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Foraging tempo: Human run patterns in multiple-target search are constrained by the rate of successive responses

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Abstract

Human foraging tasks are beginning to provide new insights into the roles of vision, attention, and working memory during complex, multiple-target search. Here, we test the idea that "foraging tempo"—the *rate* of successive target selections—helps determine patterns of behaviour in these tasks. Previously, we established that the majority of target selections during unconstrained foraging happen at regular, rapid intervals, forming the "cruise phase" of a foraging trial. Furthermore, we noted that when the temporal interval between cruise phase responses was longer, the tendency to switch between target categories increased. To directly explore this relationship, we modified our standard iPad foraging task so that observers had to synchronise each response with an auditory metronome signal. Across trials, we increased the tempo and examined how this changed patterns of foraging when targets were defined either by a single feature or by a conjunction of features. The results were very clear. Increasing tempo systematically *decreased* the tendency for participants to switch between target categories. Although this was true for both feature and conjunction trials, there was also evidence that time constraints and target complexity interacted. As in our previous work, we also observed clear individual differences in how participants responded to changes in task difficulty. Overall, our results show that foraging tempo does influence the way participants respond, and we suggest this parameter may prove to be useful in further explorations of group and individual strategies during multiple-target search.

Keywords

Foraging; foraging tempo; visual search; attention; multiple-target search; temporal constraints; individual differences

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Introduction

In a recent series of studies, we have used a range of twodimensional (2D; e.g., Jóhannesson et al., 2016, 2017; Á. Kristjánsson et al., 2014; T. Kristjánsson et al., 2018; Thornton et al., 2019) and three-dimensional (3D; T. Kristjánsson, Draschkow, et al., 2020; Prpic et al., 2019) cancellation tasks to explore human foraging under conditions of varying attentional load. This work was directly inspired by the animal foraging literature (Dawkins, 1971; Heinrich et al., 1977; Jackson & Li, 2004; Pietrewicz & Kamil, 1979; Tinbergen, 1960). In our tasks, we extended the classic human visual search paradigm—where participants are typically asked to locate a single target item embedded within a variable set size of distractor items (Hulleman & Olivers, 2017; A. Kristjánsson & Egeth, 2020; Treisman & Gelade, 1980; Wolfe, 2010; Wolfe & Horowitz, 2004, 2017)—to include situations where multiple targets from different categories must be located on each trial. Several other groups have also explored multiple-target search (e.g., Cain et al., 2012; Fougnie et al., 2015; Gilchrist et al., 2001; Hills et al., 2012, 2013; Pellicano et al., 2011; Wolfe, 2013; Wolfe et al., 2016, 2019). The common goal of such work is to better understand the relationship between vision, attention, and action in complex scenarios (see Á. Kristjánsson et al., 2019, for a recent discussion).

In our original iPad task (Å. Kristjánsson et al., 2014)—which also forms the basis of the current experimental

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work—participants were required to use their finger to touch and thus cancel 40 target items on each trial. There were always 20 targets from two different categories, randomly distributed among 40 distractor items from two other categories. The main finding was a clear difference in patterns of foraging "runs" when the individual target items were defined by a single feature (e.g., colour; feature conditions/foraging) versus a combination of features (e.g., colour and shape; conjunction conditions/foraging). A "run" in this context simply refers to a sequence of selections from the same target category.

During feature foraging, all participants switched randomly between the two target categories, producing many short-run sequences. During conjunction foraging, in contrast, the majority of participants only produced two runs, with all targets from one category being cancelled before the other. We interpreted this "exhaustive" category selection as indicating that under higher attentional load, these participants were unable or unwilling to switch rapidly between search templates, a phenomenon also discussed in the literature on animal foraging (Bond, 1983; Dawkins, 1971; Dukas & Ellner, 1993; Kamil & Bond, 2006; Tinbergen, 1960). In our original data set, we also noted that approximately 25% of participants did not show exhaustive category selection, but rather continued to switch randomly during conjunction foraging. We termed these individuals "super-foragers" as they seemed immune to the increase in attentional load. The existence of these two basic foraging profiles—and the approximate 75/25% split—has been replicated several times (e.g., Clarke et al., 2018; Jóhannesson et al., 2017), and we return to this interesting individual difference later in this article.

In subsequent studies, we also identified two other aspects of foraging behaviour that form the starting point for this study. First, examination of intertarget times (ITTs) revealed that the majority of selections happen at very regular intervals, forming what we termed the "cruise phase" of a trial (T. Kristjánsson, Thornton, et al., 2020). This regularity is interrupted only at the very start (see also Basoudan et al., 2019; Thornton & Horowitz, 2004, 2020), end, and midpoint (for conjunction trials) of a trial, where response times are significantly slowed relative to the cruise phase (see T. Kristjánsson, Thornton, et al., 2020, for details).

Second, the absolute rate of selection during the cruise phase—the "foraging tempo"—appears to impose important constraints on the pattern of runs. Specifically, by analysing several previous studies from our own group and others, Thornton et al. (2019) described a clear pattern where task variants that permitted rapid ITTs (e.g., <400 ms/item) were accompanied by a reduced tendency to switch during conjunction trials (e.g., Jóhannesson et al., 2016; Á. Kristjánsson et al., 2014; T. Kristjánsson, Thornton, et al., 2020). Conversely, those task variants where ITTs were relatively long (e.g., >700 ms/item) gave rise to an increased tendency to switch (Clarke et al., 2018;

Prpic et al., 2019; Thornton et al., 2019). These findings suggest that template complexity and temporal constraints interact to jointly determine foraging patterns. In particular, the exhaustive run behaviour found with our original iPad task may not have been solely a consequence of template complexity, but could also have relied on the fact that participants were responding rapidly.

The general idea that "search rate" can affect foraging patterns has a long and sometimes controversial history within the animal behaviour literature (Bond & Riley, 2010; Gendron & Staddon, 1983; Guilford & Dawkins, 1987, 1989a, 1989b; Hollis, 1989; Lawrence, 1989; Plaisted & Mackintosh, 1995; Reid & Shettleworth, 1992). It is generally accepted that, by searching more slowly, an animal can increase the probability of detecting prey, particularly if the prey are cryptic (Gendron & Staddon, 1983). However, precisely how search rate modulates patterns of runs and how it interacts with other constraints on foraging—such as attention (Dukas & Ellner, 1993), search images/templates (Guilford & Dawkins, 1987; Plaisted & Mackintosh, 1995), or learning (Troscianko et al., 2018)—remains less clear. For example, although search rate is incorporated into the "attentive prey" model of Dukas and Ellner (1993), their implementation assumes "that there is no interaction between search rate and attention, and that the total amount of attention devoted for foraging is constant regardless of the search rate" (p. 1339).

Here, we suggest that a useful framework that may shed further light on this relationship—and foraging tempo more generally—is the "soft constraints" approach proposed by Wayne Gray and colleagues (Gray & Boehm-Davis, 2000; Gray & Fu, 2004; Gray et al., 2006). Before describing this approach, we should note that, in the remainder of this article, we will continue to use the term "foraging tempo" to discuss temporal patterns during foraging, rather than "search rate," as we feel the former better captures the regular response patterns in multiple-target tasks and avoids confusion with temporal estimates from traditional single-target studies (Hulleman & Olivers, 2017; A. Kristjánsson & Egeth, 2020; Treisman & Gelade, 1980; Wolfe, 2010; Wolfe & Horowitz, 2004, 2017). While the term "foraging tempo" has been used previously in the animal literature to refer to global rates of return to a nest or hive (e.g., Burkhardt, 1998; Davidson, 1997; Dyer & Seeley, 1991; Oster & Wilson, 1978), we believe the context should clearly disambiguate this usage from the current meaning.

According to Gray and colleagues then, in any interactive task, a series of soft constraints govern the trade-off between low-level cognitive, perceptual, and motor operations (Gray & Boehm-Davis, 2000; Gray & Fu, 2004; Gray et al., 2006). Central to this approach is the idea that "the control system selects sequences of interactive routines that tend to minimize performance costs measured in time while achieving expected benefits" (Gray et al., 2006, p. 463). For any given task, the limiting factor(s) in

terms of time could be cognitive, perceptual, or motor operations. If rapid motor responses are possible, for example, the limiting stages may involve perceptual or cognitive operations, and constraints may be imposed on these to ensure that additional time costs are not incurred. If, on the contrary, motor responses cannot be made rapidly for some reason, the temporal bottleneck will no longer occur at the cognitive and/or perceptual stages, and constraints on the nature of the operations selected at these levels might be relaxed.

Applying these ideas to our previous findings, when using the iPad to respond, the temporal cost of cognitively switching between different conjunction templates might approach or exceed the minimum possible movement time. To avoid an increase in performance costs, constraints are applied at the cognitive level to ensure that selected operations can be completed well within the interval dictated by the motor system. Specifically, switching or activation is minimised, and a single template remains active until all targets of that category have been selected. In task variants where overall response rates are slower, however, either due to the need to navigate between target areas (Prpic et al., 2019) or because responses are being made via the mouse/keyboard rather than a touchscreen (Clarke et al., 2018; Thornton et al., 2019), conjunction template operations may not have been a limiting factor. That is, if switching between conjunction templates can be achieved within the time limit dictated by slower motor operations, then the soft constraints on the use of such a strategy may be relaxed.

The goal of this article was to directly test this foraging tempo hypothesis using a single-task variant where operations at each level (i.e., cognitive, perceptual, & motor) were held constant as we systematically varied response rate. We had participants forage through displays that were identical to those in our original iPad paper (Á. Kristjánsson et al., 2014), with the same basic success (cancel all targets from both categories) and failure (the trial terminated if a distractor was selected) criteria. However, we now also required participants to synchronise their cruise phase responses with an auditory metronome signal generated by the app. In all experimental blocks, this tempo was initially set at a moderate rate with an 800 ms ITT between required responses. Across trials, the metronome tempo adapted to performance, with the gap between responses decreasing by 25 ms after 40 correct responses (i.e., a correct foraging trial) and increasing by 25 ms after two error trials. Errors were now also generated if participants deviated from the prescribed foraging tempo, by going either too fast or too slow (see "Methods" section for details). The tempo constraints were relaxed at the start and end of the trial to account for non-cruise phase periods of responding.

As we were particularly interested in how tempo might modulate the ability to switch, we made one further important change to our usual procedure. Rather than leaving participants completely free to choose their foraging strategy, we specifically encouraged them to select targets in a "spatially efficient" manner. That is, we asked them to avoid using exhaustive runs—where they would need to pass through the display at least twice—and to try and select all locally available targets until the increasing tempo made such switching impractical. Thus, we actively encouraged participants to switch between target categories. At very slow tempos, both our review of previous studies (Thornton et al., 2019) and the soft constraint analysis described above (Gray et al., 2006) suggest that adopting such a strategy would be possible under both feature and conjunction conditions. Our primary question was whether switching could be maintained as the tempo increased and how this would vary as a function of condition.

We had two clear predictions. First, that the tendency to switch between target categories would generally reduce as foraging tempo increased. Second, that the influence of foraging tempo would be more pronounced during conjunction foraging than during feature foraging.

Methods

Participants

A total of 12 participants ($M_{\rm age} = 25$ years, SD = 5.4; 10 female; 11 right-handed) were recruited from the University of Iceland and the National Research University academic communities. Group sample size was determined prior to data collection and a detailed power analysis is provided below. All participants had normal or corrected-to-normal vision, were naïve as to the purpose of the research, and gave written informed consent before taking part in the experiment. All methods and procedures conformed to the Ethics and Data Protection Guidelines of the University of Malta, University of Iceland, and National Research University.

Equipment

The stimuli were displayed on an iPad Air (Model A1474) with screen dimensions of 20×15 cm (24.6 cm diagonal) and an effective resolution of 1024×768 pixels at 132 ppi. The iPad was placed on a table in front of the participant in landscape mode. As viewing distance could only be approximately estimated at 50 cm, we report stimulus measures in both pixels and degrees visual angle. Stimulus presentation and response collection were carried out by a custom iPad application written in objective-C using Xcode and Cocos2d libraries.

Visual stimuli

The visual displays were identical to those described in our original iPad study (see Á. Kristjánsson et al., 2014, for details). Each trial presented a display containing 80 items

randomly positioned within a $15 \times 12\,\mathrm{cm}$ (approximately $17.1 \times 13.7^\circ$) central viewing area. The overall layout was an invisible 10×8 grid, although individual items were jittered to reduce the sense of regularity. Gaps between rows and columns ensured that items never approached or occluded each other. In feature displays, the targets were red and green discs (20 pixels/ 0.46° visual angle) and the distractors were yellow and blue discs (counterbalanced across participants). In conjunction displays, the targets were red squares and green discs and the distractors were green squares and red discs (again counterbalanced). There were always 20 stimuli in each group, drawn on a black background. The overall spatial layout and the location of targets and distractors were generated independently on every trial.

Tempo manipulation

As soon as the visual display for each trial appeared, the auditory tempo cue also began. This consisted of a short (100 ms), high-frequency (fundamental freq=2.4 kHz) mechanical tick, modelled on the sound used in Apple's "Hello Metronome" sample developer application. The sound was repeated at a regular temporal frequency, which varied across trials. Note that the selection of this particular tone was arbitrary, and we explored several sounds, selecting one that was minimally invasive, but clearly detectable at all temporal frequencies. The sound file is available on the Open Science Foundation (OSF) page associated with this article at https://osf.io/ej97c/

During familiarisation, the tempo for both conditions used an ITT of 1 s, intentionally very slow to give participants practice in synchronising their responses. For both the feature and conjunction experimental blocks, the initial tempo used an ITT of 800 ms. After each correct trial (i.e., 40 correct responses), the ITT was reduced by 25 ms, so that the tempo gradually increased as the block of trials progressed. If participants had two consecutive error trials, the ITT was increased by 25 ms, slowing the tempo back into a range where successful trials had already been completed. Note that if participants completed all 25 trials without error, the final tempo would involve an ITT of 175 ms, which is almost certainly beyond human response rates. In reality, the fastest correct trial recorded had an ITT of 225 ms.

As our goal was to encourage participants to forage in synch with the metronome, rather than to directly measure the absolute temporal precision of their responses, we took a liberal approach when judging their adherence to the tempo. Beginning with the first correct selection, the app maintained a count of expected responses, incrementing the count with each auditory signal. This expected count was compared with the actual count of correct selection touches. If the actual count exceeded the expected count by more than 3, participants were judged to be responding too quickly. If the actual count lagged behind the expected

count by more than 5, they were judged to be responding too slowly. We penalised faster responding more stringently to minimise any attempts to anticipate the auditory tone. Effectively, then, participants had the entire ITT period in which to make a response that was considered temporally correct, with this period shrinking as the tempo increased. Under this scheme, it would be possible for participants to speed up and slow down within a trial to keep the actual and expected counts synchronised. While a within-trial analysis of precision might well identify such behaviour, here, we looked only at the correlation between expected and actual ITTs collapsed across trials as an indicatory of whether participants were attempting to adhere to the requested tempo (see "Results" section).

Procedure

The task was to cancel all target items by tapping on them, while avoiding distractor items. Targets disappeared immediately following the tap. If participants selected one of the distractors, the trial ended, an error message was given, and a new trial started. As already noted, we encouraged participants to switch between target categories, cancelling items in one local area, before proceeding through the display. This was suggested as a "spatially efficient" strategy and was not enforced in any way. We also made it clear to participants that such a strategy might become impractical as tempo increased.

Participants were instructed to pay attention to the auditory tempo cue at the start of each trial and to only begin responding once they had registered the new tempo. They were told to synchronise their responses to stay exactly in time with the auditory cue. If the cancellation rate ever exceeded the auditory tempo, the trial was terminated. Similarly, if the response rate lagged behind the tempo, the trial was also terminated. These tempo validation checks only began after the first response, allowing the participant to become familiar with the tempo, and were not implemented for the last five items, to take into account expected end-peaks in the response time functions (T. Kristjánsson, Thornton, et al., 2020). Each participant completed 25 trials of each condition (in counterbalanced order). One trial refers to a completed trial where all 40 targets have been cancelled.

Power analysis

As noted above, our sample size (N=12) was determined prior to data collection and was chosen to match previous studies from our group (e.g., Á. Kristjánsson et al., 2014; T. Kristjánsson, Thornton, et al., 2020; Thornton et al., 2019). Closely following the method adopted by Thornton et al. (2019), we conducted an a priori analysis to verify that this sample size provided sufficient power to detect within-subject differences between feature and conjunction foraging. Specifically, examination of the effect sizes

in two previous studies (Jóhannesson et al., 2017; Á. Kristjánsson et al., 2014) yielded Cohen's d_z calculations of 2.3 and 1.6, for the difference between the number of feature and conjunction runs. Using G*Power 3.1.9.4 (Faul et al., 2007), with assumed power of 0.95 and an alpha of .05, these effect size estimates suggested sample sizes of five and eight participants, respectively.

As in Thornton et al. (2019), we opted to be conservative and run an additional four participants relative to the sample size suggested by the smaller effect size estimate. We did this as we believed smaller sample sizes might mask expected individual differences in other aspects of run behaviour. We were also unsure of the impact of tempo on the basic feature/conjunction manipulation. Although the decision to run more participants than suggested by the a priori analysis could increase false discovery rates, as we had powered for an effect that has been replicated many times, we did not consider this a concern (e.g., Clarke et al., 2018; Á. Kristjánsson et al., 2014; Wolfe et al., 2019). Similarly, although using a more conservative expected power estimate of 0.8, rather than 0.95, may have been more appropriate, with the relatively large effect sizes from the previous studies, this would only have shifted sample size estimates down by one or two participants at most.

Subsequent to data collection, we also examined whether a different approach to a priori power analysis would have substantially altered our sample size estimates. As described by Anderson et al. (2017), the "Bias and Uncertainty Corrected Sample Size" (BUCSS) toolbox uses the reported F values and total sample size from previous factorial studies—rather than derived estimates of effect size—to generate necessary sample sizes for planned studies. As well as allowing the researcher to more easily focus on effects of interest (e.g., interactions), as the name indicates, BUCSS also corrects for other issues that can lead to underpowered studies (Anderson et al., 2017).

Here, we chose the previous study from our group (T. Kristjánsson et al., 2018) that most closely matched the current factorial design, while also involving temporal manipulations. That study included a 2 (Condition: feature/conjunction) \times 4 (Time Limit: 20, 40,60, 80) repeated measures analysis of variance (ANOVA) and had a sample size of 17. Of most interest in the current context was the significant Condition \times Time Limit interaction, $F(2.2, 33.1) = 9.4, p < .001, \eta_p^2 = .39$.

We used this F value, along with the sample size and alpha parameter from T. Kristjánsson et al. (2018) as the basis for conducting a priori analysis using the BUCSS ss. power.wa function. We made use of the default settings of assumed alpha for the planned study=.05, level of assurance=0.8, and desired power of 0.8. We specified the main factorial design of the current experiment—2 (Condition) \times 5 (Tempo)—and identified the interaction as the effect of interest. This analysis yielded a necessary sample size of 10 participants, closely approximating our original choice.

Data analysis

Data from one participant (P9) were excluded from the main analysis as they were unwilling or unable to switch between target categories, even at the very slowest tempos. Their pattern of responses was thus completely different from any other participant, and we therefore treated them as an outlier. For the sake of completeness, we present their data during the evaluation of individual differences and further discuss possible reasons for their approach to the task. The data analysis steps outlined below were thus applied to the data for the remaining 11 participants.

The staircase method we adopted was designed to steadily increase the tempo as each block of trials progressed, up to a performance limit where successive responses could no longer be made accurately, a limit which was expected to vary from participant to participant. As an initial check to verify that participants were accurately adhering to the tempo prescribed on each trial, we first compared the requested and observed ITT as a function of Tempo and Condition. In addition to reporting the slope of these functions (i.e., correlation coefficients), we also calculated the average offset between requested and observed ITT, collapsed across Tempo. This should provide a clear indication of any consistent response delay, as a function of Condition. We used separate paired sample t tests to compare the slope and offset measures across Condition. We also used onesample t tests to assess whether offset measures were significantly different from zero.

Next, to more concisely summarise patterns across blocks, we binned the 25 trials into five consecutive temporal bins. As each participant only completed one block per condition, dividing the tempo range into five sections with five repetitions per bin also allowed us to better characterise average performance within a given tempo range. To confirm that these bins captured the increase in foraging speed, we conducted a 2 (Condition) \times 5 (Trial Bin) repeated measures ANOVA on the average tempo values themselves.

Although error rates were expected to be low, given the nature of the staircase procedure, they would also be crucial in determining the overall tempo profiles. Errors could result either from incorrect category selection or from failing to maintain the designated tempo. We thus used a 2 (Condition) \times 2 (Error Type) repeated measures ANOVA to examine the error rates.

Our main analyses concerned patterns of run behaviour. A "run" in this context simply refers to a sequence of selections from the same target category. Here, we focus on three specific characteristics of run behaviour: (1) the average number of runs per trial; (2) the average run length per trial; and (3) the proportion of trials within a block where run behaviour would be classified as nonrandom. We briefly discuss each of these in turn.

When participants select randomly from two target categories, the total number of runs on a given trial should

equal approximately the total targets divided by 2. Fewer runs per trial suggest participants are limiting selections based on category identity. As noted above, in our previous studies (Jóhannesson et al., 2016, 2017; Á. Kristjánsson et al., 2014), participants typically selected targets at random during feature foraging but used exhaustive category selection (i.e., only two runs) during conjunction foraging trials. Here, we were specifically interested in how the number of runs changed as tempo increased.

The second characteristic of interest is the average run length on a given trial (total targets/number of runs). In our task, with a fixed number of targets on every trial, the average run length varies nonlinearly as an inverse proportion of the number of runs. For equal increments in the number of runs across trials, there is thus a larger increase in run length when there are fewer runs than with many runs. This nonlinearity has the potential to emphasise foraging patterns that are less obvious when only examining the number of runs. For example, previously, we have found it to be a useful indicator of individual differences (e.g., Á. Kristjánsson et al., 2014; Figure 4). We include it here as an additional probe into the nature of foraging tempo.

As an aside, the *variability* of run lengths within a trial may prove to be a particularly interesting measure to explore in future studies, in addition to or instead of the average run length. For example, with the current overall set size of 40 targets, a trial in which the two target categories are selected in four runs (i.e., T1, T2, T1, T2), the run lengths might be [8, 10, 12, 10] or [10, 10, 10, 10] or [5, 18, 15, 2], and so on. In each of these cases, the number of runs would be 4, and the average run length would be 10. However, the standard deviation would vary widely. For the sake of brevity, we do not report this measure here—there was no qualitative difference compared with average number of runs in current scenario—but we believe this observation may prove useful in future work.

Finally, although the relationship between number of runs and total targets can provide a useful heuristic to indicate whether participants select randomly from available target categories, there are additional techniques, such as the one-sample runs test (Dawkins, 1971; Á. Kristjánsson et al., 2014) or random simulation (Wolfe et al., 2019), which can provide more precise quantitative measures. Here, we followed the method previously described in Á. Kristjánsson et al. (2014) to classify each individual trial. Specifically, we applied the one-sample runs tests to each individual trial, conducting 25 separate analyses per participant and using Bonferroni correction to adjust the level of alpha for multiple tests (i.e., p < .002). We then quantified the proportion of trials of that were nonrandom at this corrected alpha level for each participant.

For each of the above run measures, we conducted two basic analyses. First, to capture overall changes in behaviour as tempo increased and to directly measure differences between feature and conjunction trials, we used the same 2 (Condition)×5 (Trial Bin) repeated measures

ANOVA described for the tempo data. Second, to more precisely measure the *change* in run behaviour as a function of tempo, we used linear regression to fit the data of individual participants. We report the average slopes of the Run Pattern \times Tempo Functions and compare them across condition using paired-samples t tests. Note that as an initial examination of feature/conjunction block order showed no influence on any measures, we did not include this factor in our main analysis. Block order is recorded in the demographics information provided in the OSF Supplementary Material along with the raw data.

Results

Figure 1a plots the relationship between requested and observed ITT across the whole tempo range as a function of Condition. It seems clear that participants adjusted their responses to stay in step with the required tempo. The correlation for both feature (r=.99) and conjunction (r=.98) conditions was almost perfect, and there was no difference between the slopes of these essentially parallel lines, t(10) = 0.38, ns (Figure 1b). However, both of these functions are shifted, indicating the presence of response delays. Specifically, the average observed ITTs for both the feature, $M=9.3 \,\mathrm{ms}$, SE=0.89, t(10)=10.5, p<.001, and conjunction, M=37.1, SE=3.2, t(10)=11.5, p<.001, conditions were significantly longer than the requested ITTs (Figure 1c). There also appears to be fairly constant offset between them of approximately $28 \,\mathrm{ms}$, t(10) = 8.7, p < .001. Thus, although participants were able to adjust their ITTs as a function of Tempo in both conditions, they did so with varying levels of precision. The relatively constant increase in observed ITTs across tempo, and the clear difference between feature and conjunction conditions, suggests the source of these offsets may relate to the attentional demands of target detection, rather than tempo reproduction per se, although additional analysis—looking at tempo precision within trials—would be required to shed further light on this issue.

As described earlier, for the remainder of our analyses, we condensed the full tempo range by averaging the responses of each participant into five consecutive temporal bins. We first wanted to verify that binning in this way still captured changes in tempo across each block of trials. Figure 2 shows how the average ITT systematically decreased across trial bin as expected, given the tempo staircase design. Note that the raw staircase data for each participant can be found in the OSF Supplementary Material. Although there were main effects of both Condition, F(1, 10)=24.2, p<.01, mean square error (MSE)=0.007, η_p^2 =0.71, and Trial Bin, F(1.8, 18.0)=1,018, p < .001, MSE=0.001, $\eta_p^2 = 0.99$, these must be evaluated in the context of a significant Condition × Trial Bin interaction, F(1.6, 16.3) = 27.6, p < .001, MSE=0.001, $\eta_n^2 = 0.73$. From the same initial starting point, participants were able to reach consistently faster final (i.e., Bin 5) tempos during

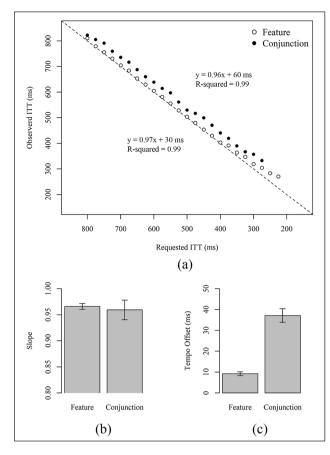


Figure 1. (a) Relationship between Requested and Observed ITT as a function of Tempo and Condition, averaged across participants; (b) Average Slope of the Requested \times Observed ITT Function; and (c) Average Offset of the Requested \times Observed ITT Function. Error bars represent standard error of the mean.

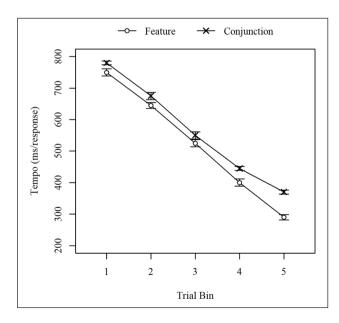


Figure 2. Foraging tempo as a function of trial bin, averaged across participants. Error bars represent standard error of the mean.

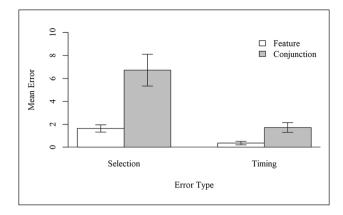


Figure 3. Average number of errors per block, classified by error type and experimental condition. Error bars represent standard error of the mean.

feature (M=284 ms/item, SE=5), as compared with conjunction (M=423 ms/item, SE=20), blocks of trials.

The shallower tempo slope during the conjunction condition suggests that participants made more errors during these trials, and this is confirmed in Figure 3. There was a main effect of Condition, with far fewer total errors during feature (M=1.0, SE=0.14) than conjunction foraging (M=4.2, SE=0.58) trials, F(1, 10)=35.6, p < .001, $MSE = 3.2, \eta_p^2 = 0.78$. There was also a main effect of Error Type, with more category selection errors (M=4.2, SE = 0.79), than tempo-related errors (M = 1.0, SE = 0.25), $F(1, 10) = 10.3, p < .01, MSE = 10.5, \eta_p^2 = 0.51.$ Both of these main effects need to be interpreted within the context of the significant Error Type × Condition interaction that can be clearly seen in Figure 3, where the overall pattern of errors is dominated by the selection errors during conjunction condition, F(1,10)=6.2, p<.05, MSE=6.2, η_p^2 =0.38. Note that the error rates reported in Figure 3 are for the entire block of trials, not per trial. As overall error rates were so low—a finding consistent with our previous studies—it was not feasible to examine possible speed–accuracy trade-offs as a function of tempo.

Figure 4 illustrates the relationship between the average number of runs and average tempo within each trial bin for both feature and conjunction conditions. There are three clear patterns. First, the number of runs consistently reduces as tempo increases in both feature and conjunction conditions. Second, participants appear to use substantially more runs during feature foraging than conjunction foraging, even at the slowest tempo, a difference maintained across all subsequent trial bins. Third, there is noticeably more variability in performance during conjunction foraging compared with feature foraging, both in terms of average number of runs and average tempo within a given trial bin. We return to these individual differences shortly.

The 2 (Condition) × 5 (Trial Bin) ANOVA used to examine changes in the number of runs during the course of a block confirmed these observations. There was a main

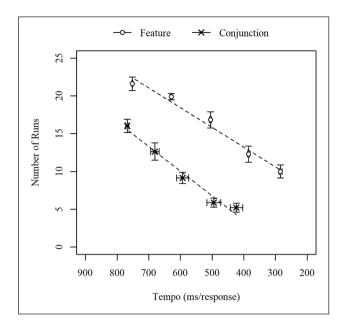


Figure 4. Scatterplot showing the relationship between average number of runs and average tempo in each of the trial bins. Data are plotted for both the feature (open symbols) and conjunction (closed symbols) conditions. Dashed lines are bestfitting linear slopes. Error bars represent standard error of the mean in both dimensions.

effect of Condition, with more runs during feature foraging (M=16.1, SE=0.49) than conjunction foraging $(M=9.8, SE=0.48), F(1, 10)=122.6, p<.001, MSE=9.1, <math>\eta_p^2=0.93$. There was also a main effect of Trial Bin, $F(4, 40)=58.3, p<.001, MSE=8.4, \eta_p^2=0.85$. The Trial Bin × Condition interaction, however, was not significant, F(2.4, 24.4)=1.0 (ns), $MSE=12.2, \eta_p^2=0.09$. Consistent with this latter finding, and the average trend line shown in Figure 4, our slope analysis indicated that there was no difference in the rate of reduction in the number of runs as a function of tempo between the feature (M=-2.63 runs/100 ms, SE=0.33) and conjunction (M=-3.22 runs/100 ms, SE=0.38) conditions, t(10)=1.5 (ns).

Figure 5 shows the pattern of run length data. There was a main effect of Condition, F(1, 10) = 40.0, p < .001, MSE = 6.3, $\eta_p^2 = 0.8$, with consistently shorter run lengths during feature foraging (M = 3.3, SE = 0.25) than conjunction foraging (M = 6.4, SE = 0.45). There was also a main effect of Trial Bin, F(1.6, 15.8) = 31.5, p < .001, MSE = 10.9, $\eta_p^2 = 0.76$. In contrast to the number of runs, here there was a significant Condition × Trial Bin interaction, F(1.9, 18.7) = 4.2, p < .05, MSE = 8.9, $\eta_p^2 = 0.3$. Direct comparisons of the Run Length × Tempo slopes confirmed that there was a more rapid increase in run length during conjunction (M = 2.37 items/100 ms, SE = 0.5) than feature (M = 0.08 items/100 ms, SE = 0.02) blocks, t(10) = 3.4, p < .01.

Figure 6 shows how the proportion of nonrandom run behaviour changes during a block, as a function of

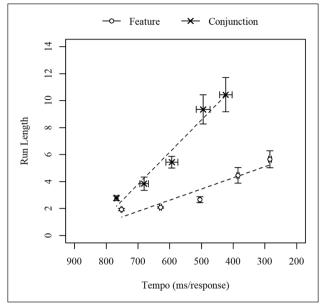


Figure 5. Scatterplot showing the relationship between average run length and average tempo in each of the trial bins. Data are plotted for both the feature (open symbols) and conjunction (closed symbols) conditions. Dashed lines are best-fitting linear slopes. Error bars represent standard error of the mean in both dimensions.

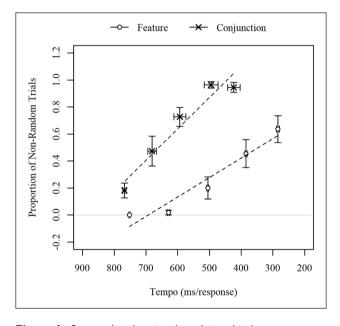


Figure 6. Scatterplot showing the relationship between the proportion of nonrandom trials and average tempo in each of the trial bins. Data are plotted for both the feature (open symbols) and conjunction (closed symbols) conditions. Dashed lines are best-fitting linear slopes. Error bars represent standard error of the mean in both dimensions.

Condition and Tempo. For the feature condition (M=0.24, SE=0.04), run behaviour was exclusively random for the two earliest trial bins. Although nonrandom foraging

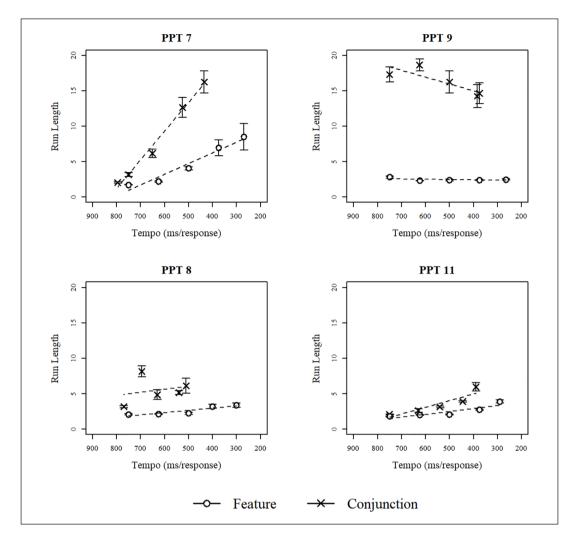


Figure 7. Example scatterplots for individual participants, showing the relationship between average run length and average tempo in each of the trial bins. Data are plotted for both the feature (open symbols) and conjunction (closed symbols) conditions. Dashed lines are best-fitting linear slopes. Error bars represent standard error of the mean in both dimensions. See OSF Supplementary Files for the remaining eight participants.

becomes more prevalent in the latter stages of the block, there is considerable between-subject variability, and even at the fastest tempo, proportions barely exceed 50%. In contrast, during conjunction foraging (M=0.69, SE=0.05), approximately 25% of trials are nonrandom even at the slowest tempos, rising quickly towards 100% in the latter two bins.

As with the other run measures, these patterns gave rise to main effects of both Condition, F(1,10)=59.7, p<.001, MSE=0.07, $\eta_p^2=0.86$, and Trial Bin, F(4,40)=43.8, p<.001, MSE=0.04, $\eta_p^2=0.81$. Although the Condition × Trial Bin interaction was not significant, F(4,40)=2.0 (ns), MSE=0.06, $\eta_p^2=0.17$, the slope analysis did indicate a consistently more rapid increase in the proportion of nonrandom trials as a function of tempo for the conjunction condition (M=0.23 units/100 ms, SE=0.02), compared with the feature condition (M=0.14 units/100 ms, SE=0.02), t(11)=2.4, t=0.05.

Individual differences

As noted in the "Introduction" section, in our previous work, we have consistently found individual differences in how participants adapt their run behaviour in response to increased attentional load. Specifically, while the majority of participants change from random category selection during feature foraging to exhaustive category selection during conjunction foraging, a subset of participants—so-called super-foragers—maintain random behaviour throughout. Here, we were interested if participants varied in terms of the influence of tempo on their foraging behaviour.

The individual data plots for all observers and dependent measures are provided in the OSF Supplementary Material. In this section, we illustrate what we consider to be the major individual differences, using example participant data from the analysis of average run length. In our

previous work, this dependent variable had provided the most stable estimates of individual differences (see Á. Kristjánsson et al., 2014; Figure 4) and in the current work, it also appeared most sensitive to changes in tempo.

Participant 7 (upper left in Figure 7; see also Participants 1, 4, 5, 10, & 12 in OSF Supplementary Figures) nicely illustrates the canonical pattern (Figure 5), with increasing run length as a function of increasing tempo, with the rate of increase being steeper for the conjunction condition. Thus, the majority of participants do appear to show the expected pattern whereby attentional load and the demands of faster responding interact.

Participant 9 (upper right in Figure 7), was excluded from the main analysis, as they showed a completely unique pattern of consistent switching during the feature condition and consistent exhaustive runs during the conjunction condition. As we had explicitly asked participants to attempt to switch between categories during the slow tempo portions of each block, this suggests that the participant was unwilling or unable to follow these instructions. Examination of the error data for this participant showed that they did not make any selection errors at all, suggesting that their performance was not mediated by difficulty in switching.

Participant 8 (see also Participant 2 in OSF Supplementary Files) shows little evidence of a systematic increase of run length with tempo. Rather, both profiles are relatively flat, but the performance in the conjunction condition is more variable, and perhaps more interestingly, compressed towards the lower end of the tempo range. This suggests that the participant attempted to frequently switch during conjunction trials, but was not very successful. Consistent with this idea, both Participants 8 and 2 had relatively high selection error rates.

Participant 11, on the contrary (see also Participants 3 & 6 in the OSF Supplementary Files), appears to have been much more successful in maintaining a pattern of conjunction switching across a wider range of tempos. The run length remains low across all trial bins, and there is a close parallel between feature and conjunction conditions. This suggests that these participants were able to cope with the dual demands of increased target complexity and increased tempo. These participants thus behaved in a manner consistent with the super-foragers from our previous studies (e.g., Jóhannesson et al., 2017; Á. Kristjánsson et al., 2014).

Discussion

In two recent papers, we suggested that foraging tempo—the rate of successive target responses within a trial—helps determine patterns of run behaviour in multiple-target search (Prpic et al., 2019; Thornton et al., 2019). Specifically, our analysis of previous studies showed that the tendency to switch randomly between target categories was more common when the interval

between responses was longer. Conversely, the tendency to use extended selection from a single category—the hallmark of attentionally demanding conjunction foraging—was more pronounced when successive responses were made rapidly. One simple explanation for these findings would be that reduced time to respond adjusts the soft constraints that are applied when selecting between available cognitive operations (Gray & Boehm-Davis, 2000; Gray & Fu, 2004; Gray et al., 2006). At faster speeds, the temporal cost of switching categories is avoided, affecting the overall pattern of foraging.

In this article, we directly tested this idea, asking participants to complete our standard iPad foraging task (Á. Kristjánsson et al., 2014) with the additional requirement of synchronising their responses to an auditory metronome signal, also produced by the app. Across trials, we increased the tempo of this metronome signal and examined patterns of runs as a function of both tempo and attentional load (i.e., feature vs. conjunction foraging). Our main finding was very clear: changes in foraging tempo were accompanied by systematic changes in run behaviour.

In the "Introduction" section, we made two specific predictions concerning foraging tempo. Below, we address these in turn, before examining other aspects of the data and drawing some general conclusions. First, we predicted that the tendency to switch between target categories would generally reduce as foraging tempo increased. If observers decrease their switching, the number of runs should decrease and the run length increase with tempo. Similarly, the tendency to use nonrandom selection from target categories should increase as tempo increases. These are exactly the patterns we see in Figures 3 to 5, and in the robust main effects of Tempo in all of the related analyses.

The finding that foraging tempo does modulate patterns of runs in this way has both theoretical and practical implications. To begin with, these results provide a further example of an interactive behaviour in which temporal factors play an important role in shaping overall performance, consistent with the soft constraint approach suggested by Gray and colleagues (Gray & Boehm-Davis, 2000; Gray & Fu, 2004; Gray et al., 2006). In terms of foraging behaviour, while we had previously argued that the appearance of exhaustive run patterns in humans was solely a consequence of changing attentional demands (Å. Kristjánsson et al., 2014), this explanation appears to be incomplete. At least in humans, increases in attentional complexity—such as the standard feature/conjunction manipulation—do not appear sufficient to trigger a complete shift from freely selecting among all available "prey" types, towards foraging for a single category. Rather, to observe this change in run behaviour, increases in attentional demand need to be accompanied by the tendency to select/respond rapidly. Although formal attempts to model the role of limited attention during foraging, for example, the "attentive prey" model (Dukas, 2002, 2004; Dukas &

Ellner, 1993), may be able to indirectly capture some aspects of this Attention×Time interaction—at least for conspicuous/cryptic prey manipulations (Gendron & Staddon, 1983)—it may be more useful to directly integrate the consequences of time constraints, along the lines suggested by the soft constraints approach (Gray & Boehm-Davis, 2000; Gray & Fu, 2004; Gray et al., 2006).

From a more practical perspective, the current results show that manipulating the time available for making selections is another useful experimental method for modulating foraging behaviour in humans. Indeed, manipulating foraging tempo would appear to give rise to graded changes in run behaviour, rather than to the random/exhaustive dichotomy we have previously observed. The virtual absence of exhaustive category selection during conjunction foraging in the current data set is almost certainly caused by our specific task instructions—a point we return to shortly—but more importantly, tempo manipulations do seem to provide a finer level of resolution for exploring the impact of increasing task demands on foraging behaviour, particularly in the context of individually determined thresholds of performance.

Furthermore, when designing new tasks, factors that can affect the rate of responding—such as response modality (e.g., touch vs. mouse) or the spatial separation between items—should clearly be borne in mind, as these may constrain run behaviour via the influence of foraging tempo (see Thornton et al., 2019, for further discussion). Similarly, when examining run behaviour in a given context, examination of response rates may shed additional light on general task demands (Gray & Boehm-Davis, 2000; Gray & Fu, 2004; Gray et al., 2006).

Our second prediction was that the influence of foraging tempo would be more pronounced during conjunction foraging than during feature foraging. Here, the pattern of results was less clear. Examination of Figure 4 suggests that the change in the number of runs as a function of tempo was very similar between the two conditions. Even at the slowest tempo, participants consistently use fewer runs during conjunction foraging, and this gap is maintained across all time bins, giving rise to very similar tempo slopes in the two conditions. In contrast, both the pattern of run length data in Figure 5 and nonrandom behaviour in Figure 6 suggest that changes in foraging tempo have an earlier impact on patterns of responding during conjunction than feature foraging.

It thus appears that the interaction between the feature/conjunction manipulation and foraging tempo is not as simple we had predicted. However, this in itself raises several interesting points. First, the lack of an interaction when considering the number of runs appears to reflect the fact that foraging tempo had a stronger influence on feature foraging than we had anticipated. Increasing time pressure may thus be a simple way to change patterns of foraging without the need to vary target type. Second, while the number of runs is a simple and intuitive

dependent variable, it may not always capture more subtle changes in behaviour. Here, for example, the very clear interaction evident in the run length data (Figure 5) is absent when only considering the number of runs (Figure 4). This reiterates the need to consider a range of dependent measures when exploring foraging behaviour.

Another aspect of performance in the current experiment was clear individual differences in response to variations in foraging tempo. Specifically, we found that some observers seemed to be less affected than others by the decreasing time limit, and these individuals seem to show performance patterns reminiscent of the participants that we called super-foragers in our previous work (Jóhannesson et al., 2017; Á. Kristjánsson et al., 2014). Taking Participant 11 as an example (Figure 7), there was little difference between feature and conjunction run patterns, the overall tempo range was similar, and the impact of tempo on run patterns was very modest.

We should note that in our original study, the feature and conjunction behaviour of super-foragers were completely indistinguishable (see Á. Kristjánsson et al., 2014; Figure 4, Participants 4, 8, 11 & 14). Here, this is not the case. Thus, although the impact of tempo for some individuals is modest, it may still add diagnostic power over and above the basic feature and conjunction manipulation. This may prove useful in terms of identifying underlying mechanisms. For example, although previous studies with children have found clear links between foraging behaviour and other, more general cognitive abilities (Ólafsdóttir et al., 2016, 2019), this has not been the case with studies of adults (Clarke et al., 2018; Jóhannesson et al., 2017). We suggest that exploring links with tasks that emphasise temporal constraints may thus be a useful avenue for future studies of individual differences in foraging behaviour.

Remaining with the topic of individual differences, it is important to remember that, in the current task, we explicitly asked participants to avoid using extended runs of selections from a single category. That is, we directly encouraged switching behaviour. We did this as we were interested in monitoring at what tempo participants would no longer be able be able to switch between target categories, and having ceiling levels of performance at the outset in one of the primary measures (i.e., number of runs) was clearly not desirable.

Our subsequent data (see Figure 4) indicate that participants were able to switch quite effectively during conjunction conditions, when encouraged to do so. So much so, in fact, that there was only very limited evidence of fully exhaustive run behaviour, even at the very fastest tempos (see individual participants plots, OSF Supplementary Figures). This strongly suggests that the use of exhaustive runs in the conjunction condition of our original study was not due to participants being unable to switch. Rather, it suggests that they either strategically chose not to switch or some other aspect of their behaviour constrained their

ability to switch. What might have caused this pattern of behaviour?

The most obvious explanation, based on the soft constraints framework already discussed above (Gray & Boehm-Davis, 2000; Gray & Fu, 2004; Gray et al., 2006), is that participants choosing an exhaustive strategy were prioritising response speed. That is, if these participants were attempting to respond close to the upper limit imposed by their perceptual-motor system, then this may have required cognitive operations that were as simple (i.e., fast) as possible, essentially precluding the use of template switching. Consistent with this idea, examination of response time from our original study (Á. Kristjánsson et al., 2014; Figure 3) shows that the six fastest participants all used exhaustive runs during conjunction foraging.

A second possibility is that these observers were more averse to making errors. During conjunction foraging, selection errors are much more likely to occur than during feature foraging (see Figure 3). Participants who want to minimise errors—either because they have prioritised accuracy or possibly because they become frustrated with having to repeat trials—would clearly do better by adopting an exhaustive strategy. Consistent with this idea, Tagu and Kristjánsson (2020) recently noted that during eyegaze foraging (Jóhannesson et al., 2016), error rates were lower for participants who adopted exhaustive search than those that would typically be classified as super-foragers. We should note, however, that in a recent study that compared performance with and without terminal error feedback, we found little impact of this factor on overall patterns of foraging (Thornton et al., 2019).

Approaching this issue from the other side, we can also ask why some participants in each of our studiesthe super-foragers—do appear so comfortable with consistently switching during conjunction conditions? There is now strong evidence the participants can routinely maintain more than one target template in working memory and are able to selectively activate or deactivate items depending on temporal expectations of task relevance (Grubert & Eimer, 2018, 2020; see also T. Kristjánsson & Kristjánsson, 2018). It seems safe to assume that during the course of a multiple-target trial, repeatedly switching activation between two conjunction templates in working memory would require more cognitive resources than maintaining activation of just one of those templates. Thus, participants who switch during conjunction conditions are choosing to place more demands on the cognitive system than those who do not.

As noted in the "Introduction" section, an important feature of the soft constraints approach to interactive behaviours is that individuals are able to adjust the balance between cognitive, perceptual, and motor operations to minimise performance costs. It seems likely that such adjustments could take into account individual differences in each of these systems (e.g., working memory capacity,

visual acuity, motor fluency) as well as allowing constraints to be "overridden by factors such as training or by deliberately adopted top-down strategies" (Gray et al., 2006, p. 463). Our original idea was that super-foragers differed from typical foragers in respect to basic cognitive abilities, such as working memory capacity or selective attention. As already mentioned, however, we have thus far not been able to identify such differences, at least in adults (Jóhannesson et al., 2017). It remains possible that differences can be found in other cognitive abilities that might more directly relate to switching, such as flexibility, or that the source of individual differences is in the perceptual or motor domains. If super-foragers have better motor fluency or more precise hand-eye coordination, for example, these could conceivably change the balance of resources across domains, freeing up cognition to handle more complex operations within a similar time frame.

In terms of top-down strategies, those participants who continue to switch during conjunction conditions may be placing more emphasis on reducing their overall movement across the display, rather than reducing time. Although we chose not to focus on intertarget distance (ITD) or overall movement in the current study, simply for the sake of brevity, our previous work has shown that there is a very strong correlation between run behaviour and spatial efficiency. That is, the use of fewer, longer runs requires travelling further distances. In our original study, for example, the correlation between the number of runs and the distance travelled was .87 and .92 for feature and conjunction conditions, respectively (A. Kristjánsson et al., 2014; Figure 3). Here, we have clearly shown that run behaviour changes as expected as a function of tempo, with fewer runs being used as tempo increases (Figure 4). Consistent with this pattern, there were also strong correlations between tempo and distance travelled, both for feature (.80) and conjunction (.83) conditions. Returning to the more general issue of individual differences, it does thus seem possible that switching could be used as a strategy by those individuals who chose to prioritise spatial efficiency over minimising time.

Of course, it is also possible that those participants who spontaneously choose to switch during conjunction conditions are simply more engaged with the task, thus affecting their levels of arousal, vigilance, or alertness (Fernandez-Duque & Posner, 1997; Kahneman, 1973; Mackworth, 1970). For example, in another variant of our iPad task, we allowed participants to respond freely, but varied the overall duration of trials (T. Kristjánsson et al., 2018). When observers had only 5, 10, or 15 s to select as many targets as they could, they tended to switch far more between target types than when they had unlimited time. We suggested that adding time pressure in this way changed their levels of concentration, facilitating switching, which in turn enabled them to select more targets than they otherwise could have with extended runs, given the spatial layout of the display. In other ongoing work in our lab, we have started

to explore how the risk of simulated predation affects patterns of human foraging (for an online example of these tasks, see https://maltacogsci.org/thePredationGame/). Consistent with the idea of a link between levels of alertness/arousal and foraging patterns, participants who were actively "hunted" by wolf objects as they foraged were significantly more likely to switch during conjunction conditions than those for whom the wolves just served as visual distractions (Thornton et al., 2020).

Finally, another approach that might yield useful insights into the nature of individual differences would be to examine whether patterns of behaviour remain stable across different forms of foraging. Several lines of evidence now support the existence of "domain general" search strategies (Hills et al., 2008) that apply not only to movement through an environment to obtain resourcesas we have modelled in our task—but also to both the internal and external search for information (Fu & Gray, 2006; Hills & Dukas, 2012; Pirolli & Card, 1999; Van den Driessche et al., 2019; see Todd & Hills, 2020, for a recent overview). Examples of internal search for information would be recalling concepts from semantic memory (Hills et al., 2012), finding anagram solutions (Hills et al., 2010), or finding mathematical solutions (Hills, 2013). Examples of external search for information would include scanning the environment for signs of predators or prey (Hills & Dukas, 2012), navigating the internet (Pirolli & Card, 1999), or making use of interactive visualisation techniques (Rensink, 2014). Behaviour across these search domains has been shown to be linked via priming studies (e.g., Hills et al., 2008, 2010), and there is also initial evidence that individual differences may be preserved across internal and external tasks (Van den Driessche et al., 2019). It would clearly be an interesting future direction to examine how the task demands of attention and tempo we have studied here impact the search for information and whether similar individual differences in response to such demands, if they exist, transfer across domains.

Conclusion

In the current study, we have demonstrated that there is a direct link between foraging tempo and run-based patterns seen during multiple-target search. Foraging tasks are increasingly being used to measure visual attention and working memory and have proven useful in identifying stable individual differences. Here, although we explicitly encouraged all participants to switch between target categories under the more demanding conjunction condition, we still found substantial individual differences in performance. Further research is required to fully characterise these differences and to identify the strategies or mechanisms that give rise to them. More generally, our results suggest that future studies should consider how the temporal demands of a given task impact expected outcomes and

that modulating foraging tempo could serve as a simple but effective way to manipulate group and individual strategies during human foraging.

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Data accessibility statement

A copy of the working app, the source code, analysis scripts, and files are all available upon request. Raw data files and individual plots for all 12 participants have been uploaded as Supplementary Material to the Open Science Foundation (OSF) page associated with this paper at https://osf.io/ej97c/

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