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Use of medial axis for reorientation by the Clark's nutcracker (*Nucifraga columbiana*)

Debbie M. Kelly[a,*], Teagan A. Bisbing[a], John F. Magnotti[b]

[a] *Department of Psychology, University of Manitoba, 190 Dysart Road, Winnipeg, MB, R3T 2N2, Canada*
[b] *Department of Neurosurgery, Baylor College of Medicine, One Baylor Plaza, Houston, TX, 77030, USA*

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ABSTRACT

Many animals are challenged with the task of reorientation. Considerable research over the years has shown a diversity of species extract geometric information (e.g., distance and direction) from continuous surfaces or boundaries to reorient. How this information is extracted from the environment is less understood. Three encoding strategies that have received the most study are the use of principal axes, medial axis or local geometric cues. We used a modeling approach to investigate which of these three general strategies best fit the spatial search data of a highly-spatial corvid, the Clark's nutcracker (*Nucifraga columbiana*). Individual nutcrackers were trained in a rectangular-shaped arena, and once accurately locating a hidden goal, received non-reinforced tests in an L-shaped arena. The specific shape of this arena allowed us to dissociate among the three general encoding strategies. Furthermore, we reanalyzed existing data from chicks, pigeons and humans using our modeling approach. Overall, we found the most support for the use of the medial axis, although we additionally found that pigeons and humans may have engaged in random guessing. As with our previous studies, we find no support for the use of principal axes.

1. Introduction

Successful navigation requires a traveler to achieve and maintain an accurate sense of orientation. Depending on the species, many types of cues may be used to orient (see Bingman and Cheng, 2005; Healy, 1998). Over the past three decades, the use of geometric information extracted from enclosed or bounded environments has received a great deal of research attention in the study of orientation and reorientation (herein collectively referred to as "reorientation"). Since the pioneer study by Ken Cheng (1986), considerable data has accrued supporting that many diverse species encode geometric information from the shape of an environment (see Cheng, 2005, 2008; Cheng and Newcombe, 2005; Cheng et al., 2013; Tommasi et al., 2012). Researchers have proposed that environmental geometry provides a robust source of spatial information (Gallistel, 1990), and thus might provide a foundation upon which the mapping of other spatial cues may be assembled (Cheng, 1986). Indeed, although not without challenge, many studies have shown that the encoding of environmental geometry is robust to learning phenomena such as blocking or overshadowing (Cheng and Newcombe, 2005; Cheng et al., 2013 but, also see Gray et al., 2005 and Pearce et al., 2006). Although we have garnered a great deal of knowledge regarding the encoding of environmental geometric information, one fundamental question remains unanswered: what information is extracted from the environment when an animal is encoding geometry?

Environmental geometry must be extracted from the environment in a robust and computationally economical way. Researchers initially proposed that one means of meeting these requirements would be through the use of an environment's principal axes (Gallistel, 1990). The principal axes are mathematically defined as two perpendicular lines bisecting the centroid of a space (considering only the two-dimensional case). The major principal axis extends through the length of the space such that "the perpendicular distances from points in the space to the axis are minimized, by the least-squares criterion, and the minor principal axis extends perpendicular to the major axis" (Cheng, 2005, p. 8). Thus, the major and minor principal axes are potentially easy to extract and computationally inexpensive. However, two perpendicular lines provide little information regarding the shape of the environment and leave the navigator with 180 degrees of rotational uncertainty. Indeed, when the use of principal axes for reorientation was tested empirically, in such a way that dissociated search locations based on principal axes from other strategies, such as medial axis (a trunk-and-branch structure) or local geometric cues (such as wall length), researchers found no support for the encoding of principal

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* Corresponding author.
E-mail addresses: Debbie.Kelly@umanitoba.ca (D.M. Kelly), tabisbing@gmail.com (T.A. Bisbing), magnotti@bcm.edu (J.F. Magnotti).

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axes. Kelly et al. (2011a) trained pigeons and chicks in the traditional fully-enclosed rectangular-shaped arena to find a reward hidden at one of two rotationally equivalent corners. The arena was void of informative featural information, requiring the birds to rely on the geometric information provided by the bounded space. Once the birds were accurately locating the reward, they received non-rewarded test trials in an L-shaped arena. This shape of this arena was developed to clearly differentiate among possible encoding strategies, including three possible means of using the principal axes, the medial axis and local geometric cues. The researchers found no support for the use of principal axes by either pigeons or chicks. Subsequently, Ambosta et al. (2013) used a similar transformation procedure, training adult humans in a rectangular arena and testing in an L-shaped arena, using a non-immersive virtual reality task, and found no support for the use of principal axes. Although others have supported the use of principal axes, such arguments have required a modification, or misunderstanding, of the definition of principal axes breaking the space into component parts of "subjectively experienced views" (Sturz and Bodily, 2011 *cf.* Kelly et al., 2011b). More recently, these researchers have developed an "I-shaped" arena, but this transformation does not dissociate between this "subjectively experienced views" definition of principal axes from the medial axis (Bodily et al., 2018), and due to the consistent starting location, the results may be more parsimoniously explained by a learned "motor' response.

Another possible method for reorientation within an enclosed space is the use of local geometric cues (e.g., McGregor et al., 2006; Pearce et al., 2004; Pecchia and Vallortigara, 2010, 2012; Sovrano and Vallortigara, 2006; Tommasi and Polli, 2004, although see Cheng and Gallistel, 2005 for a more parsimonious principal axes account for these data). For instance, within a bounded environment, the length or height of walls, the degree of angular amplitude of individual corners, and sense information (left vs. right) may provide local geometric cues. These local geometric properties may be encoded according to absolute metrics or more flexibly using relative metrics (Kelly and Spetch, 2001; Tommasi and Vallortigara, 2000). Although there has been support for the use of local cues during reorientation tasks when featural cues are uninformative (Lambinet et al., 2014), several challenges may arise when considering how this strategy might be implemented in more naturalistic environments. For instance, reliance on local cues necessitates that the animal be proximal to the source of the information, local cues are more susceptible to environmental changes (e.g., cues visible in summer may be hidden by a layer of snow during the winter) (Reichert and Kelly, 2015) and the encoding of local cues may become quickly computationally demanding (Kamil and Cheng, 2001; Kamil and Jones, 2000). Thus, local cues are likely used by many species for instance when they are already reoriented, or in conjunction with other more robust reorienting cues, such as the medial axis (Kelly et al., 2011a).

Use of the medial axis has recently been proposed as an alternative means by which the shape information of an environment maybe robustly and economically extracted (Cheng, 2005; Kelly et al., 2011a, 2011b; Kelly and Durocher, 2011). Devadoss and O'Rourke (2011) define the medial axis as "The medial axis M(P) of a polygon P (also known as the cut locus of ∂P) is the closure of the set of points in P that have two or more closest points among the points of ∂P" (where ∂P denotes the boundary of P) (p.118). Therefore, unlike the major principal axis and the corresponding perpendicular minor axis, the medial axis defines a collection of axes that provide information about the shape of a space. The medial axis has been described informally as similar to a tree, with a central trunk structure and branching vertices (see Kelly and Durocher, 2011). Thus, extracting medial axis information offers one computationally less expensive, yet robust, means of extracting shape information from a bounded space. Indeed, the aforementioned studies with pigeons, chicks (Kelly et al., 2011a), and humans (Ambosta et al., 2013) show clear support for use of the medial axis over principal axes.

Research examining how geometry is extracted from surfaces or a bounded environment has begun to accumulate. These investigations have included studies of pigeons, chicks and humans, all species for which researchers have accrued an in depth understanding of their respective spatial abilities. Although these species are known to have strong spatial abilities, how geometry is extracted from an environment has not yet been asked of a highly-spatially dependent species. Clark's nutcrackers are such a species. The Clark's nutcracker is a food-storing corvid. During years of heavy pine crops, an individual nutcracker will cache up to 33,000 seeds over the surface of a mountainside during the autumn season (Bednekoff et al., 1997; Tomback, 1983; Vander Wall and Balda, 1977). Several months later, in the winter season when the caches are covered in a thick layer of snow, the individual must rely on its spatial encoding of these food caches to return and accurately locate the food. As caches are the major food resource throughout the winter and spring, the ability to accurately and robustly encode the spatial location of these food sites is critical. Previous research has shown that nutcrackers encode metric information from individual landmarks (e.g., Kamil and Jones, 1997, 2000; Kelly et al., 2010) and that they rely strongly on geometric information when it is reliable and robust (Reichert and Kelly, 2015). As nutcrackers are faced with the problem of encoding multiple spatial locations in a robust and computationally efficient way, we were interested in examining how these birds extract geometric information from an environment. Thus, adopting the transformational approach developed by Kelly et al. (2011a), we examined whether search behavior of Clark's nutcrackers trained in a rectangular arena, and subsequently tested in an L-shaped arena, would support use of principal axes, medial axis or local geometric cues. Furthermore, as discussed above, a few species have now been examined using these similar procedures (currently, all using a reference memory task), thus we have taken the opportunity to rigorously evaluate these existing data using a quantitative model comparison. This approach goes beyond the typical null hypothesis testing framework (which tests individual models against a null model) by comparing the models directly on a given dataset. Such an approach also allows one to conclude that two models explain a given dataset equally well, avoiding problems with *accepting* a null hypothesis.

2. Methods

2.1. Subjects

Sixteen adult wild-caught Clark's nutcrackers, *Nucifraga columbiana*, having lived in captivity for 8–12 years (8 male, 8 female), participated in this experiment. All individuals had previous experience in unrelated experiments (Fairhurst et al., 2011; Clary and Kelly, 2011, 2013; Reichert and Kelly, 2015). Birds were maintained at 85–90% free-feeding weight, using a diet of Tradition® turkey starter, Lafeber® parrot pellets, sunflower seeds and peanuts (supplemented with HARI® PRIME™ vitamin), and were provided with ad libitum access to grit mixed with oyster shells and water. Birds were individually housed in metal cages (73 cm high x 48 cm wide x 48 cm deep), containing several wooden perches and swings, within a larger colony room in the Department of Psychology animal facilities at the University of Manitoba. This colony room was maintained at a constant temperature of (21 °C) with 12:12 h light/dark cycle with light onset at 07:00 Central Time zone. All animal care and experimental procedures were approved by the University of Manitoba's local animal user committee, under the purview of the Canadian Council on Animal Care, and in compliance with the Guidelines for the use of animals in research (1991).

2.2. Apparatus

2.2.1. Training apparatus

The rectangular training apparatus was constructed of Styrofoam® with a liner of white corrugated plastic secured to the inside surface (inside dimensions: 200 cm length x 60 cm width x 60 cm height). Black plastic curtains were affixed to the outside of each arena wall (237 cm from floor to ceiling) to eliminate any external visual cues. A camera was affixed to the center of the ceiling for recording all experimental trials. A white-noise machine (Conair®), located outside of the arena was used to mask external sounds; its absolute position within the room was randomized across trials.

Four identical tin containers (6.5 cm x 4 cm) were secured to the floor of the rectangular apparatus with a small square of Velcro®; one tin was located in each of the four corners. Only the two containers, associated with each bird's *correct* corners contained food reward, the others were empty [see Training section (2.3.2) below for more details]. To ensure the birds were using spatial information, not visual cues, to locate the containers with reward, the top of each container was covered with a paper towel, which was secured using an elastic band. The floor of the apparatus was covered with an even layer of aspen chip shavings.

2.2.2. Testing apparatus

The testing apparatus was an L-shaped arena constructed of the same materials as the training apparatus. The long and short walls maintained the same measurements as in the training arena, with mid-length walls of 154 cm in length. Two additional containers were placed in the arena, one at corner U and a second at corner K resulting in a total of 6 choice locations (Fig. 1). During testing, all containers were empty (non-reinforced), covered with paper towel and secured with an elastic band. All other properties of the testing apparatus were identical to the training apparatus.

2.3. Procedure

2.3.1. General procedure

Prior to the start of the experiment, an equal number of male and female birds were pseudo-randomly assigned to one of two groups: group AC or group BD. The group assignment designated the containers that would be reinforced during training (herein referred to as the *correct corners* – group AC: corners A and C, group BD: corners B and D; Fig. 1). Birds were transported in a fully-enclosed opaque container from the colony room to the experimental room, wherein they were slowly rotated within the container at a rate of 12 rpm for 1 min. This procedure was conducted to ensure the birds were disoriented and unable to use inertial cues (Kelly et al., 1998). The position, within the larger experimental room, where this disorientation procedure occurred was changed every five trials throughout all phases of training and testing. The location of the birds' entry into the training and testing arenas was randomized across trials.

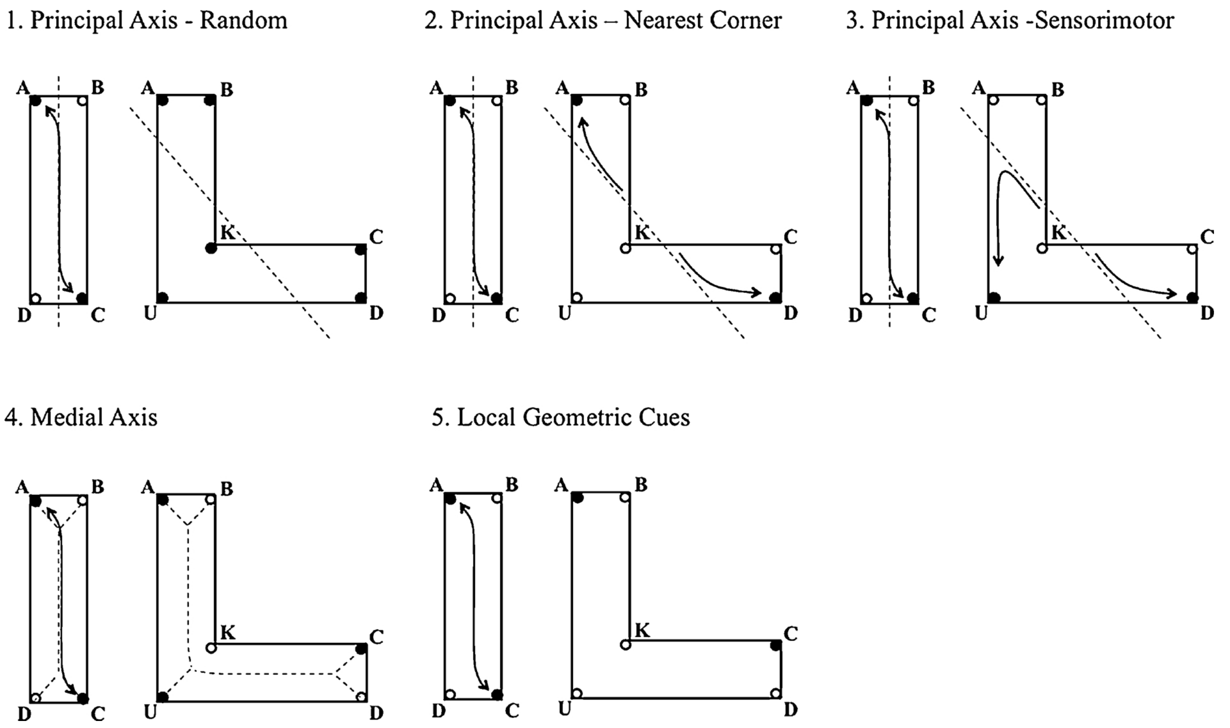
2.3.2. Training

Birds were systematically shaped to search for pine nuts hidden in the two containers positioned at the correct corners.

An initial habituation phase was used to introduce the birds to the arena. During this phase, the two containers in the correct corners were baited with 10 pine nuts each. The containers were filled with grit and the pine nuts were placed on top, fully visible from any point within the arena. Each daily session lasted approximately 15 min, with up to four trials occurring during this phase. A trial ended after the bird consumed the pine nuts from either container; therefore, the number of trials in a session was determined by the number of correct choices a bird made. If no choices were made, the habituation phase ended after a single 15-minute trial.

During the first training phase, the containers in the correct corners were baited with two pine nuts each. All containers were left uncovered to entice the birds to make choices. Each daily session consisted of ten trials. During a trial, a bird was given up to five minutes to make a choice. If a correct choice was made within the first minute of a trial, all containers were partially covered by a paper towel during the next trial. A bird advanced to the second training phase when it made a choice to at least one of the correct corners during all trials of a daily session.

The second training phase was the same as the first, except that all four containers were covered with paper towel and secured with an


1. Principal Axis - Random

2. Principal Axis – Nearest Corner

3. Principal Axis -Sensorimotor

4. Medial Axis

5. Local Geometric Cues

Fig. 1. Schematic representation of the apparatuses and the first choice predictions for each hypothesis. Nutcrackers were trained in a rectangular arena and tested in an L-shaped arena. Dashed lines represent the arena axes. These are schematics for group AC who were trained to find food in corners A and C of the rectangle arena. Filled circles represent the predicted locations of choices for each proposed hypothesis, whereas open circles represent locations predicted to *not* be chosen. Adapted from Kelly et al. (2011a).

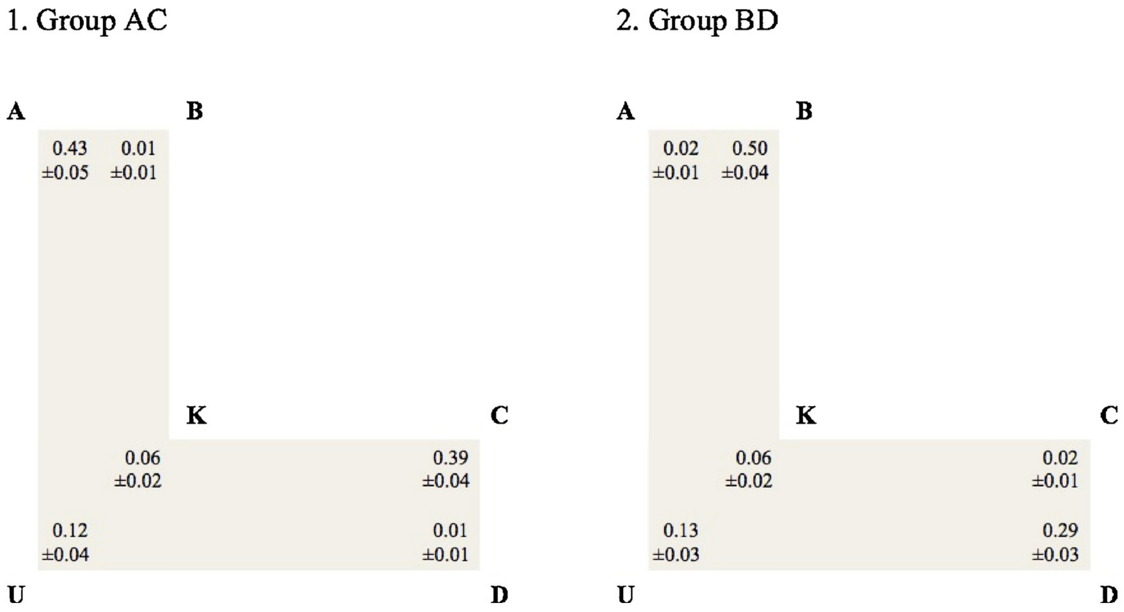


Fig. 2. Mean ± SEM proportion of choices during testing in the L-shaped arena by group AC (2.1) and group BD (2.2).

elastic band; a hole was made in the paper towel covering. Initially the holes were approximately 25 mm in diameter, but this size was incrementally reduced across successive trials until the birds were pecking through intact paper towels to access the pine nut reward. If a bird did not make a choice by the end of a five-minute trial, then the size of the hole was incrementally increased until the bird began to make choices again. Criterion was the same as during the first phase.

During the third training phase, each of the four containers was covered with an intact paper towel. The containers in the correct corners were baited with one pine nut each. Criterion for this phase required that a correct corner be chosen first in eight of the ten trials during a daily session, for two consecutive sessions. The fourth training phase was the same as the third training phase, except that every other trial was non-reinforced. Each bird completed five reinforced and five non-reinforced trials, for a total of ten trials per day, until criterion was reached. Criterion was the same as in the third phase. Two birds (from group AC) did not meet training criterion and were replaced with additional birds that met criterion to maintain equal numbers of subjects per group.

2.3.3. Testing

Each daily session of testing consisted of two alternating types of trials: baseline and test trials. A session always began with a baseline trial in the rectangular arena. The procedure for baseline trials was the same as the fourth training phase (reinforced trials) such that all four containers were covered with paper towel and the containers in the correct corners were baited with one pine nut each. These trials were used to provide the birds with food motivation and evaluate response accuracy between the groups. Test trials occurred in the L-shaped arena. These trials were never reinforced. Both types of trials ended one minute after the bird's first choice, or, if a second choice was made, 20 s after the bird's second choice, or after five minutes lapsed if no choices were made.

A daily session included five types of each trial. If a bird did not make a first choice to a correct corner during at least three of the five baseline trials, or if it did not make at least one choice during each trial of a daily session, the bird was retrained with the fourth training phase protocol until criterion was once again met (this occurred for two birds; one needed two days of retraining, the other needed four days of retraining).

2.4. Video scoring

In addition to live recording of choices, reaction times, and trial length, digital recordings were used to ensure scoring reliability. All training and testing trials were scored by two experimenters to ensure inter-rater reliability, which was 99.2% (when a conflict arose, the choice according to the real-time scoring was considered correct).

2.5. Spatial choice models

The transformational approach has proven to be a successful method to evaluate which cues animals encode when learning about, or navigating within, a spatial environment (Cheng and Spetch, 1998), and the transformation from a rectangle training arena to an L-shaped testing arena has specifically been used to dissociate theorized geometric encoding strategies (Kelly et al., 2011a; Ambosta et al., 2013). The rectangle to L-shape transformation is effective because of the discrete patterns of response that can be predicted for each encoding strategy (Kelly et al., 2011a).

We compared three general choice strategies that produced seven distinct models. The models primarily differed on whether spatial choice relied on an encoded principal axes (although we evaluate only the major principal axis, we herein refer to this strategy as *principal axes*), medial axis, or local geometric cues. According to a principal axes strategy, the subjects would follow (note: we use the terms "follow" or "lead" in a theoretical sense and not in a behavioral sense) the major principal axis of the L-shaped arena until reaching a wall at which point three distinct patterns of response emerge: (1) a *random strategy* (model PA:R) by which they default to choosing among all corners randomly – effectively a guessing strategy (Fig. 1.1); (2) a *nearest corner strategy* (PA:N) where they choose the two corners that were nearest to the ends of the axis (Fig. 1.2); or (3) a *sensorimotor strategy* (PA:S) manifesting from sensorimotor patterns learned during training (e.g., turn left) to select a corner (Fig. 1.3).

Instead of using the principal axes during training, subjects may have relied on the medial axis of the shape (model MA). In the L-shaped arena, the trunk portion would extend down the central line of the arena with branches extending out toward each salient corner (vertices). If subjects used the medial axis to reorient in this arena, they would follow along the central trunk, using sense information acquired during training to determine a direction of travel where the branches

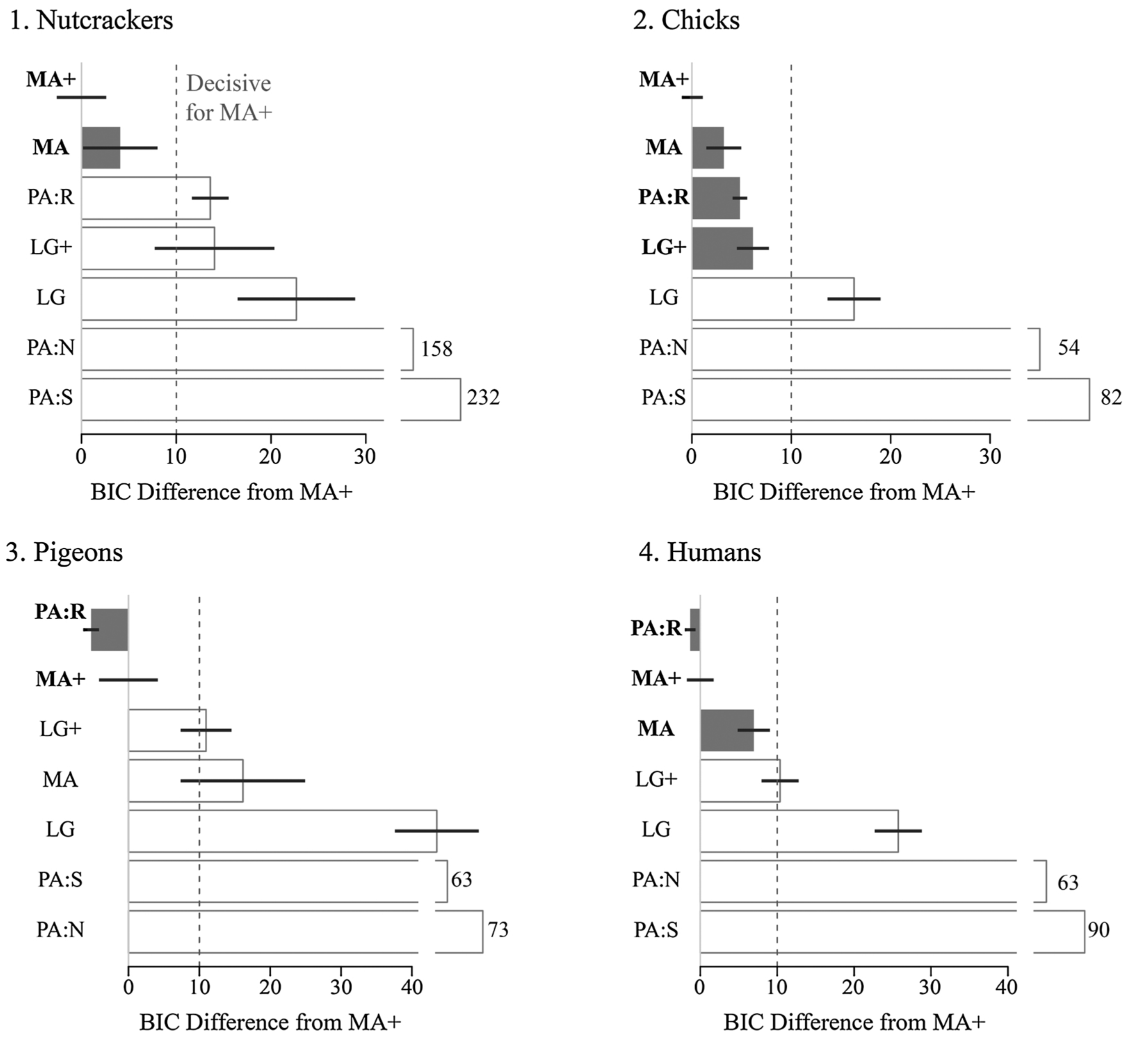


Fig. 3. Comparison of spatial models across species. Relative fit (change in BIC from MA +) for each model, positive numbers indicate better fit for the MA + model. Filled bars and bolded text indicate models with equivalent predictive power. Error bars are 1 standard error of the mean across subjects. Plain text and unfilled bars indicate models fit decisively better by the MA + model (BIC difference of at least 10; Kass & Rafferty, 1995). For all species tested, MA + was within the winning group. For nutcrackers (3.1) MA + and MA models were the best; for chicks (3.2) MA + , MA, PA:R, and LG + had similar predictive validity; for pigeons (3.3) PA:R and MA + had similar predictive validity; for humans (3.4) PA:R, MA + and MA had similar predictive validity.

diverge (Fig. 1.4).

Lastly, subjects may have relied on the combination of local geometric cues and sense information (model LG). These cues would be different in each corner of the L-shaped arena, with only two corners being geometrically identical to the baited corners of the training arena (Fig. 1.5).

Each of the above models explains how a subject would distribute choices if following a given strategy on every single test trial. Even in the trained arena, however, subjects make errors. We can reasonably assume that performance during test trials should have similar rates of errors, where an error during testing means making a choice not consistent with the learned strategy. Choices on these trials would likely be random guesses amongst all available corners. To incorporate this assumption, we created mixture models combining either the medial axis strategy or the local geometric cues strategy with such a guessing strategy (we denote these models with a "+", *i.e.*, MA + and LG + , respectively). The rate of guessing for each subject was determined entirely by that subject's accuracy in the trained arena during testing, not a free parameter. We did not create mixture models of the PA:N and PA:S models because of their vastly inferior performance. The PA:R model is already formally identical to a guessing model, so no mixture could be created.

2.6. Model comparison strategy

To determine the most likely strategy controlling nutcracker search behavior, we quantitatively compared the predictions from each of the seven spatial choice models. Because each strategy makes a quantitative prediction about the probability of choosing a given location, we can calculate the error between each bird's behavior and the proposed strategy. To measure this error, we use the Bayesian Information Criterion (BIC), a measure of the log likelihood of the data given a specific strategy plus a penalty term that is proportional to the number of free parameters in the model and the sample size. Because BIC is a measure of error, lower numbers indicate a better match to the data. Importantly, only the *relative* BIC between models is meaningful, with differences of 10 or higher considered decisive evidence for one model against another (Kass and Raftery, 1995). Because we found no difference between birds in the AC and BD groups, we ignore this factor in subsequent analyses.

To determine the number of free parameters, we counted the number of unique predictions made by each model, leading to the PA:R model having no free parameters and all other models having 1 free parameter. Recall for the mixture models the guessing rate is fixed by performance on an independent set of trials and is therefore not a free parameter.

As noted above, all of the (non-mixture) choice models except PA:R predict some corners to have a 0.0 choice probability. This extreme certainty causes the models to be immediately falsified (a log likelihood of negative infinity) if a single subject makes a single response to an unpredicted corner. To fix this numerical issue, we truncated all choice probabilities to be within the range of 0.001 to 0.999. Even the mixture models (MA + and LG+) suffer from this problem because many subjects had perfect training accuracy but still made choices during testing to unpredicted corners.

2.7. Cross-species comparison

As other studies have used this L-shaped area transformation test to examine how animals encode the geometric properties of bounded space (pigeons and chicks: Kelly et al., 2011a; humans: Ambosta et al., 2013), we applied our current modeling approach to each of these datasets in turn. We extracted training and testing data from each of these previous studies to fit the seven models (the training data for the chicks were not available and so we set the training accuracy to 95% for each subject for the MA + and LG + models). We used a linear mixed-effects model (Bates et al., 2015; Kuznetsova et al., 2017; R Core Team, 2016) of BIC across models with Species as a random factor to explore the possibility of a single choice model explaining the data across species.

3. Results

The primary goal of this study was to determine which reorientation strategy best explains how nutcrackers reorient using geometric properties from bounded environments. Before analyzing the critical test data, we first examined performance during training (phases 3 and 4) and baseline trials during testing to ensure there were no systematic differences between the counterbalanced groups (AC *vs*. BD). For all analyses, we considered only the first corner chosen during each trial. The alpha level was set at 0.05 for all statistical tests.

3.1. Phase 3 and 4 training

We found no significant differences in the number of trials to acquisition between the AC and BD groups for either phase 3 training [mean ± SEM for AC = 15.0 ± 2.7, BD = 20.0 ± 5.0; independent *t*-test, $t(14) = -0.88$, $p = 0.39$] or phase 4 training [AC = 25.0 ± 2.7, BD = 21.2 ± 1.3; $t(14) = 1.27$, $p = 0.22$] for the nutcrackers. Similar analyses have been conducted for pigeon, chick and human data, and were not repeated here (pigeons and chicks: Kelly et al., 2011a; humans: Ambosta et al., 2013).

3.2. Control trials during testing

We found no differences in control accuracy between the AC and BD groups during testing [mean ± SEM for AC = 0.98 ± 0.01, BD = 0.94 ± 0.03; $t(14) = 1.24$, $p = 0.24$]. Again, similar analyses were conducted for the pigeons, chicks and human data, so these were not re-analyzed (pigeons and chicks: Kelly et al., 2011a; humans: Ambosta et al., 2013).

3.3. Test trials

Fig. 2 shows the first-trial choice data during testing across the 16 nutcrackers. Each group responded most frequently to the “trained” locations (82% of responses to either A or C for the AC group; 79% of responses to either B or D for the BD group), followed by the U corner (12% group AC, 13% group BD). To determine the most likely strategy used across subjects, we compared BIC for seven different models, three based on an encoded principal axes (PA:R, PA:N, and PA:S), two based on the medial axis (MA and MA+; "+" denotes a model with a fixed, per-subject guessing rate), and two based on local geometric cues (LG and LG+). Fig. 3.1 shows the relative model fit (change in BIC) for each model compared to the overall best model, MA+ (*cf*. Fig. 1 for model predictions). As suggested by Kass and Rafferty (1995), we use a BIC difference of 10 to indicate decisive evidence for one model over another, given the current data. For the nutcrackers (Fig. 3.1), the two medial axis-based models (MA + and MA) are jointly the best-fitting models. For the chicks (Fig. 3.2), the medial axis models had numerically lower fit error, but were also fit well by the PA:R and LG + models (BIC difference MA+ *vs*. PA:R = 5; MA+ *vs*. LG+ = 6). For the pigeons (Fig. 3.3), the MA + and PA:R models were the best, with the PA:R model having the lowest overall fit error (BIC difference MA+ *vs*. PA:R = -5; negative because PA:R had a lower fit error). For the humans (Fig. 3.4), the MA + and PA:R models were nearly indistinguishable (BIC difference MA + vs. PA:R = -1) and not significantly different from the MA model (MA+ *vs*. MA = 7).

Overall, these results are consistent with the use of either the medial axis (especially MA+) or random guessing (only PA:R) by all species, except the nutcrackers whose data were strongly supported by the medial axis models. To quantify this pattern, we conducted an exploratory linear mixed effects analysis comparing BIC for each model (MA + was the baseline model) with Species as a random factor. We found no significant difference between PA:R and MA+ ($p = 0.86$), but all other models had significantly higher BIC than MA+ (MA, $p = 0.02$; all other models $p < 0.001$).

As a complementary analysis, we also calculated the frequency with which a given model class (principal axes, PA; medial axis, MA; or local geometric cues, LG) best explained choice behavior of a given subject, to explore the possibility of individual differences in strategy selection. For the nutcrackers, 62% were best fit by MA models and 38% were best fit by LG models. Similarly, for chicks, 70% were best fit by MA models, 15% by LG models, and 15% by PA models. Pigeons showed a stronger preference for PA (67%) compared to MA models (33%). Humans showed the most variation, PA being the greatest (39%), followed by MA models (34%) and then LG models (27%).

4. Discussion

Our results show that nutcrackers readily learned to encode the geometric information from a bounded rectangular environment. When tested in an L-shaped arena, the medial axis models best supported the nutcrackers’ search behavior. Our reanalysis of previous research, using a modeling approach that took into account error rates from training and control performance, as well as penalized choices to non-predicted corners, partially supported previous interpretations. Although the search behavior of both pigeons and chicks continued to be consistent with a medial axis encoding strategy, chicks search was now best explained by the medial axis (and not local geometric cues as previously reported), and due to the high error rates pigeons made to corner K, the PA:Random model (random guessing) best accounted for their data.

The increased explanatory power of the medial axis for the chick data was likely due to the sensitivity of our modeling approach. Previous papers used a series of significance tests to see if each model could be rejected based on the pattern of responses to a subset of the tested corners. In contrast, our approach uses all of the data and compares the likelihood of the models to one another, without resorting to rejecting a model in favor of an unspecified alternative.

Using our current modeling approach, the pigeon data (and to a small degree, the human data) were better explained by the PA:R strategy - equivalent to a guessing strategy. Indeed, we cannot dissociate choices based on the PA:R strategy from a random guessing solution – as would be the case if the subjects failed to generalize the task requirements from training to testing. At first glance, the good fit of the PA:R model is surprising – it predicts uniform responses to all corners but the response distributions are clearly clustered among particular corners. The reason for its good fit relative to other models is that maximum likelihood modelling punishes choice models in accordance with their degree of certainty—the random model is less certain everywhere and thus receives only moderate penalty for mistakes at each location. The medial axis and local geometry models, in comparison, are absolutely certain (i.e., predicts 0% responses) that certain corners will never be chosen, and thus receives a very high penalty when birds in fact choose these locations. This difference also explains why previous papers rejected the PA:R model in favor of other models – the statistical tests used did not penalize model's for their certainty against particular locations (*e.g.*, predicting with absolutely certainty that no responses should be allocated to location *K*).

Importantly, we find no other support for the encoding of principal axes by the species examined. Overall, our current results and the reanalyzes of previous data support that extraction of medial axis information is likely shared by many species.

Clark's nutcrackers are a corvid species highly dependent on their spatial abilities for caching and retrieving food stores. As these stores are critical for the survival and breeding success of nutcrackers, the birds need to extract spatial information from the environment that is robust to seasonal changes without a substantial computational cost. Nutcrackers use geometric information when it is the most reliable spatial cue, and our results suggest that they may be doing so through extraction of medial axis information. However, our data further suggest that the medial axis may be used by many species, perhaps as it affords information regarding the shape of an environmental space, or large surface areas, define locally from the point of view of the navigator.

The application of medial axis information to describe shapes has been extensively explored in fields such as computer science (e.g., Blum, 1967; Blum and Nagel, 1978; Liu et al., 2011), robotics (e.g., Lien et al., 2003), medical application (e.g., Fritsch et al., 1994), and human vision (Marr, 1982; Marr and Nishihara, 1978). Within the field of human vision, both psychophysical (Kovács and Julesz, 1994; Kovács et al., 1998) and neurophysiological (Lee et al., 1995) approaches have supported the use of medial axis. Although much of this research has focused on defining object space, we would like to propose using this substantive research as a guide to direct future investigations into the understanding of how human and non-human animals may extract shape information from surfaces, such as boundaries or enclosed environments. Although we have focused on the medial axis, guided by this literature, other models remain to be explored (Kelly and Durocher, 2011). Additionally, as all studies to date have evaluated the use of medial axis information during reference memory tasks, future research adopting working memory tasks (for instance, see Lee et al., 2012) may provide further comparative insights into how geometry is extracted from an environment.

In conclusion, our current research examining the encoding of geometric information during a spatial search task by Clark's nutcrackers, coupled with a reexamination of previous publications using a similar procedure, support the use of a medial axis strategy. We find little support for use of the major principal axis.

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Declarations of interest

None.

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