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Human foraging behavior: A virtual reality investigation on area restricted search in humans

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Abstract

The control of attention and the control of movement in space share a similar optimal control structure—mediating the trade-off between exploiting one locale and exploring others. A common spatial foraging strategy observed in many species is area-restricted search, in which animals respond to resources or their absence by moving between local and global search strategies, respectively. When resources are clustered, area-restricted search can represent an optimal foraging strategy. Surprisingly few studies have investigated whether humans display such behavior in the context of spatial navigation. Here we present two experiments in which human participants search for resources distributed over a large virtual environment. By systematically manipulating the specific distribution of the resources the first experiment investigates human's ability to perform area-restricted search. The second experiment probes for the patch-leaving rules humans apply when facing resources distributed in patches that differ in quality. Our results indicate that humans forage in space using an area-restricted search, but do so in a non-optimal way—consistent with other studies showing non-optimal search strategies in memory.

Keywords: Foraging; area-restricted search; navigation.

Introduction

Picking bananas from banana trees, searching for nebulas in the night sky, and hunting for schools of tuna in the open ocean all involve the ability to detect and respond to spatial resource distributions. Since the foundations of animal foraging behavior were laid by MacArthur and Pianka (1966) and Emlen (1966) decades of research have shown that non-human animals respond adaptively to these spatial resource distributions; moreover, their responses are often optimal with respect to long-term rate maximizing models (reviewed in Stephens & Krebs, 1987). For humans, these models have been shown to predict patterns of search in information foraging on the internet (Pirolli & Card, 1999), the foraging strategies of hunter-gatherer societies (e.g., Hawkes, Hill, & O'Connell, 1982), and the search patterns of humans in their own memory (Hills, Todd, & Jones, 2009; Hills, Todd, & Goldstone, 2008). However, surprisingly, almost nothing is known about how humans search in 3-dimensional environments like those described for the bananas, nebulas, and tuna (but cf. Smith, 1983, for an overview of anthropological research).

How *do* humans forage in space? Are they capable of detecting and localizing resources in space, with or without the help of visual cues? Moreover, are their foraging strategies adaptive, or near optimal in terms of rate maximization? In this article, we use 3-dimensional virtual representations of fields and orchards to investigate how people forage in open environments, and in particular, whether or not they show patterns consistent with area-restricted search.

Area-restricted search (ARS) is one of the most well-studied behavioral patterns in animal foraging, and has been observed in a wide variety of animals (e.g., Hills, Brockie, & Maricq, 2004; Krebs, 1973; Smith, 1974). It can also produce patterns of movement that look like Levy walks—another commonly observed foraging pattern (Benhamou, 2007). ARS involves high turning angles following resource encounters but lower turning angles elsewhere. It indicates an adaptive response to spatial distributions in clustered (or patched) environments because in clustered environments - when prior knowledge about resource locations is limited to the time since they were last encountered - ARS is optimal (Walsh, 1996; Grunbaum, 1999). ARS, like an annealing strategy, localizes animals where resources are most dense (Karieva & Odell, 1987). The success of this strategy and its minimal information requirement are consistent with the evidence that ARS had an early evolutionary origin amongst mobile animals. Moreover, the evolution of this strategy may have provided the biological building blocks for the subsequent evolution of human attention (proposed in Hills, 2006).

If humans respond to clustered resources with increased turning, but don't do so when resources are uniformly or dispersedly distributed, they are showing foraging patterns consistent with ARS. However, evidence for ARS in human

spatial foraging requires more than simply noting that humans respond to clustered resources with more turning. A number of potentially viable foraging heuristics are consistent with ARS at a gross level, but fail to meet its more strict definition of *turning mediated by decaying memories of resources*. These alternate hypotheses include the fixed-number rule and the fixed-time rule (see Stephens & Krebs, 1987).

For the *fixed-number rule*, the forager collects roughly the same amount of items in every patch regardless of the time to achieve this goal: $n_1 \approx n_2 \approx n_i$. If participants used a fixed-number-rule, they would yield insignificant differences in gathered items across patches. Additionally, re-visited (and therefore emptier) patches should receive significantly more time than during first encounter.

The *fixed-time rule* states that a foraging organism will devote roughly the same time to all patches it visits: $t_1 \approx t_2 \approx t_i$. If humans used a fixed-time-rule, there should be no significant differences in patch visit times, regardless of patch quality. Additionally, re-visited (and therefore emptier) patches should receive the same attention than during first encounter

Like the fixed-time rule, ARS uses temporal cues to determine patch departures. However, ARS adds time to the total patch residence time by incrementing the time in the patch (by turning) following each resource encounter. If a certain temporal threshold without resources is exceeded, the patch is abandoned. As Iwasa, Higashi and Yamamura (1981) mention, this heuristic—sometimes called the *incremental rule* or *Green's assessment rule* (Green, 1984) — is highly appropriate among variable patch sizes. Several studies have indicated that humans use this kind of incremental strategy when foraging in a lexical problem space (Payne, Duggan & Neth, 2007; Wilke, Todd, & Hutchinson, 2009).

In the present study we investigate human spatial foraging in a 3-dimensional environment by first asking if participants show behavior consistent with area-restricted search in clustered resource distributions (versus uniform distributions). Second, we ask if humans can detect the difference between high and low quality patches, and if so, do they respond using one of the foraging heuristics described above. That is, are their foraging patterns most consistent with an incremental rule, or are they more likely to be fixed-time or fixed-number rules?

Experiment I

Experiment 1 investigated whether human foragers are sensitive to the distribution of resources in the environment displaying a foraging pattern consistent with area-restricted search (ARS). In the experiment, participants were placed in large virtual environments that contained resource items. These were either uniformly distributed about the entire space or organized in patches. Participants could not see the items prior to encountering them; there were no visual cues to help them harvest resources. Participants had to actively navigate through the environment, searching for resource items.

Method

Environments A circular virtual environment with a radius of 110m was constructed. The environment consisted of a textured ground plane resembling a large meadow and was surrounded by a fence. Three large landmarks (mountain, city skyline, and skyscraper) surrounded the environment providing global direction cues (see Figure 1).
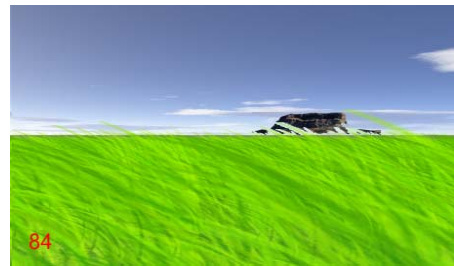

Fig. 1: Participants' perspective during the task. One of the global landmarks (mountain) is visible in the distance.

1440 individual resource items (mushrooms, modeled as 3d objects) were then either evenly distributed about the environment (*dispersed condition*) or they were arranged in 24 patches that were randomly scattered about the environment (*patched condition*; see Figure 2). Each patch had a radius of 8.65 m and contained 60 resource items. The minimal distance between any two resource items in the patched environments was 1.53m, in the distributed world it was 2.35m. For each type of resource distribution (dispersed or patched) five different environments that differed in the specific arrangement of the resource items were created. The resource items in both conditions were visible only from close proximity – i.e. from a distance smaller than 1.25m – similar to real mushrooms in long grass.
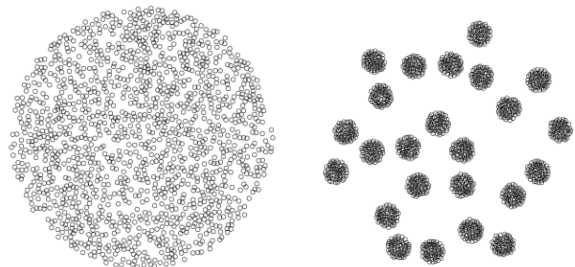

Fig. 2: The two types of resource distributions: left: one of five 'dispersed' environments; right: one out of five 'patched' environments.

Participants navigated through the environments in the first person perspective using the arrow keys of the

keyboard. Translation speed was set to 4m/s and turning velocity was set to 75°/s. The motion model allowed for either forward translations or rotations but did not allow combining translations and rotations. Thus, the resulting trajectories resembled segmented paths (see Figure 4). Participants collected resource items simply by moving closer than .75m to an item. This pick-up distance was just below half of the minimal distance between any two resource items and therefore assured that participants gathered only one item at any time. The collection of a resource item was signaled by an auditory cue. Once an item had been collected it was removed from the environment.

Participants Thirty-two participants (17 women) aged 19 to 28 (M = 22.28, SD = 2.41) took part in the experiment. They were mainly students from Freiburg University and received course credits or monetary compensation for their participation.

Procedure Participants were randomly assigned to either the dispersed or the patched condition (counterbalanced for gender) and were then briefed about the experiment: Their task was to navigate through the environment and to collect resource items. Each participant was given 5 trials. Each trial was carried out in a different environment with the same type of resource distribution (dispersed or patched). At the beginning of each trial, participants were placed in the center of the environment. A single trial was terminated either after 600 seconds or when participants collected 90 resource items. The experiment ended after participants completed all 5 trials. Participants were offered a fixed compensation, independent of the time required to do the experiment. Thus, they were motivated to finish as quickly as possible and the usual (biological) energy cost variable was transformed into a temporal equivalent.

Results

Search time A two-way mixed ANOVA (factors: trial, condition; sphericity assumed: $\chi^2(9) = 14.015$, p = .122) reveals a main effect for trials: $F(4, 120) = 4.703$, p < .01, partial-η^2 = .136 which is due to significant differences between trials one and three, and one and five (both Sidak-corrected p's < .05). Even though completion time was higher for the patched versions (M = 442.63, SE = 12.94 vs. dispersed: M = 422.95, SE = 12.94) there is no main effect of condition (F(1, 30) = 1.158, p = .291, partial- η^2 = .037), as well as no significant interaction between trials and condition: F(4, 120) < 1 (see Figure 3).

Search time results did not demonstrate a significant difference between experimental conditions (patched vs. dispersed condition). The reduction in search time over trials, however, indicates an adaptation of search strategy (see Figure 4) leading to a higher rate of item encounter.

An alternative explanation is that participants learned to control their movements more effectively as the experiment progressed.
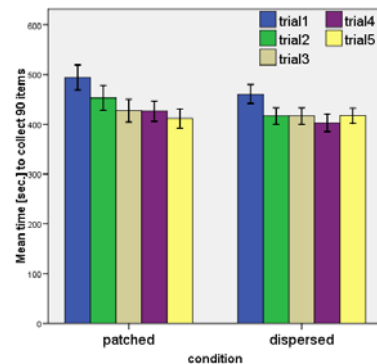

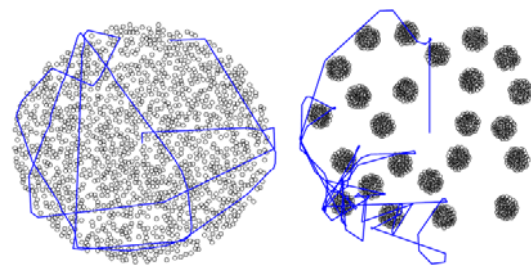Fig. 3: Mean search time for each trial in the two conditions. Error bars depict one SE.

Fig. 4: Example trajectories in the dispersed (left) and the patched condition (right).

Turning rate As argued above, an increase in overall turning rate in environments with clustered resources as compared to environments with evenly distributed resources indicates an adaptive response to spatial distributions. This would be perfectly consistent with area-restricted search. Figure 5 shows the average total turning angles per second.
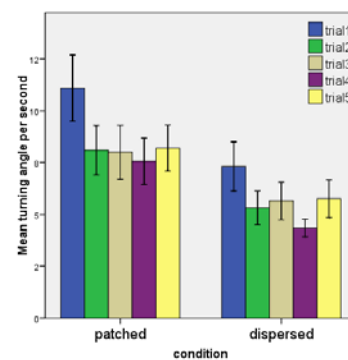

Fig. 5: Average turning angle per second for the two conditions. Error bars depict one SE.

A two-way mixed ANOVA (factors: trial, condition; due to violation of sphericity [$\chi^2(9) = 52.293$, p < .001, ε = .589] the Huynh-Feldt correction for degrees of freedom was used) demonstrates both, a main effect of trials (F(2.356, 70.675) = 6.353, p < .01, partial- η^2 = .175) as well as a main effect of condition (F(1, 30) = 5.143, p < .05, partial-η^2 = .146). Specifically, total turning angle per second in the

patched condition was higher than in the dispersed condition (patched: M = 8.59°, SE = .91; dispersed: M = 5.67°, SE = .91), demonstrating an adaptive response to the specific distribution of resources. The interaction of trial and condition did not yield a significant effect: F(4, 120) < 1.

Trajectories and turn rate after item encounter Visual inspection of the trajectories corroborates the latter analysis that demonstrates that participants search behavior differed in the patched and the dispersed condition (cf. Figure 4). These findings, however, do not necessarily demonstrate area restricted search, which specifically involves an increase in turning angle after resource encounter.
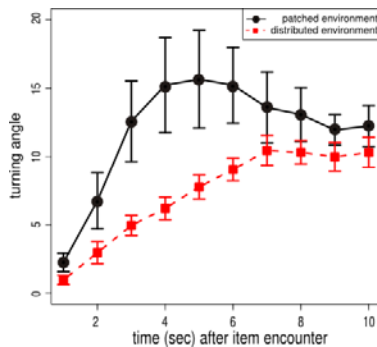

Fig. 6: Turning angle as a function of time after item encounter. Error bars represent one SE.

Figure 6 shows the effect on turning immediately after encountering a resource item. Note that in order to capture items, participants must be moving forward in a straight line. Therefore, turning angle at time of capture will always be zero. Participants in the patched condition are clearly turning more sharply following a resource encounter, as demonstrated by a mixed-model ANOVA (within-participant factor: time after item encounter; between-participant factor: condition). Due to violation of the sphericity assumption ($\chi^2(44) = 270.664$, $p < .001$, $\varepsilon = .327$) the Huynh-Feldt correction for degrees of freedom was used. The interaction of time and condition is significant (F(2.943, 88.283) = 3.616, $p < .05$, partial-$\eta^2 = .108$), because turning angles at time bins '3', '4', and '5' differed significantly (all Sidak-corrected p's $< .05$). This also resulted in a main effect of condition: F(1, 30) = 4.403, $p < .05$, partial-$\eta^2 = .128$.

Discussion
How *do* humans forage in space? Do they detect resources in the environment and adapt their search behavior when facing different distributions of resources? Experiment 1 demonstrated that participants increased their turning rate and turned more sharply after resource encounters in environments in which resources were patched. These results are consistent with area-restricted search and suggest that human foragers adapted their search strategy according to the specific distribution of resources in the environment. People do search differently when faced with different

spatial distributions of resources; moreover, they show more evidence of area-restricted search in environments where such a search strategy is optimal.

Experiment II

Results from Experiment 1 suggest that human foragers, when searching for resources in a spatial context, are sensitive to the distribution of the resources. However, in Experiment 1 all resource patches featured the same amount of items, i.e. the quality of all patches was identical. Experiment 2 was designed to investigate how human foragers interact with resource patches that differ in quality, but that are visually identified by the presence of a tree. Can they tell a good from a bad patch? And, given that foragers have a priori knowledge about the distance to the next patch (by the distribution of trees), how do they determine when to leave a patch in order to harvest at another patch? Also, this experiment allowed to more directly test for area-restricted search in comparison with the other patch leaving rules outlined in the introduction.

Method

Environment The same circular virtual environment as in Experiment 1 was used. In addition, 19 trees, arranged on a hexagonal grid (see Figure 7), were planted in the virtual environment. Resource items were distributed under the trees in patches with a radius of 8 meters. The hexagonal arrangement of the trees (patches) ensured that for each patch the distances to all neighboring patches were identical. Each patch featured either 15 (*poor patches*) or 30 (*rich patches*) resource items.
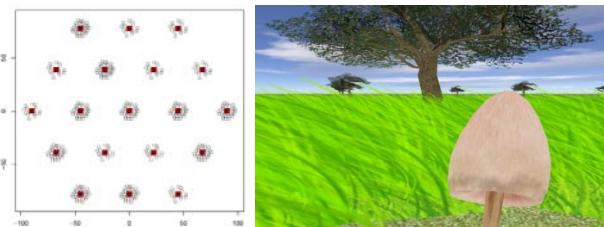

Fig. 7: Left: overview of the environment and the 19 patches (9 poor and 10 rich); right: participants' view while navigating.

As in Experiment 1, participants navigated through the environment (see Figure 7) using the arrow keys of the keyboard. They could not see resource items from the distance, but only in close proximity (viewing distance: 1m). In order to increase the costs associated with moving from one patch to another, translation speed was reduced to 2m/s. Thus, moving from one tree to a neighboring tree took 25 seconds.

Participants Thirty-two participants (16 women) aged 14 to 30 (M = 23.06, SD = 3.37) took part in the experiment. They were mainly students from Freiburg University and received course credits or monetary compensation for their

participation. None of the participants took part in Experiment 1.

Procedure Participants were first briefed about the experiment: Their task was to navigate through the environment and to collect a total of 125 resource items. Participants were also told that resource items were to be found in the vicinity of the trees: The instruction mentioned a certain type of mushroom that only grows under and in the close vicinity of trees, but never further away. Participants were unaware that the patch quality differed between patches. At the beginning of the experiment, participants were placed in the center of the environment. The experiment was terminated after participants collected the last of the 125 resource items required. As in Experiment 1, participants were motivated by being assured that they would receive a fixed compensation for their participation, independent of the time required to solve the task. For the purposes of patch leaving rule analyses, the first and the last patch participants visited were discarded from the analyses.

Results

Patches visited On average, participants visited 18.84 (SD = 10.02) patches (including re-visits). The minimum number of patches visited was seven the maximum 45 visits (see Figure 8).
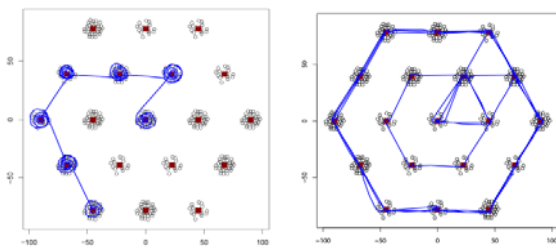

Fig. 8: Trajectories in the actual environment for the minimum (left) and maximum (right) amount of visited patches.

Time On average, participants needed 1804.87 (SD = 347.81) seconds to complete the experiment. Participants considerably differed with respect to the time needed to complete the experiment (range = 1161). Given the time required to move between patches (25 seconds), time to complete the experiment strongly correlated with the number of patches visited ($r(32) = .55$, $p < .001$).

Time spent in patches As stated above, the fixed-time rule would result in foragers devoting the same amount of time to every patch regardless of its quality. *Time in patch* is calculated as the time difference between the first and the last item encounter within each patch. In order to control for quality of the patch at time of encounter, only the first visit of each patch entered this analysis; revisits were discarded. Participants spent significantly more time – roughly twice as much – in richer patches (M = 112.25 sec, SE = 3.15) than in smaller patches (M = 64.57 sec, SE = 3.16; random-factor

ANOVA: $F(1, 34.319) = 63.663$, $p < .001$, partial-$\eta^2 = .65$). This indicates that participants were not using a fixed-time rule when foraging in this environment.

Amount of collected items The fixed-number rule predicts that foragers collect an equal amount of items in every patch, regardless of the time it would take to succeed. Again, in order to control for the patch quality at the time of encounter, only the first visit of each patch entered this analysis; revisits were discarded. Participants collected more than twice as many items in rich patches (M = 13.71, SE = .27) as compared to poorer patches (M = 6.06, SE = .27): random-factor ANOVA: $F(1, 32.405) = 95.685$, $p < .001$, partial-$\eta^2 = .747$. This poses strong evidence that participants were not using a fixed-number rule.

Giving-up-densities Giving up density was lower for rich patches (M = 54.3%, SE = .012) than for poor patches (M = 59.6%, SE = .012; $F(1, 34.552) = 5.99$, $p < .05$, partial-$\eta^2 = .148$). This may indicate that participants are leaving the different patches at different inter-item retrieval times, i.e. they are more patient in rich than in poor patches.
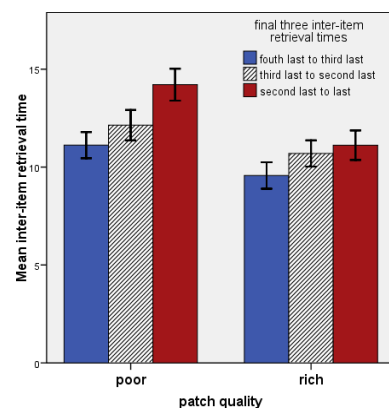

Fig. 9: Mean inter-item retrieval times for the last four item encounters over patch quality. Error bars represent one SE.

To test this, we subjected the time between encounters for the last three items within a patch to a random-factor ANOVA. Results (see Figure 9) show a significant difference between the two patch qualities[1]: $F(1, 34.28) = 6.631$, $p < .05$, partial-$\eta^2 = .162$. This is due to the last three inter-item retrieval times being higher in the poorer (M = 12.94 sec, SE = .45) than in the richer patches (M = 11.09 sec., SE = .39).

Discussion

In summary, Experiment 2 demonstrates that participants were not using fixed-time or fixed number rules, but were

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[1] There is also a main effect for the development of the last three inter-item-retrieval times ($F(2, 71.085) = 3.277$, $p < .05$, partial-$\eta^2 = .144$) which is due to an increase in time towards the last time difference. There is no interaction of the two measures ($F < 1$).

instead using a strategy similar to area-restricted search (i.e., an incremental rule) - staying longer in richer patches and shorter in poorer ones. Given the nature of the patch types (one rich and one poor), this strategy is optimal. However, unlike the optimal foraging strategy predicted by the marginal value theorem (Charnov, 1976), participants do not appear to be leaving patches at equal rates of resource capture.

General Discussion

Our results provide evidence that people are using an evolutionarily old foraging strategy—area-restricted search—when foraging in patchily distributed spatial environments. The same strategy has been observed in a variety of 'internal' foraging tasks (e.g., Payne et al., 2007; Hutchinson et al., 2008). Moreover, the same neuromolecular processes facilitate area-restricted search across species as facilitate the control of human attention, suggesting a possible evolutionary origin for human attention (reviewed in Hills, 2006). This is a fascinating possibility because fluid intelligence, working memory, executive control processes, and spatial foraging may all be largely about appropriately mediating a similar kind of trade-off between exploitation and exploration of goal structures and associative relations (e.g., Kane & Engle, 2002). Optimal control of focus is a problem common to many tasks, both internal and external.

Interestingly, while our participants show evidence of utilizing ARS, they do so non-optimally—using different departure rules for different quality patches. This too has been observed in memory search (Young, 2004), and suggests that foraging tasks may provide an important paradigm for understanding the control of attention and the influence of environmental structure on that control.

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