

**Exploitation and Exploration in Search: Priming Search in Different Cognitive Domains
and the Role of Striatal Dopamine**

Vera Nathalie Mekern

Leiden University

Name: Vera Mekern

Supervisor: Roy de Kleijn, MSc

Second reader: Prof. dr. Bernhard Hommel

Cognitive Psychology

MSc Thesis (research) Cognitive Neuroscience

Abstract

Search behavior is fundamental for adapting to the environment across species and one important aspect in search is making the appropriate tradeoff between exploration and exploitation. We intended to replicate findings of carry-over effects of exploratory and exploitative search strategies between different search domains (Hills, Todd, & Goldstone, 2008, 2010). Participants performed a visual search task in which they foraged for food tokens in either a diffuse or a clustered visual scene which should elicit exploratory and exploitative search strategies, respectively. We expected to see carry-over effects of these strategies in cognitive search in a subsequent scrabble task. Additionally, we used eye blink rate (EBR) to study the hypothesized neuromodulatory influence of striatal dopamine on exploration and exploitation in search. Contrary to our expectations, we found that participants who foraged a diffuse visual scene, showed more exploitative search behavior in the scrabble task compared to participants who foraged a clustered visual scene. The measurement of EBR might have primed all participants to take on an exploitative search strategy, precluding replication of Hills et al.'s findings, but carry-over effects of the search strategy are still apparent. We also found that the amount of exploration and exploitation was not related to EBR. The consideration of different dopaminergic systems in the control of exploratory and exploitative behavior might be important for future research into the role of dopamine in cognitive control. To comprehensively study dopamine in search behavior future research should include not only EBR but also a measure of prefrontal dopamine.

Introduction

Animals and humans spend ample time searching for resources. Consider the simple example of an animal foraging for fruits or a person shopping for groceries. Search can also be internal; for example, you may perform a cognitive search for the right words to say (Hills & Dukas, 2012). Search behavior is fundamental for adapting to the environment across species and has accordingly been the subject of much research (e.g., Hills, 2006; Hills & Dukas, 2012, Nikitin & Hills, 2016). Although hard to define, there is some agreement that search involves (a) the presence of a goal, (b) some uncertainty about the environment, (c) a way to sample the environment, and (d) a stopping rule (Hutchinson et al., 2012). The question of how an animal or human decides to persist in search or stop searching is dependent on making an appropriate tradeoff between exploration and exploitation (Mehlhorn et al., 2015; Todd, Hills, & Robbins, 2012). In cognitive search, someone naming as many animals as he knows is exploiting a source of animals by naming all farm animals that come to mind. When he runs out of farm animals to name he might make an exploratory move and start naming animals of a different type like pets. In visual search someone samples a visual scene, for example in a *Where is Waldo* book. Each time someone focuses on a particular group of people, or an area in the scene where there are many red-and-white-striped objects, she could be said to exploit that part of the scene until she decides to look for Waldo elsewhere. When she looks for a better place to find him, she explores the entire scene to exploit that new place until she finds Waldo.

This study is concerned with exploratory and exploitative behavior in human search behavior. We consider the idea that mechanisms in animal foraging behavior might have evolved to cognitive control mechanisms that control several cognitive processes in humans, among which cognitive search (Hills, 2006; Hills, Todd, & Goldstone, 2008, 2010). According to this idea we expected we could elicit either an exploratory or exploitative

cognitive style with a visual foraging task to prime exploratory or exploitative cognitive control in a cognitive search task. This would indicate that there can be carry-over effects of cognitive control style between tasks in different search domains. We also expected neuromodulatory involvement of dopamine (DA) in exploitation and exploration in human search similar to that observed in animal behavior (Hills et al., 2008, 2010). In support of both ideas we aimed to provide evidence of shared physiological mechanisms between a certain type of foraging behavior—area restricted search—and cognitive search.

Search behavior: area restricted search

Area-restricted search (ARS) is a search strategy that is used by a wide variety of animals (including humans; Kalff, Hills, & Wiener, 2010; Hills, 2006). Animals that use ARS will increase their turning frequency when they find food. This restricts their search to the area where they encountered the resource until some time has passed since the last food encounter (Hills, 2006; Kalff et al., 2010). Because resources are often found in patches in biological environments, this behavior is often optimal for foraging animals (Hills, 2006; Kalff et al., 2010). As ARS has been observed throughout a wide range of animal species including humans, it might be an evolutionary precursor to human goal-directed behavior, including goal-directed cognitive search (Hills, 2006; Kalff et al., 2010).

Evidence of a shared evolutionary mechanism: carry-over effects

If the same mechanism that underlies ARS has evolved into a mechanism that modulates cognitive control in humans, one expectation would be that cognitive control should be domain-general. In other words, it should affect external as well as internal search behavior in humans. Indeed, studies show that cognitive control effects can carry over between different types of search (Hills et al., 2008, 2010). In these studies participants

foraged a visual scene for food tokens that were distributed in either a clustered or a diffuse manner. In a consecutive *scrabble* task, in which participants had to do a cognitive search for anagrams in a set of letters, participants who foraged in the clustered visual scene tended to spend more time searching for words within each letter set compared to those who searched the diffuse scene. The visual foraging task thus seemed to prime an exploitative or exploratory cognitive style that transferred to a task in another search domain (Hills et al., 2008, 2010).

Carry-over effects are also observed in other studies that prime either flexible or persistent cognitive control. One study found that open monitoring meditation, a type of meditation that promotes an unfocused awareness, increases performance on the Alternate Uses Task, a fluency task that benefits from flexible or exploratory thinking (Colzato, Ozturk, & Hommel, 2012; Guilford, 1967). Another study showed that priming participants' cognitive control with the Remote Associates Task (RAT), a task that requires more exploitative or persistent cognitive control, helped them to focus on a primary task in a dual-task paradigm (Fischer & Hommel, 2012; Mednick, 1962). These findings indicate that exploratory and exploitative cognitive styles can carry over between tasks. This also supports the idea of one cognitive control system and thus a common evolutionary basis for control of different types of search tasks (Hills et al., 2008, 2010; Hommel, 2012).

Evidence of a shared evolutionary mechanism: dopamine

If the mechanism underlying cognitive search evolved from early foraging behavior we would expect that they share a similar physiological system. In ARS, the increase in turning frequency upon encountering food appears to be modulated by DA (Hills, 2006). For example, exogenous application of DA dramatically increases turning frequency in *C. elegans* and DA antagonists can block ARS (Hills, Brockie, & Maricq, 2004). Two regions in the human brain that are involved in search behavior are the basal ganglia – in particular the

striatum – and the prefrontal cortex (PFC; Frank, Doll, Oas-Terpstra, & Moreno, 2009; Hills, 2006; Maia & Frank, 2011). Dopaminergic receptors and projections are abundant in both the basal ganglia and PFC and there are strong reciprocal connections between them (Cools, 2015).

Over evolution, the basal ganglia have expanded considerably in humans, and this might have facilitated the coding of more complex relationships between stimuli and reward. Think, for example, of relationships between current stimuli and future rewards (Hills, 2006; Miller & Cohen, 2001). According to Miller and Cohen (2001) relationships are represented in the PFC by patterns of neuronal activity that include information about appropriate actions in a given situation. These patterns of activation can bias systems that are responsible for the execution of actions (Miller & Cohen, 2011). Moreover, these patterns of activation can be strengthened by neuromodulatory reinforcement signaling by, for example, DA (Miller & Cohen, 2001). Dopaminergic coding for reward prediction errors can then be used to relate stimuli to rewards in a representation in this correlative network through frontostriatal cortical loops (Cools, 2016; Hills, 2006; Maia & Frank, 2011; Schultz, 2016). Hills (2006) proposes that an increased dopaminergic hold on goal-related representations in search would cause a search of a more local neural assembly on the one hand. On the other hand, a decreased dopaminergic hold allows for a search of a larger neural assembly related to more global goal-related representations. In other words, a decrease in dopaminergic hold allows for exploration of more possibly appropriate actions related to the goal while an increase relates to more exploitation of the most appropriate actions (Hills, 2006).

Under the assumption that exploratory and exploitative behavior are analogous to flexible and persistent behavior, the positive relationship between DA and exploitative behavior can be observed in neurological and psychiatric disorders that have been related to aberrant dopaminergic processing (Hills, 2006; Jongkees & Colzato, 2016; Maia & Frank,

2011). For example, attention deficit/hyperactivity disorder has been related to a hypodopaminergic state and many symptoms appear as an inability to persist in behavior (Krause, Dresel, Krause, La Fougere, & Ackenheil, 2003; Schinka, Letsch, & Crawford, 2002). However, findings involving dopaminergic processing in pathologies have been inconsistent and it is difficult to judge the wide ranges of symptoms as a whole as overly flexible or persistent (Jongkees & Colzato, 2016; Maia & Frank, 2011).

More problematic, ample evidence indicates that high DA is related to exploratory behavior, not exploitation (for a recent review see Jongkees & Colzato, 2016). Hills (2006) explains that in a highly uncertain situation the striatum might increase the dopaminergic hold on so many different representations of behaviors that are possibly related to rewards, that the hold on representations actually again allows for a more global cognitive search. Exploratory behavior might thus result from possible exploitation of many different representations kept in working memory in the PFC (Cools, 2015; Durstewitz & Seamans, 2008; Hills, 2006). Indeed, widespread neuronal activation in DA-modulated frontostriatal networks has been observed in case of high uncertainty or unfamiliarity (Hills, 2006). This explanation would suggest that striatal DA is related to cognitive flexibility in a U-shaped manner, where high and low striatal DA levels would be related to flexible or exploratory search and intermediate levels to more persistent or exploitative search.

Differentiating between cognitive flexibility and performance flexibility. Some evidence seems to contradict the idea of a U-shaped relationship between the level of striatal DA and cognitive flexibility. For example, a study on divergent creativity found an inverted U-shaped relationship between DA levels and performance on a flexibility task (Akbari Chermahini & Hommel, 2012). Participants performed the Alternate Uses Task, which benefits from an ability to flexibly switch between ideas or high exploration of goal-related

representations (Guilford, 1967). Those with high and low DA levels scored lower on flexibility than those with intermediate DA levels (Akbari Chermahini & Hommel, 2012). These seemingly conflicting findings might be reconciled when we differentiate between the level of flexible switching between representations in the frontostriatal DA network (from here on ‘cognitive flexibility’) and the level of performance in tasks that require flexible switching between ideas (from here on ‘performance flexibility’). A U-shaped relationship between DA and cognitive flexibility as suggested by Hills (2006) does not exclude an inverted U-shaped relationship between DA and performance flexibility as found by Akbari and Chermahini (2012). As discussed earlier, high cognitive flexibility can come from either a lack of a dopaminergic hold on any appropriate representation or a global dopaminergic hold on many different representations (Hills, 2006). Performance flexibility might suffer from a search that is too global due to high cognitive flexibility such that non-goal-related representations are considered in the search for an appropriate response (Hills, 2006; Jongkees & Colzato, 2016). Thus, at low and high levels of DA cognitive flexibility may be high and go together with low performance flexibility.

Differentiating between dopaminergic exploratory and exploitative systems.

Instead of two ends of one dimension ranging from flexibility to persistence, flexibility (or exploration) and persistence (or exploitation) can also be thought of as two different systems in cognitive control (Akbari Chermahini & Hommel, 2012; Cools, 2015; Cools & D’Esposito, 2011). This idea is supported by the observation that performance in divergent thinking tasks is not correlated to performance in convergent thinking tasks (Akbari Chermahini & Hommel, 2012). Moreover, DA seems to be related to performance in the two types of tasks in different manners. Where DA level seemed to be related to performance on a divergent thinking task in an inverted-U shaped manner, DA might be linearly and negatively related to convergent

thinking, although this finding was not very reliable (Akbari Chermahini & Hommel, 2012). Cools and D'Esposito (2011) propose that cognitive control is indeed dependent on two competing dopaminergic states. They propose a functional opponency between the PFC and the striatum. On the one hand, dopaminergic activation in the PFC promotes stability of representations, allowing for exploitation. On the other hand striatal dopaminergic activity promotes flexibility, allowing for exploration (Cools, 2015; Cools & D'Esposito, 2011). Intermediate levels of DA are then associated with a balance between the two systems that allows for adaptive cognitive control in terms of behaving in a flexible or persistent manner. Sub- or supraoptimal levels of DA in either system would be associated with decreased cognitive performance (Cools, 2015).

Dual-state theory states that this balance depends on different types of DA activity in the PFC: D1- and D2 receptor-mediated (Durstewitz & Seamans, 2008). With intermediate levels of DA the PFC assumes a D1 receptor-mediated state in which a high-energy barrier between representations precludes the switching between them and thus promotes the stabilization of representations. High or low levels of DA, on the other hand, are associated with a D2 receptor-mediated PFC state. The D2 receptor-mediated state involves a low-energy barrier that promotes switching between representations and exploratory behavior (Durstewitz & Seamans, 2008). As there are predominantly D1 receptors in the PFC and D2 receptors in the striatum the theories proposed by Cools and D'Esposito (2011) and Durstewitz and Seamans (2008) are compatible (Hommel, 2015).

Hommel (2015) proposes the metacontrol state model (MSM) that generalizes these ideas and states that metacontrol depends on a balance between one state that promotes flexible cognitive control and another state that promotes focused or persistent cognitive control. He explains that the increased impact of a goal representation and/or a high competitiveness between different representations increase persistence. Flexible behavior, on

the other hand, should be related to a lesser impact of goal representation and/or low competitiveness between representations (Hommel, 2015).

Eye blink rate and dopamine. In summary, DA likely has a role in control of exploratory and exploitative behavior, possibly in two different systems. The dopaminergic system that underlies simple search behavior like ARS might have evolved into the dopaminergic systems that now afford complex processing in cognitive search. Based on the theory on two different systems in cognitive control mentioned earlier, we might conclude the striatum to be implicated in the control of cognitive flexibility.

One way of measuring DA levels is eye blink rate (EBR). This is an indirect measure of DA where higher EBR indicates a higher level of striatal DA (Jongkees & Colzato, 2016; Stevens, 1978). EBR has been used to study how differences in striatal DA are related to differences in reinforcement learning, cognitive control, cognitive flexibility, and working memory (Jongkees & Colzato, 2016). To our knowledge, EBR has not been used before to study how differences in striatal DA are related to differences in search behavior. In this study we assumed that the level of exploration in cognitive control in search might be related to or even the same as the level of flexibility in cognitive control. EBR as a measure of striatal DA then offers the opportunity to study the relationships between striatal DA and differences in exploratory behavior in cognitive search.

The current study

In this study we tried to replicate the studies on carry-over effects between different domains of search that were described earlier (Hills et al., 2008, 2010; Wilke, 2006; Wilke et al., 2004). Participants performed a cognitive word search task twice in which they had to search for anagrams from letter sets, the so-called *scrabble task*. In between the pretest and

posttest scrabble task they foraged a visual scene for food tokens, the *visual foraging task*. The food tokens in the visual scene were distributed either in a clustered or diffuse manner throughout the scene. We added EBR as a measure of DA levels to study the neuromodulatory effects of DA in human search behavior. As discussed above we expected to find a relationship between DA and exploratory search behavior.

Hypotheses

First, we expected to replicate the main findings of Hills et al. (2008, 2010). We expected that there would be carry-over effects of exploratory and exploitative search strategies between tasks: Those participants who would search for food tokens in a clustered environment should search within letter sets for longer in the scrabble posttest compared to the pretest. This would indicate less exploration between letter sets and more exploitation within letter sets. The other way around, participants in the diffuse condition should search for words within letter sets in the posttest for a shorter time compared to the pretest. This would indicate more exploration between letter sets and less exploitation within letter sets.

Second, we expected that participants with different EBRs would show different search behavior in the scrabble tasks. We expected an inverted U-shaped relation between the time spent searching for words in a letter set and EBR such that those with low and high EBR stayed in the letter sets the shortest, showing higher exploratory behavior. This would be in line with Hills' (2006) expectation of more exploration for low and high DA levels and more exploitation for intermediate levels (Hills, 2006). We also expected participants with low and high DA levels to turn less immediately after finding food tokens, indicating higher exploratory behavior even in response to possible patches of reward. Again, this finding would offer evidence for the suggestion that cognitive flexibility is regulated by dopaminergic holds on representations in the striatum (Hills, 2006).

Method

Participants

Participants were sampled from an undergraduate psychology and child studies population at Leiden University. We visited lectures, approached students in the faculty hallways, and sampled via Facebook groups, posters in the faculty hallways, and a participant management system. We included 54 undergraduate participants with a mean age of 21.55 years ($SD = 6.54$ years, 76% females) in this study. All participants were native Dutch speakers and in self-reported excellent physical and mental health. Participants with contact lenses were asked to wear their glasses during the tasks and take them off for the EBR measures. Those participants who smoked were asked to refrain from smoking before participating in our study. As EBR has been found to relate to arousal, and thus might vary over different times of day, all participants were tested between 9 AM and 5 PM (Chandler, Waterhouse, & Gao, 2014; Jongkees & Colzato, 2016). Informed consent was required for every participant and they received course credit for their participation.

Procedure

Participants were informed about the study and signed informed consent. They were then taken to a room where artificial lighting was kept constant over all participants and they were seated in front of a computer. Before they performed any tasks we measured their EBR. All participants then performed the scrabble pretest followed by the visual foraging task. After measuring their EBR for the second time they performed the scrabble posttest.

Materials

Eye blink rate. EBR was measured twice during the experiment. Participants sat in front of the computer screen with a fixation cross on it and were asked to look at the cross in a relaxed state. We filmed them with a webcam for 6 minutes. Based on video images we counted the number of blinks in 6 minutes manually. We divided the total number of blinks by 6 to get a measure of their EBR per minute.

Scrabble task. We replicated the scrabble task from the studies by Hills et al. as closely as possible (2008, 2010). This task was used to study internal, cognitive search behavior. Participants were asked to find as many anagrams as possible from a set of letters. For example, the letter set TNIERW contains among other words the Dutch words ‘winter’ (winter), ‘trein’ (train), and ‘niet’ (not). Each word had to be a Dutch word consisting of at least four letters and could not be plural or a proper name. Every letter in the set could be used only once. Participants could enter as many words as they wanted when a letterset was shown. Feedback was given about whether the word was correct immediately after entering the word. They could change to the next letterset whenever they wanted but the next set was shown only after a waiting penalty of 15 seconds to represent ‘travel costs’ between patches. A total of 18 lettersets was created with a mean number of 15.2 valid words ($SD = 4.9$). Words were judged as correct words based on an online anagram dictionary (www.wordfeudhelp.nl) and every word was cross referenced with a Dutch dictionary for outdatedness and correct spelling. No additional correct words were found in the participants’ responses that were not in the original list of correct words.

Participants were allowed to practice on one letter set before starting the scrabble pretest. In the pretest each participant was shown four consecutive lettersets (the same sets in the same order for each participant) from which they were asked to form words. In the posttest participants were told to find 30 words in total and to not spend too little or too much

time in each letter set. They had to form the words within the remaining 14 letter sets that were the same for each participant but presented in random order.

Visual foraging task. The visual foraging task was used to study external search behavior (similar to Hills et al., 2010). Participants were presented with a 200 x 200 pixel blank field in which they could control a foraging icon using the 'J' to initiate a 35° counterclockwise turn and 'L' for a 35° clockwise turn. The foraging icon moved at a speed of approximately 20 pixels per second and participants practiced its controls for 30 seconds. Whenever the participant moved the foraging icon over a food pixel ('food token') the pixel would turn green and remain green for the rest of the trial. They could not see where they had been before neither where food pixels could be found. Participants were randomly assigned to either the clustered condition or the diffuse condition. In the clustered condition 3044 food pixels were distributed in four diamond-shaped patches. In the diffuse condition the food pixels were distributed over the blank field in 624 patches of five pixels each. Both the clustered and diffuse patches were distributed randomly over the visual scenes.

The participants were told to search for as many food pixels as they could find in five different visual scenes. Each search lasted for two minutes. The participants were not told about the exact duration of each trial, but a sweeping hand clock in the top right corner was used to indicate that time was passing without an explicit report of how much time was left. We measured the turning angle immediately after finding food by counting the number of 35°-turns within 0.3 s after every encounter with food.

Results

All participants ($N = 54$) were randomly assigned to either the clustered ($n = 27$) or diffuse ($n = 27$) condition. Upon initial data inspection we found that one participant did not

finish the task properly but instead stopped searching for words in the posttest and skipped the final six letter sets before finding 30 words. A second participant spent longer than 3 or more standard deviations above the mean ($M = 82.57$ s, $SD = 46.49$ s) in all but the last letter set to search for words in the scrabble posttest. A third participant failed to meet the 30-word criterion in the scrabble posttest within 14 letter sets and used dextroamphetamine on a regular basis, which affects DA levels and EBR (Strakowski & Sax, 1998). All three participants were removed from the data before analysis. After exclusion of these three participants, 26 participants remained in the clustered condition and 25 in the diffuse condition.

Due to technical issues we could not use the videos of the first 12 participants to measure their EBR and their data was excluded from the analyses of the second hypothesis. However, we did include data of these participants in the analyses of those hypotheses for which all necessary values were available. Wherever we report medians instead of means the data were not distributed normally and nonparametric Wilcoxon rank sum tests were used to test for differences between medians.

Carry-over effects between visual search and cognitive search

The clustered ($Mdn = 67.75$ s) and diffuse ($Mdn = 76.02$ s) groups spent the same amount of time in each letter set in the scrabble pretest ($z = -0.45$, $p = .651$), indicating no difference in cognitive search behavior between the two conditions before the visual foraging task. The combined median time spent in letter sets in the pretest was 74.77 s. The groups found different amounts of food tokens in the visual foraging task. Participants from the clustered condition ($Mdn = 740.2$ tokens) found more tokens than participants in the diffuse condition, $Mdn = 134.2$ tokens, $z = 5.32$, $p < .001$. Because of this difference we corrected the turning angle after food for the amount of food tokens that were encountered, effectively

calculating the mean turning angle after food per encountered food token. We used this measure as a manipulation check to see if our participants were sensitive to the spatial layout of the foraging scenes in the visual foraging task. We expected that the participants in the clustered condition would respond to food tokens by turning—to exploit the patch the tokens were in—more than participants in the diffuse condition (as found by Hills et al., 2010). Contrary to our expectations, we found that the clustered group had a smaller turning angle after encountering food ($Mdn = 7.11^\circ$) than the diffuse group, $Mdn = 12.75^\circ$, $z = -4.42$, $p < .001$. Participants in the clustered condition thus turned *less* in response to food compared to the participants in the diffuse condition and behaved thus less exploitative according to Hills et al.'s reasoning (2008, 2010).

Our first hypothesis was that participants' search behavior would be primed by the visual foraging task like Hills et al. (2008, 2010) found. Similar to these studies, we used the difference in time spent in letter sets between the pre- and posttest to test this hypothesis. Participants usually stayed in the final set in the posttest for a shorter time, as the task finished when they found their 30th word, therefore we used the difference between their median time in letter sets in the pre- and posttest as their central tendency. On average, participants in the clustered condition spent 6.51 s longer in the scrabble posttest than in the pretest, while participants in the diffuse condition spent 19.76 s longer in the posttest, $t(46.66) = -2.06$, $p = .045$ (Figure 1). Again, this was not what we expected based on the study by Hills et al. (2008, 2010). In our study, participants who foraged a clustered visual scene increased their search time per letter set *less* than participants who foraged a diffuse visual scene. In other words, it seems as if participants in the diffuse condition showed more exploitative behavior than those in the clustered condition after searching the diffuse scene in the visual foraging task.

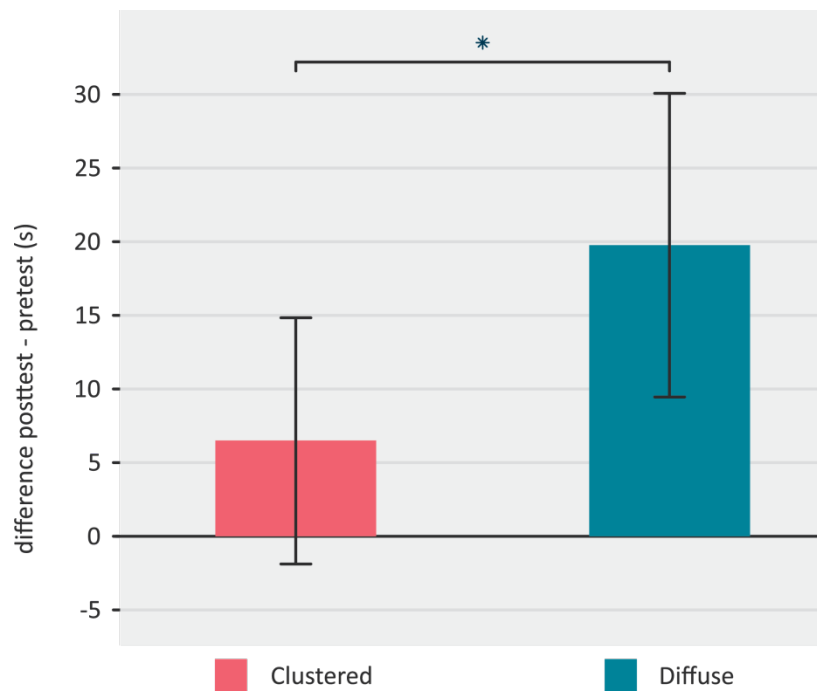


Figure 1 The mean difference in seconds between the stay in the pretest and posttest letter sets for the clustered and diffuse group. Error bars indicate 95% confidence intervals. * $p < .05$.

Eye Blink Rate, Exploration, and Exploitation

For our second hypothesis, we expected that EBR would be related in an inverse-U shaped manner to exploitation. Participants with low and high EBR should then stay shorter in each letter set, making exploratory moves between letter sets, than participants with intermediate EBR, who would exploit more within letter sets. We tested this hypothesis with mean time spent in a letter set in the scrabble pretest (as a measure of trait exploratory behavior) and their initial EBR measurement (a measure of trait EBR). Other than expected, there was no quadratic relationship between EBR and the time spent in a letter set in the pretest, $F(2,36) = 0.11$, $p = .892$, $R^2 = 0.01$.

We also tested whether there was an inverted U-shaped quadratic relationship between EBR and turning angle after food. Here a low or high EBR should be related to smaller turning angle or exploratory behavior, while intermediate EBR should be related to a larger turning angle after food or exploitative behavior. Because the difference in turning angle after

finding food between the clustered and diffuse group was significant as mentioned earlier, the regression analysis was performed for each group separately. Again, no quadratic relationship was found between EBR and turning angle immediately after encountering food tokens in the clustered group ($F(2,17) = 0.56, p = .58, R^2 = 0.06$) or in the diffuse group, $F(2,15) = 0.61, p = .56, R^2 = 0.07$.

Discussion

We set out to replicate findings that showed that exploratory or exploitative search strategies could carry-over between search tasks in different domains of search (i.e., visual search and cognitive search; Hills et al., 2008, 2010). We predicted that participants who foraged a visual scene with clustered food tokens would show ARS-like behavior: They should exploit these clusters by turning immediately after finding food (Kalff et al., 2010; Hills, 2006; Hills et al., 2008, 2010). On the other hand we expected those who foraged a scene with diffusely spread out food tokens to explore more or turn less in response to food. This should then prime exploitation and exploration, respectively, in a subsequent cognitive search task: the scrabble task. However, we found a different effect, already starting in the visual foraging task. Participants in the diffuse condition turned more after encountering food compared to those in the clustered condition, showing more ARS-like behavior than participants in the clustered condition. This difference between the clustered and the diffuse group still existed in the scrabble posttest. Compared to the pretest, the diffuse group increased the time they spent in a letter set more than the clustered group did. These findings suggest that there are priming effects of a visual search task on a cognitive search task as more exploitative behavior in the diffuse group carried over from the visual foraging task to the scrabble posttest. However, the question remains why our diffuse group showed more

exploitative behavior in search than the clustered group, contrary to what Hills et al. found (2008, 2010).

To our knowledge the only difference between this study and the studies by Hills et al. (2008, 2010) were the added measures of EBR. We measured EBR before the scrabble pretest and again between the visual foraging task and the scrabble posttest to study the influence of differences in striatal DA levels on search behavior. During the EBR measurement participants focused on a fixation cross for six minutes, which might have acted as a form of focused attention meditation. This is a form of meditation in which the practitioner concentrates attention on one object, such as their breathing (Lippelt, Hommel, & Colzato, 2014; Lutz, Slagter, Dunne, & Davidson, 2008). Another type of meditation is open monitoring meditation, in which the practitioner tries to reach an open monitoring awareness, without focus on anything specific (Lippelt et al., 2014; Lutz et al., 2008). Where open monitoring meditation can induce a more flexible or exploratory cognitive style (e.g., Colzato, Sellaro, Samara, Baas, & Hommel, 2015; Colzato, Sellaro, Samara, & Hommel, 2015), focused attention meditation is thought to increase a persistent or exploitative cognitive style (Hommel, 2015). For example, it has been related to a narrowed attentional focus (e.g., Colzato, Sellaro, Samara, Baas, & Hommel, 2015), increased cognitive persistence (e.g., Colzato, Van der Wel, & Sellaro, 2016), and increased cognitive control (e.g., Colzato, Sellaro, Samara, & Hommel, 2015). If the EBR measurements acted as a form of focused meditation, this might have induced an exploitative cognitive style in both groups. However, this would only explain why the diffuse group did not decrease their time spent in a letter set in the scrabble posttest, not why they increased their time spent in a letter set more than the clustered group.

One explanation might be that the induced exploitative cognitive style and the nature of the diffuse visual foraging task interacted to increase the exploitative cognitive style in the

scrabble posttest. The food tokens in the diffuse search fields were distributed in small patches of five pixels and the EBR measurement might have primed participants to consider the diffuse condition to consist of many small patches of food tokens. Indeed, some participants spontaneously mentioned the challenge they saw in completing the small patches of food tokens. Exploiting these small patches would require larger turning angles than exploiting patches in the clustered condition. Exploiting patches in the diffuse search fields could thus have induced a very focused, exploitative cognitive style which carried over to the scrabble task.

Exploitation of the small patches in the diffuse condition might also have increased the difficulty of the visual foraging task. Participants had to turn more vigorously and had to exploit more patches to find as many food tokens as possible. Increased difficulty can cause an increase in effort and this might have caused participants in the diffuse condition to be more persistent in their exploitative search than those in the clustered condition (Brehm & Self, 1989; Higgins, 2006; Klinger, 1975).

We interpreted the larger turning angle after finding food in the diffuse group as an indication of more exploitative behavior, however, it could be interpreted differently. The turning angle was measured by adding up all turns (each with an angle of 35°) within 0.3 s after finding food. A larger cumulative turning angle does then not necessarily indicate that a participant turned around to go back and exploit an encountered patch. Another possibility is that the participants in the diffuse condition performed a more frantic, exploratory search, in which they turned more but in different consecutive directions. Unfortunately, we did not record the search paths that our participants used, and can thus only speculate about the diffuse group having turned more because they tried to exploit the small patches of food tokens. However, a frantic exploratory style would also relate to very fast switches between

letter sets in the scrabble posttest and still cause the diffuse group to decrease their stay in letter sets compared to their scrabble pretest.

According to our second hypothesis we expected an inverse-U shaped relationship between the time spent searching for words in a letter set and EBR. This would have suggested that those participants with high and low striatal DA would show the highest exploratory behavior. However, there was no difference in the time spent in letter sets between participants with high or low and intermediate EBR. This can be explained if we assume two different dopaminergic systems to control cognitive style as discussed before, one for control of flexibility and one for persistence (Cools & D'Esposito, 2011; Durstewitz & Seamans, 2008; Hommel, 2015). EBR as a measure of striatal DA, in contrast to prefrontal DA, has been related more often to cognitive flexibility and exploration than to cognitive persistence and exploitation (Cools & D'Esposito, 2011; Frank et al., 2009; Jongkees & Colzato, 2016). Moreover, the findings by Akbari Chermahini and Hommel (2012) suggested that convergent thinking and EBR were unreliably related if related at all. If all participants were indeed primed to a more exploitative cognitive style, EBR may not be the correct measure of individual differences in DA. Rather, it would be interesting to consider differences in prefrontal DA levels to study differences in cognitive persistence or exploitation, for example by measuring the *COMT* genotype (Meyer-Lindenberg et al., 2005).

Limitations

The most obvious limitation in this study is the possible interference of the EBR measurement with the replication of the results by Hills et al. (2008, 2010). Although the effects the EBR measurement may have had as a form of focused meditation might have led to some interesting results, it was not our intention to use EBR as such. Future studies that

would like to include EBR as a measurement to study striatal DA effects in cognitive control must consider measuring baseline EBR in a separate session.

Another limitation is the homogeneity of the sample. Although we did not register participant characteristics such as ethnic background, social economic status, or religion, undergraduate student samples are quite homogenous (Henrich, Heine, & Norenzayan, 2010). This might affect the range of exploratory and exploitative search behavior as cultural differences influence cognitive control styles (Hommel, 2015). For example, people from Western cultures employ a more analytic cognitive style compared to people from Eastern cultures, whose reasoning is more holistic (e.g., Nisbett & Miyamoto, 2005). However, Hills et al. (2010) also used an undergraduate participant sample in the studies we were aiming to replicate. The homogeneity of the sample may thus preclude generalization of results to a wider population but should not have precluded the replication of Hills et al.'s earlier findings.

Finally, we measured EBR by visual inspection of video, which leaves the possibility of human error. However, when videos were hard to judge (e.g., because someone blinked very often or had many partial blinks) videos were watched at a slower speed or frame-by-frame.

Conclusion

To sum up, we aimed to replicate the findings of Hills et al. (2008, 2010) and supplement these findings with an indirect measure of striatal DA to be able to study the dopaminergic mechanisms in cognitive search. The inclusion of EBR in this study seems to have changed the nature of the study to such an extent that we were not able to replicate Hills et al. (2008, 2010). However, our findings are interesting as they do still suggest that

cognitive control styles in search can be induced, for example by meditation, and that effects carry over between tasks. We also found that striatal DA was not related to search behavior in either visual search or cognitive search as predicted, which might relate to different dopaminergic systems in exploitative versus exploratory cognitive control. It appears that studying the role of DA in search behavior might require measures of prefrontal DA as well.

To conclude, different dopaminergic systems should be considered in the study of human search behavior and studies of carry-over effects of cognitive styles in search should be designed very carefully. Nevertheless, the study of foraging and search behavior can increase our knowledge on cognitive control and perhaps offer different interesting methods and models.

References

- Akbari Chermahini, S., & Hommel, B. (2012). The (b)link between creativity and dopamine: Spontaneous eye blink rates predict and dissociate divergent and convergent thinking. *Cognition, 115*, 458-465. doi:10.1016/j.cognition.2010.03.007
- Brehm, J. W., & Self, E. A. (1989). The intensity of motivation. *Annual Review of Psychology, 40*, 109-131. doi:10.1146/annurev.ps.40.020189.000545
- Chandler, D. J., Waterhouse, B. D., & Gao, W-J. (2014). New perspectives on catecholaminergic regulation of executive circuits: Evidence for independent modulation of prefrontal functions by midbrain dopaminergic and noradrenergic neurons. *Frontiers in Neural Circuits, 8*(53), 1-10. doi:10.3389/fncir.2014.00053
- Colzato, L. S., Ozturk, A., & Hommel, B. (2012). Meditate to create: The impact of focused-attention and open-monitoring training on convergent and divergent thinking. *Frontiers in Psychology, 3*(116), 1-5. doi:10.3389/fpsyg.2012.00116
- Colzato, L. S., Sellaro, R., Samara, I., Baas, M., & Hommel, B. (2015). Meditation-induced states predict attentional control over time. *Consciousness and Cognition, 37*, 57-62. doi:10.1016/j.concog.2015.08.006
- Colzato, L. S., Sellaro, R., Samara, I., & Hommel, B. (2015). Meditation-induced cognitive-control states regulate response-conflict adaptation: Evidence from trial-to-trial adjustments in the Simon task. *Consciousness and Cognition, 35*, 110-114. doi:10.1016/j.concog.2015.04.012
- Colzato, L. S., Van der Wel, P., Sellaro, R., & Hommel, B. (2016). A single bout of meditation biases cognitive control but not attentional focusing: Evidence from the global-local task. *Consciousness and Cognition, 39*, 1-7. doi:10.1016/j.concog.2015.11.003

- Cools, R. (2015). The cost of dopamine for dynamic cognitive control. *Current Opinion in Behavioral Sciences*, 4, 152-159. doi:10.1016/j.cobeha.2015.05.007
- Cools, R. (2016). The costs and benefits of brain dopamine for cognitive control. *WIREs Cognitive Science*, 7, 317-329. doi:10.1002/wcs.1401
- Cools, R., & D'Esposito, M. (2011). Inverted-U shaped dopamine actions on human working memory and cognitive control. *Biological Psychiatry*, 69(12), e113-e125. doi:10.1016/j.biopsych.2011.03.028.
- Durstewitz, D., & Seamans, J. K. (2008). The Dual-State Theory of prefrontal cortex dopamine function with relevance to catechol-*O*-methyltransferase genotypes and schizophrenia. *Biological Psychiatry*, 64, 739-749. doi:10.1016/j.biopsych.2008.05.015
- Fischer, R., & Hommel, B. (2012). Deep thinking increases task-set shielding and reduces shifting flexibility in dual-task performance. *Cognition*, 123, 303-307. doi:10.1016/j.cognition.2011.11.015
- Frank, M. J., Doll, B. B., Oas-Terpstra, J., & Moreno, F. (2009). Prefrontal and striatal dopaminergic genes predict individual differences in exploration and exploitation. *Nature Neuroscience*, 12(8), 1062-1068. doi:10.1038/nn.2342
- Guilford, J. P. (1967) . *The nature of human intelligence*. New York, NY: McGraw-Hill.
- Higgins, E. T. (2006). Value from hedonic experience and engagement. *Psychological Review*, 113(3), 439-460. doi:10.1037/0033-295X.113.3.439
- Hills, T. T. (2006). Animal foraging and the evolution of goal-directed cognition. *Cognitive Science*, 30, 3-41. doi:10.1207/s15516709cog000050
- Hills, T. T., Brockie, P., & Maricq, A. V. (2004). Dopamine and glutamate control area-restricted search behavior in *Caenorhabditis elegans*. *The Journal of Neuroscience*, 24(5), 1217-1225. doi:10.1523/JNEUROSCI.1569-03.2004

- Hills, T. T. & Dukas, R. (2012) The evolution of cognitive search. In P. M. Todd, T. T. Hills, & T. W. Robbins (Eds.), *Cognitive search. Evolution, algorithms, and the brain*. (pp. 11-24). Cambridge, MA: MIT Press.
- Hills, T. T., Todd, P. M., & Goldstone, R. L. (2008). Search in external and internal spaces. Evidence for generalized cognitive search processes. *Psychological Science, 19*(8), 802-808. doi:10.1111/j.1467-9280.2008.02160.x
- Hills, T. T., Todd, P. M., & Goldstone, R. L. (2010). The central executive as a search process: Priming exploration and exploitation across domains. *Journal of Experimental Psychology: General, 139*(4), 590-609. doi:10.1037/a0020666
- Hommel, B. (2012). Convergent and divergent operations in cognitive search. In P. M. Todd, T. T. Hills, & T. W. Robbins (Eds.), *Cognitive search. Evolution, algorithms, and the brain*. (pp. 221-236). Cambridge, MA: MIT Press.
- Hommel, B. (2015). Between persistence and flexibility: The Yin and Yang of action control. In: A.J. Elliot (ed.), *Advances in motivation science, Vol. 2* (pp. 33-67). New York, NY: Elsevier.
- Hutchinson, J. M. C., Stephens, D. W., Bateson, M., Couzin, I., Dukas, R., Giraldeau, L.-A., . . . Winterhalder, B. (2012). . In P. M. Todd, T. T. Hills, & T. W. Robbins (Eds.), *Cognitive search. Evolution, algorithms, and the brain*. (pp. 47-65). Cambridge, MA: MIT Press.
- Jongkees, B. J., & Colzato, L. S. (2016). Spontaneous eye blink rate as predictor of dopamine-related cognitive function – A review. *Neuroscience and Biobehavioral Reviews, 71*, 58-82. doi:10.1016/j.neubiorev.2016.08.020
- Kalff, C., Hills, T. T., & Wiener, J. M. (2010). Human foraging behavior : a virtual reality investigation on area restricted search in humans. In S. Ohlsson & R. Catrambone

- (Eds.), *Proceedings of the 32nd Annual Conference of the Cognitive Science Society* (pp. 168-173). Austin, TX: Cognitive Science Society.
- Klinger, E. (1975). Consequences of commitment to and disengagement from incentives. *Psychological Review*, 82(1), 1-25. doi:10.1037/h0076171
- Krause, K. H., Dresel, S. H., Krause, J., La Fougere, C., & Ackenheil, M. (2003). The dopamine transporter and neuroimaging in attention deficit hyperactivity disorder. *Neuroscience & Biobehavioral Reviews*, 27(7), 605-613.
- Lippelt, D. P., Hommel, B., & Colzato, L. S. (2014). Focused attention, open monitoring and loving kindness meditation: effects on attention, conflict monitoring, and creativity – A review. *Frontiers in Psychology*, 5, 1-5. doi:10.3389/fpsyg.2014.01083
- Lutz, A., Slagter, H. A., Dunne, J. D., Davidson, R. J. (2008). Attention regulation and monitoring in meditation. *Trends in Cognitive Sciences*, 12(4). doi:10.1016/j.tics.2008.01.005
- Maia T. V., & Frank, M. J. (2011). From reinforcement learning models to psychiatric and neurological disorders. *Nature Neuroscience*, 14(2), 154-162. doi:10.1038/nn.2723
- Mednick, S. (1962). The associative basis of creative problem solving process. *Psychological Review*, 69, 200–232.
- Mehlhorn, K., Newell, B. R., Todd, P. M., Lee, M. D., Morgan, K., Braithwaite, V. A., . . . Gonzalez, C. (2015). Unpacking the exploration exploitation tradeoff: A synthesis of human and animal literatures. *Decision*, 2(3), 191-215. doi:10.1037/dec0000033
- Meyer-Lindenberg, A., Kohn, P. D., Kolachana, B., Kippenhan, S., McInerney-Leo, A., Nussbaum, . . . Berman, K. F. (2005). Midbrain dopamine and prefrontal function in humans: interaction and modulation by COMT genotype. *Nature Neuroscience*, 8(5), 594-596. doi: 10.1038/nn1438

- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24*, 167-202. doi:10.1146/annurev.neuro.24.1.167
- Nikitin, E., & Hills, T. T. (2016). Strategic search in semantic memory. In A. Papafragou, D. Grodner, D. Mirman, & J.C. Trueswell (Eds.), *Proceedings of the 38th Annual Conference of the Cognitive Science Society* (pp. 1565-1570). Austin, TX: Cognitive Science Society.
- 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. doi:10.1002/ajmg.10649
- Schultz, W. (2016). Dopamine reward prediction-error signaling: a two-component response. *Nature Reviews Neuroscience, 17*, 183-195. doi:10.1038/nrn.2015.26.
- Stevens, J.R. (1978). Eye blink and schizophrenia: psychosis or tardive dyskinesia? *American Journal of Psychiatry, 135*(2), 223–226. doi:10.1176/ajp.135.2.223
- Strakowski, M. S., & Sax, K. W. (1998). Progressive behavioral response to repeated d-Amphetamine challenge: further evidence for sensitization in humans. *Biological Psychiatry, 44*(11), 1171-1177.
- Todd, P. M., Hills, T. T., & Robbins T. W. (2012). Building a foundation for cognitive search. In P. M. Todd, T. T. Hills, & T. W. Robbins (Eds.), *Cognitive search. Evolution, algorithms, and the brain*. (pp. 1-10). Cambridge, MA: MIT Press.
- Wilke, A. (2006). *Evolved responses to an uncertain world* (Doctoral dissertation). Retrieved from www.diss.fu-berlin.de/2006/14/indexe.html
- Wilke, A., Hutchinson, J. M. C., & Todd, P. M. (2005). Testing simple rules for human foraging in patchy environments. In K. Forbus, D. Gentner, & T. Regier (Eds.), *Proceedings of the 26th Annual Conference of the Cognitive Science Society* (pp. 1656-1656). Mahwah, NJ: Erlbaum.