Separate Geometric and Non-Geometric Modules for Spatial Reorientation: Evidence from a Lopsided Animal Brain

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Abstract

Research has proved that disoriented children and nonhuman animals can reorient themselves using geometric and nongeometric features of the environment, showing conjoined use of both types of information to different degree depending on species and developmental level. Little is known of the neurobiological bases of these spatial reorientation processes. Here we take advantage of the neuroanatomical peculiarities of the visual system of birds (showing segregation of information between the two sides of the brain to a considerable degree) to investigate the way in which geometric and nongeometric information is encoded and used by the left and right hemispheres. Domestic chicks were trained binocularly in an environment with a distinctive geometry (a rectangular cage) with panels at the corners providing nongeometric cues. Between trials, chicks were passively disoriented to disable dead reckoning. When tested after removal of the panels, left-eyed chicks, but not right-eyed chicks, reoriented using the residual information provided by the geometry of the cage. When tested after removal of geometric information (i.e., in a square-shaped cage), both right- and left-eyed chicks reoriented using the residual nongeometric information provided by the panels. When trained binocularly with only geometric information, at test, left-eyed chicks reoriented better than right-eyed chicks. Finally, when geometric and nongeometric cues provided contradictory information, left-eyed chicks showed more reliance on geometric cues, whereas right-eyed chicks showed more reliance on nongeometric cues. The results suggest separate mechanisms for dealing with spatial reorientation problems, with the right hemisphere taking charge of large-scale geometry of the environment and with both hemispheres taking charge of local, nongeometric cues when available in isolation, but with a predominance of the left hemisphere when competition between geometric and nongeometric information occurs.

INTRODUCTION

The finding that human children (Hermer & Spelke, 1994, 1996) and a variety of nonhuman vertebrates (fish: Sovrano, Bisazza, & Vallortigara, 2002; domestic chicks: Vallortigara, Zanforlin, & Pasti, 1990; pigeons: Kelly, Spetch, & Heth, 1998; rats: Cheng, 1986; rhesus monkeys: Gouteux, Thinus-Blanc, & Vauclair, 2001; tamarins: Deipolyi, Santos, & Hauser, 2001) can reorient themselves using purely geometric information provided by the distribution of surfaces as surfaces in the environment has generated considerable interest among researchers of spatial cognition (reviews in Carruthers, 2002). Usually, in these reorientation tasks, subjects are placed in a rectangular enclosure perfectly homogeneous and without distinctive featural information; the location of a goal that is subsequently hidden is shown; then subjects are disoriented and allowed to search for the hidden goal. In the absence of featural information, subjects rely on the shape of the enclosure to locate the goal, searching equally at the location of the goal and at the geometrically equivalent location at the opposite side of the rectangular room (i.e., in the corner located at a 180° rotation from the goal to the center; Figure 1). Human adults (Hermer & Spelke, 1994) and several nonhuman species (e.g., fish; Sovrano et al., 2002; rhesus monkeys: Gouteux et al., 2001) appear to be able also to conjoin geometric and nongeometric information to reorient themselves, whereas in certain conditions human children (up to 5 years old in small, but not in large, rooms; Learmonth, Nadel, & Newcombe, 2002; Hermer & Spelke, 1994, 1996) and rats (in working memory tasks, but not in reference memory tasks, Cheng, 1986) seem to rely exclusively on geometric information.

The issue of whether or not the encoding of geometric information possess the characteristics of a “module” (sensu Fodor, 1983) is currently debated (e.g., Learmonth, Newcombe, & Huttenlocher, 2001). On one hand, as noted above, comparative cognition research has suggested that conjoining of geometric and nongeometric information can be achieved in several species, irrespective of possession of a verbal language (one very interesting suggestion put forward by Hermer and Spelke, 1994, 1996, is in fact that language can serve as the medium to integrate information from different modules; see also Hermer-Vasquez, Spelke, & Katsnelson, 1999; Hermer-Vasquez, Moffet, & Munkholm, 2001). On the other hand, a weaker version of modularity can be claimed for based on the observation of a “primacy” of geometric information over nongeometric information. For instance, results obtained with chicks (Vallortigara

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birds present some anatomical peculiarities that have made them prominent as system models for the investigation of cerebral lateralization (see Vallortigara, Rogers, & Bisazza, 1999; Vallortigara, 2000; Güntürkün, 1997; Rogers, 1993; Rogers & Andrew, 2002). The domestic chick is probably the most used of these models (Andrew, 1991; Rogers, 1991, 1996; see also Matsushima, Izawa, Aoki, & Yanagihara, 2003, for a general review on the use of the chick model in neurocognitive research). Because of almost complete decussation at the optic chiasma, primary visual projections ascend mostly to the contralateral hemisphere in this species (Rogers, 1995). Crossover at the thalamic level in the chick (Deng & Rogers, 1998a, 1998b) allows indirect ipsilateral input to forebrain neurons. However, independent scanning movements of the eyes are usual in birds (Andrew, 1991); as a result, even the frontal visual fields (which are used in binocular fixation when the eyes are converged) will commonly each provide an independent (and quite different) input to the contralateral forebrain. This means that temporary eye patching reproduces a natural condition in which most of what is seen by the left (or right) eye is processed by the contralateral right (or left) hemisphere. Monocular vision produced experimentally by covering one eye is thus much less abnormal in birds than in mammals.

It is worth stressing what is peculiar to the type of investigation that can be carried out using the bird model. We shall not be concerned here with direct comparison of the ability of chicks to learn spatial disorientation tasks in monocular conditions. It is likely that, when forced, both eye systems could learn (this sort of experimental strategy is usually employed to investigate interocular transfer, see Rogers, 1995). Our approach is somewhat different. Our aim was to unravel the way in which different types of information, which are available in the ordinary, binocular condition of vision, are segregated into the two hemispheres. To this end, we exploited the crucial observation (Andrew, 1991; Vallortigara & Andrew, 1991; Vallortigara, 1992) that birds, like chicks, form and store two separate and very different records of an episode experienced in binocular condition, one in each hemisphere, apparently serving different purposes. An example comes from some recent studies on place finding task (Tommasi & Vallortigara, 2000, 2001; Vallortigara, 2000; see also Prior & Güntürkün, 2001; Clayton & Krebs, 1994, for evidence in other species of birds). Chicks were trained binocularly to find food buried under sawdust in the center of a square enclosure; the position of food being indicated by a conspicuous landmark. Then the landmark was displaced in a novel position and chicks were tested with only one eye in use. Results showed that left-eyed chicks searched in the center (disregarding the local cue provided by the landmark), whereas right-eyed chicks searched close to the landmark (disregarding the cen-

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**Figure 1.** Sketch of the geometric information that is available in a rectangular-shaped environment. The target (filled dot) stands in the same geometric relations to the shape of the environment as its rotational equivalent (open dot). Metric information (i.e., distinction between a short and a long wall) together with sense (i.e., distinction between left and right) is sufficient to distinguish between locations A–C and B–D, but not to distinguish between A and C (or between B and D).
tral position of the enclosure defined by large-scale spatial cues). In this article, we adopt a similar strategy for the spatial reorientation tasks.

**EXPERIMENT 1**

In our first experiment, chicks were first trained binocularly in a rectangular enclosure with distinctive features (panels) located at the corners. Thus, both geometric and nongeometric cues were available for spatial reorientation during training in binocular condition. Then the panels were removed and chicks were tested in the rectangular cage in binocular or in monocular conditions. We know from previous work (Vallortigara et al., 1990) that after removal of nongeometric information chicks tested in the binocular condition reoriented based on the residual (purely geometric) information provided by the shape of the environment; this demonstrates that training with nongeometric information (panels) does not overshadow encoding of purely geometric information. The issue we addressed here is whether encoding of purely geometric information takes place in both hemisphere or it is actually confined to only one hemisphere.

**Figure 2.** Results of Experiment 1. Chicks were trained binocularly in a rectangular environment with panels at the corners (left) and then tested after removal of the panels (right). Mean percentages of choices for each corner are shown (with SEM in brackets) for chicks tested binocularly (right, top) or with only their left (right, middle) or only their right (right, bottom) eye in use.
Results

Chicks took on average 5.67 (SE = 0.37) sessions to learn the task. Results (Figure 2) showed that after removal of the panels binocular chicks did not go back to random choices: They preferentially chose the two geometrically correct (and equivalent) corners A and C (A–C vs. B–D: n = 6, T+ = 21, p = .03; two-tailed Wilcoxon test). The same occurred with chicks tested with only their left eye in use (A–C vs. B–D: n = 6, T+ = 21, p = .03; two-tailed Wilcoxon test), but not with chicks tested with only their right eye in use, which searched at random among the four corners (A–C vs. B–D: n = 6, T+ = 0, ns).

Choices for the geometrically correct corners (A–C) were higher in chicks tested with only their left eye in use than in chicks tested with only their right eye in use (n1 = 6, n2 = 6, U = 0, p = .002, two-tailed Mann–Whitney U test). There were no significant differences between binocular chicks and chicks tested with only their left eye in use.

Discussion

Results for binocular chicks confirm previous results (Vallortigara et al., 1990) that chicks encode information concerning the geometry of the environment even when featural, nongeometric information provided by the panels is sufficient to disambiguate completely the reorientation task during training. However, the results also reveal a striking asymmetry: Geometric information seems to be encoded (or perhaps can be retrieved) only by the left eye (right hemisphere).
EXPERIMENT 2

In Experiment 1, chicks were first trained with both geometric and nongeometric cues available, and then tested after removal of nongeometric cues. In the following experiment, a complementary procedure was devised. Chicks were trained as in Experiment 1 with both geometric and nongeometric cues. Then at test, geometric information was removed by changing the shape of the test cage from rectangular to square (leaving unchanged the nongeometric information provided by the panels). Reorientation by geometric information requires the use of metric properties (i.e., short vs. long wall) and sense (i.e., right vs. left). In a square-shaped environment, no metric differences are available to allow the animals to distinguish between two geometrically correct locations (A–C) and two geometrically incorrect locations (B–D). Thus, when testing chicks in a square-shaped environment, only featural, nongeometric information provided by the panels remains available.

Results

Chicks took on average 6.20 (SE = 0.27) sessions to learn the task. Results of test are shown in Figure 3. There was no difference between chicks tested using only their right eye and chicks tested using only their left eye (n1 = 8, n2 = 7, U = 42.5, p > .1, two-tailed Mann–Whitney U test). As can be seen, in both monocular groups, chicks reoriented very well using the residual nongeometric information provided by the panels.

Discussion

The results thus suggest that encoding of nongeometric information occurs in both sides of the brain during training with addition of geometric and nongeometric cues.

EXPERIMENT 3

The results of the first two experiments suggest that during training in binocular condition in a rectangular cage with panels at the corners, information concerning the geometry of the environment can be segregated into the right hemisphere and can be retrieved only when chicks use the contralateral left eye, whereas information concerning local cues provided by the panels seems to be shared by the two hemispheres and can be retrieved irrespective of the eye in use. Does segregation of geometric information only occur when multiple sources of information are available? Or does it occur anyway associated with binocular training in an environment with a distinctive geometry? To address this issue in the following experiment, chicks were first trained binocularly in the rectangular cage without any nongeometric cues and then tested for their remembering of purely geometric information with only their left or their right eye in use.

Results

Chicks took on average 6.45 (SE = 0.18) sessions to learn the task. Results of test are shown in Figure 4. Choices for the two geometrically correct corners (A–C) were slightly higher in left-eyed chicks than in right-eyed chicks (n1 = 8, n2 = 10, U = 17, p < .05, two-tailed Mann–Whitney U test). Left-eyed chicks also were shown to choose preferentially the two geometrically correct (and equivalent) corners A and C with respect to the two geometrically incorrect corners B and D (n = 10, T+ = 55, p = .002, two-tailed Wilcoxon test). Right-eyed chicks, in contrast, showed only a nonsignificant trend for a similar choice (n = 8, T+ = 15, three cases eliminated for difference = 0, p = .06, two-tailed Wilcoxon test).

Discussion

Although stronger reliance on geometric information in chicks using their left eye seems to be revealed in this experiment, the difference between the two monocular conditions is rather weak when compared with the results of the Experiment 1. This may suggest that specialization of function appears more clearly when both sources of information, geometric and nongeometric, are available, particularly when they provide conflicting cues. This hypothesis is tested in the last experiment.

EXPERIMENT 4

As a final test of the dissociation of geometric and nongeometric information in the two hemispheres, we tested chicks in a condition in which the two types of cues (geometric and nongeometric) provided contradictory information. Previous work has shown that rats rely mainly on geometric cues in this condition (Cheng, 1986), whereas chicks (Vallortigara et al., 1990), pigeons (Kelly et al., 1998), and rhesus monkeys (Gouteux et al., 2001) rely mainly on local, nongeometric cues. However, based on the results obtained with monocular tests in chicks, we can predict that reliance on geometric information should be more prominent when the right hemisphere is in control (i.e., in left-eyed chicks) than when the left hemisphere is in control (i.e., in right-eyed chicks).

Chicks were trained binocularly as in Experiment 1 in a rectangular cage with panels at the corners. In monocular conditions, chicks were tested with a transformation in the arrangement of panels that alters the geometric relations between the target and the shape of the environment (the so-called affine transformation, see Figure 5). As a result of the affine transformation, the correct panel is moved in a novel, geometrically incorrect, location (Figure 5). Based on the results of the previous experiments, we expected that right-eyed chicks would be little affected by the affine transforma-
tion, whereas left-eyed chicks would be severely affected, showing systematic errors in correspondence to the previously learned geometrically correct locations.

Results
Chicks took on average 6.56 ($SE = 0.26$) sessions to learn the task. Results of test (Figure 5) revealed a striking asymmetry: Chicks using only their left eye made several errors on the two (previously) correct geometric locations A–C ($n_1 = 8$, $n_2 = 8$, $U = 12$, $p < .05$ two-tailed Mann–Whitney $U$ test). No differences were apparent between the two eye conditions with respect to errors in the geometrically incorrect D location.

Discussion
Results confirmed the evidence collected in the previous experiments. Both hemispheres are able to process landmark information well (as shown in Experiment 2), but in left-eyed chicks, the geometric and nongeometric information tend to interfere, resulting in a drop in performance, as measured by the correct location (panel) selection.

GENERAL DISCUSSION
The results of the experiments show that (1) when tested after removal of nongeometric information, left-eyed chicks, but not right-eyed chicks, reoriented using the residual information provided by the geometry of the environment; (2) when tested after removal of geometric information, both left- and right-eyed chicks reoriented correctly using the residual nongeometric information provided by panels; (3) when trained with only geometric information, left-eyed chicks reoriented slightly better than right-eyed chicks; (4) when geometric and nongeometric cues provided contradictory information, left-eyed chicks rely on geometric cues more than right-eyed chicks did. Overall, these results suggest that encoding of purely geometric information takes

**Figure 4.** Results of Experiment 3. Chicks were trained binocularly in a rectangular environment without any featural information and then tested in the same environment in monocular conditions. Mean percentages of choices for each corner are shown (with $SEM$ in brackets) for chicks tested with only their left (top) or only their right (bottom) eye in use.
place mainly in the right hemisphere. Such a segrega-
tion emerges more clearly when both types of informa-
tion are available during binocular training (e.g.,
compare Experiments 1 and 3), suggesting relative
rather than absolute hemispheric specialization to deal
with parallel and simultaneous encoding of multiple
sources of information. There is no clear evidence for
a similar segregation of function with respect to non-
geometric cues. Although when tested with contradic-
tory cues (Experiment 4), right-eyed chicks rely heavily
on nongeometric information, when tested after remov-
al of geometric information (i.e., in a square-shaped
cage), both right- and left-eyed chicks appeared to be
able to reorient using the residual nongeometric infor-
mation provided by the panels (Experiment 2).

These findings thus suggest that anatomically separ-
ated mechanisms for dealing with spatial reorientation
problems exist. It appears that the right hemisphere
takes charge of the large-scale geometry of the environ-
ment, whereas both hemispheres can take charge of
local, nongeometric cues when these cues are available
in isolation, but the left hemisphere tends to become
dominant when competing cues, some geometric and
some nongeometric, are available.

**Figure 5.** Results of Experiment 4. Chicks were
trained binocularly in a rectangular environment
with panels at the corners (leftmost figure) and then
tested monocularly after an affine transformation in the
spatial arrangements of panels (right), so as contradictory
geometric and nongeometric information were provided
(after the affine transformation the correct panel is located
in a geometrically incorrect corner). Mean percentages
of choices for each corner are shown (with SEM in
brackets) for chicks tested with only their left (top)
or only their right (bottom) eye in use.
Although these data certainly do not provide evidence for the “strong” version of modularity in spatial reorientation claimed for by Hermer and Spelke (1994) and Cheng (1986), because chicks can clearly conjoin geometric and nongeometric information to reorient themselves (see also Vallortigara & Sovrano, 2002, for a discussion of the evidence in other species), they do support the notion of a “weak” modularity in showing that separate neural mechanisms seem to be at work in dealing with the different aspects (geometric and nongeometric) of a spatial reorientation problem. There is recent evidence that the avian hippocampus exhibits functional lateralization in spatial cognition, with the right hippocampus mainly involved in the use of the geometric properties of the environment (Tommasi, Gagliardo, Andrew, & Vallortigara, 2003). However, these data have been obtained in place finding tasks, which are quite different from the reorientation tasks involving passive disorientation used here (for the latter any involvement of the hippocampus is, at least in humans, quite uncertain, see Nadel, 1995, and Introduction).

As to the extent these data obtained with the avian brain can be generalized to mammals, and to humans in particular, little evidence is currently available. Clearly, birds are special in having more complete decussation at the optic chiasma, lack of callosum, and (relatively) reduced interhemispheric communication (Vallortigara, in press). Nonetheless, hemispheric differences quite like those reported here for chicks have been observed in rats. La Mendola and Bever (1997) tested rats in an eight-arm radial maze, the same five arms of which were always baited. Fewer errors (scored as returns to a baited arm that had already been visited or entry of one of three arms that were never baited) were made when left whiskers were anesthetized (and so only right whiskers were in use) than when only left whiskers were in use. The dependence of this effect on a left hemisphere involvement in the analysis of right whisker input was confirmed by unilateral spreading depression of the left or right cortex, with left-hemisphere depression producing more errors in rats with both sets of whiskers in use. This left hemisphere dominance was likely due to the fact that local intramaze cues provided a unique and conspicuous label for each arm. When the maze was rotated, so that intramaze and extramaze cues were no longer in their usual relationship, a reversal in the relative performance of right- and left-whisker rats was observed; use of extramaze cues seems to favor dependence on a record based on the overall layout of the maze and thus dominance of the right hemisphere.

Some recent data may suggest dissociations along similar lines in humans. For instance, right hippocampal activation has been documented in taxi drivers asked to mentally navigate the streets of London (Maguire, Frackowiack, & Frith, 1997). Using the rectangular room task, Pizzamiglio, Guariglia, and Cosentino (1998) showed that patients with right brain damage with hemineglect are deficient in reorienting (although it proved difficult to establish a precise correlation between the site of the lesion and the deficit in the use of geometric and/or nongeometric information). More recently, however, Guariglia, Coriale, Cosentino, and Pizzamiglio (2000) found that in neglect patients transcutaneous electrical neural stimulation significantly improved the ability to code geometric information, but was ineffective with nongeometric information. All these suggest the existence of separate systems for processing geometric and nongeometric information similar to that reported here for the avian brain.

It could be, therefore, that we are dealing with a very general and possibly ancient functional organization of the vertebrate brain to deal with the treatment of spatial information or, alternatively, with the fact that similar selective pressures produced, independently, analogous neural architectures in the avian and mammalian classes.

METHODS

Experiment 1

Subjects

Subjects were 18 domestic chicks (Gallus gallus) of the Hybro strain (a local variety derived from White Leghorn), supplied from a commercial hatchery when they were only a few hours old. The animals were reared singly at a controlled temperature (30°C), with food and water at libitum. Rearing cages, 45 cm wide × 25 cm high × 35 cm deep, were illuminated by fluorescent lamps.

Apparatus

The experimental apparatus was a uniformly white-colored rectangular cage (70 × 35 × 35 cm). Four different cardboard panels (21 × 6.5 cm) were placed, one for each corner, in the test cage. Two panels were uniformly colored (blue and orange); the third panel was a series of black and white horizontal stripes (1.5 cm in size); the fourth panel was a red disk (5 cm in diameter) on a black ground. A different positive panel (i.e., the one that indicated the corner with the food) was used for different chicks (thus, for each panel there were three chicks trained with that panel as “reinforced” in each eye condition, see below). A transparent glass container (5 cm in diameter; 5 cm in height) was located in each corner (it was identical to the food container that was present in the chicks’ homecage). On the top of the container, a wire net prevented the chicks from scattering the food during pecking.
**Procedure**

Chicks were trained binocularly to search for the reinforced glass container associated with a particular panel and a fixed position in the test cage. All four containers were filled with food, but in three containers, a transparent sheet was glued on top, just behind the wire net, preventing the chicks to feed from them. The same transparent sheet was located also in the correct, reinforced container, but a small hole (2 cm in diameter) was cut onto it to allow chicks access the food while making the four containers to appear indistinguishable to each other. Training started on day 3 of life and consisted of two daily sessions of 10 trials (intertrial interval was 2 min), separated by a 2-h interval. In each trial, the chick was placed in the middle of the cage and allowed to approach one food container. When the food container in the correct position was chosen, the chick was allowed four to five pecks (reinforcement); after that, the chick was removed and placed in a small closed cardboard box (20\times20\times30 cm) outside the test cage. During the intertrial interval, the small box containing the chick was rotated slowly on a rotating chair to eliminate compass or inertial information (disorientation procedure, see also Vallortigara et al., 1990). When the food container in the incorrect positions was chosen, the chick was immediately removed from the test cage and, after the disorientation procedure, given another trial. Learning criterion was 90% correct in a single session of 10 trials.

Ninety minutes after chicks had reached learning criterion, the four panels were removed. During this test phase, the chicks were given 10 test trials in the absence of food reinforcement (i.e., in which access to food was prevented by transparent sheets in all four containers). Choices for the four corners were recorded. A choice was considered valid when the chick approached a container entering with its head in an arc of circle area of 12 cm in diameter centered on each corner, irrespective of emission of pecking responses. Soon after an approach response, the chick was removed from the test cage and, after the disorientation procedure, given another trial. Thus, only first choices were considered. An extinction procedure with recording of only the first responses is usually preferred in these tasks to avoid both learning effects associated with repeated unsuccessful trials and decrease of motivation (see e.g., Gouteux et al., 2001; Kelly et al., 1998).

**Experiment 2**

**Subjects**

Fifteen chicks were used. Strain and rearing conditions were the same as in Experiment 1.

**Apparatus and Procedure**

The apparatus and procedure used during training were identical to those of Experiment 1. At test, however, chicks were located in a square-shaped cage (50 cm in size; the height was the same as in Experiment 1) with the same panels used during training located at the corners. Thus, apart from the shape of the cage test, all other conditions were the same as in Experiment 1. Seven animals were tested with only their right eye in use and 8 animals with only their left eye in use. Eye-patching procedures were the same as in the previous experiment.

**EXPERIMENT 3**

**Subjects**

Eighteen chicks were used. Strain and rearing conditions were the same as in Experiment 1.

**Apparatus and Procedure**

The apparatus and procedure used during training were identical to those of Experiment 1, except that no panels or other nongeometric cues were available for spatial reorientation. After training, chicks were tested in the same apparatus in monocular conditions. Eight animals were tested with only their right eye in use and 10 animals with only their left eye in use. Eye-patching procedures were the same as in the previous experiments.

**EXPERIMENT 4**

**Subjects**

Sixteen naive chicks were used. Strain and rearing conditions were the same as in Experiment 1.

**Apparatus and Procedure**

The apparatus and procedure used during training were identical to those of Experiment 1. At test, chicks were presented with a different arrangement of panels, corresponding to an affine transformation (Figure 5). Eight animals were tested with only their right eye in use and 8 animals with only their left eye in use. Eye-patching and all other procedures were the same as in the previous experiments.

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