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Biol. Lett. 2005 **1**, 314-317
doi: 10.1098/rsbl.2005.0347

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Spatial encoding in mountain chickadees: features overshadow geometry

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Encoding the global geometric shape of an enclosed environment is a principal means of orientation in human and non-human animals. Animals spontaneously encode the geometry of an enclosure even when featural information is available. Although features can be used, they typically do not overshadow geometry. However, all previously tested organisms have been reared in human-made environments with salient geometrical cues. Here, we show that wild-caught mountain chickadees (*Poecile gambeli*) do not spontaneously encode the geometry of an enclosure when salient features are present near the goal. However, chickadees trained without salient features encode geometric information, but this encoding is overshadowed by features.

Keywords: mountain chickadees; spatial orientation; geometry

1. INTRODUCTION

Developing a directional frame of reference, often referred to as ‘getting oriented’ or ‘determining heading’, is an integral part of solving many spatial navigation problems (Gallistel 1990). One way of determining heading is to use geometric properties of the environment (Cheng 1986). Encoding the global geometric shape of an enclosed environment is a ubiquitous and predominant means of orientation in humans and other animal species (see Cheng & Newcombe (2005) for a review). Cheng (1986) found that rats predominantly rely on the geometry of a rectangular enclosure, frequently making rotational errors even when features were present. Similar results have been found in human children (Hermer & Spelke 1994; Learmonth *et al.* 2002), rhesus monkeys (Gouteux *et al.* 2001) and fishes (Sovrano *et al.* 2003; Vargas *et al.* 2004). Pigeons (Kelly *et al.* 1998; Kelly & Spetch 2001) and chicks (Vallortigara *et al.* 1990) also use geometric information to reorient, but rely more on featural information.

The finding that most animals learn the geometric properties of an environment despite the availability of salient featural information contrasts with evidence that cue competition effects, such as overshadowing and blocking, occur in spatial learning tasks. For example, both pigeons (Spetch 1995) and rats (e.g. Biegler & Morris 1999; Sanchez-Moreno *et al.* 1999) learn less about spatial cues when other salient or closer cues are simultaneously available (i.e. overshadowing). Interestingly, however, overshadowing was not found when pigeons (Kelly *et al.* 1998), fishes (Sovrano *et al.* 2003), rats (Wall *et al.* 2004), or humans (Kelly & Spetch 2004) were trained with both featural and geometric information simultaneously; all species spontaneously used geometry to find the correct corner when the featural information was removed. Furthermore, chicks trained to locate a beacon in the middle of a square arena continued to focus their search in the centre of the arena when tested without the beacon (Tommasi & Vallortigara 2000). Similar results have been found with rats (Pearce *et al.* 2001). Thus, encoding of geometry, unlike encoding of other spatial cues, appears to be robust and resilient to cue competition effects (see Cheng & Newcombe (2005) for a review).

Interestingly, all species tested so far in this paradigm are typically raised in an environment rich in geometrical cues, and thus have had considerable experience with right-angled environments (see Cheng & Newcombe 2005). As food-caching birds, chickadees (*Poecile gambeli*) have well-developed spatial memory abilities (Sherry 1984). However, living in forested areas limits their experience with salient geometry and continuous surfaces, making them ideal subjects for studying the encoding of geometry in the absence of extensive early experience.

2. METHODS

(a) *Participants*

Seven male and five female adult mountain chickadees participated in the study. None had any previous experience with spatial tasks or with the apparatus. Chickadees were captured between January 2002 and March 2004 at the Barrier Lake Field Research Station in Kananaskis Valley, Alberta, Canada (51°02′ N, 115°03′ W). The birds were maintained on a light–dark cycle typical for the season in Edmonton, Alberta. Temperature was maintained at about 20 °C.

(b) *Apparatus*

The experimental apparatus was located within a 2.9×3.3 m laboratory room. The birds were transported to and from the experimental room in a black semi-translucent case with a guillotine style door. The experimental apparatus was a uniformly white Plexiglas rectangular chamber, 50×100 cm (60 cm high). Centred at the bottom of each wall was a 13×13 cm guillotine style door through which the birds entered and exited the chamber. The top of the chamber was covered with a wire mesh screen and the floor of the arena was covered with approximately 1 cm depth of aspen chips. Small 15 W lights were affixed to the top of each corner of the chamber. White curtains surrounded the apparatus to block the use of visual room cues for directionality.

On each wall, four white Velcro pieces were attached in the corners so that a blue plastic wall could be attached to any of the walls. Identical white perches were placed 2–3 cm from each corner. The perches were 15 cm tall cylinders (diameter: 5 cm) with a second smaller cylinder (diameter: 1.3 cm) affixed horizontally 7.5 cm from the bottom. Above the small cylinder was a hole (diameter: 1.3 cm), which could be covered with a Velcro piece to hide a reward.

The entire apparatus was randomly rotated by either 90°, 180° or 270° within the curtains approximately every two days.

(c) *Procedure*

All birds were initially trained in their home cages to retrieve a worm from the perch and were habituated to handling and to being placed in the carrying case. Once the bird quickly and consistently obtained the worm, training in the experimental chamber commenced.

All birds received three trials per day, five days per week. One group ($n=4$) was trained without any distinctive features in the enclosure (geometry group), a second group ($n=4$) was trained with one differently coloured wall adjacent to the correct corner

Received 20 January 2005
Accepted 12 May 2005

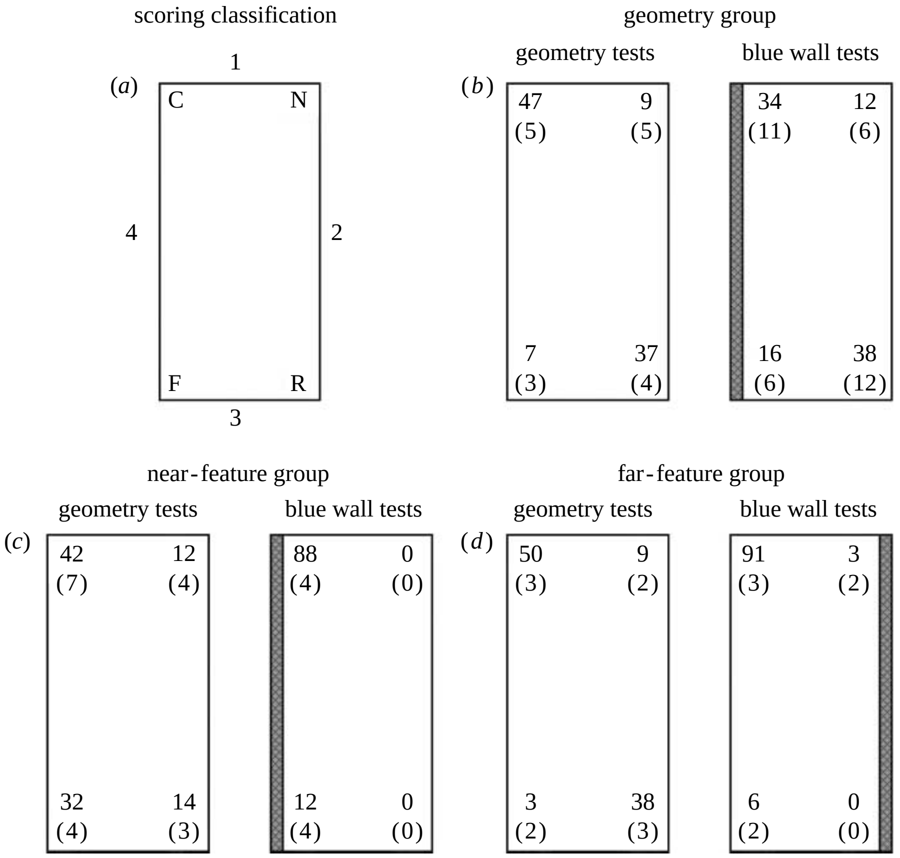

Figure 1. Panel (*a*) shows the classification of corners as correct 'C', the rotational equivalent 'R' and the geometrically incorrect corner nearest the correct one 'N' and far from the correct corner 'F'. For the near-feature birds, the blue wall was placed on either wall 1 or 4, and for the far-feature birds the blue wall was placed on either wall 2 or 3. Panels (*b*)–(*d*) show percentage (s.e.m.) of first choices to each corner during the blue wall tests and geometry tests for the geometry, near- and far-feature groups, respectively. The data are averaged across birds. The correct corner is shown as the top left (the actual correct corner was counterbalanced across birds).

(near-feature group) and the third group was trained with a differently coloured wall opposite the correct corner (far-feature group). The blue wall was on a short wall for half of the birds and a long wall for the remaining birds in each group.

To begin a training session, the bird was removed from its home cage, placed in the carrying case and taken to the experimental room. The chamber lights were lit and the room lights were extinguished. The carrying case was placed flush against a randomly selected entry door and the doors to the chamber and carrying case were opened. Upon entry, both doors were closed. The bird was allowed up to 10 min during initial training sessions and 5 min during regular training to obtain the worm. The chamber lights were then turned off and both entry doors were re-opened. A flashlight was placed above the carrying case to illuminate it; if the bird did not enter the case, the experimenter gently guided the bird towards the door. Between trials, the aspen chip on the floor was swept, the perches were swapped between corners, and the perch in the correct corner was baited. The carrying case was moved to another randomly selected door, and the above procedure was repeated.

In the initial phase of training, only the correct corner contained a perch. Once the bird reached a criterion of obtaining the worm within 5 min on the first two trials for three consecutive days, identical perches were placed in the remaining three corners of the chamber.

Four-perch training continued for a minimum of 10 days and until an accuracy criterion was met. For this criterion, only the first two trials of each session were used because performance on the third trial was variable, probably due to satiation. For the geometry birds, the accuracy criterion was a first choice to either the correct corner or the geometrically correct corner on 8 out of 10 trials. For the feature birds, the accuracy criterion was a first choice to the correct corner on 8 out of 10 trials. In all cases, a choice was counted when the bird's beak touched the Velcro covering the hole of a perch, as determined by video analysis.

Tests were conducted Tuesday through Friday, with Monday being a training day. The test trial was randomly selected as either the first or second trial of the day. All groups were tested with and without the featural information available (blue wall and geometry tests, respectively). The birds received eight trials of each of these test types. The feature birds also underwent two additional sets of tests (five of each type), one in which the location of the blue wall was moved so that it conflicted with the geometry (conflict tests) and one in which the location of the blue wall was moved but did not provide a conflict (opposite wall tests). In conflict tests, the blue feature was rotated one wall over from training. In this test, the featural information conflicts with the geometric information. In opposite wall tests, the blue feature was moved to the diametrically opposite wall from training, which essentially rotated the bird's frame of reference by 180° but did not provide a conflict. No reinforcement was available during test trials. All percentage scores were compared using *t*-tests with both raw and transformed (arcsine square root) percentages to normalize the distributions; the patterns of results from each were comparable and therefore only results for the raw data are reported here.

3. RESULTS

The mean percentage of first choices made at each corner during the geometry and blue wall tests for the geometry group is shown in figure 1*b*. The percentage of first choices by the geometry birds to either the correct corner or its geometric equivalent was significantly above chance level (50%) during both the geometry tests (84%; $t(3)=7.33$, $p=0.005$) and the blue wall tests (72%; $t(3)=3.40$, $p=0.04$). When the blue wall was present, the geometry birds always made their first choice at a corner that was not

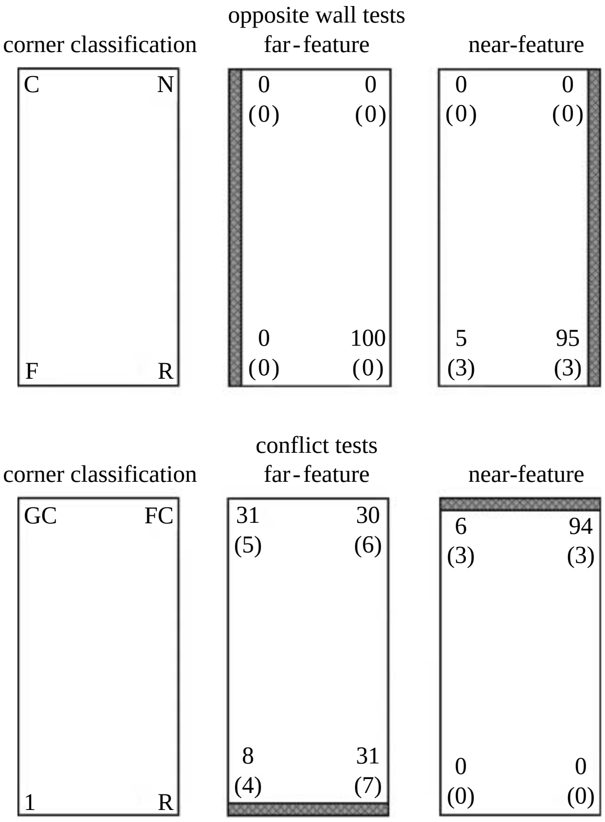

Figure 2. Percentage of first choices to each corner for both the near- and far-feature groups during: (*a*) opposite wall tests and (*b*) conflict tests. The data are averaged across birds. The geometrically correct corner is shown as the top left, however the actual correct corner was counterbalanced across birds. The first panel in each row shows the classification of corners. The opposite wall tests were classified as indicated in figure 1 and the conflict tests were classified as geometrically correct 'GC', featurally correct 'FC', the rotational equivalent of the geometrically correct corner 'R' and an incorrect corner 'I'.

adjacent to the blue wall, but this was usually a geometrically correct corner. Thus, the geometry birds learned to use the shape of the environment to locate the correct corner.

For both groups of feature birds, the blue wall tests served as control tests. These test trials were the same as training trials for these groups except that test trials were not reinforced to rule out the possibility that the chickadees might have been using cues from the mealworm (e.g. odour) to locate the correct corner. Both groups learned to effectively locate the correct corner using the blue wall (figure 1*c*,*d*). The percentage of first choices to the correct corner on control tests significantly exceeded chance (25%) for both the near-feature group (88%; $t(3)=14.14$, $p<0.001$), and far-feature group (91%; $t(3)=21.93$, $p<0.001$).

When tested on geometry only, the far-feature group made their first choice at either the correct corner or rotational equivalent 88% of the time. This was significantly above chance level (50%) ($t(3)=14.70$, $p<0.001$). Choices to the correct corner did not significantly exceed choices to the rotational equivalent corner (paired $t(3)=1.414$, $p=0.25$). The near-feature group performed quite differently from the far-feature group, choosing correct or rotationally equivalent corners only 56% of the time. This was not significantly above chance ($t(3)=1.06$, $p=0.37$) indicating that the birds trained in the near-feature group did not learn the geometry of the enclosure. Choice of the correct corner was not significantly higher than choice of the geometrically equivalent corner (paired $t(3)=1.40$, $p=0.26$).

An ANOVA comparing choices to the correct corner or rotational equivalent for the three groups showed a significant main effect of group, $F_{2,9}=4.53$, $p=0.04$. Planned comparisons showed that the near-feature group differed significantly from both the geometry group ($F_{1,9}=2.46$, $p=0.04$) and the far-feature group ($F_{1,9}=2.73$, $p=0.02$). There was no significant difference between the geometry and far-feature groups ($F_{1,9}=0.26$, $p=0.79$).

During the opposite wall tests, both groups of birds almost exclusively chose the rotational corner, 95% for the near-feature group and 100% for the far-feature group (figure 2). On the conflict tests, the near-feature group chose the featurally correct (but geometrically incorrect) corner 94% of the time, significantly more than chance (25%) ($t(3)=22.00$, $p<0.001$). In contrast, the far-feature group divided their searches between the featurally correct corner and the geometrically correct corners. Although they did not choose any of those three corners significantly above chance, they chose the incorrect corner significantly below chance level (25%) ($t(3)=4.00$, $p=0.03$).

4. DISCUSSION

The chickadees trained with featural information adjacent to the correct corner did not spontaneously encode the geometry of the enclosure, whereas the chickadees trained with geometry only or the far feature learned to use the geometric information of the environment to reorient. It should be noted that encoding of geometry does not appear to be disrupted by either being tested in an impoverished and unnatural environment or by the mere presence of a feature. Specifically, all birds were tested in the same environment, and birds trained with the far feature present did in fact encode this feature but not to the detriment of geometric encoding. Thus, the overshadowing observed in the near-feature group appears to reflect a difference in encoding, presumably because the near feature functioned as a beacon. This is the first report, to our knowledge, of overshadowing of geometry by featural information and it suggests that use of geometry is not a predominant strategy for wild-caught mountain chickadees.

Our finding that features overshadow geometry in wild-caught mountain chickadees contrasts with the results obtained from more traditional laboratory species. This leads to the obvious question of why this is the case. One explanation is that wild-caught birds have little experience with salient right-angle cues, thus leading to reliance on featural over geometric information. Another testable alternative is that at least some laboratory species (e.g. rats and pigeons) may respond differently from wild-caught animals because of the effects of years of artificial selection. Further research will address the nature versus nurture issue by, for example, comparing chickadees reared in the laboratory with wild-caught chickadees to assess whether early experience with salient geometric environments affects the propensity to encode geometric information.

We thank A. Brown, F. Hasham, Z. Kassam, D. Ludeman, S. McAnsh, M. Modanu and E. Verbeek for their help in collecting and scoring the data, and I. Lank for help with the apparatus and technical support. This research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grants to M.L.S. and C.B.S.; post-graduate scholarship to L.L.B.), the Alberta Ingenuity Fund (New Faculty Grant to C.B.S.), the Canada Foundation for Innovation (New Opportunities Grant to C.B.S.) and the University of Alberta (start-up and CFI partner funding to C.B.S.).

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