Behavioural Processes 102 (2014) 3–11

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Size does not matter, but features do: Clark's nutcrackers (*Nucifraga columbiana*) weigh features more heavily than geometry in large and small enclosures

Veronika Lambinet[a], Christiane Wilzeck[a], Debbie M. Kelly[a,b,*]

[a] *Department of Psychology, University of Saskatchewan, Canada*
[b] *Department of Psychology, University of Manitoba, Canada*

ARTICLE INFO

Article history:
Received 10 September 2013
Received in revised form
12 December 2013
Accepted 12 December 2013

Keywords:
Clark's nutcrackers
Reorientation
Features
Geometry
Environment size

ABSTRACT

Two groups of Clark's nutcrackers (*Nucifraga columbiana*) were trained to locate a hidden goal which was consistently located at one corner of a fully enclosed rectangular environment with distinctive cues available at each corner. One group was trained in a small enclosure, whereas the second group was trained in a large enclosure. Once the birds were showing accurate search behavior, they were presented with non-reinforced tests in either the same sized environment as training or the novel sized environment, as well as in a square-shaped environment. The birds were able to accurately search at the two geometrically correct corners when the four distinctive features were removed showing that they had encoded geometry. Although accuracy was greater when tested in the same sized environment as during training, accuracy was above chance in both environments. Regardless of the size of training enclosure both groups showed primary control by features along with secondary control by geometry. Furthermore, when the features and geometric cues provided conflicting information as to the goal location, both groups weighed featural cues over geometry, and this was independent of whether the size of the testing environment was maintained or manipulated. These results show that for Clark's nutcrackers the size of the environment had little effect on the weighing of featural and geometric cues. Furthermore, although nutcrackers encoded both features and geometry, when spatial cues provided discrepant information as to the goal location, nutcrackers relied primarily on features.

This article is part of a Special Issue entitled: CO3 2013.

1. Introduction

Kamil (1988) proposed the *synthetic approach* for the study of animal cognition. At the time, he argued that the current approaches used by many psychologists needed to be broadened by placing the species under investigation within its evolutionary framework and by widening the scope of phenomena under examination. Over the years, Alan Kamil's research has provided many examples of how this approach has successfully enriched our understanding of animal cognition and intelligence. One such area of study, and the one that sets the context for this manuscript, is the study of spatial abilities by food storing corvids.

Animals are faced with the ongoing problem of securing food sources. One strategy that may be used as a provision for times of food scarcity is food storing. Several species store food, with strategies ranging from larder hoarding to scatter hoarding. The former is defined by large quantities of food stored in one or a few main locations, whereas the latter is defined by small quantities of food stored in many locations. Scatter hoarding, in particular, has attracted the attention of several researchers interested in animal cognition. As an example of scatter hoarding, an individual Clark's nutcracker will make thousands of caches during the late summer and autumn, returning to the sites months later to provision itself and offspring (Kamil and Balda, 1985; Tomback, 1983; Vander Wall and Balda, 1977). Mounting evidence over the years has shown that for many scatter hoarding species the solution to relocating these food stores is through spatial memory (Balda and Kamil, 1992, 2006; Gibson and Kamil, 2001, 2009; Gould et al., 2010; Kamil, 1988; Kamil and Balda, 1990, 1995; Kamil and Gould, 2008).

Studies which have directly compared species of food storing birds suggest that the degree to which a species depends on food stores correlates positively with accuracy for cache retrieval. For instance, Balda and Kamil (1989) examined the ability of Clark's nutcrackers, pinyon jays and Western scrub jays to relocate food stores seven days post caching. The researchers reported that the

---

[*] Corresponding author at: Department of Psychology, University of Manitoba, 190 Dysart Road, Winnipeg, Manitoba R3T 2N2, Canada. Tel.: +1 204 474 9489.
E-mail address: Debbie.Kelly@umanitoba.ca (D.M. Kelly).

0376-6357/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.beproc.2013.12.008

two species most dependent on their caches, nutcrackers and pinyon jays, were able to more accurately locate the hidden caches compared to the less cache reliant Western scrub jay. Similar findings were also reported by Bednekoff et al. (1997) who also examined Mexican jays (also see Kamil et al., 1994 for a study using an analog of the radial arm maze). These studies support that, of the food storing birds examined, those which rely most on food storing also remember cache locations more accurately than those less dependent. However, showing that food storing birds are able to remember cache locations more accurately than non-storing birds does not allow one to understand what information the birds are using to relocate the food stores (e.g., spatial memory, olfactory cues, or site fidelity).

Kamil (1988) suggested that when examining whether food storing and non-storing species differ in their spatial abilities, a variety of paradigms should be adopted. This approach would allow researchers to select tasks for which the pattern of results would be predictable as well as tasks for which a pattern of results would not be predictable. For instance, it would be expected that food storing birds should show greater accuracy on tasks of spatial memory compared to non-storing birds, whereas there would be no a priori reason to expect that food storing birds should be more accurate at non-spatial tasks (such as color associations) compared to non-storing birds (see Olson et al., 1995 for an example). This approach has proven fruitful. In combination with a systematic approach to examine possible alternative hypotheses, Kamil and colleagues have shown that food storing corvids, and in particular the Clark's nutcracker, rely on excellent spatial abilities to relocate food caches (for some examples of empirical and review articles the interested reader is directed to the following: Balda and Kamil, 1992, 2006; Gibson and Kamil, 2001, 2009; Gould et al., 2010; Kamil, 1988; Kamil and Balda, 1990, 1995; Kamil and Gould, 2008).

Many studies have focused on the Clark's nutcracker, in particular, to understand what aspects of a spatial environment are encoded when a food storing bird needs to relocate a cache site or hidden goal. For instance, Goodyear and Kamil (2004) showed that Clark's nutcrackers trained to search for food hidden in relation to an array of landmarks, weighed the closest landmark more heavily than ones further away from a target location. They also found that the landmark closest to the goal location may overshadow more distant landmarks. Kelly (2010) investigated the ability of nutcrackers to use the configuration of a multiple object array. Two groups of birds were trained to locate food that was consistently positioned near one object in a four landmark array in the shape of a rectangle. One group was trained with four distinctive objects forming the array, whereas the other group was trained with identical objects forming the array. The birds with the distinctive objects learned the task readily, whereas the birds with identical objects failed to learn the task after many training sessions. Interestingly, when the birds trained with the distinctive objects were presented with the identical object array, they were able to limit their searches to the two correct locations within the array. These results suggested that the presence of distinctive featural information facilitated learning about the configuration of the array. Furthermore, studies which have provided multiple cue types, such as edges, proximal and distal landmarks, even point of entry into the testing arena, have shown that nutcrackers rely on multiple cue types when learning about a goal location (Gould-Beierle and Kamil, 1996, 1999; Kelly et al., 2010).

The metric relationship among landmarks and a goal location has also been shown to be important in the formation of a spatial representation. Kamil and Jones (1997) showed that Clark's nutcrackers are able to learn to search for a hidden goal situated halfway between two landmarks, when the distance between the two landmarks was varied during training. The researchers went on to show that the nutcrackers could not only learn to locate a goal defined along a line connecting two landmarks (either ¼ or ½ of the distance from one landmark) but the birds could also learn to search at the third point of a triangle made by the two landmarks and the goal location using either a constant distance rule or a constant bearing rule (Kamil and Jones, 2000). The birds learning the constant distance rule learned more slowly and did not show as accurate transfer as the other three groups, suggesting that for nutcrackers learning about directional information may be more salient or weighed more heavily than distance information. Based on such studies, Kamil and Cheng (2001) presented a formalized model, the Multiple-Bearings Hypothesis, which provides clear predictions as to how Clark's nutcrackers encode the spatial relationship among a goal location and several landmarks to achieve such precise search abilities.

Geometric information can also be provided by large surfaces or boundaries, such as the shape of the experimental environment itself. Cheng (1986) showed that animals may use the geometric information from an environment's surfaces when reorienting. Cheng trained rats to locate food that was hidden at one corner of a fully enclosed rectangular environment. Featurally distinctive panels were positioned at each corner and could be used to accurately locate the food. During a reference memory task, Cheng found that disoriented rats could learn to use the distinctive features, but also showed a reliance on the geometric properties of the rectangular enclosure to relocate the hidden food. Over the years, many species have been shown to incidentally encode surface geometry when reorienting, and that featural and geometric cues are integrated when forming a spatial representation of the environment (see Cheng, 2008; Cheng et al., 2013; Cheng and Newcombe, 2005). Recently, researchers have also shown that the size of the search space may be important for the relative weighing of featural and geometric information (e.g., chicks: Chiandetti et al., 2007; Chiandetti and Vallortigara, 2008; Vallortigara et al., 2005; fish: Sovrano et al., 2005, 2007; humans: Learmonth et al., 2002, 2008; Ratliff and Newcombe, 2008; Sturz and Kelly, 2013; rats: Maes et al., 2009).

Hermer and Spelke (1994) reported that human toddlers did not encode featural cues when examined using a reference memory task similar to Cheng (1986). Yet, when Learmonth et al. (2001) replicated the study but in a larger environment, toddlers of a similar age were able to use features. These seemingly contradictory results lead to the question of whether environment size affects the encoding of featural and geometric information. Subsequently, several nonhuman animals have been examined and although the effect of enclosure size on the relative weighing of featural and geometric cues is complicated, the general trend seems to be that when searching for a goal location in a large rectangular environment, animals weigh featural information more heavily than surface geometry; when searching in a small rectangular environment, animals weigh surface geometric information more heavily than features. For instance, redtail split fins and chicks encode features and geometry in both small and large environments (fish: Sovrano et al., 2005, 2007; chicks: Chiandetti et al., 2007; Chiandetti and Vallortigara, 2008; Vallortigara et al., 2005). When the fish are trained in an environment of one size and subsequently presented with transfer tests in the environment of the other size, their search behavior followed this general trend. Chicks also showed this general trend, but only when tested with an affine transformation, which places geometric and featural cues in conflict (i.e., a stronger reliance on features when tested with an affine transformation in a large enclosure, but a stronger reliance on geometry when tested with an affine transformation in a small enclosure). Thus, size of the environment seems to bias the encoding of featural and geometric information in a consistent way, but how this pattern of cue use is expressed may differ among species.