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S35-1 Spatial and object cognition in the domestic chicken

Giorgio VALLORTIGARA
Dept. of Psychology and B.R.A.I.N. Centre for Neuroscience, University of Trieste, Via S. Anastasio 12, 34123 Trieste, Italy; vallorti@univ.trieste.it

Abstract The ability of the chicken to encode different aspects of spatial layout were investigated. In a first series of experiments, chickens were disoriented in a rectangular environment, where they proved able to reorient themselves using both geometric and non-geometric properties of the environment. In a second series of experiments, chickens were trained to find the central position of an arena using only the spatial arrangement of the walls for orientation. When subsequently tested in an arena of identical shape but a larger area, chickens displayed searching behavior at two different distances, one corresponding to the original distance (i.e., center) in the smaller, training arena, the other to the actual center of the test arena. When training was performed in the presence of a conspicuous landmark at the center of the arena, animals searched at the central location even after the removal of the landmark. Chickens are thus able to encode information about absolute and relative distance from the walls of the arena, even when orientation by a single landmark suffices for spatial localization. Temporary occlusion of the left or the right eye during testing revealed that the right hemisphere (served by the left eye) is primarily concerned with encoding geometric and relational spatial information, whereas the left hemisphere (served by the right eye) is concerned with absolute metric information, possibly as part of an encoding strategy based on local spatial and non-spatial information.

Key words Cognition, Spatial memory, Cerebral lateralization, Domestic chicken, *Gallus gallus*

1 Introduction

When considering spatial cognition in birds, cognitive ethologists usually think of the surprising feats of food-storing birds or of the remarkable orienting abilities of homing pigeons. In contrast, the protagonist of my paper is the humble domestic chicken (*Gallus gallus*). I shall report on the ability of the chicken to make use of different features of spatial layout in its environment for orientation, and on the way in which these different features are encoded separately in left and right hemispheres of the brain.

2 Encoding of geometric and non-geometric information

My analysis begins with the ability of the chicken to use so-called purely geometric information, namely the information provided by the spatial arrangement of surfaces as surfaces. In a rectangular space similar to that used by Cheng (1986) for rats and Hermer and Spelke (1994) for children, a filled dot in corner A indicates the location where the chicken can find visible food (Fig. 1). After several trials, the food is progressively hidden until it becomes completely invisible. At the same time, the chicken is disoriented by slow rotation on a chair, and then is replaced in the rectangular arena. In the absence of topographical cues, there is no way that it can relocate the correct corner. Nevertheless, if it can encode and use geometric information, a partial solution to its problem is possible. There is only one other location that is truly indistinguishable from corner A, and that is its rotational equivalent, corner C (empty dot). Corners B and D can be discarded on the basis of geometric information alone. We found that chickens, after brief training, could learn to choose the correct corners A and B. Surprisingly, it has been found that human infants (Hermer and Spelke, 1994) and adult rats (Cheng, 1986) failed to reorient. They tended to use only purely geometric information, persisting in confusing corners A and C.

These findings have been interpreted as suggesting that spatial reorientation depends on an encapsulated, task-specific mechanism, a "geometric module" (Cheng, 1986). Such a module would encode only the geometric properties in the arrangement of surfaces as surfaces. In the case of the spatial reorientation task in the rectangular environment, for instance, the geometric module would use only "metric properties" (i.e., the distinction between a long and a short

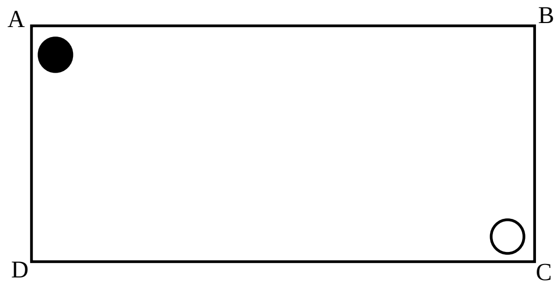

Fig. 1 Rectangular space for testing encoding of geometric information by the chicken

wall) and what is known in geometry as “sense” (i.e., the distinction between right and left).

It was found that chickens, in contrast to rats and young children, can easily learn to reorient by combining geometric and non-geometric information (Vallortigara et al., 1990). Rats showed the clearest evidence of informational encapsulation of the geometric module when tested with geometric transformations of the arrangement of panels, particularly with transformations that modify the geometric relations between the target and the shape of the environment (Cheng, 1986).

Chickens behave very differently. We studied the effects of two geometric transformations: the diagonal transposition and the affinal transformation. Both transformations alter the original spatial arrangement of the panels; the affinal transformation, however, also modifies geometric relations between the target and the shape of the environment, whereas the diagonal transposition does not. Results showed that chickens were completely unaffected by these transformations. They searched on the basis of featural information alone, making virtually no errors at the locations specified by geometric information. Thus, chickens perform better than rats and young children in such spatial reorientation tasks, encoding and combining geometric and non-geometric information to position themselves (also Sovrano et al., 2002 for fish).

Recently, the possibility that different processing modules in the two cerebral hemispheres encode these different spatial processes has aroused interest. The avian brain provides an excellent model for analyzing brain lateralization in the vision domain, because there is complete crossing (decussation) at the optic chiasma, and the two visual pathways, the thalamofugal and tectofugal, ascend in the main contralaterally. This means that by occluding one eye temporarily, we can study how information is stored in the left and right parts of the brain.

Chickens were first trained in the rectangular-cage test, with four panels at the corners, as described before, and then tested with one eye covered in the affinal transformation test. Although chickens oriented mainly on the basis of non-geometric information whatever the eye condition, left-eyed chickens made more errors in the geometrically correct corners and tended to choose incorrect panels more often. This would suggest that purely geometric information, based on large-scale spatial information, is processed by the right hemisphere (left eye), whereas object-centered, local information is processed by the left hemisphere (right eye).

3 Learning to localize the center of an environment

An even more striking example of dissociation between position-specific and object-specific cues has been obtained in a different task. Young chickens were trained to find food hidden below sawdust on the floor by ground scratching in the center of a closed uniform arena: the center was indicated by a conspicuous landmark (a red stick). After learning, the landmark was shifted to a novel position and chickens were tested with both or only one eye uncovered. It was found that chickens with both or only the left eye uncovered searched at the center, ignoring the landmark, whereas chickens using only their right eye searched at the corner centered by the landmark, ignoring purely spatial information. It is interesting to note that here global cues prevailed over local cues in binocular and left-eye viewing conditions. The reason for it is unclear at present, but even so, whatever cues dominate in binocular conditions, the left eye tends to attend to global geometric cues and the right eye to local, non-geometric cues.

Our investigations then turned to a search for the neural bases of these spatial processes in the brain, in particular for specific areas in the left and right hemispheres that could be involved in these tasks. The hippocampus is very important for spatial memory in mammals, and patterns of connectivity suggest that its function could be homologous in birds. To test this, chickens were trained to find the center of an arena with a central landmark. Lesioned birds learned the task as well as sham-operated controls. Then the landmark was removed. Chickens lesioned bilaterally or at the right hippocampus appeared to be completely disoriented; lesions to the left hippocampus, in contrast, were ineffective.

In a second experiment, the landmark was not removed but transferred to a different position. Control, sham-operated chickens behaved as binocular chickens, searching in the center and ignoring the landmark. Bilateral- and right-hemisphere lesioned chickens (but not left-lesioned chickens), in contrast, searched near the landmark. In the absence of the right hippocampus, then, chickens could only use local information (i.e., the landmark), and were unable to process large-scale, geometric spatial information.

A similar dissociation between object-specific and position-specific cues has been observed in a working memory task. Young chickens were confined to a transparent cage through which they could see their “mother” (an imprinted object) at a distance. The mother object was then moved and hidden behind one of two different opaque screens. After a delay of 30 seconds, the cage was opened and the chicks allowed to search for the mother object behind the screens. In each trial, the position of the screen behind which the mother object was hidden was changed at random such that the task for the chicken was to remember the “correct” screen.

The chickens managed this task quite well. In one version, however, an opaque partition was placed in front of the transparent cage during the 30-second delay, and the experimenter, not visible, changed the left-right position of the screens so as to produce contradictory spatial and object-specific information. The chicken was thus faced with the dilemma of choosing the screen in the correct position but with the wrong color, or of choosing the screen in the wrong position but with the right color. It was found that left-eyed chickens searched behind the screen in the correct position, and right-eyed chicks behind the screen of the correct color. Once again, the right hemisphere (left eye) attends to position, and the left hemisphere (right eye) to visual characteristics.

The finding that birds are capable of using the metric configuration of distances between surfaces in the environment opens the door to the previously uninvestigated field of spatial performance. Take, for example, the task of localizing the perceptual center of a closed environment, and orienting by it, a task easily accomplished by humans. If the environment lacks distinctive landmarks, localization of the center would require the use of abstract metric information concerning spatial relations and distances between surfaces in the environment. We trained young chickens to find food by ground scratching in the center of a closed square-shaped uniform arena, and then tested them in arenas of similar size but different shape. The birds showed localized searching behavior in the square arena, and maintained it when placed in circular or triangular arenas. In a rectangular arena formed by doubling the original square, chickens dispersed their searching more along the major axis, yet searching tended to be concentrated around the centers of the composing squares and around the center of the rectangle itself.

When trained in a square-shaped arena and then tested in an arena of the same shape but larger area, chickens displayed searching behavior at two different distances from the wall, one corresponding to the original distance (i.e. center) in the smaller, training arena, the other to the actual center of the test arena. The same was found in triangular-shaped arenas. In circular arenas, however, chickens searched mainly at a distance midway between the radius of the small, training and large, testing arenas when moved to the latter. These results suggest that, during training, the chickens encoded information about both the absolute and relative distances of the food from the walls of the arenas, the latter information being more accurate when the arena provided identifiable features such as corners.

This task was used to investigate the way in which distances from the center were encoded in the two hemispheres. Left- and right- eyed chickens were strikingly different: chickens using their left hemisphere (right eye) searched only at absolute distances, whereas chickens using their right hemisphere (left eye) searched only at relative distances.

4 Conclusion

Overall, these results suggest that, for vision, the right hemisphere of the avian brain is concerned primarily with encoding relational spatial information, and the left with absolute metric information, possibly as part of an encoding strategy based on local spatial and non-spatial information.

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