

INTERFERENCE EFFECTS IN THE SPATIAL MEMORY
OF SEED CACHING CORVIDS

by

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DISSERTATION TITLE

Interference Effects in the Spatial Memory of Seed Caching Corvids

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INTERFERENCE EFFECTS IN THE SPATIAL MEMORY OF SEED CACHING CORVIDS

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University of Nebraska, 2005

Advisor: Alan C. Kamil

I tested the spatial memory of serially presented locations in Clark's nutcrackers (*Nucifraga columbiana*). Birds were presented with lists of locations in an open room by offering a buried seed in a sand filled cup at each location, one at a time. Birds were then tested for their memory for each location by opening clusters of cups surrounding the correct location. Accuracy was measured by how many tries the bird required to find the correct location. In chapter 2, I found no evidence of serial position effects, but did find evidence for proactive and retroactive interference after the presentation of two lists of locations. Nutcrackers performed worse on a list whether the interfering information came before (proactive) or after (retroactive) the target list. Furthermore, when items from two lists were located close to each other, nutcrackers made errors by visiting the interfering list locations during recall of the target list. This suggests that the majority of interference in nutcracker memory is due to revisits to depleted locations. Two experiments, presented in chapter 3, were conducted to determine whether increasing the interval between lists or changing the landmark array during study and recall of each list would decrease proactive interference. Increasing the interval did not affect interference, but changing the landmark array eliminated errors made in repeat clusters during recall of list 2. Finally, chapter 4 demonstrates that there was no difference between the performance of nutcrackers and scrub jays (*Aphelocoma coerulescens*) for their susceptibility to proactive interference in this task.

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PREVIEW

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Chapter 1: Introduction

The ecological and evolutionary approach to studying animal cognition

The modern study of animal cognition falls into one of two common viewpoints, the general process or the ecological view. The general process view assumes that basic learning and associative mechanisms are shared by all organisms because of the common need to make associations between events in the environment (see Macphail & Bolhuis, 2001). Those that approach the study of animal behavior using the ecological view assume that cognitive mechanisms have evolved to solve specific ecological problems in the organism's environment (Shettleworth, 1998).

In this adaptive view of researching behavior, learning and cognition are studied within an ecological and evolutionary framework. Unlike studying questions that are centered around understanding human cognition, the adaptive framework helps researchers to formulate meaningful questions centered around the animal and its natural history. Studying cognition with an ecological approach also provides a framework for understanding the function and evolutionary history of a cognitive mechanism. Prior research with food storing birds, such as the Clark's nutcracker, has demonstrated that an understanding of the ecology and evolutionary history of the animal helps to provide a framework for understanding spatial memory. This framework is beneficial by helping us to ask appropriate research questions. For example, understanding the natural history of the nutcracker helps to formulate questions about what characteristics of memory are most adaptive for remembering large amounts of information over a long period of time. By understanding the evolutionary history of food storing corvids, one can also ask whether birds that are highly dependent on stored food have better spatial memory

abilities than birds that do not store food. The natural history of the bird can also provide a framework for understanding why a particular species does or does not perform well on a particular task. Therefore, understanding the spatial memory abilities of a food storing bird can only come from understanding the natural history of the bird.

The natural history of nutcrackers and other food storing corvids

Clark's nutcrackers (*Nucifraga columbiana*) reside in high altitude environments in the western United States and Canada and survive harsh winters by recovering food stored the previous fall. Each year, in the late summer and autumn, nutcrackers spend their time foraging for seeds from several species of pine such as pinyon pine (*Pinus edulis*), southwestern white pine (*P. strobiformis*), and whitebark pine (*P. albicaulis*; Tomback, 1977; VanderWall & Balda, 1977). As a bird harvests seeds, it fills its sublingual pouch (Bock, Balda, & VanderWall, 1973) with up to 35 to 150 seeds and will often carry those seeds up to 22 km away from the collecting site for caching (Tomback, 1980).

In the fall, nutcrackers store seeds in storage sites that typically include south facing slopes that are likely to experience rapid snowmelt. Large macrosites used by nutcrackers include open or cleared areas, meadows, and burn sites. More refined microsites include caching near rocks, trees, roots, and plants (Tomback, 1977; 1986). Anywhere from one to 30 seeds (with a mean of about 6-8) are placed in a single cache location which are spatially distributed from 10 to 300 centimeters apart (Tomback, 1977). Nutcrackers recover caches throughout the winter months into spring and early summer and feed recovered seeds to nestlings (Tomback, 1977; VanderWall, & Hutchins,

1983). A single nutcracker may cache close to 30 thousand seeds in one year and will recover them with an accuracy of approximately 67% (Tomback, 1980).

Two other closely related species of food caching corvid, the pinyon jay (*Gymnorhinus cyanocephalus*) and the scrub jay (*Aphelocoma coerulescens*) have diverged from the nutcracker in their dependence on stored food and the number of specialized adaptations to storing food. The nutcracker is more adapted to food storing than the pinyon jay, which relies slightly less on stored food than the nutcracker (Vanderwall & Balda, 1981). Pinyon jays and nutcrackers have similar long and tapered beaks and can harvest seeds from unripe cones. Scrub jays have short beaks that are not adapted for opening closed cones (Vanderwall & Balda, 1981). Scrub jays also have no adaptive structure for carrying seeds like the sublingual pouch of the nutcracker. Pinyon jays have a flexible esophagus in which they can carry about half the number of seeds of a nutcracker (VanderWall & Balda, 1981). Nutcrackers also feed their nestlings a larger diet of stored seeds than either pinyon jays or scrub jays (Vanderwall & Balda, 1981).

In the field, Tomback (1980) found that the success rate for locating a cache was above chance levels which suggests that nutcrackers do not use trial and error search. Therefore, she suggested that nutcrackers probably have memories for specific cache sites. In more controlled laboratory environments, researchers have found that nutcrackers find their caches via memory for specific cache locations (see Balda & Turek, 1984; VanderWall, 1982; Balda, 1980). For example, VanderWall (1982) allowed nutcrackers to cache seeds in a large experimental room and recorded their searching behavior. Birds that had previously cached seeds had better success rates at finding buried seeds in the testing room than birds that did not cache seeds. This suggests that

the birds who cached seeds were using something other than trial and error search to locate seeds. These results also suggest that nutcrackers do not use general rules to search randomly in preferred sites and nutcrackers do not use olfactory cues to locate caches.

The memory capabilities of Clark's nutcrackers have been found to be quite exceptional which is highly related to their dependence on stored food. The important characteristics of nutcracker memory are high load (they store thousands of seeds) and long retention interval (they remember caches for months at a time). Nutcrackers are highly dependent on stored food to survive the winter and for the success of its progeny, and therefore there is a strong selective pressure on spatial memory abilities for recovering stored food.

Laboratory experiments which test the memory of nutcrackers

Much of what we know about nutcracker memory comes from laboratory experiments conducted in semi-naturalistic environments. These experiments have revealed many important characteristics of nutcracker memory. For example, landmarks are important for recovering stored food. Removing or displacing landmarks can significantly disrupt performance during cache recovery (Balda & Turek, 1984; VanderWall, 1982). Nutcrackers also make many revisits to depleted sites during recovery (Balda, Kamil, & Grim, 1986; Kamil & Balda, 1985; Kamil, Balda, Olson, & Good, 1993). However, site preferences in a caching room play a minor role in the selection of a cache and have no relation to recovery accuracy (Balda, Kamil, & Racz, 1997; Kamil & Balda, 1985). Nutcrackers also tend to visit the best remembered sites

first during cache recovery (Kamil & Balda, 1990). In the laboratory, nutcrackers can remember their caches for up to 285 days and the majority of forgetting doesn't occur until after 183 days (Balda & Kamil, 1992). Comparative experiments with nutcrackers, pinyon jays, and scrub jays show that performance on caching experiments correlate with each species dependence on stored food. Nutcrackers and Pinyon Jays outperform Scrub Jays at recovering their caches (Bednekoff, Balda, Kamil, & Hile, 1997; Balda & Kamil, 1989). However, species differences disappear at longer intervals over 150 days as nutcrackers and pinyon jays did as poorly as scrub jays (Bednekoff et al., 1997).

Nutcrackers have also been tested with traditional methods of measuring memory in animals. For example, nutcrackers have been tested for their memory of locations using operant procedures. Basil (1992) found that performance during recall of spatial lists of locations declines as the memory load and the retention interval increases. Operant tests of non-matching to sample have also revealed that memory for spatial information, but not color samples, is correlated with the dependency on stored food between nutcrackers, pinyon jays, and scrub jays (Olson, 1991; Olson, Kamil, Balda, & Nims, 1995).

Nutcrackers also perform well in an analogue of the radial arm maze over retention intervals of up to 6 hours (Balda & Kamil, 1988). There are no differences in nutcracker' performance whether the maze is a stay (returning to rewarded holes) or shift (returning to unrewarded holes) task (Olson, Kamil, & Balda, 1993). However, when the birds cache seeds in a testing room, they cannot learn to shift away from their own cache sites (Kamil, Balda, & Olson, 1994). Most radial arm maze experiments with nutcrackers, pinyon jays, and scrub jays have also revealed a correlation between

performance on the task and dependence on cached food. Kamil, Balda, and Olson (1994) found that nutcrackers and pinyon jays perform better than scrub jays in an analogue of the radial maze at short retention intervals. However, nutcrackers do not outperform other species on other radial maze experiments that involve a three-dimensional version of the task (Balda, Kamil, Bednekoff, & Hile, 1997), or involve both working and reference memory tasks (Gould-Beirle, 2000).

The importance of considering interference when studying memory

The study of memory must be assessed behaviorally by how an organism performs on a test of remembered items. A performance deficit on a memory test could be due to the inability to encode the item, problems retaining, or difficulty retrieving the item (Kamil et al., 1994). Many memory researchers agree that performance deficits on memory tests are most often due to retrieval failures (e.g. Loftus & Loftus, 1980; Roediger & Guynn, 1996). That is, poor performance on a memory test is usually due to a failure to retrieve the appropriate memory, and not because the memory is lost (Capaldi & Neath, 1995; Spear, 1971). According to McGeoch (1932) old information is never lost but exists along with new information. In support of this, there are many examples of when a subject is unable to recall information at time A, but does recall the information later at time B (e.g. Brown, 1923).

McGeoch (1932) states that like rust develops over time, memories also fade with time. However, oxidation is the process which causes rust, not time. Therefore, he suggests that interference is the process that causes forgetting. Time is only an important factor in forgetting because it increases the probability that interference will occur

(Nairne, 2002). Therefore, Capaldi and Neath (1995) suggest that remembering information is essentially discrimination learning. In order to accurately retrieve a target memory, the organism must learn what cues uniquely distinguish the memory from competing memories.

The important factors for recalling information are the relationship between the target memory and the stimuli that cue the retrieval of the memory, and whether the retrieval cue uniquely identifies the target (Tulving, 1974; Anderson & Neely; Capaldi and Neath, 1995; Nairne, 2002; Roediger & Gynn, 1996). Interference occurs when the retrieval cue fails to cue a specific target memory over competing memories. Interference is likely to occur if one retrieval cue is tied to more than one target. Therefore, when the cue is used to retrieve a memory, the cue will trigger more than one memory associated with this cue and the memories will compete for access during recall. For example, in the paired associate paradigm, humans are asked to learn a pair of words in one list (A-B). The participant is then given the cue (A) and is asked to provide the correct word (B). When given a second paired list of words, people are typically better at recall when given a list with completely different words (C-D) than a list that reuses words from the first list (A-C; see Neath, 1998).

Interference, such as that occurs in the paired associate paradigm, can act proactively or retroactively on remembered information. Proactive interference occurs when the recall of information is hampered by previously acquired information. Conversely, interference can also occur between the time when information is encoded and when memory is tested. This type of interference is called retroactive, because it acts retroactively on the target information.

Another important characteristic of interference is that organisms are subject to more interference the greater the similarity between old and new learned information. This phenomenon can be seen most readily in experiments that demonstrate release from proactive interference when the item type is changed. Wickens, Born, and Allen (1963) gave humans lists of three consonants for three trials. Performance declined over the trials because of a build up of proactive interference from the previous trials. On the fourth trial, the participants in the experimental group were asked to remember a list of three numbers and those in the control group were asked to remember another list of consonants. The group that was asked to remember a new category of stimuli performed better than the control group. This release from proactive interference was also demonstrated for participants who remembered lists of numbers over three trials and then were switched to lists of consonants (Wickens, et al., 1963).

Another type of similarity that produces a strong interference effect is when target memories are repeatedly reused over multiple trials (Wright et al., 1986). Often, organisms have a difficult time determining which of the appropriate items was correct on a given trial. As a result, they often make incorrect choices to previously rewarded targets. For example, Sands and Wright (1980a, b) developed a serial-probe-recognition task in order to examine the effects of interference with repeated items. In this procedure a monkey was given a serial presentation of stimuli and then given a recognition test. During this test, a probe item is presented and the monkey must identify whether it was the item it had seen in the list (same) or not seen in the list (different). They tested the monkey's memory for three item lists of sample stimuli with high and low levels of interference. In the high interference condition, lists were constructed from a pool of six

items and in the low interference condition, lists were chosen from a pool of 211 items (without replacement; Sands & Wright, 1980a,b). They found poorer performance when the lists were derived from small pools of samples that consequently have higher number of samples that are reused. Similar results have been found in tests of delayed matching-to-sample, which show better performance using trial-unique stimuli than using repeated stimuli (Overman & Doty, 1980). Furthermore, Sands and Wright (1980a,b) discovered that monkeys are susceptible to proactive interference (PI) and typically make mistakes by responding “same” to a stimulus that was seen in a previous list. Wright, Urcuioli, and Sands (1986) call this the “repeated-item PI effect” in which every trial, not just the previous trial, has the potential to include conflicting memories of prior samples. In turn, Wright et al. (1986) argue that an animal’s true capabilities on a given memory test are likely underestimated because the item repetition causes a high level of interference throughout the entire test.

Repeated PI effects are also enhanced in other tests of memory (such as DMTS, and operant tests of spatial memory) that include a small pool of possible samples (Basil, 1992; Olson, 1991; Wright et al., 1986). Matching-to-sample is a common method used to study animal memory. In this design animals are shown a sample, give a retention interval, and are then given two choices. One of the choices is the correct sample and the other is a distracter. Because there are few samples and few choices in the design of these experiments, there are numerous chances for interference to occur. Interference can come from the immediately prior trial, within the trial itself, and within the entire session (Capaldi & Neath, 1995).

Interference effects during the recall of spatial items will occur the more similar spatial information is over multiple lists. However, determining what constitutes similarity on a spatial task may be complicated. Determining what are similar items to cause interference during recall of lists of words in human memory is also a difficult task. For example, humans are given a list of words; pear, lion, match. What would constitute a similar list? A list that sounds similar to the target list: peer, lying, mask? Or a list that is similar in meaning to the original list: apple, tiger, lighter (Spear & Riccio, 1994). Locations that are close to each other in space between several lists may produce interference. For example, locations in space can obtain stimulus control (Cheng, Spetch, & Johnston, 1997). A rewarded location can produce a peak level of responding at that location and a generalization gradient along a spatial dimension (Cheng, et al., 1997). However, other environmental features are also encoded when an animal must remember a location in space such as the shape of the testing environment (Cheng, 1986), and landmarks (VanderWall, 1982). Therefore, increasing the similarity between lists of locations may also include choosing similar testing environments and between old and new to-be-remembered locations.

Questions addressed in this dissertation

Interference is an important component of memory and should be considered when studying the spatial memory of food storing animals. All of the experiments in this dissertation focus on questions concerning spatial memory and interference effects in food storing corvids such as the Clark's nutcracker. The first experiment in chapter 2, demonstrates that a list learning procedure can be a promising way to test spatial memory

in food storing birds. This is a successful procedure for testing nutcracker's memory for locations, and is used for subsequent experiments in this dissertation. Experiments 2 and 3 address initial questions as to whether Clark's nutcrackers are susceptible to the effects of proactive and retroactive interference. More specifically, if interference affects nutcrackers' memory for locations I wanted to examine the nature of this interference. Because interference is most likely to occur when interfering and target information are most similar to each other, similarity on a spatial task may vary depending on how close in space interfering information is to the target information. For example, interference could occur during the memory of caches made between years or between cache sites that are close in space to each other. Interference could also occur between memories for depleted and previously emptied cache sites. This type of interference could occur if a target location is seen by the bird more than once during a test. I was most interested in whether nutcrackers would make errors when recalling spatial information by revisiting previously rewarded locations.

It was also important to examine what factors were important for minimizing the effects of proactive interference. In chapter 3, I examine what variables may be important for nutcrackers for keeping interfering and target spatial memories separate. These sets of experiments provide support for whether increasing the time interval between lists, or changing the landmark array during recall of each lists decreases the effects of interference.

The last chapter in this dissertation reports the results from a comparative experiment between Clark's nutcrackers and scrub jays. Nutcrackers rely more heavily on stored food for survival and reproduction than scrub jays, and typically outperform

scrub jays on spatial memory tasks. The purpose of the final experiment in chapter 4 was to determine whether the difference in spatial memory abilities between nutcrackers and scrub jays are due to differences in their susceptibility to interference. I predicted that nutcrackers would also outperform scrub jays on the spatial list learning task and be less susceptible to interference.

PREVIEW

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PREVIEW

Chapter 2: Interference effects in the memory for serially presented locations in Clark's nutcrackers, *Nucifraga columbiana*.

Many seed-storing birds rely on memory to re-locate stored food (Balda, 1980; Shettleworth & Krebs, 1982; VanderWall, 1982). However, the importance of memory can vary between species depending on how much they rely on food stores for survival and reproduction. Furthermore, species who subsist primarily on stored food often perform more accurately during spatial memory tasks than species less dependent on stored food (Balda, Kamil, & Bednekoff, 1996; Shettleworth, 1995). Food storing birds' memory for spatial information may be enhanced because they are more resistant to interference (Clayton & Krebs, 1994; Hampton & Shettleworth, 1996; Hampton, Shettleworth, & Westwood, 1998; Shettleworth & Hampton, 1998).

Because interference effects could hamper recall of caches, they may be an important component of memory in food storing birds. Extraneous information acquired close in time to acquisition of the target information could affect memory through interference effects. For example, spatial information obtained before placing caches could hamper recall of those cache locations (proactive interference) as could spatial information obtained after the placement of caches, but before their recovery (retroactive interference). Interference could also occur between memories for caches made the present year versus the previous year, between memories for caches located close to each other and encoded in terms of the same environmental cues, or between memories for full and depleted cache sites. Food storing birds may be less susceptible to revisiting emptied sites than birds that do not store food (Clayton & Krebs, 1994; Healy & Krebs, 1992). Revisits to depleted cache sites pose a potential cost, in terms of both time and energy expended and exposure to predation. Food storing birds therefore would be expected to