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Title
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Permalink
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Journal
International Journal of Comparative Psychology, 25(4)

ISSN
0889-3675

Authors
Watanabe, Shigeru
Bischof, Hans-Joachim

Publication Date
2012

DOI
10.46867/ijcp.2012.25.04.04

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International Journal of Comparative Psychology, 2012, 25, 276-284.
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Spatial Cognition of Zebra Finches in a Morris-maze Analogue Apparatus

Shigeru Watanabe
Keio University, Japan

Hans-Joachim Bischof
Bielefeld University, Germany

There are many studies of spatial memory in food-storing birds, but comparable studies in songbirds are rather rare. We have devised a Morris-maze analogue for zebra finches (*Taeniopygia guttata*). Here we examined the discriminative behavior of zebra finches (N = 10) in the maze analogue used in previous experiments. The birds, when released from different positions into the aviary, had to choose one baited feeder from four feeders. When the birds had learned this task, their performance in trials with a modified arrangement of the feeders was tested. Removal of a non-baited feeder did not disturb discrimination performance, while displacement of the position of the baited feeder (so as to move it closer to other feeders) disturbed discrimination. These results suggest that the birds identified the baited feeder by absolute position in reference to extra-maze cues, and that the non-baited feeders affected the discriminative behavior by acting as distractors.

For finding a particular location within the environment, for example a food source, animals rely on a variety of different cues. Long distance orientation is mainly based on global cues like the earth's magnetic field, the sun, or constellations of stars (e.g., Schöne, 1980). Near field orientation is mainly based on the use of landmarks, that is, conspicuous objects scattered around the landscape. By learning relations between the goal and one or several landmarks, the animal acquires a "neuronal representation" of the environment which can be used to find the goal location independent of the animal's own position within the environment (Bennett, 1996; Gallistel, 1989). Orientation after landmarks independent of own position is called "allocentric," in contrast to "egocentric" orientation, in which the location of the goal is determined by using relations between landmarks and own position.

Foraging behavior may affect spatial cognition strategy. Experimental work in the laboratory has shown that food-storing birds like nutcrackers depend mainly on distant cues, while non storing birds have been shown to use both local and distant cues, with a preference for local ones (Brodbeck, 1994). LaDage, Roth, Fox, and Pravosudov (2009) showed that, in food-storing birds, the percentage of local or distant cues used varies according to the situation. If the local environment changes often, it is much safer to use distant cues. By contrast, in a stable configuration of local landmarks, locating the goal might be easier using local cues.

Researchers have applied the Olton-type radial maze to birds (Bond, Cook, & Lamb, 1981). But for different species the same apparatus may not give ecologically correct comparative data. Walking on the arms to reach the feeder

The experiment was supported by Global COE Program at Keio University in Japan. Correspondence concerning this article should be addressed to Shigeru Watanabe, Department of Psychology, Keio University, Mita 2-15-45, Minato-ku, Tokyo, Japan. (swat@flet.keio.ac.jp)

may be unnatural foraging behavior for birds. Hence, researchers have modified the original radial maze in two different ways. One is the so-called radial maze analogue, in which feeders can be accessed through open space instead of walking on the arms (Spetch & Edwards, 1986). Another modification was placing a large-scale radial maze outside (Lipp et al., 2001). Birds were able to fly and walk through radial tunnels to reach feeders, but the arrangement of the arms was the same as in the original radial maze. There is a considerable amount of avian data using such modified radial mazes (see Pleskacheva, 2009, for a review).

On the other hand, the Morris water maze has been rarely applied to birds. Because the water escape paradigm cannot be applied to birds, we invented a dry type Morris-maze analogue for small birds. One baited feeder and three non-baited feeders were placed in an aviary. Birds released from different positions had to detect a baited feeder at a particular position to obtain a food reward. Zebra finches (a non-storing species) were able to learn this task (Watanabe & Bischof, 2001). After the training, we tested their spatial cognition with the aviary covered by white paper and rotated by 90 degrees to eliminate possible local cues. The birds again showed good discrimination. The finches apparently used extra-maze cues for finding the desired feeder. We found deficits of this spatial learning after lesions in hippocampus or visual Wulst but not after lesions in entopallium (Bischof, Lieshoff, & Watanabe, 2006; Watanabe & Bischof, 2004; Watanabe, Mayer, & Bischof, 2008, 2011).

In the present study, we wanted to know whether spatial cognition based on distant cues would be affected by the rearrangement of local cues. For this purpose, we removed two of the four feeders in order to examine whether the birds needed the complete arrangement of the four feeders for correct recall of the task. If so, the removal should disturb their discrimination. Second, we displaced the baited feeder in order to examine whether the absolute position controls the birds' spatial discrimination. Third, the distances between the four feeders were scaled down -- that is, they were placed closer together, but their geometric relation to each other was maintained. If the birds used the relative position of the baited feeder among the four feeders as a cue for their spatial discrimination, this operation should not disturb their discriminative behavior. Finally, the color of the baited feeder was changed to examine whether or not the feeder's position provided enough information for the birds to make a correct choice.

Method

Subjects

Ten zebra finch males (*Taeniopygia guttata*) between 100 and 150 days of age were used for this study. They were housed in individual cages, and water was freely available. The light cycle was 12L: 12D. Food was available after the daily experiments (around 4:00 PM), but was removed at 9:00 PM.

Apparatus

As shown in Figure 1, the experimental chamber was a cubic aviary (180 x 180 x 180 cm) made of wire mesh, situated in the middle of a sound isolated room (3 x 3 x 2.40 m). Each wall had a release site with a flap door (10 x 7.5 cm). A wooden platform on which the individual home cage of the experimental animal could be placed was fixed at the outside of the walls below the release sites.

The height of the platforms was 120 cm from the floor. There was a long perch at one corner inside the aviary (74 cm) and seven short perches (9 cm) attached to the walls. The floor was covered with white paper. Four feeders were placed on the floor. The feeders were cylindrical white feeders, consisting of the base part of a commercially available pet bird feeder (3.5 cm in diameter, 3.5 cm high), each with a hollow arm (1.0 cm wide, 3.5 cm high) allowing the bird to reach and eat the mixed grain.

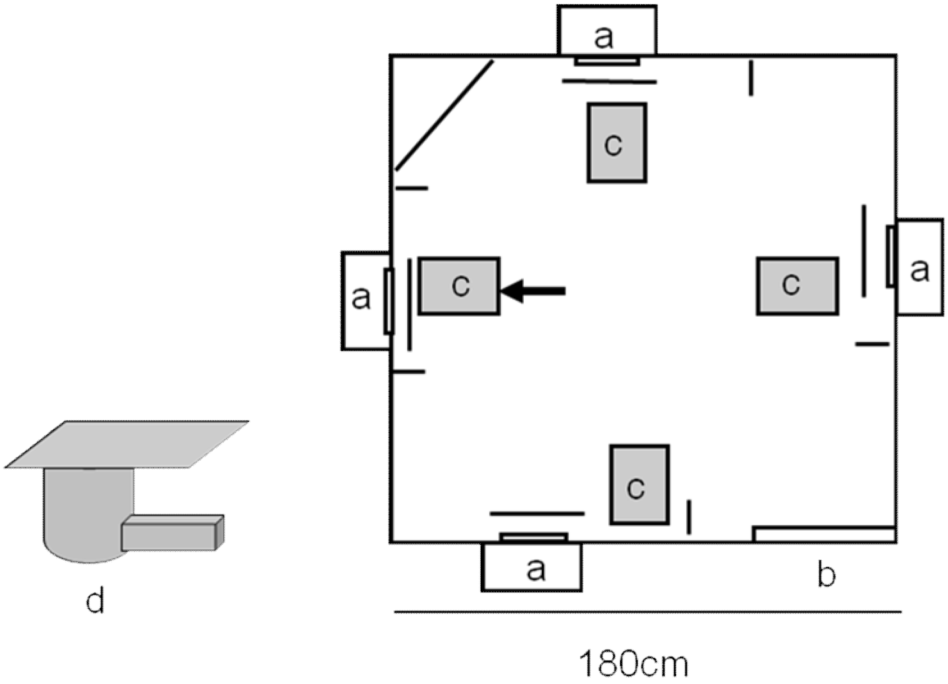

Figure 1. Apparatus. **a**) releasing points. Home cage was placed on the platform and a flap door in front of the cage and a guillotine door of the cage were opened to release the bird, **b**) door. **c**) feeders, **d**) original feeder for small birds, with a yellow flap and covered by yellow paper. A bird can eat food from an arm. The non-baited feeder also has food but the arm is covered by transparent tape; thus the bird can see but cannot eat the food.

Each feeder was covered by a piece of yellow cardboard (5 x 8.5 cm) concealing the cylindrical part and the arm of the feeder so that the birds could not see the inside of the arm from above. The feeders contained mixed seeds for small birds. Further details of the setup and the basic experiment are given in Watanabe and Bischof (2001).

Procedure

Habituation. The four cages were placed on the floor of the aviary, where the feeder for the bird's home cage and the experimental ones were placed for the first day of habituation. The doors of the cages were opened and the birds were allowed to eat from either the home cage feeders or the experimental feeders for 1 hr. The second day of habituation consisted of three trials. On the first trial, only the four experimental feeders were placed in the aviary, and four birds were released from the four platforms. They were allowed to eat food from any feeder for 30 min, and were then returned to their cages. The second trial started 2 hrs later. The birds were released singly into the aviary, using the following procedure. The home cage was placed on a platform, its ceiling lamp (DC12V) was turned off, and a string attached to the guillotine door of the cage was pulled to open it and to release the bird into the aviary. The bird was allowed to eat food from any feeder for 2 min.

Then, the ceiling lamp of the cage was turned on and illumination of the aviary was turned off. The bird spontaneously returned to the home cage in most cases. If the bird did not return to the cage, it was gently chased to the cage. Then, the next bird was released into the aviary. The third trial started 2 hrs later. The procedure of the third trial was identical to that of the second trial. Two birds did not come out of their cages and so were excluded from further training.

Training. Only one of the four feeders was baited during discrimination training. The other three feeders also contained food, but their hollow arm was covered with transparent adhesive tape to block access to the food. Thus, the birds could see the food but could not eat it. Each training session consisted of four trials. The birds received one training session on any given day. The position of the baited feeder was the same for all trials, but the birds were released randomly from four different positions, so they had to use their spatial memory to remember the baited feeder's location. The time each bird needed to reach the baited feeder after entering the aviary (latency) was measured, and the number of visits to incorrect feeders until reaching the baited feeder was counted. The first visit of a given trial was used to determine whether the trial was counted as a correct or an incorrect choice. A trial ended when a bird had eaten food for 2 minutes. The inter-trial interval was greater than 90 min but less than 120 min. The training continued until the birds had reached a minimum of three correct choices out of four in two consecutive sessions ($\geq$ 75%). Time to reach the baited feeder was counted as search time. More details of the procedure were given in Watanabe and Bischof (2001).

Tests. After the subjects accomplished the learning task, they received the following six different tests. In the partial cue tests, only two of the feeders remained in the aviary. In one of the two tests, the two feeders on the left and right of the baited feeder were removed; in the second one, the feeders removed were those on the right of and opposite to the baited feeder. In the color test, the arrangement of the feeders was not altered, but the color of the baited feeder was changed to green. In the position tests, the position of the baited feeder was changed, horizontally or vertically, as shown in Figure 3. In the scale reduction test, the distance between the feeders was reduced to 60 cm.

In the test phase, the first trial was an assessment of the learning, namely a trial with the same arrangement of the feeders as used in the training sessions. If the birds chose the baited feeder correctly in this assessment trial, the four test trials followed. If they failed, they received a second set of the usual training trials, followed by the four test trials. The order of tests was counterbalanced.

Data Analysis

We employed paired t-tests with Holm's correction for multiple comparisons. Corrected *p* values for 0.05 were 0.008, 0.01, 0.0125, 0.0167, 0.025 and 0.05.

Results

Figure 2 presents the averaged backward learning curve. The upper and lower graphs show the mean percentage of correct choices and the latency to reach the goal, respectively. Small numbers on the learning curves indicate numbers of subjects in the backward averaging. Every bird reached the criterion within six sessions and the fastest birds reached the criterion in three sessions. The training also reduced the time to reach the goal. These results were similar to those of our previous studies (Watanabe & Bischof, 2001).

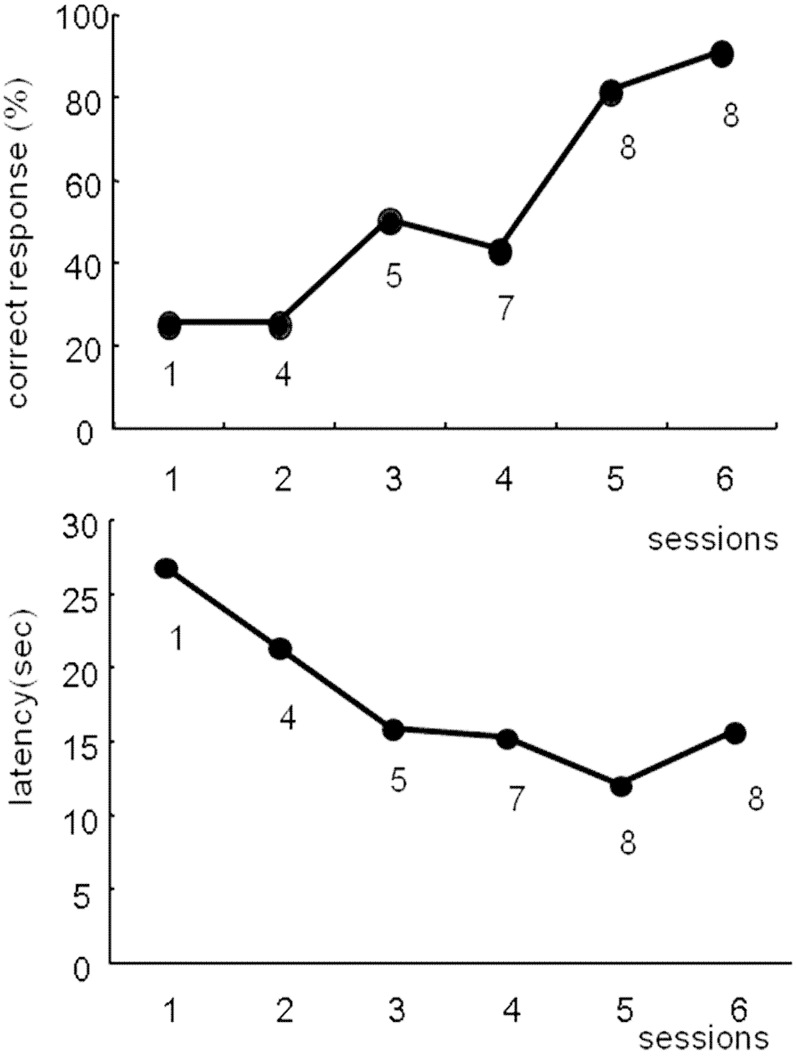

Figure 2. Backward averaged learning curves. The upper panel shows percentage correct response and the lower latency to reach the baited feeder. Small numbers indicate number of subjects for averaging.

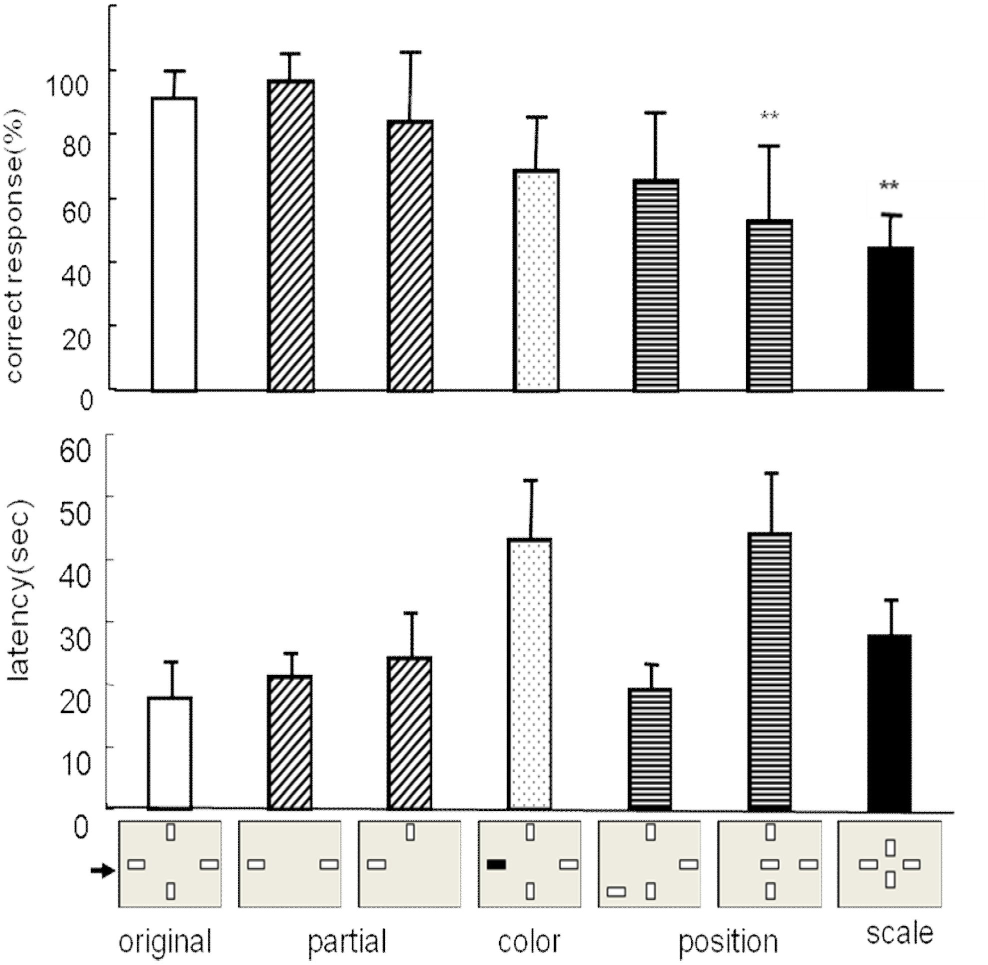

Figure 3. Results of the tests. The upper and lower panels show percentage correct response and latency to reach the baited feeder. The arrow in the original setting indicates position of the baited feeder. Two of the three non-baited feeders were removed in the two partial tests. The color of the baited feeder was changed in the color test. The position of the baited feeder was moved in the two position tests. The arrangement of the feeders was reduced in the scale reduction test.

The results of the six tests are shown in Figure 3. During the testing, only three of the 48 cases failed in the first assessment trial, and these failed birds chose correctly on the second training trial. The upper and lower graphs present the mean percentage of correct choices and the latency to reach the goal, respectively. The baseline performance was calculated from the last training sessions before each test session. There was a significant difference between the baseline and the horizontal movement of the baited feeder position (paired t-test, $t(8) = 4.79$, $p < 0.01$, but not between the baseline and the vertical movement, $t(8) = 2.43$, $p < 0.017$. In these tests, the birds often jumped to the location where the baited feeder used to be placed and appeared to look for the displaced feeder. There were no significant differences between the baseline and the color test, $t(8) = 3.24$, $p >$

0.0125). Interestingly, the birds often approached the green feeder but hesitated to eat from it, and then moved to one of the yellow feeders.

There were no statistically significant differences between the baseline and the two partial elimination tests, $t(8) = 0.86$, $p > 0.05$ and $t(8) = 1.52$, $p > 0.10$, respectively. Although we have to take into account the fact that the chance level of these two tests was 50% rather than 25% (two feeders rather than four), the elimination of two feeders did not disturb the orientation of the birds.

The birds took more time to reach the baited feeder in the horizontally moved test, the scale reduction test, and the color test. But there were no statistically significant differences in these cases after the Holm's correction, $t(8)$s = 2.26, 2.38, 1.00 *(p = 0.06, 0.04, 0.33, respectively)).*

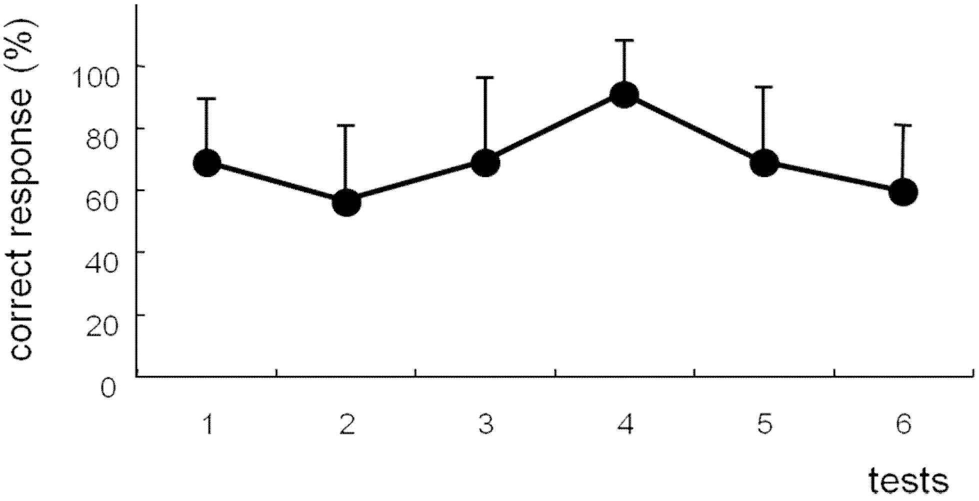

Figure 4. Percentage correct responses to tests arranged in serial order. Six tests were carried out in random order. If birds learned something during testing, they should have shown improvement through the six tests.

Because each subject received 6 tests successively, they may have learned something during the tests. The subjects received the tests in random order, and Figure 4 presents the averaged correct response percentages from the first to the sixth test of the sequence. There was no systematic improvement during the testing.

Discussion

In the present experiment, partial removal of the feeders did not disturb the discriminative behavior of zebra finches. Thus, the absolute position of the baited feeder provided enough spatial information to detect the correct feeder.

On the other hand, when the absolute position of the baited feeder was changed, the birds showed disturbance of their discriminative behavior. One possible explanation of this disturbance is a stimulus generalization gradient along the distance from the original position. If this occurred, the larger distance should have resulted in poor performance. However, the distance from the original position was 80 cm in both the horizontal and vertical displacement tests, and only 50 cm in the scale reduction test; it was the latter in which the subjects showed the worst performance. Thus, the generalization gradient hypothesis based on displacement distance does not explain the results.

Another possible explanation is based on the spatial arrangement among the feeders. The non-baited feeders may have been distractors for detection of the baited feeder, with the disturbance depending upon the distance between the baited feeder and the distractors. A closer distance between the distractors and the baited feeder should have resulted in disturbance in detection of the correct feeder. In the horizontal and vertical displacement tests, the 4 feeders stood within 80 cm distance of each other. In the scale reduction test, the 4 feeders were placed within 60 cm distance of each other. Thus, shortening the distance among the feeders disturbed the birds' discriminative behavior. One problem with this explanation is the difference between the vertical and horizontal displacement. Although the difference between the baseline and vertical displacement was not significant after the Holm's correction, a direct comparison between the vertical and horizontal displacement tests did not reveal a significant difference (paired t-test, $t(8) = 1.89$, $p = 0.35$). Thus, the vertical displacement may have had a disturbing effect on discriminative behavior. Another possibility is the relationship to the extra-maze cues. The vertical relationship may have differed from the horizontal relationship. Such a difference may have caused a different disturbing effect.

In our previous experiment (Watanabe & Bischof, 2001), we examined the effects of changing colors. In that case, we changed the color of all the feeders, and the birds showed good discrimination. In the present experiment, only the color of the baited feeder was changed. Thus, the birds may have used two strategies in choosing the baited feeder, namely, to select the feeder in the correct position (but in an unfamiliar color), or to select a feeder that had a familiar color (but was at an incorrect position). The results supported the former case and agreed with our previous experiment.

Considering the present study's findings together with those from our previous study (Watanabe & Bischof, 2001), it appears that zebra finches preferentially learn the absolute position of the baited feeder in reference to extra-maze cues, and non-baited feeders disturb their discrimination.

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