Contents lists available at ScienceDirect

Behavioural Processes

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

Pattern of visuospatial lateralization in two corvid species, black-billed magpies and Clark's nutcrackers

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ARTICLE INFO

ABSTRACT

Article history: Received 7 March 2014 Received in revised form 8 June 2014 Accepted 30 July 2014 Available online 15 August 2014

Keywords: Black-billed magpies Clark's nutcrackers Lateralization Visuospatial attention Cerebral lateralization is widespread amongst vertebrate species suggesting advantages are gained by having one of the brain's hemispheres exert dominant control over certain cognitive functions. A recently devised task for assessing lateralization of visuospatial attention by birds (Diekamp et al., 2005) has allowed researchers to suggest the corpus callosum may not be necessary for the emergence of such asymmetries. More recently, this task has been adopted to examine the embryonic development of lateralization in birds, research which may provide important insights as to the underlying genetic mechanisms (Chiandetti, 2011; Chiandetti et al., 2013) of vertebrate cerebral lateralization. However, to date only chicks and pigeons have been used in this paradigm. Thus, it is unclear whether other avian species will also show lateralization of visuospatial attention during this task. Here, we examined the pattern of visuospatial lateralization in two corvid species: social black-billed magpies (*Pica hudsonia*) and non-social Clark's nutcrackers (*Nucifraga columbiana*). We find that neither the magpies nor the nutcrackers show evidence for population level lateralization or predictable individual level lateralization, as only a subset of individuals of each species showed a significant individual bias, which were rarely stable over repeated testing.

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1. Introduction

Cerebral lateralization is ubiquitous amongst vertebrates (Rogers and Andrew, 2002). The prevalence of lateralized brains and resulting behavioral responses suggests lateralization provides individuals with advantages, such as increasing neural efficiency by avoiding redundant neural circuitry (Levy, 1977) or preventing the initiation of conflicting behavioral responses (Andrew, 1991; Vallortigara, 2000). Indeed, strongly lateralized individuals have been shown to have enhanced efficiency when performing dual tasks (Rogers, 2000; Rogers et al., 2004) and lateralization may enhance cognition in general (Magat and Brown, 2009). However, the factors that promote lateralization are still unclear.

Birds are often used as an animal model for understanding hemispheric lateralization (Rogers and Andrew, 2002) with issues such as predator (Franklin and Lima, 2001; Randler, 2005; Rogers, 2000) and prey detection (Rogers, 2000; Templeton and Christensen-Dykema, 2008), mate choice (Templeton et al., 2012), spatial memory (Clayton and Krebs, 1994a,b), or visual discrimination

http://dx.doi.org/10.1016/j.beproc.2014.07.020 0376-6357/© 2014 Elsevier B.V. All rights reserved. (Templeton and Gonzalez, 2004) a few examples of topics investigated.

Diekamp et al. (2005) developed a simple task for examining lateralization of visuospatial attention in birds – an adapted version of the cancelation task used with humans to identify visuospatial biases (Mesulam, 1999; Uttl and Pilkenton-Taylor, 2001; Vingiano, 1991). They presented chicks and pigeons with an array of grains from which the birds could freely forage. Both species' visuospatial attention was found to be lateralized at the population level as indicated by the birds' over-selection of grains from their left side. This procedure has since been adopted to study mechanisms influencing avian visuospatial lateralization (aging: Wilzeck and Kelly, 2012; development: Chiandetti, 2011; gene activation: Chiandetti et al., 2013), with the leftward bias being replicated in each of these studies (including the study conducted in our own laboratory, Wilzeck and Kelly, 2012).

One appeal of the procedure developed by Diekamp and colleagues is it only requires slight modifications to permit comparative examinations, which may allow for the elucidation of the ecological factors involved in lateralization. Thus, our study will provide the first comparative examination using this procedure beyond chicks and pigeons. We assessed the pattern of individual and population level lateralization of two corvid species: black-billed magpies (*Pica hudsonia*) and Clark's nutcrackers (*Nucifraga*)



Short report





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columbiana). Black-billed magpies are a relatively social corvid (Trost, 1999) that makes short-term caches (Birkhead, 1991), whereas Clark's nutcrackers are a relatively non-social corvid that makes long-term caches (Tomback, 1998). Sociality has been proffered as the evolutionary impetus for the development of population level lateralization (Vallortigara and Rogers, 2005), and the spatial abilities required for food caching have been implicated in brain organization (Clayton and Krebs, 1995). Therefore, sociality and cache reliance were examined as two potential factors that may influence lateralization of visuospatial attention.

2. Materials and methods

2.1. Subjects

Seventeen black-billed magpies (12 male, 5 female) and eighteen Clark's nutcrackers (8 male, 10 female) were used. The magpies were wild-caught as nestlings and hand-reared, whereas the nutcrackers were wild-caught as adults. At the time of initial testing the magpies were approximately 10 months of age; the nutcrackers were of unknown age, but had been in the laboratory for 7-15 years. The colony rooms were maintained at 22 °C with a 12 h light cycle. Birds were housed in individual cages (magpies: $64 \text{ cm} \times 61 \text{ cm} \times 66 \text{ cm}$; nutcrackers: $48 \text{ cm} \times 48 \text{ cm} \times 73 \text{ cm}$ length, width, and height, respectively) with water provided ad libitum. All birds were food restricted to 85-90% of the ad libitum weight. Magpies were fed a diet of Pedigree® wet dog food, Kirkland Signatures[®] dry dog food, mixed fruits and vegetables, and a vitamin supplement. Nutcrackers were fed a diet of turkey starter, parrot pellets, sunflower seeds, mealworms, peanuts, pine nuts, oyster shells, and a vitamin supplement. All housing and experimental procedures adhered to the Canadian Council on Animal Care.

2.2. Apparatus

Prior to a trial, a bird was placed in a holding container (magpies: $47 \text{ cm} \times 13 \text{ cm} \times 24 \text{ cm}$; nutcrackers: $30 \text{ cm} \times 12 \text{ cm} \times 23 \text{ cm}$ length, width, and height, respectively), with a small opening at one end (4 cm width $\times 17$ cm height), which the bird could protrude its head and neck through. During a trial, the opening of the holding container was aligned with an equally sized opening in one wall of a wooden testing arena (61 cm length $\times 33$ cm width $\times 61$ cm height). The interior walls of the testing arena were covered with white Bristol board and the floor with a piece of white plastic containing a matrix of 1 cm³ cells. All cells were filled with sand to allow pine seeds to be placed visibly on the surface. White noise was played to mask external noise. Trials were recorded with an Ever Focus EQ350 color digital camera connected to a Sony Digital Video Cassette Recorder (GV-D1000 NTSC).

2.3. Procedure

2.3.1. Training

Training occurred for four consecutive days. The first day was comprised of a single trial, whereas the following three days each consisted of two trials. During training, ten halved pine seeds were placed in adjacent cells to form a straight line from the first cell of the central column. The holding container was placed in front of the testing arena such that the openings of the container and testing arena were aligned. After 30 s, a partition separating the holding container and the testing arena was lifted allowing the bird to protrude its head and consume the seeds. A trial was terminated once the bird consumed the seeds or after 2 min of inactivity after consuming a seed. If a bird did not consume any seeds, the trial was continued for 40 min to allow further habituation. If a bird consumed at least four seeds during the final two training trials it advanced to testing, otherwise training was continued until this criterion was met.

2.3.2. Testing

Testing was conducted over four days, with a single trial per day. During testing, halved pine seeds were placed in every other cell (checkerboard pattern) of nine columns. A total of 32 half seeds were available. All other procedures were identical to training. To complete testing, the birds had to obtain at least ten seeds in each session. If this criterion was not met additional testing trials were conducted. If a bird did not meet this criterion after five days it was returned to training and required to meet the original training criteria. Both species were tested during two time frames separated by 18–20 months (magpies) or 22–24 months (nutcrackers) to assess whether biases were stable over time.

2.4. Statistical analysis

Analysis was limited to each bird's first 10 choices so as to not restrict seed selection due to decreasing seed availability. Each choice was given a weighted score; the first choice received a score of 10, the second choice a score of 9, and so on. Subsequently, each column was summed to provide a cumulative score of the bird's choices for each trial. The mean cumulative scores for the four trials were used for the analysis.

Alpha was set at 0.05. Population level biases were assessed using $2 \times 2 \times 4$ repeated measures ANOVA with *Time frame* – first versus second time birds participated in the experiment, *Side* – the difference between the mean cumulative scores of the left and right side, and *Distance* – the difference in cumulative scores among the columns on either side of the midline. Individual level biases were assessed using one-sample *t*-tests with laterality index as the dependent variable. The laterality index was calculated as:

Mean cumulative score on right – mean cumulative score on left Total of right and left mean cumulative scores

The resulting value was compared against zero (i.e., no bias).

3. Results

3.1. Magpies

3.1.1. Criteria attainment

During the first time frame, 8/17 magpies required additional training days before moving to testing. Once in testing, 13/17 magpies required additional testing days to reach the criterion of 4 test days with at least 10 choices. Four of these birds required additional training because of incomplete testing sessions.

During the second time frame, 5/17 magpies required additional training days before moving to testing. Once in testing, 3/17 magpies required additional testing days to reach the criterion. None of these birds required additional training because of incomplete testing sessions.

3.1.2. Population level

There was no main effect of *Time frame* ($F_{(1,16)} = 0.090$, p = 0.768) or *Side* ($F_{(1,16)} = 0.204$, p = 0.657) and no *Time frame* × *Side* interaction ($F_{(1,16)} = 1.075$, p = 0.315, Fig. 1). There was a significant effect of *Distance*, indicating less seeds were selected from columns further from the center column ($F_{(3,14)} = 259.519$, p < 0.001).

3.1.3. Individual level

During the first time frame, 4 of 17 magpies showed a significant preference for one side. Two biases were to the left (Thelma: $t_{(3)} = -5.090$, p = 0.015; Heckle: $t_{(3)} = -3.654$, p = 0.035) and two

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