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Giorgio VALLORTIGARA

Dept. of Psychology and B.R.A.I.N. Centre for Neuroscience, Univ. of Trieste, Italy

Comparative Neuropsychology of the Dual Brain: A Stroll through Animals' Left and Right Perceptual Worlds

Giorgio Vallortigara

Department of Psychology, Laboratory of Animal Cognition and Comparative Neuroscience, and B.R.A.I.N. Center for Neuroscience, University of Trieste, Trieste, Italy

Perceptual asymmetries in humans typically manifest themselves under quite unnatural settings (e.g., tachistoscopic viewing and dichotic listening) and this has put into question their real biological significance. In animals with laterally placed eyes, however, perceptual asymmetries are ubiquitous in the normal, everyday behavior, as revealed by the differential use of the lateral visual field of the left and right eye in a variety of tasks. Data are presented showing how preferential use of the left and right eyes influences visual discrimination learning and detour behavior in chicks; similarities with detour tests performed in fish and evidence for asymmetries in eye use in animals with larger binocular overlap (e.g., anuran amphibians) are discussed. Implications of these perceptual asymmetries on the formation and fate of memory traces are put forward, with examples from unihemispheric sleep and lateralization of spatial memory in chicks. Finally, speculations about the evolutionary origins and possible adaptive advantages of perceptual asymmetries in vertebrates are presented. © 2000 Academic Press

INTRODUCTION

For more than a century, the study of the specialization of the left and right sides of the brain was confined to the human species. Now we know that cerebral lateralization is widespread among warm-blooded vertebrates, i.e., birds and mammals (see Bradshaw & Rogers, 1993). Oddly enough, however, evidence for lateralization in nonhuman species first appeared in the so-called "lower" vertebrates (fish, amphibians, and reptiles), concerning anatomical asymmetries in the diencephalic regions (review in Harris et al., 1996). These early data had been, however, largely neglected (see Bisazza, Rogers, & Vallortigara, 1998 for a review), partly because lower vertebrates are not usually regarded as interesting preparations by neuropsychologists. As a result, until very recently, we failed to notice that functional

Address correspondence and reprint requests to Giorgio Vallortigara, Department of Psychology, University of Trieste, Via S. Anastasio, 12, 34123 Trieste, Italy. Fax: +39 040 4528022. E-mail: vallorti@univ.trieste.it.

lateralization is in fact widespread among a variety of vertebrate species and can reveal itself in a striking and very straightforward way: namely through asymmetries in the use of the eyes.

In animals with laterally placed eyes, as in most species of fishes, reptiles, and birds, primary visual projections ascend mainly to the contralateral side of the brain. Direct inferences between left/right eye and right/left side of the brain should be taken with some caution, however, particularly for birds. Animals like fish or reptiles usually combine the fact that their eyes are placed on the sides of the head (and thus each of them has limited access to hemifields of space accessible to the contralateral eye) together with very reduced ipsilateral projections. They have no structure homologous to the corpus callosum, instead possessing only a small anterior commissure and a small interhemispheric hippocampal commissure that interconnects regions of the dorsal part of the telencephalon. Neuroanatomically, they can be considered quite close to "split brain" preparations (see Deckel, 1995, 1997). In birds, however, things are more complicated. When laterality is revealed by monocular testing only, one can never be sure that it is exclusively the contralateral hemisphere that is involved. This is because ipsilateral and contralateral projections are both present in the thalamofugal as well as in the tectofugal pathways (Deng & Rogers, 1997, 1998a, 1998b). Nonetheless, whatever the relative contribution of the left and right parts of the two visual pathways—which are differently associated with lateral (monocular) and frontal (binocular) vision—asymmetries in modes of analysis of perceptual information entering the left and the right eyes are clear from birds' behavior.

The first evidence of visual lateralization in the intact animal was obtained in the domestic chick (*Gallus gallus*) by temporary occlusion of either the left or right eye (Rogers & Anson, 1979; Andrew, 1983). This procedure revealed that the right eye is better at discriminating visual stimuli, such as grains from pebbles, and that the left is more reactive to emotionally charged stimuli (Rogers & Anson, 1979; Andrew, Mench, & Rainey, 1982; Gaston, 1983; Andrew, 1988). These results met with initial incredulity; a comment by an eminent animal lateralization researcher, involved in studies of split-brain monkeys, clearly expressed this concern: *"These results lead to the plausible but revolutionary inference that a bird more effectively searches for food with its right eye while it watches for danger with its left!"* (Hamilton, 1988). However, what at first seemed unbelievable turned out to be absolutely correct and was confirmed in a variety of other species of birds (pigeons: Güntürkün & Kesh, 1987; von Fersen & Güntürkün, 1990; Güntürkün, 1997; parids: Clayton & Krebs, 1993; corvids: Clayton & Krebs, 1994; zebra finches: Alonso, 1998). What is more interesting, it soon became clear that asymmetries in eye use in birds are apparent even in the more "ecological" condition of normal, unobstructed two-eyed vision.

FUNCTIONAL SPECIALIZATIONS OF THE LEFT AND RIGHT SIDES OF ANIMALS' PERCEPTUAL WORLDS

Chicks

Dharmaretnam and Andrew (1994) first devised a method to study the lateral viewing of stimuli by placing chicks at a distance from objects and allowing them to sit with their heads through a hole in a wall and then using videtaped recording to assess fixation with the right or left eye (see also Wokman & Andrew, 1986; Andrew & Dharmaretnam, 1993). They found that different stimuli evoked different patterns of eye use: a hen tended to be viewed with the right eye, whereas a novel stimulus (a small light) was viewed with the left. More recent work has confirmed that preferential eye use also occurs in adult hens (McKenzie et al., 1998).

These phenomena were revealed under conditions in which the animals were relatively restrained in order to precisely measure angular head positions as referred to the stimuli placed in front of the chicks. However, it seems very likely that preferential eye use normally occurs in the everyday behavior of these animals. It has been found, for example, that hens responding to a playback of an aerial predator alarm call (when turning their heads to one side to look up) are more likely to use their left rather than their right eye (Evans et al., 1993; see also Rogers, 2000).

We wondered whether such a preferential use of one eye may affect motor responses of chicks when negotiating obstacles (Vallortigara, Regolin, & Pagni, 1999). We devised a simple detour test (see Regolin, Vallortigara, & Zanforlin, 1994a, 1994b) which enabled us to study asymmetries of response. Chicks were faced with a vertical-bar barrier behind which an imprinting object (a red ball chicks had been reared with since soon after hatching) was located (Fig. 1). Chicks exhibited a stereotyped behavioral strategy in this apparatus. They kept very close to the barrier with their heads turned left or right so that the goal was under lateral fixation by one eye and then moved along the barrier (i.e., according to their head orientation) until they circled around the obstacle while maintaining visual contact with the goal. As a result of this behavior, the left or right direction of turning around the barrier largely reflected preferential fixation by the contralateral eye (i.e., detour to the left, preferential right-eye use; detour to the right, preferential left-eye use).

Figures 2 and 3 show the results of a study in which independent groups of 2-, 3-, and 4-day-old chicks were tested in the apparatus using a familiar imprinted ball as a goal. There were separate groups tested in binocular condition or with the left or the right eye temporarily covered by an eye patch. Times needed to detour the barrier (Fig. 2) and directions of detour (Fig. 3) were recorded.

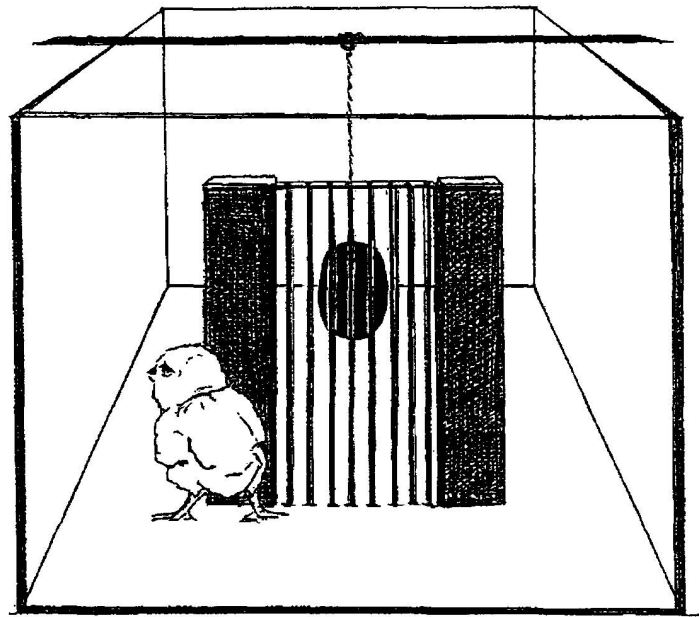Chicks using their right eye took less time to detour the barrier than chicks

FIG. 1. Schematic representation of the test apparatus used to investigate asymmetries of detour responses in chicks. In order to rejoin the imprinted ball, chicks performed a detour around the barrier either on the left or on the right side. (Modified from Vallortigara, Regolin, & Pagni, 1999.)

using their left eye (the effect was small but consistent at all ages studied and in both sexes). As can be seen from Fig. 3, monocular chicks were constrained in their choice of the direction of detour by the eye in use: those using the left eye made the detour on the right, those using the right eye made the detour on the left. Responses of binocular chicks were, however, not random, but more similar to monocular chicks with the right eye in use. Binocular chicks thus showed a bias to detour the barrier on the left side (which is consistent with preferential right-eye use).

It seems very unlikely that these asymmetries were due to a motor bias because the chicks' direction of turn could be reversed by simply changing the visual characteristics of the imprinting ball. Figure 4 shows biases in direction of detour responses in 2-day-old chicks tested with a visual transformation of the imprinted ball (i.e., a yellow, a blue, and a half yellow–half red ball). As can be seen, there was a shift to left-eye use with some of these novel stimuli. The shift in eye use seemed to depend on an estimation of the degree of novelty of the unfamiliar ball and, interestingly, the judgement seemed to differ between males and females (see also Vallortigara & Andrew, 1994a, 1994b). Assuming that there is an increase in the degree of novelty ranking from the red/yellow ball (slight novelty) to the yellow ball (novelty) to the blue ball (strong novelty), then results for females suggested a corresponding shift from right- to left-eye use with increasing degree of novelty. Results for males were more puzzling in that they indeed shifted to left-eye use when faced with moderate novelty (red/yellow and yellow balls) but then switched back to right-eye use when faced with strong novelty (blue ball). An entirely speculative but interesting hypothesis (see Vallorti-
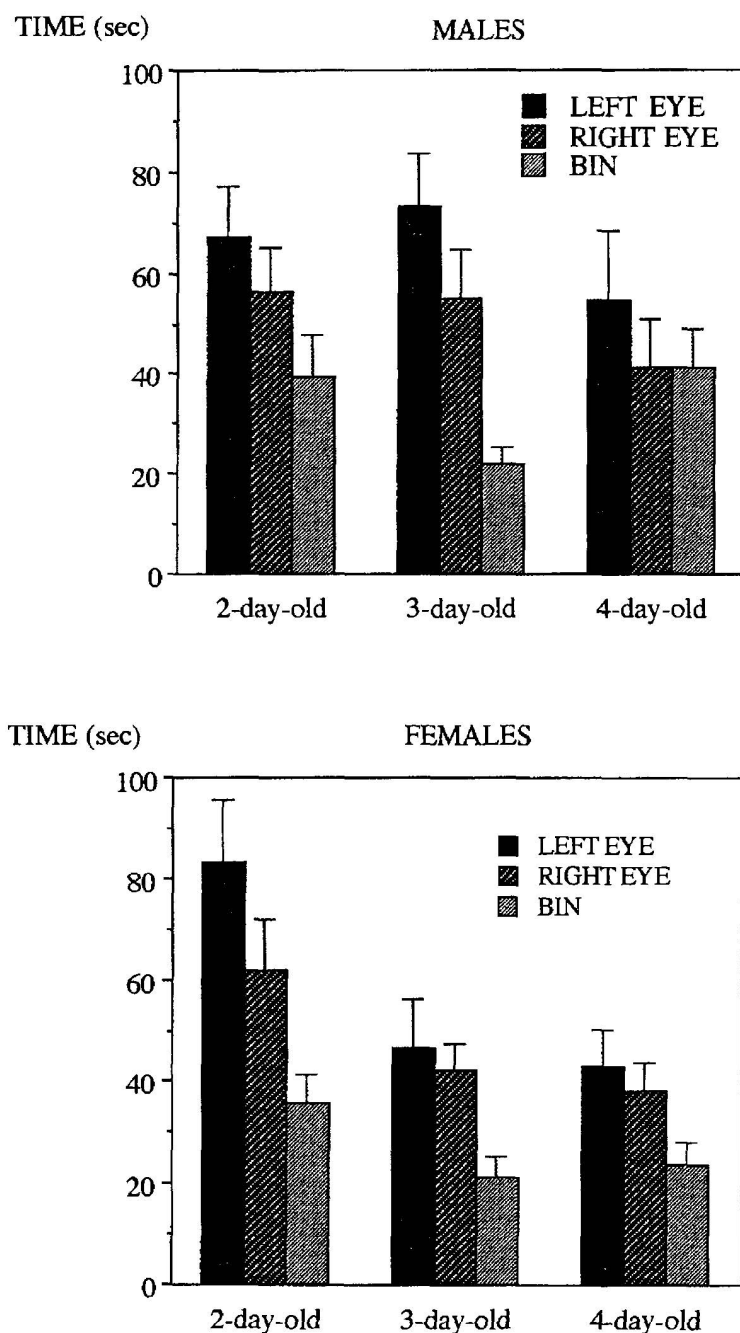
FIG. 2. Mean times (with SEM) needed to detour the barrier in binocular (BIN) chicks and in right-eyed (RE) and left-eyed (LE) chicks using a familiar imprinted ball as a goal (top: males; bottom: females). The analysis of variance revealed significant effects of age [$F(2, 153) = 8.210, p < .001$] and eye in use [$F(2, 153) = 22.989, p < .001$]; there were no other statistically significant effects. Right-eyed chicks showed lower times to detour the barrier than left-eyed chicks [$F(1, 103) = 4.741, p = .029$]. (Modified from Vallortigara, Regolin, & Pagni, 1999.)

gara et al., 1999 for details) would be that male chicks faced with the blue ball were using the right eye in order "to ignore" the broad change involved with the use of such a stimulus, which is well known to be very fearful to young chicks (see Andrew & Brennan, 1983; Clifton & Andrew, 1983).

These results would suggest that the hemisphere not directly stimulated can nonetheless access experiences and memory traces in the other hemi-
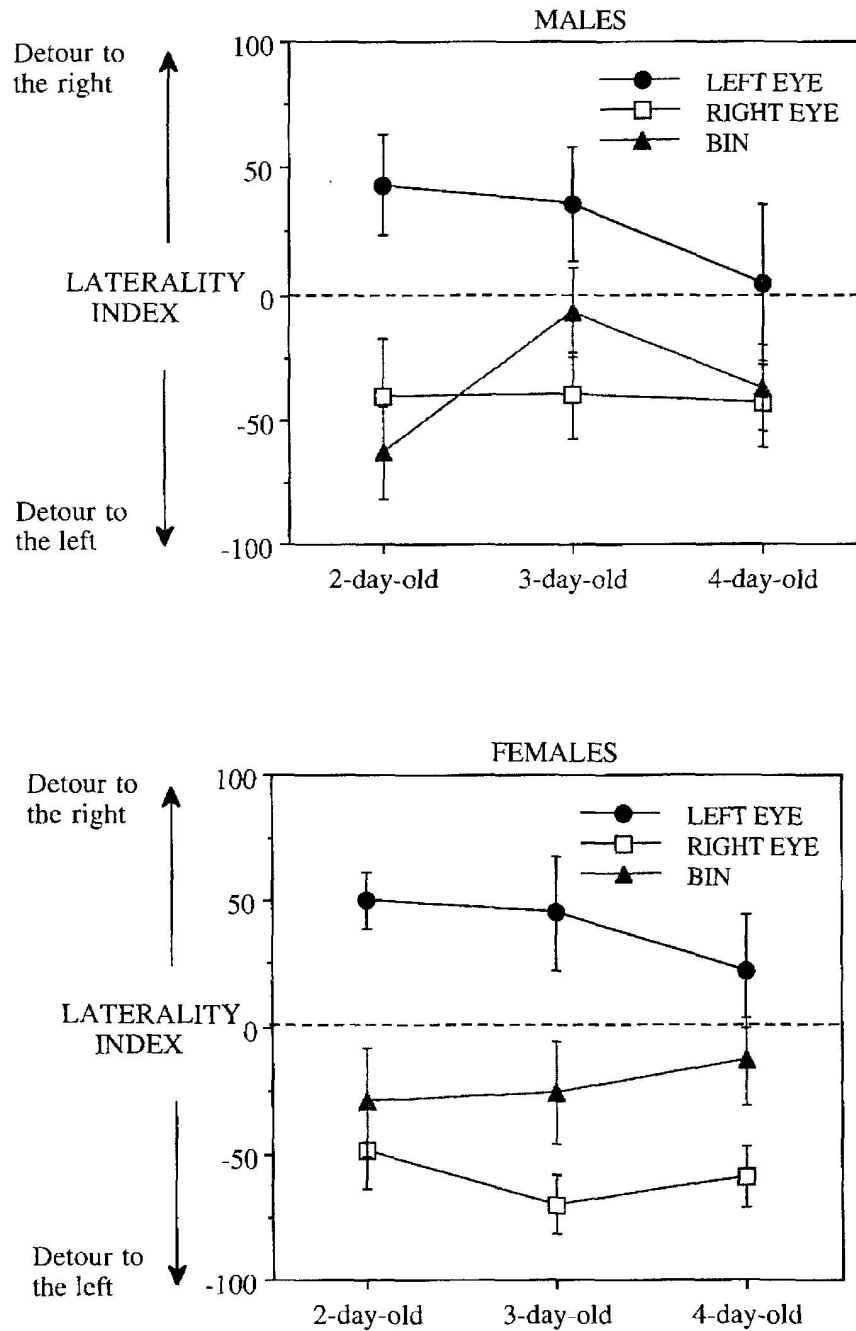
FIG. 3. Direction of detour responses [(detour on the right − detour on the left/(detour on the right + detour on the left) × 100; group means with SEM are shown] in binocular (BIN) chicks and in right-eyed (RE) and left-eyed (LE) chicks using a familiar imprinted ball as a goal (top: males; bottom: females). The analysis of variance revealed only a statistically significant effect of the eye in use [$F(2, 154) = 30.912, p < .001$]. Left-eyed chicks showed a preference to detour to the right [$t(56) = 3.953, p < .001$]; binocular chicks showed a preference to detour to the left [$t(55) = -3.745, p < .001$] as did right-eyed chicks [$t(57) = -7.599, p < .001$]. (Modified from Vallortigara, Regolin, & Pagni, 1999.)

sphere, sometimes even taking control of overt behavior. More generally, what is interesting in these findings is that cerebral lateralization in birds can directly affect visually guided motor responses through selective use of the lateral field of vision of the eye contralateral to the hemisphere which has to be put in charge of control of behavior (see also Vallortigara et al.,
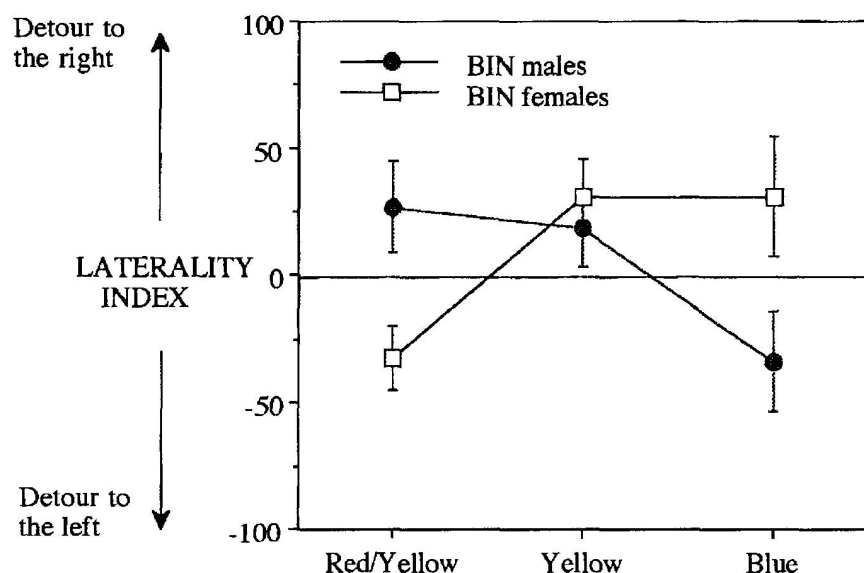
FIG. 4. Direction of detour responses [(detour on the right − detour on the left/(detour on the right + detour on the left) × 100]; group means with SEM are shown] in binocular male and female chicks reared with a red ball and tested with a novel ball as a goal. The ANOVA revealed a significant sex × stimulus interaction [$F(2, 49) = 6.73, p < .002$]. There were no other statistically significant effects. Females tended to turn on the right side (left-eye use) when using the yellow and the blue balls [$t(17) = 2.533, p = .0211$], whereas males did the same when using the red/yellow and the yellow balls [$t(17) = 2.182, p = .0403$]. Detour on the left side (right-eye use) was, in contrast, predominant in males tested with the blue ball and females tested with the red/yellow ball [$t(19) = −3.104, p = .005$]. (Modified from Vallortigara, Regolin, & Pagni, 1999.)

1996). It is not simply that the two hemispheres show different specializations, the animal can actively put incoming sensory stimulation in control of the more "appropriate" hemisphere by locating it into its left or right lateral field of vision.

Fish, Toads, and (Possibly) Humans

The work I have carried out in recent years with my colleague Angelo Bisazza, a behavioral ecologist, has shown that several species of fish show lateral asymmetries in detour behavior very similar to those described here for the chick (Bisazza, Pignatti, & Vallortigara, 1997a, 1997b). Male mosquitofish (*Gambusia holbrooki*), faced with an obstacle (a vertical-bar barrier) behind which a group of females was visible, preferentially circled around the obstacle leftward (thus maintaining fixation on the target with their right eye). The same bias was observed using a dummy predator as a target (that, in this species, can induce detouring of the barrier to perform predator-inspection responses). The lateral asymmetry was task- and stimulus-dependent. It disappeared when the task was made difficult by forcing the fish to lose visual contact with the goal (i.e., employing a U-shaped barrier) or by using less attractive targets (i.e., a group of males or an empty environment).

More recently, we studied detour responses of two species of poeciliid fish (*G. hoolbroki* and *Girardinus falcatus*) faced with a vertical-bar barrier through which conspecifics of different sex or a dummy predator were visible (Bisazza, Facchin, Pignatti, & Vallortigara, 1998). Both species showed a consistent bias to turn leftward when faced with the predator. Sexual stimuli elicited a leftward bias only in females that had been deprived of the presence of males for 2 months, while no bias was apparent in nondeprived females.

We have been able to show that lateral asymmetries in detour behavior are due to preferences in eye use (Facchin, Bisazza, & Vallortigara, 1999). Viewing tests revealed in fact that fish (*G. falcatus*) that tended to detour the barrier on the left side used the right eye to scrutinize a dummy predator and the left eye to scrutinize a neutral stimulus, whereas fish that tended to detour the barrier on the right side showed the reverse pattern of eye use; fish that did not show any consistent bias in the detour test did not reveal any significant preference in the viewing test.

It may appear somewhat counterintuitive that cerebral lateralization can impose a differential use of the two eyes. Biologically relevant stimuli could appear equally often on either side, and therefore there should be selective pressures maintaining the right and left eye equally capable of performing visual-processing tasks. However, it should be noted that sustained viewing in birds and in fish is commonly monocular; therefore, after initial detection and recognition has been performed, a choice of the right or left eye for viewing might well be affected by lateralization of function. Even more, the choice for left- or right-eye viewing might determine the sort of visual analysis that should be carried out. Apparently, in fact, birds and fish are able to bring into action the hemisphere most appropriate to particular conditions and to particular stimuli by using lateral fixation with the contralateral eye.

It cannot be excluded that perceptual asymmetries during sustained fixation arise (or are somewhat facilitated) from motor asymmetries associated with escape behavior. When confronted with an approaching predator, fish react with a ''C-bend'' of the trunk in the horizontal plane, either to the left or to the right, followed by a ''tail flip'' during which the fish gains considerable acceleration (Eaton, Bombardieri, & Meyer, 1977). There is evidence for behavioral (Cantalupo, Bisazza, & Vallortigara, 1995), muscular (Heuts, 1999), and neuroanatomical (Moulton & Barron, 1967) asymmetries associated with the C-start reaction in fish. The reaction is controlled by a pair of giant reticulospinal neurons, the Mauthner cells, each decussating and innervating contralateral muscles (Eaton et al., 1977). In the goldfish, the Mauthner cell on the left brain stem is larger than on the right (Moulton & Barron, 1967). It may be considered nonsense having a left–right asymmetry in a predator-escape response: predators may appear on the right or on the left side with the same probability. The reason for such an asymmetry could be that left/right-specialized individuals can develop higher speeds and accelerations than ''ambidextrous'' individuals and can therefore escape better

from a predator (see Heuts, 1999). It could be that these motor asymmetries form the basis for subsequent specializations in eye use. After an initial C-start reaction to the sight of a noxious stimulus has occurred, sustained monitoring of the stimulus with the lateral field of the left or the right eye could in fact arise as a result of the fish's lateral body posture, thus promoting specializations of the left and right monocular visual fields.

Mammals like human beings, accustomed to use obligate conjugate eye movements to binocularly fixate stimuli of interest, do not obviously show any directly comparable phenomena. However, it has been suggested that a mechanism somewhat similar to that observed in birds could be available to humans as well (see Dharmaretnam & Andrew, 1994). The engagement of one or the other hemisphere in verbal or spatial tasks is revealed by eye movements to the right or the left, respectively, provided that there are no external factors affecting gaze (Gur & Gur, 1977). Also, direction of gaze to the left tends to promote analysis by right-hemisphere strategies, whereas gaze to the right brings in left-hemisphere strategies (Gross, Franco, & Lewin, 1978). Adjustment of head position and eye movements may thus play a similar role in mammals with frontal vision, as the choice for right or left lateral visual fields does in birds.

Obviously, because of complete decussation at the optic chiasma, in fish and in birds primary visual projections ascend mainly to neural structures on the contralateral side of the brain. But it should be noted that even in mammals with frontally placed eyes there are differences in the inputs from one eye to each of the two hemispheres. In fact, although each eye relays inputs to both the right and left hemispheres, the fibers from the medial half of the retina that cross to the contralateral hemisphere are larger than those that arise from the lateral half of the retina and go to the ipsilateral hemisphere (Bishop, Jeremy, & Lance, 1953). Fibers which cross and go to the contralateral hemisphere, therefore, conduct neural signals faster and they may dominate the uncrossed fibers during binocular stimulation (Proudfoot, 1953; Walls, 1953). Consistent with this, eye preferences for viewing in both human (Adam, Szilagyi, & Lang, 1992) and nonhuman primates (Rogers, Ward, & Stafford, 1994; Hook-Costigan & Rogers, 1995) have been observed.

We recently obtained a striking demonstration of complementary eye use in a species with large binocular overlap (Vallortigara et al., 1998). Prey-catching behavior was studied in three species of toads (the European green toad *Bufo viridis,* the European common toad *Bufo bufo,* and the South American cane toad, *Bufo marinus,* introduced to Australia) using a modification of the classic procedure known as the "worm-test" (Ewert, 1980). A preferred prey was attached to a thread and suspended from a wire support that moved it mechanically in a horizontal plane around the toad, entering first either its right or its left monocular visual field depending on the direction of rotation. When the prey moved clockwise, and thus entered first the
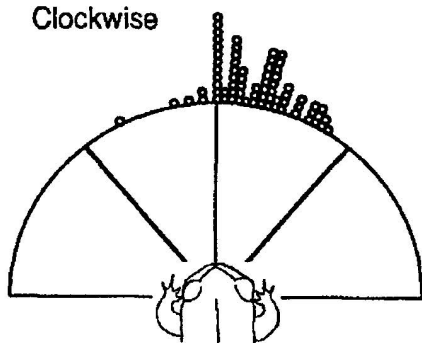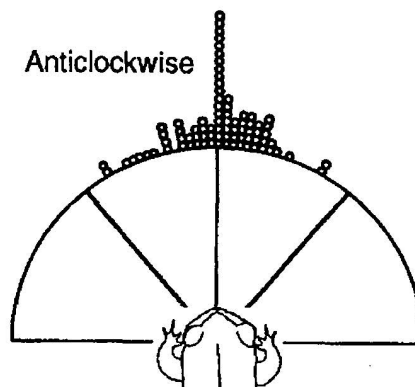
A. *Bufo bufo*
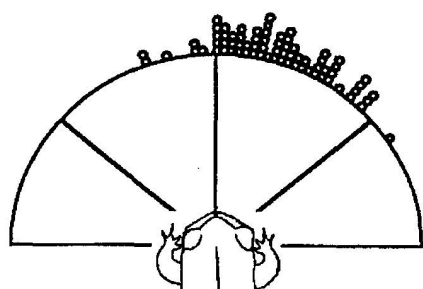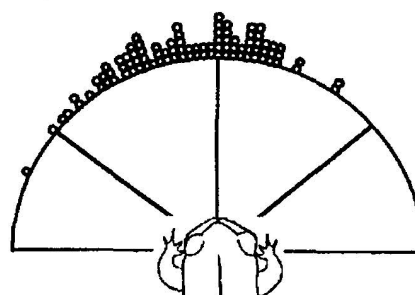
B. *Bufo viridis*

FIG. 5. Positions of tongue-striking responses to a moving prey in two species of toads as a function of the direction of rotation (modified from Vallortigara et al., 1998).

left and then the binocular field of vision, almost all of the tongue-strikes occurred in the right half of the binocular field (Fig. 5). When the prey moved counterclockwise, and thus entered first the right and then the binocular field of vision, a more symmetrical distribution of strikes in the left and right halves of the binocular fields occurred (Fig. 5). Thus, it seems necessary that prey enter the right half of the binocular visual field in order to evoke predatory behavior. Initial detection in the left visual field does not allow the toad to show prey catching until prey have moved into the right half of the binocular visual field. In contrast, initial detection of prey in the right visual field allows the toad to orient toward and follow prey and strike at it anywhere in the binocular field. Functionally, it is as if the toads' left hemifield shows a form of stimulus-specific visual "hemineglect."

The same toads were also tested for agonistic behaviors in the form of tongue-strikes at competitors during feeding. Toads showed a population bias to strike with the tongue at conspecifics when these were occupying their left visual field (Fig. 6; see also Robins et al., 1998). Thus toads are
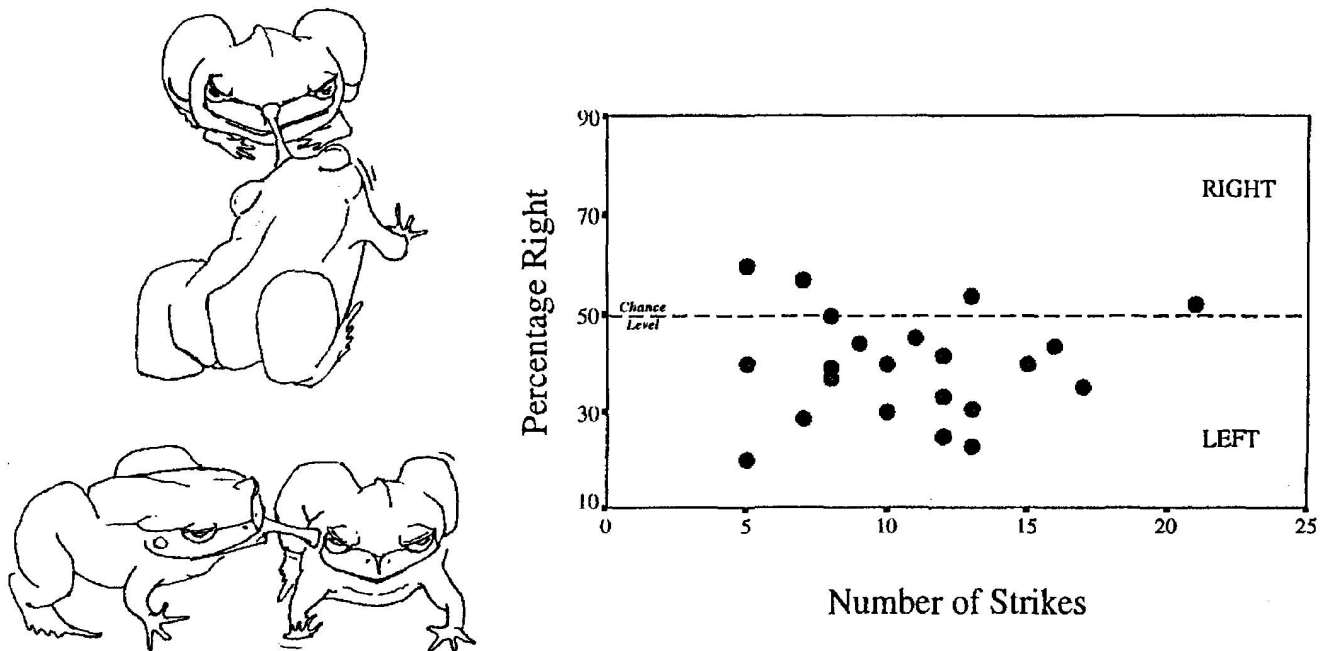
FIG. 6. Proportion of strikes directed at targets in the right hemifield in each individual in *B. marinus* toads. Significantly higher proportions of strikes were directed more toward the left than the right [$G(21)$ = 57.7, p < .001]. (Modified from Vallortigara et al., 1998.)

more likely to attack prey to their right side (and ignore them to their left side) and to attack a conspecific to their left side (and ignore them to their right side). There is a striking similarity between the complementary behavioral lateralizations of toads described here and those found in "higher" vertebrates. Use of the right eye in categorizing food and nonfood is well demonstrated for chicks (Mench & Andrew, 1986) and pigeons (Güntürkün & Kesh, 1987). Domestic fowls (Rogers et al., 1985, Bullock & Rogers, 1986), baboons (Casperd & Dunbar, 1996), and lizards (Deckel, 1995) are all more likely to attack conspecifics to their left side. Therefore, despite substantial differences between species in the general structures of the brain and visual pathways, these particular functional specializations appear to be conserved throughout a wide evolutionary spectrum.

AN EYE FOR A CHANGE? MONOCULAR SLEEPING IN CHICKS

A very surprising manifestation of preferential eye use in the chick is associated with sleep. Rogers and Chaffey (1994) first reported behavioral evidence for lateralization of eye closure during sleep in the chick (see Ball et al., 1988 for a review of unihemispheric sleep in other bird species). In the 2nd week posthatch, monocular sleep with left-eye closure occurs more frequently than that with right-eye closure. Ball et al. (1988) have shown that closure of one eye is associated with sleep EEG patterns in the contralateral hemisphere only. Therefore, there is strong evidence to argue for contralateral hemispheric sleep on the basis of the pattern of eye closure. We have

recently confirmed and extended Rogers and Chaffey's results (see Mascetti, Rugger, & Vallortigara, 1999). Behavioral sleep during the first 2 weeks of life was investigated in female chicks reared with an imprinting object or in social (visual) isolation. Binocular sleep tended to decrease and monocular sleep to increase with age in both rearing conditions. In chicks reared with an imprinted object, during the 1st week monocular sleep with either right- or left-eye closure occurred with approximately the same frequency, except that on day 5 right-eye closure dominated. During the 2nd week, however, there was a clear bias toward more monocular sleep with left-eye closure. During the 2nd week the pattern of monocular sleep was similar in both rearing conditions, but during the 1st week chicks reared with the imprinting object showed relatively more right-eye closure compared to chicks reared without the imprinting object, an effect that might tentatively be associated with consolidation of imprinting memories in the left hemisphere (see Horn, 1990; McCabe, 1991; Rogers, 1993; Andrew, 1997). Binocular sleep occurred in all four body postures mainly adopted by chicks during sleep: standing sleep, sleep with bill forward, sleep with bill on the ground, and sleep with head on the ground. Monocular sleep, in contrast, only occurred when chicks adopted the bill-forward posture, in which there is high neck tonus—an association that would fit with a vigilance function for monocular sleep. When the color of the imprinting object was suddenly changed, on day 8, a striking shift toward predominant right-eye closure during monocular sleep was observed (Fig. 7). The same effect occurred when the imprinting object was suddenly removed from the home cage on day 8, but not with other types of changes (i.e., when a novel object was introduced into the home cage or when a novel-colored imprinting object was inserted into the home cage together with the original one). It is tempting to suggest that this phenomenon could be associated with right-hemisphere involvement in response to novelty. There is striking evidence for a selective use of the left eye in response to novelty in the chick in a variety of behavioral tasks, including changes in spatial position of food objects (Andrew, 1991) and changes in position and other visual characteristics of social (imprinted) objects (Vallortigara, 1992; Vallortigara & Andrew, 1991, 1994). It is possible, therefore, that monocular sleep in chicks (and no doubt also in other species of birds) is not simply an epiphenomenon related to lateralization of memory processing; rather, it could be adaptive for the animal to have one eye (and one half of the brain) devoted to the periodical monitoring of the environment to check for potentially important events (see also Rattenborg, Lima, & Amlaner, 1999). Given that the right hemisphere is normally dedicated to this task in the waking state (Vallortigara & Andrew, 1991; Regolin & Vallortigara, 1996), it should be the left eye that is open during unihemispheric sleep, particularly after the occurrence of very stressful events such as any change regarding the chicks' mother.
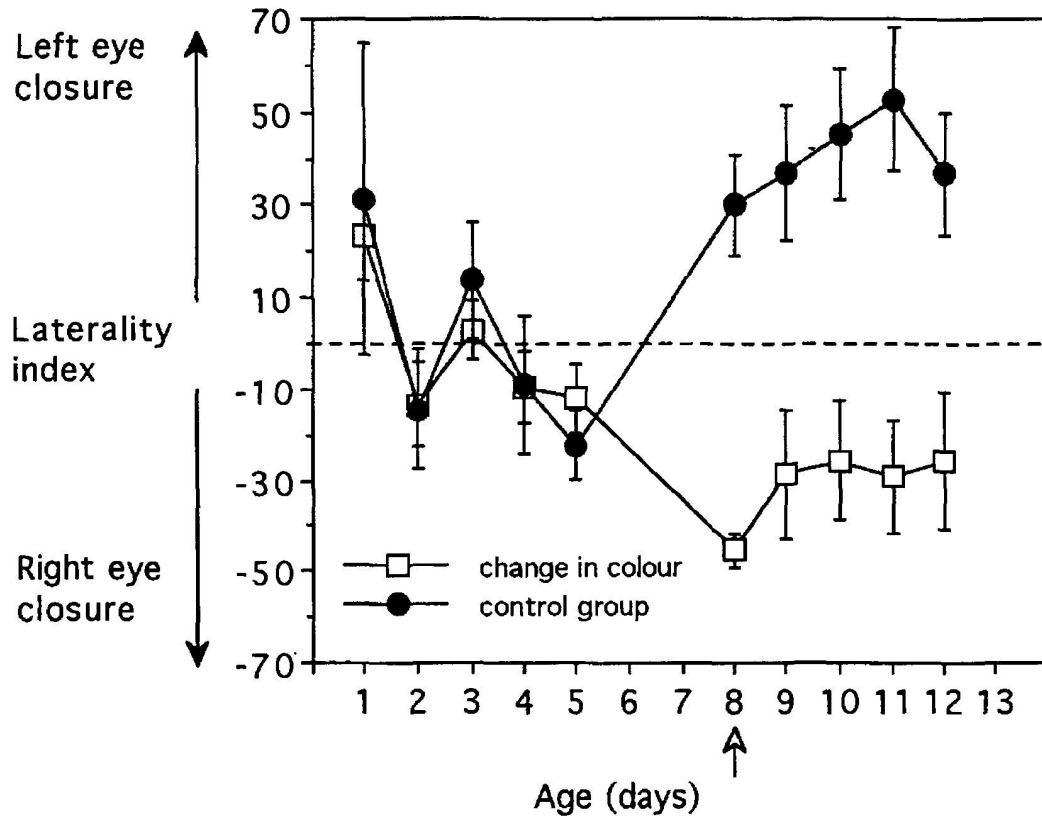
FIG. 7. Percentage of time (with SEM) spent with the left or the right eye closed during sleep in female chicks reared with an artificial imprinting object (a red ball) during the first 2 weeks of life who underwent an abrupt change in the color of the imprinting object (from red to yellow) on day 8. The arrow indicates the day in which the change in color was introduced; in the control group no changes occurred in the imprinted object throughout the entire period of observation. There was a highly significant difference between the control group and the group for which the imprinted object was modified from day 8 onward [$F(1, 10)$ = 30.525, p = .0003]. (Modified from Mascetti et al., 1999.)

FUNCTIONAL SPECIALIZATIONS OF LEFT AND RIGHT MEMORY TRACES OF RIGHT AND LEFT ANIMALS' PERCEPTUAL WORLDS

Complementary use of the left and right lateral visual fields seems to be associated with differential modes of analyses of perceptual information in the avian brain. As a consequence, both encoding and subsequent retrieval of memories are likely to be affected by such a differential use of the two eyes during acquisition of incoming sensory information. Let us consider some evidence of this.

We trained chicks to discriminate between two boxes of the same color (white) on the basis of their left–right positions using the pecking response (Vallortigara et al., 1996; see also Vallortigara, 1989). Chicks were then retrained with two boxes of different colors (one red, the other green): in one group of chicks the position of the two boxes was randomly alternated in the various trials, in the other group the position was maintained as fixed. A control group was retrained with two white boxes identical to those used

during training. In all three groups chicks had to discriminate between the two boxes (for food reinforcement) on the basis of their positions. We found that during training chicks took fewer trials and made fewer errors to learn when the positive box was placed on their right side, and the same occurred during retraining with boxes that maintained a fixed position and during retraining in the control condition. During retraining with position alternation, on the contrary, chicks took fewer trials and errors to learn when the positive box was placed on their left side.

A simple explanation of this phenomenon could arise from the observation of chicks' behavior while approaching the boxes (see Fig. 8, bottom). The animals moved along the runway with their bodies and heads turned to one
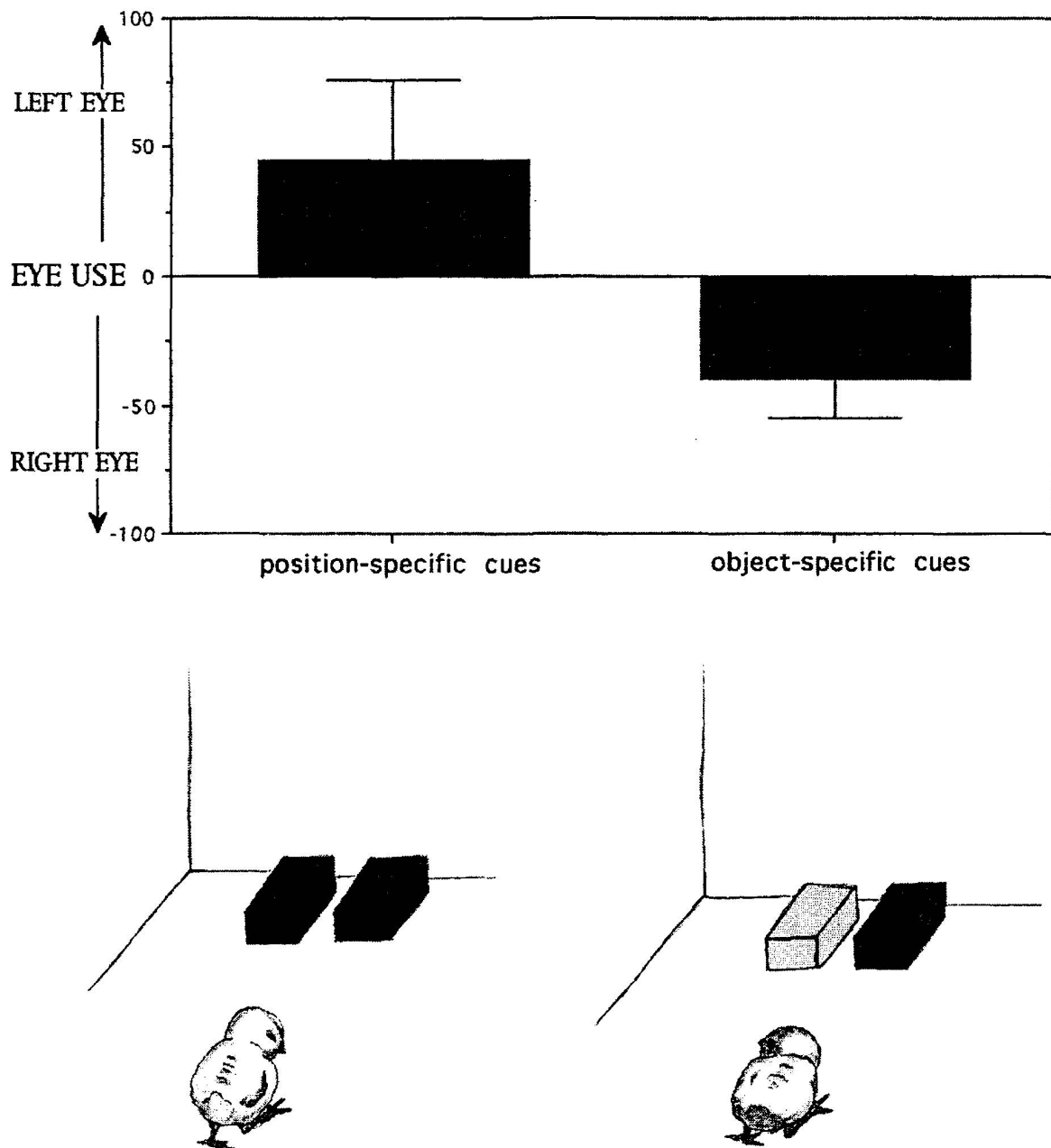

FIG. 8. Preferential left- or right-eye use of chicks in viewing the box to be pecked when using only position-specific cues (identical boxes) or in the presence of object-specific cues (boxes of two different colors). (Modified from Vallortigara et al., 1996.)

side to allow lateral viewing of the boxes. Birds usually employed their lateral, monocular, fields of vision to look at distant objects, whereas binocular vision is typically used during fixation of close, small peckable objects. As a result, head turning to the right (or to the left) to allow lateral viewing with the left (or right) eye might produce a bias to peck the box on the right (or left) side. Videorecording of the chicks' behavior while approaching the boxes confirmed that these lateral asymmetries reflect head and body turning associated with preferences in eye use, likely due to the different specializations of contralateral brain structures (see Fig. 8). It seems that positional cues engage the right hemisphere, with consequent head turning to the right to allow lateral viewing by the left eye, whereas object-specific cues (like color) engage the left hemisphere, with consequent head turning to the left to allow lateral viewing by the right eye.

In the experiments described below, we tried a sort of inverse procedure, looking for a demonstration of the fact that, following binocular learning in a task in which object- and position-specific cues were simultaneously available, chicks show differential use of either cue, depending on whether the right or the left eye is in use at retrieval. Two experiments are presented, one involving reference memory, the other involving working memory.

EXPERIMENT 1: LEFT AND RIGHT HEMISPHERE ENCODING OF OBJECT- AND POSITION-SPECIFIC CUES IN A REFERENCE MEMORY TASK

In this experiment we used a procedure developed in my laboratory to study spatial cognition in chicks (see Tommasi et al., 1997). Young chickens are trained to find food by ground-scratching in the center of an arena. The position of the food is indicated by a conspicuous landmark. After learning attainment, the landmark could be displaced to a novel position in such a way as to generate conflicting local (the landmark as such) and global (the spatial location within the arena) information as regard to food location (see Tommasi & Vallortigara, in preparation).

Methods

The subjects were 15 male chicks of the Hybro strain (a local variety derived from the White Leghorn breed) obtained from a commercial hatchery (Incubatoio "La Pellegrina," Ponte di Castegnero, Vicenza, Italy) when they were only a few hours old. Chicks were reared individually, at a controlled temperature (30–35°C) in metal cages (35 cm wide × 35 cm deep × 38 cm high) lit from above by fluorescent lamps with food and water *ad libitum*.

Apparatus and general procedure have been described in detail elsewhere (Tommasi et al., 1997). Chicks were trained daily for 1 week starting on day 8 and were tested on days 16 and 17. Chicks were food deprived 12 h before each daily session of training started. They were trained in a square-shaped arena (70 cm) with a sawdust-covered floor (5 cm in depth). The arena was made of wooden walls (40 cm high) uniformly white-painted, covered by a one-way screen that prevented the chicks from seeing outside, while allowing videorecording.

The arena was illuminated by light bulbs (25 W) located at the corners and/or at random positions along the walls (the positions of the bulbs were changed at random throughout experimental sessions).

At the beginning of each training session, a small rectangular plastic box (5 × 10 × 2 cm) containing grains of food was placed on the floor in the center of the arena. Attached to the box was a red plastic stick (15 cm in length, 0.5 cm in diameter) that served as the landmark to indicate food location. The box had a small hole in it (2 × 2 cm) through which food could be reached. Each chick was introduced into the arena from above at one of the corners; it was given time to reach the box and allowed to eat some grains of food. At the end of each trial the chick was taken from the arena and the food box was buried a few millimeters more in the sawdust. During the intertrial period (1 min), while the animal was outside of the arena, it was confined in a small closed cardboard box (10 × 15 × 10 cm) and slowly rotated to avoid subsequent usage of inertial or compass information. The corner into which it was released in the arena varied randomly from trial to trial and so did the position of the experimenter with respect to the arena when reintroducing the animal. After some trials the box was completely buried and therefore invisible to the animal, leaving visible only the landmark. When faced with the disappearance of the food box, chicks started searching for it under the sawdust by means of the ground-scratching response. Each training session consisted of a sequence of five series of trials, each series ending with the disappearance of the food box.

At day 16 of life, chicks' performance in the training arena was assessed by videorecording their search activity during a 3-min session. Before videorecording started, the food was completely removed from the arena and sawdust was systematically mixed to rule out any spatially localized olfactory or visual cues. The video camera was mounted above the arena and the image was displayed on a TV monitor with a cartesian grid superimposed onto it. Scratching responses were recorded on the grid as sets of cartesian (x, y) coordinates for subsequent analyses. All chicks were trained in binocular conditions. After videorecording in the training arena, chicks were given a retraining session in the presence of food in order to reinstate motivation. Chicks were then tested with the landmark relocated to a corner (different corners were used for different animals, and data have been subsequently normalized and reported conventionally to a single corner, see figures below). Chicks were tested in binocular (N =
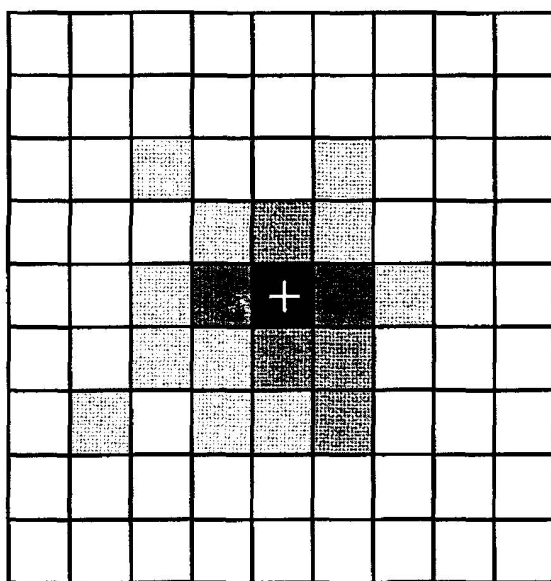
FIG. 9. Searching behavior in binocular chicks trained to find food in the spatial center of a square-shaped arena. The position of the food was indicated by a landmark (indicated by the white cross in the figure). The darkest areas represent the zones of maximal ground scratching.

FIG. 10. Searching behavior of chicks after the displacement of the landmark in a novel position (the position of the landmark is indicated by the black cross). Binocular (top) and left-eyed chicks (middle) ignored the novel position of the landmark and persisted in searching in the center, whereas right-eyed chicks (bottom) ignored the spatial center and searched close to the landmark.

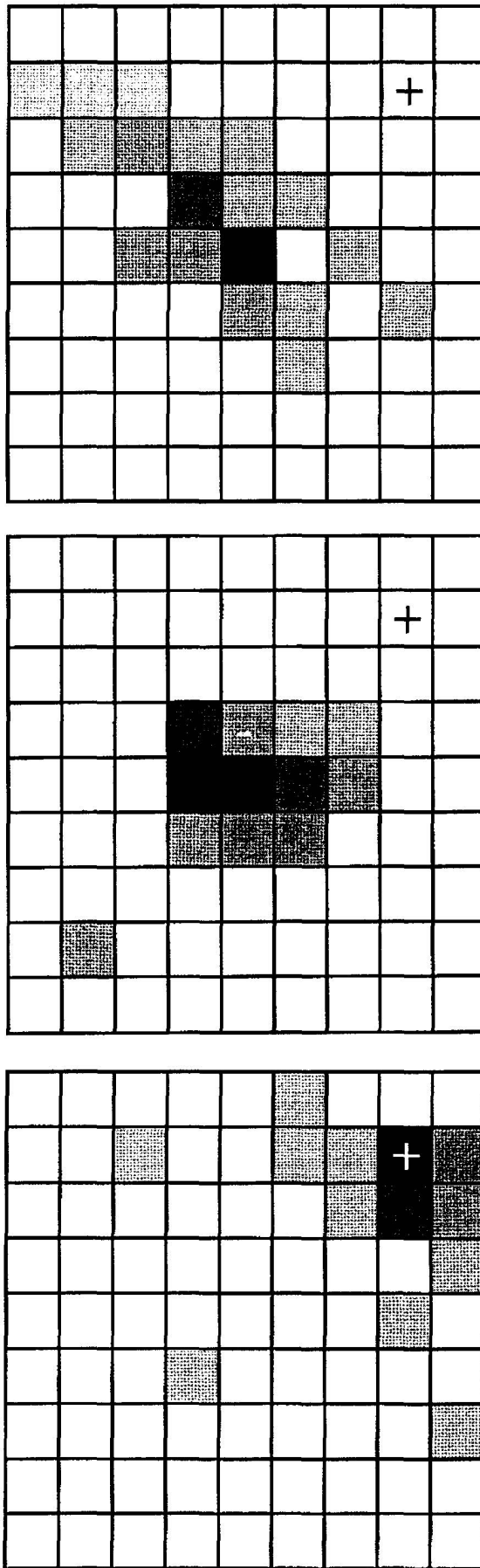5) and monocular conditions (left-eyed chicks $N = 5$; right-eyed chicks $N = 5$). Monocular testing was carried out by means of eye patches made of special, removable, sticky tape, worn by the chicks 20 min before testing to get them acquainted to the new condition (binocular chicks were not eye-patched but received an equivalent amount of handling and acquainting time as monocular chicks). Even in this phase chicks were tested in the absence of food and after sawdust had been systematically mixed to rule out spatially localized olfactory or visual cues. Searching behavior after landmark displacement was videorecorded for 3 min and the locations of the ground-scratching responses were recorded as before.

Data collected from videorecordings were represented graphically to show the spatial components associated with the search activity. The floor of the arena was partitioned into equivalent areas: for each of these areas the weighted mean of the number of scratches was calculated (mean of all the response ratios in which the single animal's ratio was computed as the number of scratches in that area divided by the total number of scratches in the whole arena). The weighted means ranged between a minimum (always zero) and a maximum; these values were represented with a 10-level gray scale, where white stands for zero and dark gray for maximal proportion of scratches. An additional representation of results was obtained by dividing the arena into concentric annuli of the same width and calculating the search intensity in each annulus (computed as the weighted mean of the responses of all the animals divided by the area). The gray gradient obtained in this way is a representation of the intensity of search behavior as a function of distance from the center (see Figs. 9 and 10, rightmost graphs).

Results

Chicks developed very precise and localized searching behavior during the training phase, exhibiting almost all of their ground-scratching behavior near the landmark in the center of the arena (Fig. 9). After landmark displacement, left-eyed chicks searched in the center (Fig. 10, middle), completely ignoring the novel position of the landmark, whereas right-eyed chicks (Fig. 10, bottom) did exactly the opposite, searching close to the landmark and ignoring the global spatial information provided by the environment. Thus, the left-eye system (right hemisphere) appeared to have encoded position-specific cues (the global spatial information provided by the walls of the arena) and the right-eye system (left hemisphere) to have encoded object-specific cues (the local information provided by the landmark). It is also apparent that in the normal, binocular condition (Fig. 10, top), the left eye is dominant, given that responses of binocular chicks clearly resembled more those of left-eyed than right-eyed chicks.

EXPERIMENT 2: LEFT AND RIGHT HEMISPHERE ENCODING OF OBJECT- AND POSITION-SPECIFIC CUES IN A WORKING MEMORY TASK

In the following experiment a similar dissociation between object- and position-specific cues by chicks' left and right eyes was investigated with a technique developed in my laboratory to investigate working memory in the avian brain (Vallortigara, Regolin, Rigoni, & Zanforlin, 1998). Basically, chicks were trained to perform a delayed-response task. A very attractive goal (an imprinted object) was hidden behind one of two different opaque

screens and the chicks were allowed to search for the goal after a fixed delay. In each trial, the position of the screen behind which the goal object was hidden was changed at random and, during the delay, the left–right position of the screens was interchanged so as to locate the "correct" screen in the wrong position and the "incorrect" screen in the correct position. Our aim was to check whether right-eyed and left-eyed chicks would rely on different cues for search, i.e., the position of the screen for left-eyed chicks and its visual characteristics for right-eyed chicks (see Vallortigara & Garzotto, in preparation).

Methods

The subjects were 18 female Hybro chicks, obtained from a commercial hatchery (Incubatoio 'La Pellegrina', Ponte di Castegnero, Vicenza) when they were only a few hours old. Chicks were reared singly, at a controlled temperature (30–35°C), with food and water available *ad libitum*. The rearing cages (45 cm wide × 25 cm high × 35 cm deep) were illuminated from above by fluorescent lamps. A small red plastic ball (4 × 3 × 3 cm) was suspended by a fine thread (at about chicks' head height) in the center of the rearing cage and served as the imprinting object (previous studies showed that this stimulus is very effective in producing social attachment in this strain of chicks; see Vallortigara & Andrew, 1991).

The apparatus and general procedure have been described in detail elsewhere (Vallortigara et al., 1998). The test apparatus consisted in a circular arena (95 cm in diameter, 30 cm high) with the floor uniformly covered by sawdust (1 cm thick). Within the arena, adjacent to the outer wall, was positioned a small clear glass cage (10 × 20 × 20 cm), where the chick could be confined for the delay period during the test phase. The side of the glass cage facing the center of the arena was removable (the experimenter could lift it from above) in order to release the test chick in the arena. Two opaque screens (16 × 8 cm; with 3-cm sides bent back to prevent chicks from spotting the hidden ball), visually different in color and patterning (i.e., one was blue with a yellow "X," and the other white with a red "Florence lily" pattern) were positioned symmetrically with respect to the glass cage in the center of the arena, 20 cm apart from each other and 31 cm away from the closest side of the glass cage.

On day 4 of life, each chick underwent preliminary training. For the training, only one of the screens was used (the blue one for half of the animals, the white one for the other half) and positioned in front of and 31 cm away from the glass cage. The chick, together with the imprinting red ball, was at first placed within the arena for a couple of minutes, free to move around and get acquainted to the novel environment. The rearing ball, held from above (by a fine thread) by the experimenter (not visible to the chick), was slowly moved and made to disappear behind the screen. This was repeated a few times, until the chick promptly responded by following, and finding, the ball behind the screen. Thereafter, the test chick was confined in the glass cage. The red ball, outside the cage, was slowly moved until it disappeared behind the screen; the experimenter took care that the chick was watching this happening. The chick was then immediately set free in the arena, and every time the chick rejoined the ball behind the screen it was allowed to spend a few seconds next to its artificial social partner. Training ended when the chick reached the ball behind the screen within 10 s from release for six consecutive times.

Testing took place 2 h after training. Both screens were positioned in the arena. The chick was confined in the transparent glass cage, from where it could see and track the ball disappearing behind one of the two screens. After the disappearance of the ball, an opaque partition was located in front of the glass cage, preventing the chick from seeing the two screens for 30 s. During this delay, the experimenter swapped the positions of the two screens so that,
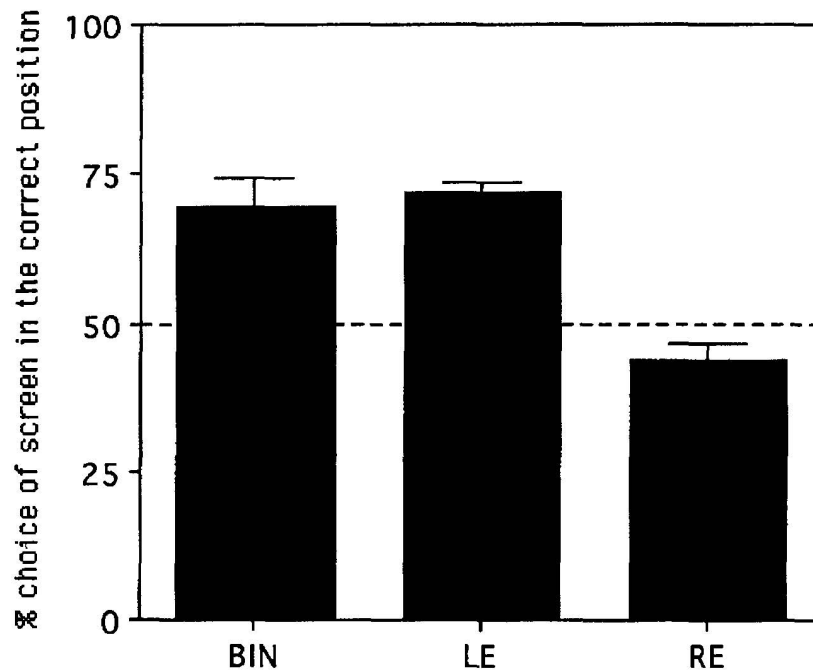
FIG. 11. Percentage of choice for the screen in the correct position (and with the wrong color and patterning) in chicks tested binocularly (BIN) or with only the left (LE) or the right (RE) eye in use in the delayed-response task.

after the removal of the opaque partition and the release of the chick, the animal was allowed to choose between a screen that was in the correct position but had the wrong color and patterning and a screen that was in the wrong position but had the correct color and patterning. Each chick performed 16 trials, and the screen behind which the ball disappeared was changed according to a semirandom sequence (Fellows, 1967). The screen first chosen and searched by the chick was recorded. Separate groups of chicks were tested in binocular conditions ($N = 6$) and in monocular conditions (temporarily eye-patched right-eyed chicks, $N = 6$; left-eyed chicks, $N = 8$). Procedures for eye-patching and acquaintance of animals to eye-patching were the same as in the previous experiment.

Results

The results are shown in Fig. 11, depicting percentages of choice for the screen in the correct position. The analysis of variance revealed a significant main effect of the eye in use [$F(2, 30) = 19.396, p = .0001$]. Post hoc comparisons (Tukey test) showed that there were significant differences between right-eyed and left-eyed chicks ($p = .0001$) and between right-eyed and binocular chicks ($p = .0001$), but not between left-eyed and binocular chicks. Results suggest that chicks using their left eye relied on the position of the screen, ignoring its color and pattern, whereas chicks using their right eye relied on the color and pattern of the screen, ignoring its position.

EVOLUTIONARY BIOLOGY AND COMPARATIVE NEUROPSYCHOLOGY: ESTABLISHING A MISSING LINK

Consider again the issues associated with the possibility that animals might use their left and right visual fields differently, and in a sense may

also "see" differently, through their left and right monocular visual fields. The problem, of course, is that any asymmetry of responding to visual stimuli could cause serious problems in some circumstances. Predators, for instance, should be detected and avoided with identical probability regardless of whether detection occurred in one or the other monocular visual field. However, as we have already mentioned, asymmetries in turning may arise from advantages associated with faster escape responses (Heuts, 1999), thus producing postural asymmetries that result in asymmetric lateral viewing. But even aside from postural asymmetries associated to asymmetric predator-escape responses, after initial detection of a stimulus has occurred, more sustained viewing may well take place into one or other monocular field.

It can be argued that species with laterally placed eyes could turn their heads to ensure that the stimulus is seen with both eyes, either by using alternatively both monocular fields to view the stimulus or by detecting it in one monocular field and then turning to use the binocular field. However, head movements may present problems, for they can be detected by predators (or by prey) and also increase time of processing. It is likely, therefore, that some processing occurs without any lateralization in both monocular visual fields, whereas other analyses are carried out quite differently by the left and right eyes. (Interestingly, chicks show no lateralization of habituation of the orientation response to a large, novel stimulus viewed by either monocular field, and in this respect they could differ from fish and toads, see Rogers & Anson, 1979).

Rogers (1989) has stressed that if possessing an asymmetric brain confers some biological advantage to the individual, there is no reason why the direction of asymmetries should be the same in all (or most) individuals of a population. Perhaps the original condition of early vertebrates could have been that of brain asymmetry at the individual level. However, if lateralization manifests its effects on organisms' everyday behavior, for instance, producing preferential eye use in animals with laterally placed eyes and thus determining conspicuous lateral biases in motor behavior, then the direction of the asymmetries would be of extreme importance in all the conditions in which an asymmetric individual must coordinate its behavior in relation to that of other asymmetric individuals. This may be particularly important when the other individuals are conspecifics. To a fish in a school, for instance, the best direction of predator-escape response depends on the direction taken by the majority of individuals within the same school. Also, having one eye (and one side of the brain) that, say, recognizes a stimulus as a dangerous predator and the other eye treating the same stimulus as innocuous, would similarly disrupt cohesion of a school. This reasoning leads to the intriguing possibility that population asymmetries (as opposed to individual asymmetries) would be more typically encountered among social rather than solitary species. Obviously, gregarious behavior is in some sense a matter of degree rather than an all-or-none characteristic of a species, and higher

vertebrates are virtually all "social" animals. Among fish, however, quite a clear-cut distinction can be drawn between "social" species showing shoaling tendencies and "solitary" species that do not form schools. Up to now, we have tested 20 species of fish in the detour task (see Bisazza et al., 1999; Vallortigara et al., 1999). All the most social species, estimated on the basis of both previous ethological literature and of direct tests of shoaling tendencies, showed lateralization at the population level; among the less gregarious species only 40% showed population lateralization, the others showing only individual lateralization (see Bisazza et al., 1999).

Obviously, this sort of very general hypothesis cannot be easily proved or disproved within a single experiment. Comparative behavioral studies with large numbers of species are difficult to perform and extremely time-consuming. Nevertheless, I believe that the increased availability of these sorts of comparative data would be crucial to the development of our understanding of the evolutionary origins of cerebral lateralization. Although the field of hemispheric specialization has been a domain for neurologists and neuropsychologists, there are recent signs of interest by evolutionary biologists as well (Raymond et al. 1996; Hori, 1993). If, as the evidence reviewed here suggests, behavioral asymmetries are important in the everyday behavior of animals, then the evolutionary pressures and genetic mechanisms that maintain these asymmetries should be of concern to evolutionary biologists. In particular, it would be crucial to establish why and when the advantages of having asymmetric brains could have overcome the disadvantages of displaying evident (and *predictable*) asymmetric behavioral patterns.

In order to investigate this issue, my colleagues and I (see Bisazza, De Santi, & Vallortigara, 1999) recently took advantage of an experimental paradigm which has been widely used in the field of behavioral ecology. It is common among fish that pairs of individuals leave their shoal in order to approach and inspect a potential predator (Magurran & Pitcher 1987; Magurran & Segers 1990). The risk of being preyed upon is shared if both fish simultaneously inspect the predator, but not if one of the fish remains at a distance. Fish are thus believed to face a classic Prisoner's Dilemma in this situation, and predator-inspection behavior has been used as a model to analyze the evolution of mutual cooperation among unrelated individuals. In an influential paper, Milinski (1987) found that sticklebacks are more likely to approach a predator when a mirror is placed parallel to the tank so that the image appears to swim along with the fish (simulating a cooperative partner) than when the mirror is angled so that the image appears to swim away from the fish (simulating a noncooperative, "betraying" partner).

In our study we duplicated Milinsky's original procedure, checking for the effects of positioning a mirror on either the left or the right side of the fish. We found that predator inspection is more likely to occur when the mirror image is visible on the left rather than on the right side of mosquitofish (*G. holbrooki*). The same occurred even when a videorecorded stimulus pre-

sentation was used in which sequences of the predator were mixed with their mirror-image equivalents, thus showing that the asymmetry was not due to behavioral or morphological asymmetries of the predator itself. Moreover, irrespective of being tested with either a cooperative (parallel mirror) or a noncooperative (angled mirror) partner, mosquitofish moved closer to the predator when the mirror was located on their left side. These findings suggest, once again, that the visual scenes seen on the right and left sides by a fish may evoke different types of social behavior, likely because of different modes of analysis of perceptual information carried out by the left and right sides of the brain.

Considering that during these tests mosquitofish typically swam very close to the mirror, it seems likely that positioning the mirror on the left side produced the best arrangement of monocular lateral stimulation, with the right eye fixating the predator and the left eye monitoring the companion. However, no data to disentangle the relative roles played by right eye use in fixation of the predator and left eye use in fixation of the companion were available in this experimental condition; in principle, either one of the effects would suffice for producing the reported asymmetry. More recently we thus measured the time spent in monocular viewing during inspection of their own mirror images in females of five species of fish, belonging to different families (Sovrano et al., 1999) Results revealed a consistent left-eye preference during sustained fixation in all of the five species. Thus, the hypothesis that fish use the right eye for fixation of the predator and the left eye for monitoring their mirror image seems to be fully confirmed.

The use of conditional strategies like tit-for-tat rests on a monitoring of the cooperative or noncooperative behavior of the other member of the pair and on the recognition of its identity. There is widespread evidence among birds and mammals for a dominant role of the neural structures located in the right side of the brain in recognition of individual conspecifics (review in Vallortigara & Andrew, 1994a). It is unknown whether similar specializations hold for lower vertebrates such as fish, but if so that may explain why it is the left eye (mainly feeding neural structures on the right side of the brain) that is used to monitor the behavior of the image on the mirror.

There is an intriguing difference with regard to the direction of lateralization in different species here. Although the direction of asymmetry of response to predators tends to remain the same among closely related species (fish belonging to the same family, i.e., Gobidae, Poeciliidae, and Cyprinidae, showed identical direction of lateralization), it varies among less closely related species. In contrast, the species so far studied for lateralization of response to their mirror image all showed identical direction of lateralization (i.e., left-eye use), in spite of the fact that they were very unrelated phylogenetically. It could be argued that the sample tested (five species) is too small to generalize, but some of the species that show different patterns of eye use during predator-inspection responses show identical direction of

lateralization during mirror-image conspecific viewing. It could be, therefore, that this would reflect the different costs and benefits associated with directional asymmetries in relation to antipredatory and social behaviors (see Sovrano et al., 1999). A problem with directional asymmetries is that they are costly and risky because they can be exploited by other species. A predator could learn about the fact that its prey tends to escape in a particular direction as a consequence of a behavioral lateralization (e.g., of a preference in eye use). Thus, it could be adaptive for individuals of a species to develop a different direction of lateralization at the population level. This could also produce phenomena of frequency-dependent selection, as it has been documented among scale-eating Cichlid fish (Hori, 1993). Thus, selective pressures for changes in the direction of lateralization in different species associated to predator-evasion responses should be expected. In contrast, selective pressures can exist for the maintenance of directional asymmetries associated with social interactions among individuals of the same species. The demands associated with living in groups are the most obvious candidate, for example, with respect to courtship behavior and agonistic interaction as well as with respect to schooling behavior (to be a "left-handed" fish within a small shoal could be terribly dangerous because that individual would increase its risk of being preyed upon). Therefore, it could be predicted that behaviors associated with some sort of social interactions among conspecifics should manifest more easily an invariant pattern of directional asymmetries even in unrelated species (providing that they have been inherited by a common ancestor), whereas for behaviors involving interspecies interactions and competitions there could have been advantages for ecologically determined species-specific changes in the direction of lateral asymmetries (note that within each species the advantages to maintain an identical direction of lateralization in the various individuals remain important: the argument here is that a different direction of lateralization could be advantageous to differentiate behavior of individuals of a species from that of other species that are at risk of similar predation). Such changes in the direction of lateralization can be expected even when lateralization is controlled by genes. Evidence obtained in birds has shown clearly that the alignment of brain and behavioral asymmetries at the population level could easily be obtained (and even modified) through an interplay of embryologic and environmental factors. In chicks (Rogers, 1990, 1991, 1995, 1996, 1997) and in pigeons (Güntürkün, 1993), for instance, the position of the eye in the embryo soon after hatching, and the consequent different amount of light stimulation of the two eyes, causes at least some of the asymmetries documented at both the anatomical and behavioral levels. Individuals hatched in the dark are still lateralized, but with equiprobable distribution within the population (Rogers, 1982, 1986, 1990). There is at present no evidence of similar phenomena in fish, but the issue is worth testing.

Obviously, fish use more than their eyes when interacting with schooling

partners (e.g., lateral line and olfaction). In natural situations fish will thus have a variety of sensory information that could potentially compensate for any laterality arising solely from vision. The possibility that these phenomena of behavioral lateralization produce asymmetries in the organization of social structures such as fish schooling deserves consideration (lateralization in other sensory modalities may well be possible, for birds see Vallortigara & Andrew, 1994b; and Miklòsi, Andrew, & Dharmaretnam, 1996).

In conclusion, it seems to me that there are reasons to believe that the early origins of brain lateralization could have been associated with simple computational advantages associated with the possession of asymmetric brains by single individuals (and thus with an equiprobable distribution of "left" and "right" phenotypes within the population). Such very simple advantages could have been related to the increase in the speed of predator-evasion responses of creatures with (roughly) bilaterally symmetrical bodies that possessed neural circuits such as those of the Mauthner cells. The intrinsic asymmetry needed for performing this sort of escape response sets a requirement for an asymmetry at the neuronal, muscular, and behavioral levels, which in turn could have produced other asymmetries at the sensory and perceptual levels. But there are even other possible advantages associated with the appearance of asymmetries in the nervous system, which have been largely discussed in the literature. For example, the need to avoid useless duplication of function in relation to the saving of neural space (Nottebohm, 1979), or the particular logical demands associated with phenomena of functional incompatibility within neural mechanisms originally devoted to the solution of a particular and circumscribed problem when they have to be coopted for novel tasks (Vallortigara, Rogers, & Bisazza, 1999). The crucial point is, however, that all these advantages could be gained and maintained within individually asymmetric brains, without any need to align the direction of the asymmetries at the population level. To understand directional asymmetries, i.e., asymmetries in which direction is the same among the majority of individuals in a population, we need a further (simple) logical step. After natural selection had built up behaviorally asymmetric organisms, the problem appeared that some of these asymmetric organisms could interact with each other and that, in some circumstances, disadvantages could arise for an individual if the direction of its behavioral asymmetries was different from that of the majority of the other asymmetric individuals of the population. Hence, evolution of population lateralization (which is therefore an example of what J. Maynard-Smith has called an "evolutionarily stable strategy," see Maynard-Smith, 1976).

I believe that such an evolutionary approach could prove useful in facing issues that have long been problematic in neuropsychology, such as that of left-handedness. Apparently, what we have said here would argue against the possibility of left-handedness as an adaptive strategy. Let us consider again our hypothetical school of primitive fish. If it is advantageous for all

the individuals to be synchronized in their lateral responses and, for instance, to escape to the right as a group, then a "left-handed" fish escaping to the left would be an isolated fish and probably a dead fish. That is true, but it is probably not the entire story. "Left-handers" could have their own advantages, and these advantages could be, paradoxically, associated with the fact that they are only a *few* individuals within a large "right-handed" population. This is what evolutionary biologists call "frequency-dependent selection." Suppose that a predator could learn about and thus exploit the right-side escapes tendencies of our hypothetical school of fish, for instance paying more attention to a particular side or by developing a motor bias. As a result of such a predator's learning, a "left-handed" fish would have a selective advantage. But, and this is the point, the advantage of the left-handed fish is frequency-dependent, it works only if left-handed fish remain a minority within a large group of fish that are right-handed. Hori (1993) has provided evidence of right–left morphological asymmetries associated with frequency-dependent natural selection in scale-eating Cichlid fish. Work by Raymond et al. (1996) has provided evidence for frequency-dependent maintenance of left-handedness in humans. They proposed that left-handers have a frequency-dependent advantage in fights and for that reason a fitness advantage. Consistent with this hypothesis, they found a higher proportion of left-handed individuals in interactive sports (reflecting some fighting elements) but not in noninteractive sports. I would guess that introducing the study of brain lateralization into the framework of evolutionary biology could prove to be an extraordinarily fruitful enterprise.

ACKNOWLEDGMENTS

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