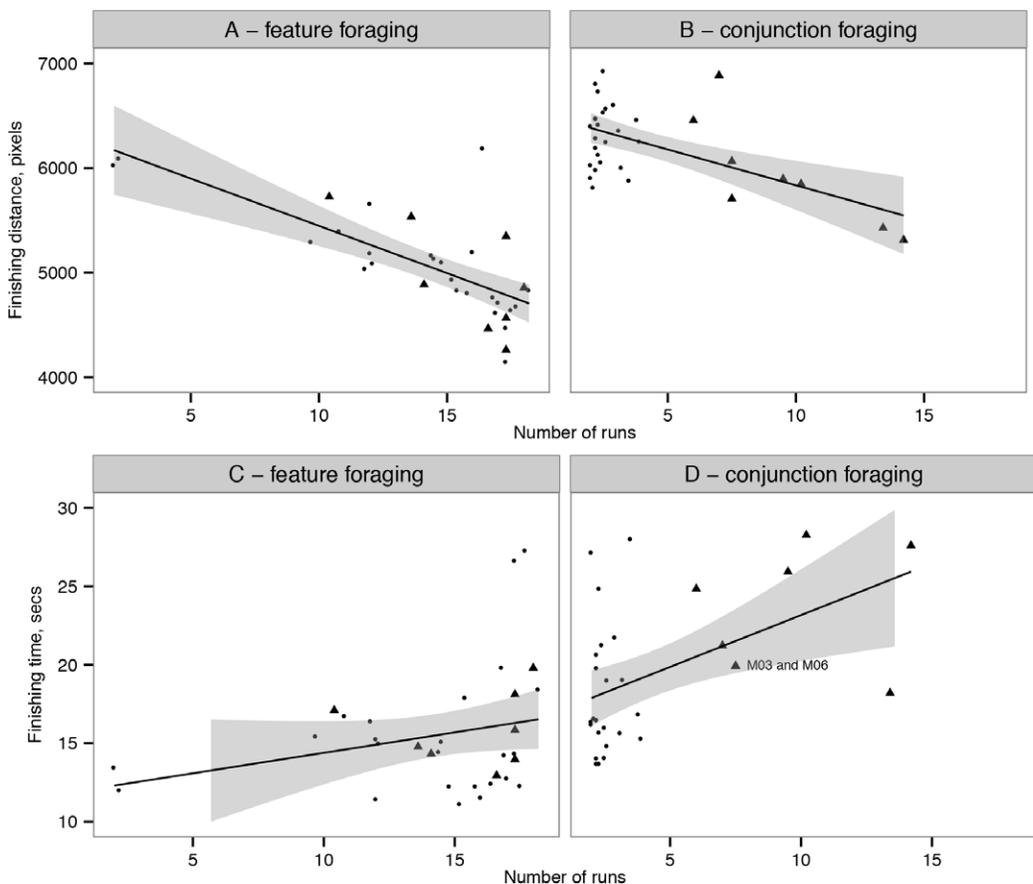
Figure 3 The relationship between the finishing distance and number of runs in the (A) feature and (B) conjunction conditions. The relationship between number of runs and finishing time in the (C) feature and (D) conjunction conditions. Note: The number of runs and finishing time for participants M03 and M06 were almost the same and their plot-symbols completely overlap in (D). The triangles represent the super-foragers and the dots represent the normal-foragers.

Table 4 Overview of the results from the multiple regression analyses

Factor	Task	Slope	SE	t-value	p-value
Intercept	Feature	15.899	3.938	4.037	<.001
Country	Feature	1.881	6.480	0.290	.774
Stroop	Feature	−0.009	0.383	−0.023	.982
WM	Feature	−0.013	0.055	−0.231	.819
Country:Stroop	Feature	−0.328	0.699	−0.469	.643
Country:WM	Feature	0.017	0.093	0.187	.853
Stroop:WM	Feature	0.001	0.006	0.112	.911
Country:Stroop:WM	Feature	−0.001	0.012	−0.733	.470
Intercept	Conjunction	5.281	0.351	1.447	.161
Country	Conjunction	−3.189	6.007	−0.531	.600
Stroop	Conjunction	−0.026	0.355	−0.074	.941
WM	Conjunction	−0.026	0.051	−0.517	.610
Country:Stroop	Conjunction	0.144	0.649	0.222	.826
Country:WM	Conjunction	0.093	0.086	1.087	.288
Stroop:WM	Conjunction	0.003	0.005	0.504	.619
Country:Stroop:WM	Conjunction	−0.010	0.011	−0.904	.375

Note. In these analyses we used the treatment contrast coding, which is default in *R* and Iceland was therefore the reference point for the categorical variable Country.

variables seem to contribute to the overall run behavior. Furthermore, since there are no significant effects in Table 4, we cannot expect that the predictor variables contribute to the observed difference in run behavior.

General Discussion

We have replicated our previous results of large differences in foraging behavior depending on whether targets are defined by a single feature or by a conjunction of features (Jóhannesson et al., 2016; Á. Kristjánsson et al., 2014). At the same time, a subset of observers showed similar patterns of foraging during feature- and conjunction-foraging, suggesting that they do not have the same difficulty switching during conjunction-foraging as the other participants. These individual differences in foraging performance, which again replicate our previous findings, clearly demand an explanation (Jóhannesson et al., 2016; Á. Kristjánsson et al., 2014).

Here, we examined whether individual differences in attentional control and/or WM capacity help determine such conjunction-foraging patterns. We hypothesized that participants who

showed less interference on the Stroop task would be more likely to switch between conjunction target categories as they would more easily overcome the current "primed" response during a run (Brascamp et al., 2011; Chetverikov & Kristjánsson, 2015). Similarly, we hypothesized that WM capacity might predict switching patterns, if greater capacity made it easier to hold and respond to more than one target template at a time (Jóhannesson et al., 2016; Á. Kristjánsson et al., 2014).

Our current data provided no support for either of these hypotheses. That is, when participants were classified—based on their conjunction-foraging behavior—as either SFs or NFs, there were absolutely no group differences in either Stroop interference or WM performance. Furthermore, correlation and regression analyses that included the whole dataset, irrespective of grouping, also showed no hint of a predictive relationship between these measures and run-based behavior. The current findings thus cast doubt on a strong, direct link between individual foraging patterns and more general attention and WM performance. However, several aspects of the current study require us to urge some caution before completely abandoning the notion of such a link.

First, in our attempt to statistically compare "groups" of participants, we may have been too liberal in our definition of "super-foraging." To recap, this grouping was based solely on the distribution of run-length behavior during conjunction trials. In both of our previous papers, this categorization clearly identified individuals with almost identical feature- and conjunction-foraging patterns (see Figure 2, Jóhannesson et al., 2016; Figure 4, Á. Kristjánsson et al., 2014). By contrast, in the current dataset, none of our SF participants used exactly the same number of runs in both feature and conjunction conditions, and more importantly, there was considerable variability in the difference between the number of feature versus conjunction runs within the SF group. For example, compare the run patterns of I06–I07 to those of M05–M06 in Figure 1 and Table 2. In addition to raising questions about the homogeneity of this group, this variability almost certainly contributes to the decrease in non-random runs, the marginal distance effects, and the slowing of completion times for the SF group noted in the results section.

Clearly, in future studies involving individual difference, it may be more appropriate to adopt a more conservative definition of SF behavior. This could be achieved in a number of ways. For example, by enforcing a specific distance between the number of runs in the feature versus conjunction conditions, by restricting selection based on random run behavior during conjunction trials, or by supplementing run behavior with other measures of foraging performance, such as more efficient use of space or a lack of obvious RT costs.

The above suggestions for grouping participants brings into focus the more general issue of defining SF behavior. To date, we have focused solely on run-based measures. That is, the "super" aspect of performance referred to the relatively rare tendency to "switch" with conjunction categories rather than an overall evaluation of "optimal" foraging performance. It is possible that by refining this definition to include additional foraging parameters, we might better identify more stable and/or measurable SF traits. One practical concern with

this suggestion is that within our typical sample of between 12 and 20 participants, this might only identify one or two individuals per study, making group comparisons impossible. Another approach might be to specifically pre-screen for SF behavior and/or revisit our previous participants' pools to re-test individuals who have already shown this behavior in the past.

The variability within the current SF group also raises a number of other interesting points. It suggests, for example, that switching behavior may not be all or none, but might vary, depending on, for example, task demands or strategy. Indeed, in several other studies from our group, we have observed such flexibility. For example, Jóhannesson et al. (2016) found that the same group of participants was much more likely to exhibit SF behavior when foraging with their eyes, than when foraging, as here, with their fingers. We noted that this argued against SF behavior being a fixed trait and suggested that in this particular case, eye gaze may be a more fluent, independent behavior than finger movement, consuming fewer resources, that can instead be allocated to support category switching.

We have also been exploring how imposing time limits on foraging can influence switching behavior (T. Kristjánsson, Thornton, & Kristjánsson, 2016; Thornton, Johannesson, & Kristjánsson, 2015). Typically, when response time is constrained, all participants are more likely to switch between categories, even during conjunction trials. Note importantly, that although it appears possible to encourage switching, for most observers, this is accompanied by greatly increased error rates and/or significant slowing of response times.

Does this potential flexibility in foraging style invalidate the current "individual differences" approach? We believe not. Rather, the question simply shifts to focus on strategy choice—for example, why do most people typically opt not to switch between categories during conjunction-foraging? Clearly there could be a strong strategic component. Individuals who exhibit SF behavior might, for example, feel compelled to follow the layout

of the display, to move systematically through the display in a preferred left-to-right or up-down direction. Conversely, our two observers (M11 & I15) who used long, exhaustive runs for both feature and conjunction conditions almost certainly did so as a strategic choice. But what influences these strategy choices? And how might individual abilities interact with any such choices?

We continue to believe that one major influence will be individual differences in cognitive ability. That is, most individuals—including the current authors—subjectively report that switching between conjunction target categories is effortful and feels more likely to produce errors. Indeed, some form of risk aversion might also influence strategy choice. In one recent variant of these tasks, we removed trial termination on the first error and this substantially increased the general incidence of switching during conjunction trials (Thornton, de'Sperati, & Kristjánsson, 2016).

To return to the issue of strategy choice and cognitive constraints, one aspect of our original dataset (Á. Kristjánsson et al., 2014) seems to neatly illustrate this point. The four SF individuals in that study appeared to use short runs very consistently across both feature and conjunction conditions (see Figure 4, Á. Kristjánsson et al., 2014). In contrast, those participants who generally used long, exhaustive runs (i.e., those that would be classified here in the NF group) did typically try to switch during conjunction-foraging on one or two trials out of 20, but seem not to have adopted switching. Our hunch was that these attempts at switching were felt to be too demanding or risky, and were quickly abandoned in favor of their usual strategy. Our point then, is that strategy choice may be directly affected by more general cognitive ability—as we have tried to investigate here—but clearly we need to examine this idea further in future studies.

The second issue that should be borne in mind when interpreting the current findings relates to our specific choice of attention and WM tasks. We were able to consistently

measure a Stroop effect, but this did not seem related to patterns of runs. Clearly, it is quite possible that other tasks might tap into aspects of attentional control that are more related to foraging. For example, in future studies, it could prove useful to concurrently measure standard conjunction search (Treisman, 1988), task-switching behavior (Hsieh, 2012), or to use tasks deigned to more generally assess attentional factors, such as the Attention Network Test (Fan, McCandliss, Sommer, Raz, & Posner, 2002). Similarly, rather than using digit span to assess memory capacity, we could use some form of visuospatial WM task or even a hybrid task, such as Multiple Object Tracking (Pylyshyn & Storm, 1988), which taps into both capacity limits and attentional control.

Finally, we should qualify the lack of correlation seen in the current study between run-based behavior and our attention and WM measures. We had included these as exploratory measures in recognition of the fact that our experimental groups were likely to be of unequal size and also in recognition of the fact that defining SF behavior might be difficult. Our idea was therefore to see if there was any sign of a relationship irrespective of grouping. We note, however, that our relatively small sample size ($N = 32$) does limit the conclusions that we should draw. For example, our a priori power analysis (assuming standard Type I and Type II error rates of 0.05 and 0.2, respectively) indicated that our design might only expect to find significant effects for relatively strong correlations, specifically those approaching $r = 0.5$ (Lachin, 1981). This was acceptable as our main interest was to determine whether attentional control and WM capacity strongly influenced run-based behavior. Perhaps of more concern, however, is that with such a small sample size, the precision of such an observed effect (i.e., $r = 0.5$) might be very poor (i.e. confidence intervals could be ±0.3; Moinester & Gottfried, 2014). In short, we should acknowledge that our design may not have had the sensitivity to detect relatively subtle relationships between our variables of interest, and it remains a possibility that such links do exist.

Theoretical Implications, Related Findings, and Future Directions

The general pattern of switching between target categories noted here and in our previous work may be problematic for theories of WM and attention that propose that only one feature value (such as, say, one color value) can be stored in WM at any given time (Huang & Pashler, 2007; van Moorselaar et al., 2014; Olivers et al., 2011). That is, rapid switching between target types, as almost all observers exhibit during feature-foraging and quite a few during conjunction-foraging, is inconsistent with the predictions of these theories unless such switching between WM representations can be very fast and with minimal cost. Measuring how rapidly switching between memory templates can occur would therefore be valuable.

As mentioned in the introduction, the current work can be seen as a contribution to a small, but rapidly growing, literature on human foraging (Cain et el., 2012; Jóhannesson et al., 2016; Á. Kristjánsson et al., 2014; Smith et al., 2008; Wolfe, 2013). A study by Wolfe, Aizenman, Boettcher, and Cain (2016) deserves particular mention as it replicates our initial report that humans, like other species, forage in "runs" when presented with multiple targets (Á. Kristjánsson et al., 2014). To our knowledge, only a handful of previous studies have explicitly measured run-like behavior in this way (i.e., Bond, 1983; Dawkins, 1971; Á. Kristjánsson et al., 2014). Wolfe et al. (2016) used a "hybrid foraging search" paradigm, that combines search of the contents of memory and foraging. They found that not only is performance biased toward the previous target type, but, in addition, memory has been reconfigured such that a repeated target type can be confirmed faster than a new target type. Selection within runs is therefore more efficient than during switches (see also Jóhannesson et al., 2016).

Unfortunately, Wolfe et al. (2016) did not discuss the question of individual differences, so the possible existence of "super-foragers" in their task remains an open question. They did, however, address another important aspect of foraging. That is, Wolfe et al. (2016) also measured at what point observers leave the search area—to go into an area that may have higher target yield. In our task, observers had to finish all targets. Clearly, this manipulation could easily affect within-trial strategies and studies are currently under way in our laboratory to directly address this question.

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