

## Research Article

# Search in External and Internal Spaces

## Evidence for Generalized Cognitive Search Processes

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**ABSTRACT**—*There is compelling molecular and behavioral evidence that goal-directed cognition is an evolutionary descendant of spatial-foraging behavior. Across animal species, similar dopaminergic processes modulate between exploratory and exploitative foraging behaviors and control attention. Consequently, we hypothesized that spatial-foraging activity could prime attentional cognitive activity. We examined how searching in physical space influences subsequent search in abstract cognitive space by presenting participants with a spatial-foraging task followed by a repeated Scrabble task involving search for words that could be made from letter sets. Participants who searched through clumpier distributions in space behaved as if words were more densely clumped in the Scrabble task. This was not a function of arousal, but was consistent with predictions of optimal-foraging theory. Furthermore, individual differences in exploratory search were conserved across the two types of tasks. Along with the biological evidence, our results support the idea that there are generalized cognitive search processes.*

More than a hundred years ago, James (1890) noted, “We make search in our memory for a forgotten idea, just as we rummage our house for a lost object” (p. 654). This analogy is anecdotally supported by the fact that cognitive representations of both spatial and semantic knowledge are often characterized as maps or networks (Steyvers & Tenenbaum, 2005; Tolman, 1948). Though these internal representations may differ in particular contexts, the search processes required to navigate them may be more general. The commonality stems from the fact that in all

cases, cognitively controlled navigation of internal space relies on appropriate modulation—that is, dynamic control—of attention between exploration and exploitation, much as animal foraging in physical space does (Kareiva & Odell, 1987; Walsh, 1996).

Significant evidence from various fields suggests that the similarity between spatial foraging and internal cognitive search is a consequence not just of convergent evolution, but also of evolutionary homology (i.e., shared descent—see Hills, 2006). Research from neuroscience, genetics, and the study of human cognitive pathologies provides evidence that molecular and neural mechanisms that evolved for the purpose of modulating between exploration and exploitation in spatial foraging have subsequently been exapted in later species for the purpose of modulating attention. This exaptation hypothesis is supported by the observation that, across species, similar dopaminergic processes modulate goal-directed behaviors and attention in multiple behavioral modalities (Floresco, Seamans, & Phillips, 1996; Schultz, 2004; Wang, Vijayraghavan, & Goldman-Rakic, 2004; Watanabe, Kodama, & Hikosaka, 1997; for a review, see Hills, 2006). For example, the basal ganglia control both attention and movement via dopaminergic processes that are conserved across vertebrates and share the same microlevel circuitry as that proposed for the control of foraging in invertebrates (Dani & Zhou, 2004; Hills, Brockie, & Maricq, 2004; Nassel, 1996; Reiner, Medina, & Veenman, 1998).

Further evidence that animal foraging is a precursor to goal-directed cognition is provided by particular human pathologies of goal-directed cognition, such as attention-deficit/hyperactivity disorder (ADHD), drug addiction, Parkinson’s disease, and specific variants of obsessive-compulsive disorder, schizophrenia, and stereotypies in autism. All of these pathologies involve dopaminergic defects or respond to dopaminergic drugs in ways that are consistent with dopaminergic effects on spatial movement behavior (Berke & Hyman, 2000; Nieoullon, 2002;

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Schinka, Letsch, & Crawford, 2002)—effects that are also found in, for example, the nematode and the fruit fly (Hills et al., 2004; Kume, Kume, Park, Hirsh, & Jackson, 2005).

These observations suggest that spatial search in physical space and abstract search in cognitive space share a common basis in the brain and may therefore share key control features. Previous research using arguments from optimality or robust decision heuristics has shown that animal foraging theory can be successfully used to understand human search behavior (Pirolli & Card, 1999; Wilke, 2006). Our argument, by contrast, is based on the premise of a common biological basis for goal-directed cognition and spatial foraging, which implies that spatial and cognitive foraging are not simply the convergent outcomes of similar selective forces in their respective environments, but are themselves constrained by similar underlying physiologies. Extending this reasoning, if the search mechanisms for different domains are physiologically related to one another, then activity in one “environment” may influence activity in another. For example, we hypothesized that prior experience with resource distributions in a spatial environment could prime foraging behavior in an abstract cognitive environment. Similarly, we hypothesized that an individual’s exploratory behavior in a spatial environment could be indicative of that individual’s exploratory behavior in an abstract environment. Such cross-task dependencies could go in either direction: Focused resource exploitation in one task could lead to focused resource exploitation in another task, or individuals could rebound from initial exploitation behavior and engage in the opposite, exploratory behavior during the next task. Either effect would contrast with the lack of cross-task dependencies that would be predicted by more fine-grained, domain-specific theories of modular cognitive abilities (Barrett & Kurzban, 2006; cf. Barrett & Fiddick, 1999).

To investigate the relationship between spatial and conceptual search, we had participants forage in external and internal search spaces. The external search space was represented by a two-dimensional region on a computer screen; participants foraged over this region by controlling the movement of an icon. For the internal space, we focused on word construction and memory, having participants search for words that could be made from some of the letters in each of a sequence of letter sets, as in the game Scrabble (e.g., words that could be created with four or more of the letters in the set “SULMPA”—Wilke, 2006; Wilke, Hutchinson, & Todd, 2004). Each letter set could be used to form multiple words and therefore was equivalent to a finite resource patch that got depleted as words were found by a participant. When participants decided they had foraged sufficiently in a given letter set, they could proceed to a new letter set. Thus, we created an abstract conceptual space analogous to a patchy spatial-foraging environment. We used the external and internal search tasks to address two questions concerning the priming and conservation of search strategies between spatial and conceptual search domains: (a) Does the experience of

searching in larger patches in a spatial setting prime individuals to search longer in each letter-set patch in the repeated Scrabble task? (b) Do individuals who explore more extensively in space show similar tendencies to explore more in the Scrabble task?

## METHOD

### Participants

Forty-one undergraduate students at Indiana University participated in the experiment. All were recruited on a volunteer basis and received class credit; there was no financial reward for participation.

### Materials and Procedure

Participants were seated in front of a computer and asked to follow written instructions that appeared on the screen. The instructions guided participants through three activities: a training and pretest session in the word-search (Scrabble) task, followed by a spatial-foraging task, and then a posttest session in the Scrabble task. All participants saw the same sequence of tasks and same letter sets in the same order, but were randomly assigned by the computer to either of two spatial-foraging treatments (in a between-participants fashion): *clumpy* ( $n = 19$ ) or *diffuse* ( $n = 22$ ).

### Repeated Scrabble Task

In the internal search task, participants were presented with a sequence of letter sets and asked to find words (anagrams) made up of at least 4 letters from each set (e.g., the letter set “SULMPA” could be used to form, among other words, “SLAP” and “PLUM”). Plurals and proper names were disallowed. Once a letter set was displayed, participants could type in as many words as they wanted, or click on a button at any time to move to the next set. Letter sets were constructed using only the 20 most common letters in English (i.e., *K*, *V*, *X*, *Z*, *J*, and *Q* were excluded), as previous work has shown that participants performing this task are sensitive to letter frequency, which is associated with number of possible solutions (Wilke, 2006), and we did not want there to be obvious cues to “patch size” for each letter set. Immediately following each word participants entered, they were given on-screen feedback as to whether it was correct (i.e., an English word, not plural, and formed from the appropriate letters) or incorrect. There were on average 14.7 ( $SD = 5.5$ ) valid solution words per letter set, as judged according to the wordsmith.org anagram dictionary. Participants could leave a letter set at any time but had to wait 15 s before the next letter set was shown. After leaving a letter set, participants could not visit it again.

Participants received instructions and training on one letter set before moving to the pretest session. In the pretest, participants went through three letter sets, receiving no directions regarding how many words to find before moving on to the next letter set. The pretest session ended when participants left the

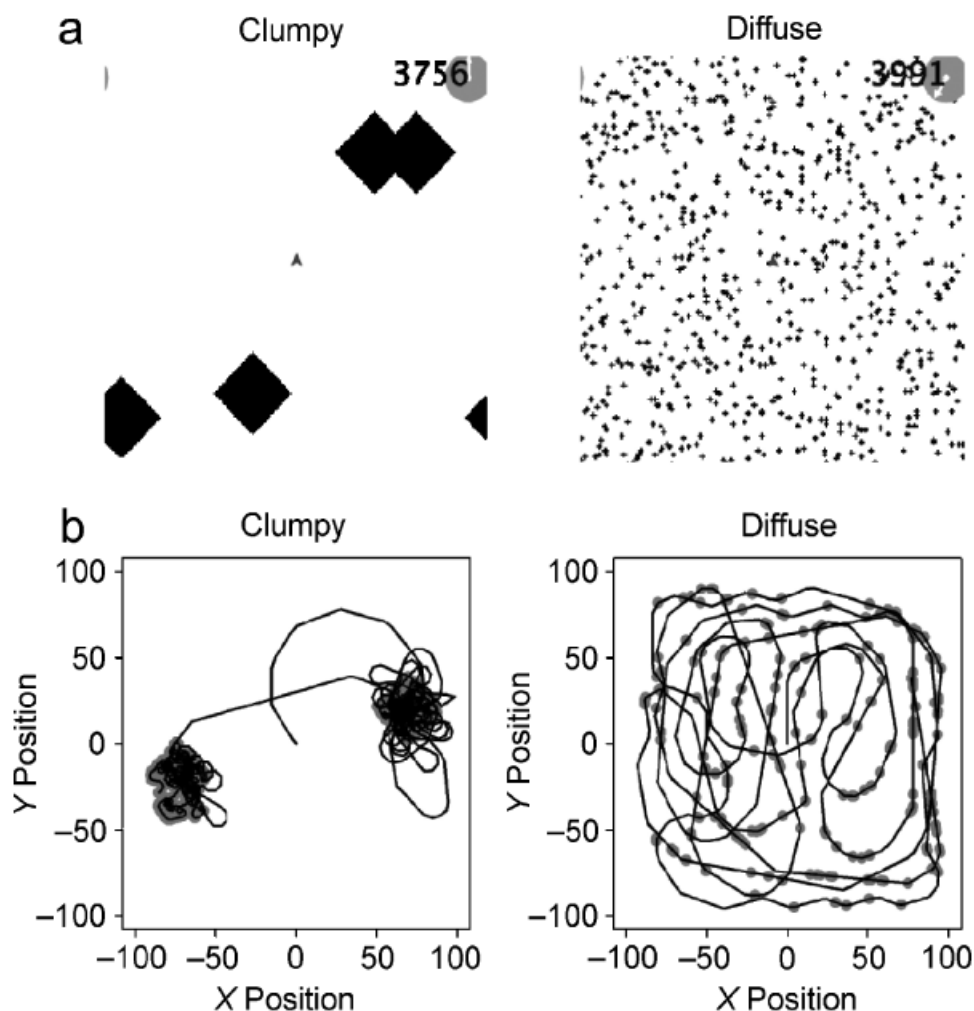
third letter set. In the posttest word-search session (following the spatial-foraging treatment), participants were told that they needed to find a total of 30 correct words across any number of letter sets to finish the experiment, that they could spend as much time as they liked on any given letter set, and that they should allocate their time appropriately so as not to spend too much or too little time with any given letter set.

#### *Spatial-Foraging Task*

In the external search task, participants controlled the movement of a foraging icon by using the “I,” “J,” “L,” and “K” keys, which represented “go,” “left,” “right,” and “stop,” respectively. The “left” and “right” keys initiated turns of  $35^\circ$  per step, and forward (“go”) speed was approximately 20 pixels per second. No participant used the stop key more than 1% of the time. To become familiarized with the controls, participants first had to

navigate a two-dimensional maze. Then, in the foraging treatment, they saw a blank field that measured  $200 \times 200$  pixels. Their search icon was in the center, and they were told to move the icon to find as many hidden “resource” pixels as they could in the allotted time, which was indicated by a sweeping clock hand in the upper right screen corner (clock units indicated the number of remaining search steps possible, measured in pixels).

Participants were randomly assigned to one of two resource distributions, clumpy or diffuse. In the clumpy distribution, the 3,124 resource pixels were located in 4 patches of 781 pixels each, and in the diffuse distribution, the 3,120 resource pixels were located in 624 patches of 5 pixels each. Figure 1 shows example resource distributions for the two spatial-foraging treatments and a typical foraging path for each treatment. Resource pixels were not visible to participants until they were encountered and changed color, nor could participants see the



**Fig. 1.** Examples of (a) clumpy and diffuse resource distributions and (b) paths of 2 participants in the clumpy and diffuse treatments. In the example distributions, black pixels represent resources (not seen by participants until they passed over them). The clock in the upper right corner counted down during the task, showing the number of remaining search steps possible, given the time limit; search steps were measured in pixels (20 pixels per second). In the example paths, gray circles are positioned over the pixels where participants found a resource.

path they had taken (except where they encountered resource pixels). Participants searched through five spatial-foraging displays for 2 min each; each display had a different random arrangement of patch locations.

We measured spatial exploratory behavior for each individual by overlaying a square grid with cell width of three pixels (half the size of the minimal possible path loop that could be made by movement of the icon) on the spatial arena, counting how many of the cells the individual entered, and dividing that number by the total number of cells to compute the proportion of the area visited. Also, turning angles were measured at 0.3-s intervals by taking the angle between the current direction and the previous direction.

## RESULTS

The conventional patch-based model of optimal-foraging theory specifies the optimal allocation of time to individual resource patches (Stephens & Krebs, 1986). Foragers should leave resource patches sooner when the patches are depleted sooner and travel times between patches are shorter (e.g., our diffuse spatial treatment), compared with when patches are richer and further apart. This means that individuals in our diffuse condition should have turned less frequently after encountering resources, to avoid revisiting areas they had already depleted, whereas individuals in our clumpy condition should have done the opposite, turning more frequently after finding resources because their presence indicated more resources nearby. This optimal turning behavior can be demonstrated using a genetic algorithm that evolves appropriate behaviors for simulated agents facing resource distributions similar to those used in the present study (Hills, 2006). Consistent with this reasoning, Figure 2 shows that participants' average turning angle immediately after encountering resources was significantly lower in the diffuse treatment

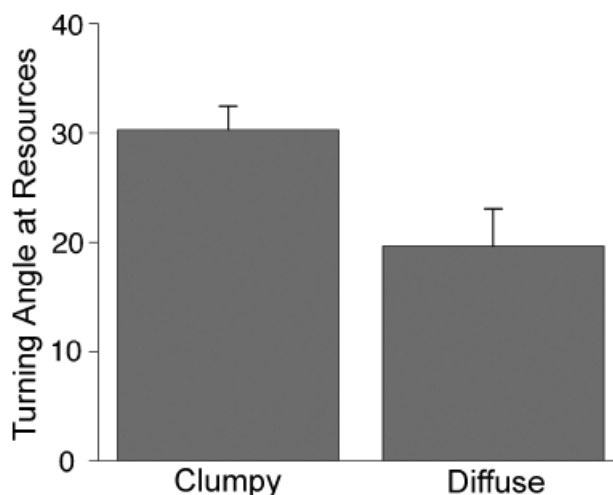


Fig. 2. Results from the spatial-foraging task: mean turning angle when participants encountered resources in the clumpy versus diffuse environments. Error bars show standard errors of the means.

than in the clumpy treatment ( $19.7^\circ$  vs.  $30^\circ$ ),  $t(39) = 2.72$ ,  $p < .01$ ,  $p_{\text{rep}} = .97$ ,  $d = 0.84$ . Thus, participants were sensitive to the spatial correlations in the two environments, and any observed between-treatment differences in the subsequent Scrabble task were potentially a consequence of this sensitivity (though we also tested other hypotheses).

### Priming of Exploration in Conceptual Space by Experience in Spatial Resource Distributions

To test the potential priming effects of searching among spatially clumped resources on patch-exploitation times in a subsequent abstract conceptual search task, we compared the mean time each participant spent in a letter-set patch before and after the two types of spatial-foraging treatments. As should be the case, in the pretest phase before spatial foraging, the mean letter-set times were not significantly different between the two treatments ( $p = .66$ ); the combined mean was 85.7 s. However, in the posttest after the spatial-foraging task, changes in mean letter-set times differed significantly between the two treatment groups,  $t(39) = 2.65$ ,  $p < .05$ ,  $p_{\text{rep}} = .96$ ,  $d = 0.83$  (see Fig. 3). Individuals who were primed for goal-directed exploitation in the clumpy spatial-resource environment stayed within letter sets approximately 17.1 s longer in the posttest than in the pretest, whereas individuals who experienced diffuse resource distributions stayed within letter sets approximately 16.3 s shorter in the posttest than in the pretest.

To evaluate better the process by which spatial foraging influenced abstract problem solving, we also measured patch exploitation in terms of giving-up time (GUT), which is the time between when the last resource item is found and when the forager actually leaves the patch. Using optimal-foraging theory, McNair (1982) showed that organisms should use longer or shorter GUTs depending on patch quality, with longer GUTs being used for better patches. In the repeated Scrabble task, GUT is analogous to latency to switch to a new letter set (i.e., the time between the last word submitted and the switch). If

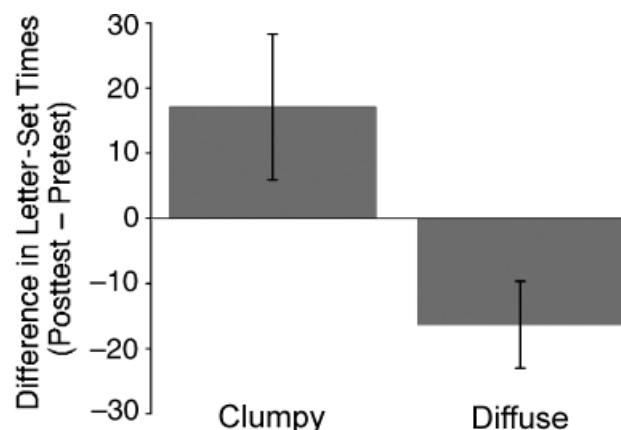


Fig. 3. Mean difference in time spent within letter sets between the posttest and the pretest (in seconds), for the clumpy versus diffuse environments. Error bars show standard errors of the means.

participants who foraged in the spatially clumpy environment—where longer GUTs would be adaptive—were acting as if letter sets in the posttest were also clumpy, then their latencies to switch between letter sets should have been longer than the latencies of participants who experienced diffuse spatial resources.

Figure 4 shows that the latencies to switch in the word-search posttest were indeed significantly longer for individuals in the clumpy spatial treatment than for those in the diffuse treatment (21.2 s vs. 13.8 s),  $t(39) = 2.24$ ,  $p < .05$ ,  $p_{\text{rep}} = .93$ ,  $d = 0.70$ . This is consistent with the biological and behavioral evidence suggesting common cognitive mechanisms for foraging across external and internal domains. However, we also tested other possible explanations for the cross-domain priming we observed.

It is possible that this priming effect was a consequence of the total resources received during foraging and therefore was due to a greater anticipation of reward, regardless of the particular form of the distribution. In other words, individuals who found more in either of the spatial-foraging environments may have been primed to act as if abstract cognitive environments were also richer, and may have stayed longer at individual letter sets for this reason. The average number of resource pixels encountered by participants was 2,185 ( $SD = 1,008$ ) in the clumpy treatment and 816 ( $SD = 104$ ) in the diffuse treatment. To test the hypothesis that this difference in resources encountered explains the priming effect observed, we conducted a linear regression across both treatments. This analysis showed that the number of spatial resources found was not a significant predictor of mean changes in letter-set time,  $t(39) = 1.13$ ,  $p = .26$ . To be thorough, we also included resources found as a covariate in an analysis of variance (ANOVA) with treatment condition as a between-subjects variable. As before, treatment condition was a significant predictor,  $F(1, 37) = 6.9$ ,  $p < .05$ ,  $p_{\text{rep}} = .94$ ,  $\eta^2 = .19$ ,

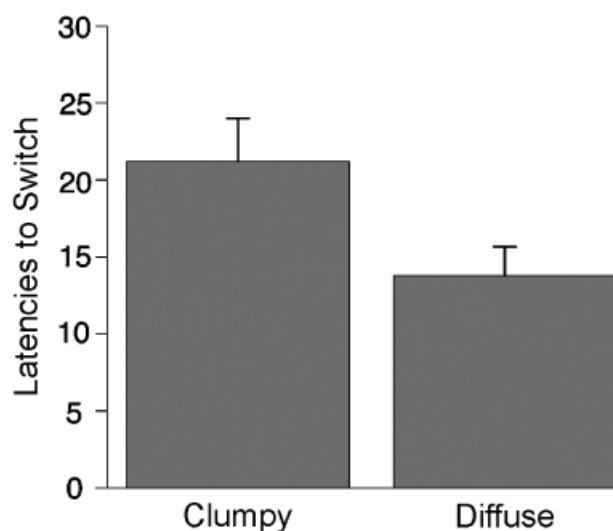
but the main effect of resources found and the interaction of resources found and treatment condition were not significant,  $F_s(1, 37) < 1.5$ .

Another alternative explanation is that individuals in the clumpy treatment could have been in a higher state of arousal than those in the diffuse treatment because they pressed the response keys more frequently; higher arousal could have led to longer search times in subsequent word patches. Including number of key presses as a covariate in an ANOVA showed that key presses were not a significant predictor of letter-set times,  $F(1, 37) = 1.08$ ,  $p = .30$ ,  $\eta^2 = .03$ , whereas the significance of the original treatment effect was not affected. Furthermore, if participants in the clumpy treatment were in a higher state of arousal than those in the diffuse treatment, their overall word-submission rates in the posttest task should also have been higher. However, the treatment groups did not differ significantly in mean time to submit correct or incorrect words,  $t(39) = 1.61$ ,  $p = .12$ , and  $t(39) = 1.27$ ,  $p = .21$ , respectively. These results suggest that arousal, as measured by number of key presses or word-submission rates, was not the cause of the greater time spent exploring each letter set following clumpy spatial foraging.

#### Conservation Between Spatial and Conceptual Foraging

If a generalized cognitive search process underlies search in different types of environments, then there may be consistent individual differences in search across domains. In particular, if an individual is prone to perseverative search—exploiting found resources—in one environment, that individual should display similar perseverative tendencies in other environments. Though individual differences in sensitivity to novel environments may lessen the effect, we expected to find that levels of exploration correlated within subjects across tasks.

Our hypothesis was that individuals who explored more in the spatial-foraging task (in either condition) would also explore more in the Scrabble task, and hence leave letter-set patches earlier. In the spatial-foraging task, we measured exploration as the proportion of the total surface area visited, using the grid-based count described earlier. We had to take into account the fact that the mean proportion of the area explored was significantly larger for the diffuse-treatment group than for the clumpy-treatment group (.12 vs. .08),  $t(39) = -4.70$ ,  $p < .001$ ,  $p_{\text{rep}} = .99$ ,  $d = 1.49$ . To control for this variance in exploration due to the treatment condition, but still maintain our statistical power, we ran an analysis of covariance with mean letter-set time as the dependent variable, treatment condition as a between-subjects factor, and proportion of spatial coverage as a covariate. Exploratory behavior in the spatial-foraging task was a significant predictor of letter-set time,  $F(1, 37) = 4.57$ ,  $p < .05$ ,  $p_{\text{rep}} = .89$ ,  $\eta^2 = .12$ : Participants who explored more in space also explored more across letter sets, spending less time in each letter set.



**Fig. 4.** Latencies to switch (in seconds) to the next letter set following the last word submitted, for the clumpy versus diffuse environments. Error bars show standard errors of the means.



## DISCUSSION

The present study examined the search strategies of individuals as they moved from a concrete spatial-foraging task to an abstract word-search task. We found that, between subjects, exploitation- and exploration-inducing spatial-foraging tasks are capable of priming corresponding exploitation and exploration during abstract conceptual search in a repeated Scrabble task. We also found that, within subjects, individual differences in exploration and exploitation were conserved as subjects moved from the spatial to the abstract task.

These results strongly suggest that there are general search processes underlying cognition and that these processes are used to search both in external physical space and in internal cognitive space. This conclusion fits well with the evidence supporting a common biological basis in the brain for spatial and abstract goal-directed cognition (Hills, 2006). When an individual moves from one task to another, strategies for exploration or exploitation fostered by the first task can remain to influence search in the second, even if the two tasks involve domains that are traditionally conceived to be highly dissimilar. We propose that this is because people perform the tasks (e.g., foraging in two-dimensional space and searching in high-dimensional memory) using similar underlying mechanisms to handle the dynamic modulation between exploitation and exploration.

We believe that the general search process produces priming across domains because it operates on expectations regarding environment structure that develop during performance of a task, not simply because the individual perseverates on the behavioral strategies that were used to solve the first task. This idea is supported by preliminary evidence from a study that was very similar to the present study except that spatial resources were visible the entire time; in that study, the foraging behavior as measured by turning angle was the same as in the results reported here, but the development of expectations about environment structure was not needed (because all resources were visible). We found no evidence of cross-task priming in that case, a result that points to the importance of search, rather than overt behaviors, in producing the priming effect.

Processes that dynamically modulate between exploitative and exploratory search have been seen in other types of cognitive tasks as well. Recent neural studies have shown dynamic changes from global brain activation during learning to more localized activation following learning. More global activation is considered to be consistent with more exploratory processing, and local activation is interpreted as due to more focused, or exploitative, processing (Jog, Kubota, Connolly, Hillegaat, & Graybiel, 1999; Qin et al., 2003). Similarly, spreading-activation theories of semantic processing (Collins & Loftus, 1975) also are based on modulation between global and local search (Neely, 1977) that can be influenced dopaminergically

(Kischka et al., 1996). Combining such findings with our results suggests that these local/global focus-shifting mechanisms underlie a general cognitive search process. Hence, we predict that exploratory spatial movement may be tightly linked not only with expectations about distributions of abstract resources, as shown here, but also with memory retrieval, problem solving, learning, control of attention, and other cognitive functions.

Identifying the extent and boundaries of a generalized cognitive search process will require substantial further research employing other tasks beyond the two we used here. For instance, because the letter set is constantly displayed in the Scrabble task, this task is more stimulus driven than other potential search tasks (e.g., “name all the cities you can think of in a given state,” a task in which states represent depleting patches). Nonetheless, we chose to start with the Scrabble task specifically because it allows for fairly direct control of the possible solution-set size, and because individual performance is unlikely to be influenced by previous experience with the letter sets we used.

Our proposal that there is a generalized cognitive search process was partly inspired by the observation that increases in extracellular dopamine increase behaviors associated with exploitation of and attention to resources, whereas reductions in extracellular dopamine lead to more exploratory or inattentive behavior (for a review, see Hills, 2006). Though we did not measure dopamine in the present study, our research may provide insight into dopamine-related clinical disorders of attentional focus, such as ADHD and schizophrenia, by showing how cognitive tendencies for attentional persistence (or lack thereof) may be revealed in tasks involving spatial search. Furthermore, we have shown that tasks that modulate attention in space can alter the persistence of attention in subsequent nonspatial tasks. If particular spatial tasks could be made to have long-lasting effects on the generalized cognitive search process—for example, by exposing individuals to the tasks during development—this could provide useful hints toward nonpharmacological treatments for disorders of attention.

Just how general this generalized cognitive search process is must still be determined. On the one hand, it is able to operate at a level of abstraction concerning patterns of resource distribution that can apply to many different domains, allowing modulation between exploration and exploitation in similar ways across different contexts. On the other hand, it is also context sensitive, which we see in the fact that the search process adapted to the spatial distribution in the spatial-foraging task, thus influencing behavior in subsequent contexts and resulting in possibly maladaptive priming effects across domains. But this balance of domain generality and context sensitivity presumably comes with advantages as well, combining increased speed of decision making within a given context with the ability to adapt search to a wide range of novel environments with greatly varying statistical structure.

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## REFERENCES

- Barrett, H.C., & Fiddick, L. (1999). Evolution and risky decisions. *Trends in Cognitive Sciences*, 4, 251–252.
- Barrett, H.C., & Kurzban, R. (2006). Modularity in cognition: Framing the debate. *Psychological Review*, 113, 628–647.
- Berke, J.D., & Hyman, S.E. (2000). Addiction, dopamine, and the molecular mechanisms of memory. *Neuron*, 25, 515–532.
- Collins, A.M., & Loftus, E.F. (1975). A spreading activation theory of semantic processing. *Psychological Review*, 82, 407–428.
- Dani, J.A., & Zhou, F. (2004). Selective dopamine filter of glutamate striatal afferents. *Neuron*, 42, 522–524.
- Floresco, S.B., Seamans, J.K., & Phillips, A.G. (1996). A selective role of dopamine in the nucleus accumbens of the rat in random foraging but not delayed spatial win-shift-based foraging. *Behavioral Brain Research*, 80, 161–168.
- Hills, T. (2006). Animal foraging and the evolution of goal-directed cognition. *Cognitive Science*, 30, 3–41.
- Hills, T., Brockie, P.J., & Maricq, A.V. (2004). Dopamine and glutamate control area-restricted search behavior in *Caenorhabditis elegans*. *Journal of Neuroscience*, 24, 1217–1225.
- James, W. (1890). *The principles of psychology*. New York: Holt.
- Jog, M.S., Kubota, Y., Connolly, C.I., Hillegaart, V., & Graybiel, A.M. (1999). Building neural representations of habits. *Science*, 286, 1745–1749.
- Kareiva, P., & Odell, G. (1987). Swarms of predators exhibit “prey-taxis” if individual predators use area-restricted search. *American Naturalist*, 130, 233–270.
- Kischka, U., Kammer, T.H., Maier, S., Weisbrod, M., Thimm, M., & Spitzer, M. (1996). Dopaminergic modulation of semantic network activation. *Neuropsychologia*, 34, 1107–1113.
- Kume, K., Kume, S., Park, S.K., Hirsh, J., & Jackson, F.R. (2005). Dopamine as a regulator of arousal in the fruit fly. *Journal of Neuroscience*, 25, 7377–7384.
- McNair, J.N. (1982). Optimal giving-up times and the marginal value theorem. *American Naturalist*, 119, 511–529.
- Nassel, D.R. (1996). Neuropeptides, amines and amino acids in an elementary insect ganglion: Functional chemical anatomy of the unfused abdominal ganglion. *Progress in Neurobiology*, 48, 325–420.
- Neely, J.H. (1977). Semantic priming and retrieval from lexical memory: Roles of inhibitionless spreading activation and limited capacity attention. *Journal of Experimental Psychology: General*, 106, 226–254.
- Nieoullon, A. (2002). Dopamine and the regulation of cognition and attention. *Progress in Neurobiology*, 67, 53–83.
- Pirolli, P., & Card, S.K. (1999). Information foraging. *Psychological Review*, 29, 343–373.
- Qin, Y., Sohn, M.H., Anderson, J.R., Stenger, V.A., Fissell, K., Goode, A., & Carter, C.S. (2003). Predicting the practice effects on the blood oxygenation level-dependent (BOLD) function of fMRI in a symbolic manipulation task. *Proceedings of the National Academy of Sciences, USA*, 100, 4951–4956.
- Reiner, A., Medina, L., & Veenman, C.L. (1998). Structural and functional evolution of the basal ganglia in vertebrates. *Brain Research Reviews*, 28, 235–285.
- Schinka, J.A., Letsch, E.A., & Crawford, F.C. (2002). DRD4 and novelty seeking: Results of meta-analyses. *American Journal of Medical Genetics: Neuropsychiatric Genetics*, 114, 643–648.
- Schultz, W. (2004). Neural coding of basic reward terms of animal learning, game theory, microeconomics and behavioral ecology. *Current Opinions in Neurobiology*, 14, 139–144.
- Stephens, D.W., & Krebs, J.R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.
- Steyvers, M., & Tenenbaum, J.B. (2005). The large-scale structure of semantic networks: Statistical analyses and a model of semantic growth. *Cognitive Science*, 29, 41–78.
- Tolman, E.C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55, 189–208.
- Walsh, P.D. (1996). Area-restricted search and the scale dependence of patch quality discrimination. *Journal of Theoretical Biology*, 183, 351–361.
- Wang, M., Vijayraghavan, S., & Goldman-Rakic, P.S. (2004). Selective D2 receptor actions on the functional circuitry of working memory. *Science*, 303, 853–856.
- Watanabe, M., Kodama, T., & Hikosaka, K. (1997). Increase of extracellular dopamine in primate prefrontal cortex during a working memory task. *Journal of Neurophysiology*, 78, 2795–2798.
- Wilke, A. (2006). *Evolved responses to an uncertain world*. Retrieved May 2007 from [www.diss.fu-berlin.de/2006/14/indexe.html](http://www.diss.fu-berlin.de/2006/14/indexe.html)
- Wilke, A., Hutchinson, J.M.C., & Todd, P.M. (2004). Testing simple rules for human foraging in patchy environments [Abstract]. In K. Forbus, D. Gentner, & T. Regier (Eds.), *Proceedings of the 26th annual conference of the Cognitive Science Society* (p. 1656). Mahwah, NJ: Erlbaum.

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