Full length review

Possible evolutionary origins of cognitive brain lateralization

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Abstract

Despite the substantial literature on the functional architecture of the asymmetries of the human brain, which has been accumulating for more than 130 years since Dax and Broca's early reports, the biological foundations of cerebral asymmetries are still poorly understood. Recent advances in comparative cognitive neurosciences have made available new animal models that have started to provide unexpected insights into the evolutionary origins and neuronal mechanisms of cerebral asymmetries. Animal model-systems, particularly those provided by the avian brain, highlight the interrelations of genetic, hormonal and environmental events to produce neural and behavioural asymmetries. Novel evidences showing that functional and structural lateralization of the brain is widespread among vertebrates (including fish, reptiles and amphibians) have accumulated rapidly. Perceptual asymmetries, in particular, seem to be ubiquitous in everyday behaviour of most species of animals with laterally placed eyes; in organisms with wider binocular overlap (e.g., amphibians), they appear to be retained for initial detection of stimuli in the extreme lateral fields. We speculate that adjustment of head position and eye movements may play a similar role in mammals with frontal vision as does the choice for right or left lateral visual fields in animals with laterally placed eyes. A first attempt to trace back the origins of brain asymmetry to early vertebrates is presented, based on the hypothesis that functional incompatibility between the logical demands associated with very basic cognitive functions is central to the phenomenon of cerebral lateralization. © 1999 Published by Elsevier Science B.V. All rights reserved.

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1. Introduction

As recently as the early 1970s, hemispheric specialization of function was thought to be a unique human trait, part of a phenomenon that included handedness, language and superior cognitive abilities. Now we know that our species shares brain lateralization with many species of vertebrates [20,30,31,75]. Paradoxically, increasing interest in studies of cerebral asymmetry in animals has coincided with a decline of interest in this topic among human neuropsychologists [36]; we believe that this disaffection has arisen because of misguided focusing on issues related to localization of functions and on models of cerebral lateralization bearing little relation to biology. As pointed out by Corballis [27], there are, however, signs that research on lateralization in humans is now moving towards a more realistic and biologically based understanding of the nature of cerebral asymmetry. Animal studies appear crucial to this enterprise.

Research with animals has provided invaluable model-systems for investigating the neurobiological bases of asymmetries, as well as the possibility of determining the roles of genetic and epigenetic factors in the establishment of asymmetries. Further, comparative work may shed light on the evolutionary origins of cerebral asymmetry, and thus on its ultimate causation.

2. How ancient is brain lateralization?

Comparative psychologists and neurobiologists cannot rely on fossil records to reconstruct evolutionary history. With some caution, however, reasonable inferences can be drawn from data obtained on current living animal species. Until a few years ago, the state of the art was that there was clear evidence for the presence of both structural and functional lateralization in mammals and in birds [20]. Disputes concerned the extent to which lateralization in other species was similar in strength of bias to that of the human species, but not the existence of the phenomenon. Nonetheless, the relevance of animal lateralization to human lateralization has been questioned. For instance, it was claimed that lateralization in birds could be an example of convergent evolution, bearing no relation to lateralization in mammals, and even the presence of lateralization in mammals was disqualified from being a valid model relevant to humans on the grounds that mammals were seen to be *less* strongly lateralized than humans (see, however, Section 5).

Nevertheless, a completely different story is at hand. No doubt birds are only distantly related to humans. Lineages of the amniote groups were separated about 300 million years ago from the ancestral 'stem reptiles'. Lateralization in birds and in mammals might have arisen independently in the two classes. This does not make their study less important from a biological point of view, however. If two species with a common phylogenetic history exhibit structurally similar traits, we call such traits homologous [23]; if two species lack a common phylogenetic history but exhibit structurally similar traits, we call such traits homoplasies [52]. Both of these considerations are important for reconstructing the phylogenetic history of a trait, and both contribute to an understanding of the functional and adaptive aspects of a trait. Homoplasy typically emerges because even distantly related species may confront environmental problems with only a limited set of possible adaptive solutions. Different evolutionary forces can be responsible for generating homologous and homoplasic similarities.

In order to understand such a prominent biological character as brain lateralization, we must know what these forces might have been. If cerebral asymmetries of birds and mammals are homologous phenomena, we should find widespread traces of lateralization among current living 'lower' vertebrates — fish, amphibians and reptiles. Note that, in order to make an argument for homology, it is crucial for lateralization among lower vertebrates to be a diffuse or ubiquitous phenomenon. Discovering a single isolated case of lateralization at population level in, say, a species of frog would leave open the door to the possibility that, as a result of similar evolutionary forces, similar (homoplasic) asymmetries emerged in the particular species of frog and in humans without the trait being inherited from any common ancestor. Thus, there is no straightforward solution to the question of homoplasy vs. homology other than by painstaking collection of enough data from different species.

It is likely that research on brain asymmetries among lower vertebrate species will be regarded as the tracing of one of the most convoluted paths in the history of neuroscience. As noted by Braintenberg and Kemali [21], the existence of structural asymmetries in the brain (particularly the diencephalon) of lower vertebrates was common knowledge among neuroanatomists at the beginning of the century, but subsequently the mention of these asymmetries disappeared from anatomy textbooks. Only recently were they 'rediscovered' [51]. But the history of research on functional asymmetries is even more bizarre. Virtually no papers on functional lateralization in lower vertebrates appeared until very recently (see Bisazza et al. [11] for a review of the few exceptions), probably because lower vertebrates are not the most typical animal models to which neuropsychologists usually refer. Then, the *zeitgeist* did its job and several lines of evidence appeared quite simultaneously from different laboratories. In 1993, Bauer [7] reported neural asymmetries favoring the left side of the brain in the control of clasping vocalizations in frogs; in 1995, Deckel [29] found preferential left eye use during aggressive responses in lizards, and in the same year, Cantalupo et al. [24] first reported a lateral bias favoring the right side of the brain in predator escape-responding in a teleost species of fish. Other important findings con-

cerned the discovery of pawedness in several species of toads (Section 5), lateralization of pectoral stridulation sounds in catfish [40], and lateralization of sexual behaviour in newts [43]. In a period as short as only 5 to 6 years, evidence for behavioural lateralization at the population level became available for more than a dozen species of fish, six species of amphibians and two species of reptiles [11]. This, together with widespread evidence for structural asymmetries in the diencephalon of lower vertebrates, really makes the case for a possible ancient evolutionary origin of cerebral lateralization.

3. Modes of processing by right and left hemispheres: hints from avian brains

Similarities in the direction of lateralization in different tasks among different species may be seen as evidence for possible homologies, but the direction of the lateralization is probably not as important as the fact that there is *different* functional specialization of the two sides of the brain. Similarity in direction is not very informative considering that there are only two possible directions for an asymmetry to occur, either favoring the right or the left side, and that the direction of lateralization could be influenced by embryological and other environmental factors (see Section 4). Even assuming a direct genetic control for the direction of lateralization, the possibility of variations between species as a function of environmental variables should be taken into account. Actually, there is evidence that similarities in the direction of brain asymmetries are more likely to occur among closely related species within the same order than across different orders. Fig. 1 shows the phylogenetic relationships among the species of fish that have been tested up to now in our laboratories for lateral asymmetries during detour behaviour (see Section 6).

The direction of lateralization is similar among closely related species; for instance among species of the Poeciliidae, Gobidae and Cyprinidae families, but not in species
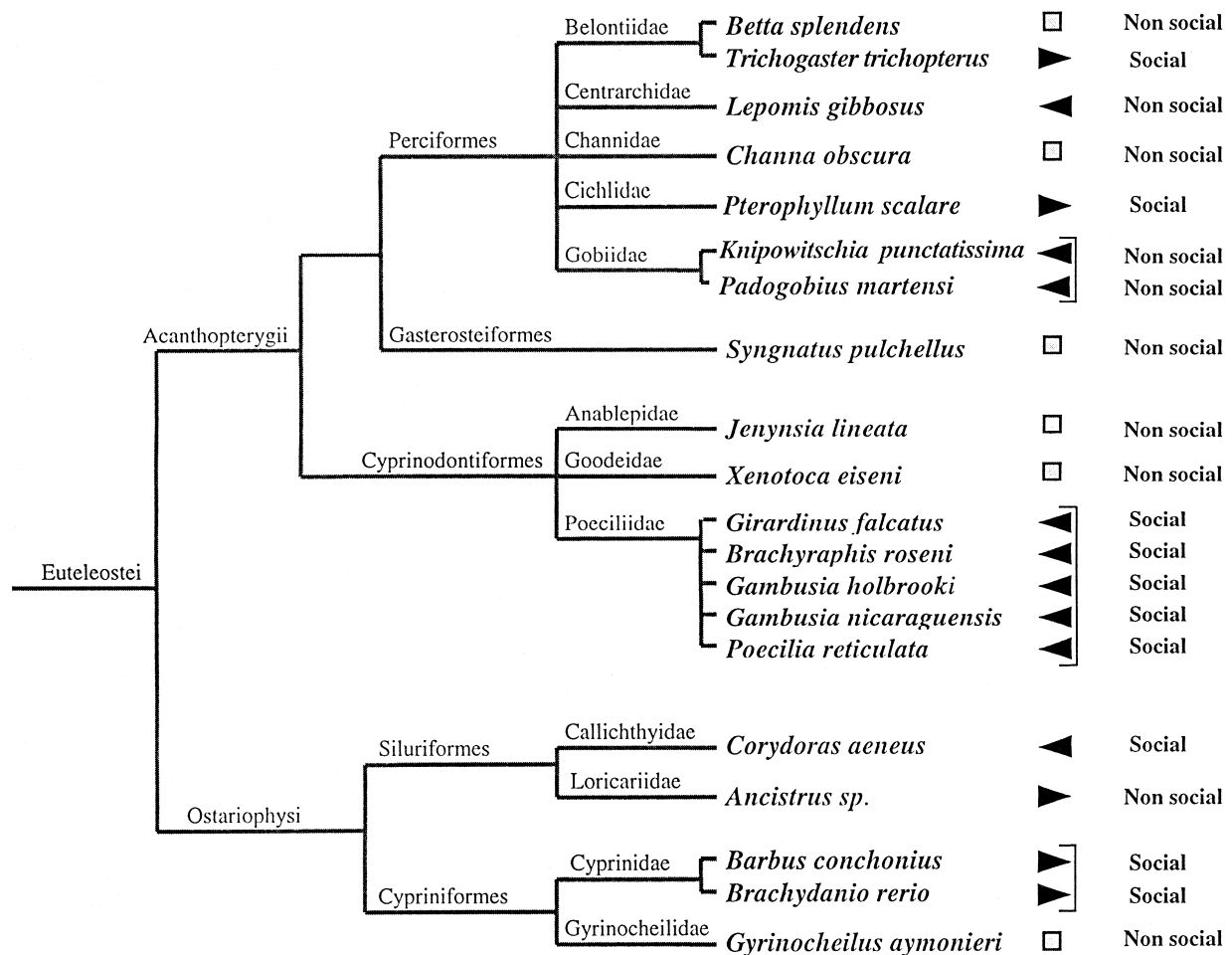
Fig. 1. Phylogenetic tree of the fish species studied for turning asymmetries during detour behaviour. The arrows show the direction of turning bias; social and non-social species are also indicated. Note that all social species showed lateralization at the population level, whereas solitary species are more likely to show lateralization only at the individual level (i.e., individuals exhibit asymmetries but in the population there is approximately an identical number of individuals showing rightward or leftward biases).

which are phylogenetically more distant. This suggests that the need for an asymmetrical brain is widespread among vertebrates, but that the determination of the precise direction of lateralization in different families may vary, probably as a result of epigenetic factors that modulate on a basically similar genetic program. (Note, also, that there is evidence that motivational/emotional factors can influence the direction of behavioural asymmetries, and it is likely that closely related species resemble each other in terms of motivational/emotional responses [10].) Thus, although we can expect a certain degree of correspondence in the direction of lateralization among vertebrates, this particular facet of lateralization is not crucial to the argument that brain lateralization appeared early in vertebrate evolution.

We believe that the essence of brain lateralization lies in the fact that one side of the brain performs certain types of computational operations and the other side performs other, different computational operations. When faced with complex computational problems, brains might perform better if they segregate them into sub-problems that differ in a typical ways. What sort of separation between sub-aspects of natural computations has animal research revealed? Birds have provided the most important insights.

In the domestic chick, lateralization of brain functions has been investigated in far more detail than in any other species. a variety of behavioural and neurobiological methods [3,5,83,84,56,96] has revealed that the two hemispheres differ in fundamental ways in modes of perceptual analysis and storage of information. Procedures which restrict direct sensory input to one or other hemisphere have proved particularly valuable. Chicks using the left eye tend to choose between objects to which they are socially attached on the basis of small changes in their appearance, whereas these same changes tend to be ignored by chicks using the right eye [102,103]. Chicks using the right nostril (and so predominantly the right hemisphere) show a similar pattern of choice based on olfactory changes [104]. Chicks using the left eye have also a marked advantage in topographical orientation based on visual cues [79]. Overall, therefore, these findings suggest a special competence of the right hemisphere in spatial analysis and in response to novelty [103,105, 79,102], whereas the left hemisphere is involved in the selection of cues that allow stimuli to be assigned to categories [4–6], as occurs when pecking at grains of food vs. pebbles (see Refs. [30,111] for similar evidences in mammals, including humans).

Imprinting has provided another important source of information about brain asymmetry in the chick. When newly hatched chicks are exposed to a visually conspicuous object, they approach it, learn its characteristics and form a social attachment to it. (In a natural environment, the object is usually the hen, but in the laboratory imprinting can be obtained using a variety of simple artificial objects.) The intermediate part of the hyperstriatum ventrale (IMHV), an associative forebrain structure, is part of a memory system which encodes a representation of the imprinting object [56]. The right and the left IMHV appear, however, to have different roles in storing the memory of the imprinting object. Evidence from lesion and electrophysiological studies suggest that both the right and the left IMHV act as short-term memory stores [68], but only the left IMHV is used as a long-term store. The right IMHV is crucial in establishing another store, somewhere outside the IMHV region, referred to as S' [56]. The right IMHV passes information on to S' over a period of several hours [68]. It has been also suggested that the passing the memory from the right IMHV to S' may add to the depth of processing by allowing the storage of contextual information and thus enriching simple representations initially stored in the IMHV [57]. This hypothesis is consistent with behavioural evidence from monocular tests showing that chicks using the right eye (mainly feeding neural structures in the contralateral left hemisphere) responds only to large changes in the visual appearance of an imprinting stimulus, whereas the left eye (mainly feeding structures in the right hemisphere) responds to more subtle changes in at least some visual characteristics of the imprinting object [103,105]. (It should be noted that optic fibers projections are mainly, but not completely, contralateral: there is complete decussation of the optic fibers at the optic chiasma but then some partial recrossing of the midline occurs in the projections from OPT in the thalamus to the Wulst and in the projections from the optic tecta to the ectostriata, see Ref. [33].) Recent evidence [76] from single unit recordings in the IMHV has revealed that, while exposure to an imprinting object results in increased activity of left IMHV cells without affecting their responses to other stimuli, in the right IMHV the same increase in activity is accompanied by a decrease in responsiveness to other stimuli. Thus, overall, the signal-to-noise ratio should be higher in the right than in the left IMHV and this again may be related to the specialization of the right hemisphere in the analysis and estimation of novelty (and possibly to the specialization of the left hemisphere to single out key features of stimuli and so classify together visual stimuli which differ widely in some visual properties but not others). There are also lateralized changes in the number and affinity of NMDA receptors, which are important for neural plasticity and learning: imprinting leads to a delayed increase in binding to NMDA receptors in the left IMHV but not in the right IMHV [62,68]. However, glutamatergic mechanisms in the right hemisphere are involved in recall of imprinting memory, as shown by disruption of memory recall by glutamate treatment of the right [61].

It is interesting to note that, in several respects, the pattern of lateralization observed in chicks is reminiscent of features of human lateralization. Andrew [5] has provided a comparison under three main headings: motor behaviour, emotional behaviour and cognitive processes,

showing that lateralization of all three is paralleled sufficiently close in humans and chicks. Let us consider cognitive processes which are of concern to us here. In humans, the right hemisphere has advantages in the analysis of spatial relations and topography [34] and in the recognition of complex and relatively unfamiliar stimuli [19]. Attentional processes under right hemisphere control tend to be global rather than focused, and memory storage in the right hemisphere tends to be organized in overall patterns rather than in a series of single items [115]. Similarly, in the chick the right hemisphere is especially concerned with spatial relations and shows interest in a wide range of stimulus properties, which suggests global attention [5]. In humans, of course, the left hemisphere is specialized for language and speech, but this could, in a sense, be regarded as a manifestation of a more general 'categorizing' ability of this hemisphere. A left-hemisphere advantage tends to emerge during the process of recognizing and becoming familiar with stimuli that cannot be named easily (e.g., 'nonsense', complex visual stimuli) and this reflects its use in categorizing stimuli [42]. Also, the left hemisphere tends to group visual stimuli according to the functions which they may serve, rather than their general appearance [111], and this hemisphere dominates in the production of appropriate practiced responses to a series of stimuli [114]. Similarly, in the chick it appears that the left hemisphere is concerned with selecting cues which allow stimuli to be assigned to categories on the basis of a single property, despite variation between stimuli in a variety of other properties [5]. Similar features hold for several different species of birds as well [39,46,26].

All of these suggest that the basic aspects of lateralization are common to both birds and mammals (a point also stressed by Denenberg [30]). But why should it be so? From a phylogenetic point of view, this indicates that lateralization emerged early in vertebrate evolution. From a computational point of view, it may have come about because the segregation of functions of the separate halves of the brain represents a solution to a problem of 'functional incompatibility' [98]. When assessing a novel stimulus, an event likely to be faced quite commonly even by most primitive vertebrates, an organism must carry out two different types of analyses [5]. First, it must rely on previous comparable experiences to estimate the degree of novelty of the stimulus, and to do it must recall stored memories and then elaborate on them for future use. Secondly, certain appropriate cues, based on past experience or on phylogenetically-based information, must be used to try to assign the stimulus to a category, and so to decide what sort of response (if any) should be given. Categorization must be made on the basis of selected stimulus properties, despite variation in many other properties. All this is reminiscent of the functional incompatibility among logical demands, a condition hypothesized to underlie the evolution of multiple memory systems [98]. To categorize events (or stimuli), the organism must recognize, and memorize, those features of an experience (or of a stimulus) that recur in different episodes (or stimuli) and, at the same time, ignore or discard unique and idiosyncratic features that do not recur and thus are not essential to learning. The selective attention that results is one of the brain's main functions, as it enables the smooth, and eventually automatic, execution of skilled motor behaviour, performed in response to certain invariant features of episodes. In contrast, to detect novelty and to build up a detailed record of episodic experiences the organism must attend to the contextual details that mark individual experiences uniquely, i.e., to recognize variance across episodes rather than invariance. Andrew [5] has stressed that these two types of processing need to be carried out simultaneously if an animal is to be able both to detect novelty (which can depend on detecting features that cannot be predicted in advance), and to categorize objects and events so that they can be responded to appropriately by 'practiced' responses and skills. However, it may be functional incompatibility, rather than the need of simultaneous parallel processing per se, that provides the clue for hemispheric specialization. Processing and storing of information about invariances and variances among experiences are mutually incompatible problems, that might best be handled by functionally separate systems [98]. This, together with competition for space within the brain, has probably generated basic patterns of hemispheric specialization.

4. Genes, environment, and embryos: roots of lateralized brains

Study of the chick embryo has revealed that genetic, hormonal and experiential factors interact to determine lateralized organization of some of the visual connections to the forebrain and lateralized visual function [84]. Most avian embryos, including the chick embryo, are oriented inside the egg during the final few days before hatching in a way that occludes the left eye by the body and leaves the right eye positioned next to the membranes of the air sac. As a result, light that passes through the shell and membranes of the egg stimulates the right eye but not the left eye. It is this asymmetrical stimulation that leads to the development of asymmetry in the visual projections that arise in the thalamus and cross the midline of the brain to project to the visual Wulst in the contralateral hemisphere of the brain [33]. Provided that the embryo is exposed to light during the final days of incubation when these connections are becoming functional, there are more projections from the left side of the thalamus (which receives input from the right, stimulated eye) to the right Wulst than from the right side of the thalamus (which receives input from the left, occluded eye) to the left Wulst [2,18,87,90]. This asymmetry is triggered by light exposure before hatching and becomes apparent after hatching. It does not develop in chicks that are hatched from eggs

incubated in the dark [86] and it can be reversed by occluding the embryo's right eye and then exposing its left eye to light [90].

In chicks exposed to light before hatching, the visual Wulst region in the *left*, and not the right, hemisphere of the forebrain is essential for performance of a task requiring the chick to search for grains of food scattered on a background of small pebbles that differ from grain in texture and brightness but not ranges of colours, shapes or sizes [32]. If the functioning of the left visual Wulst is impaired by an intracranial injection of glutamate on day 2 after hatching, the chick, tested binocularly, is unable to avoid pecking pebbles and so pecks at grain and pebbles randomly, whereas no such impairment follows the same treatment of the right Wulst.

Hence, it appears that light exposure before hatching generates a population bias in at least those forms of visual lateralization that depend on the visual Wulst. Chicks hatched from eggs incubated in the dark have no population bias for asymmetry of performance on the pebble-grain search task [82,85]. Other behaviours that depend on the other visual system, the tectofugal system, are unlikely to be so affected by light exposure because, as recently shown, there is no obvious asymmetry in this visual pathway in the chick [87].

In the pigeon, however, light exposure of the embryo does generate asymmetry in the tectofugal visual system, in the projections to the rotundal nuclei [45,47], and thus might affect lateralization in other types of visual behaviour. These species differences are likely to depend on the precocial nature of the chick at hatching compared to the pigeon at hatching and the consequent relative stage of development of the two visual systems in each species when the asymmetrical exposure to light occurs.

The hormonal condition of the embryo also has an influence on the light-induced asymmetry that develops in the thalamofugal visual projections of the chick. If the testosterone or oestrogen levels of the late embryo are artificially elevated, no asymmetry develops in response to the asymmetrical light stimulation [89,97]. In fact, there is a sex difference in the degree of asymmetry in these projections, males having greater asymmetry than females [78], and this is likely to result from the occurrence of a trough in circulating testosterone in male embryos at the time when light exposure is effective. Low levels of testosterone in male embryos at this time allow the developing projects to the Wulst to be sensitive to the influence of light stimulation, whereas in females relatively high levels of oestrogen override the effects of light.

Therefore, early experience provided by exposure to light affects the development of some important aspects of lateralization, both structural and functional, in the avian embryo. It also alters the levels of certain neurotransmitters in regions of the left and right hemispheres [63]. Other lateralities in the avian brain are not dependent on light exposure, and these include the various forms of laterality associated with imprinting and choice to approach a preferred stimulus as well as lateralization of auditory and olfactory processing [94]. Nevertheless, these results alert us to the possibility that lateralized experience in non-visual modalities could influence lateralization in those sensory systems and lateralized sensory experience during development might also affect lateralization in other species.

5. Did 'handedness' appear first in early tetrapods?

It has long been denied that other animal species show differences in the use of the limbs in any way comparable to human handedness — meaning consistent preferential use of one hand in most individuals and across most tasks. But this view does not appear valid. Avian species that use their feet to manipulate food and objects have shown significant 'footedness' present at the population level, with proportions similar to those of handedness in humans [41,50,81,92,99–101]. Even in rodents, previously credited to exhibit limb preferences only at the individual but not population level, a recent report, in which large samples of inbred mice were used, showed significant right pawedness on one test of lateral paw preference and left pawedness on another reaching test [112]. Among primates, though controversies still exist, a reassessment of the data seems to suggest that handedness is present after all [64] (but see also Ref. [70]). The lower primates seem to be left handed for holding food, whereas their right hand is stronger and used for holding on to the tree branches [110]. MacNeilage et al. [64] suggested that, as primates became less arboreal, the right hand became available for manipulation, with a shift to right handedness for fine motor acts. There is indeed some evidence in support of a right-hand bias in tool using by capuchin monkeys [113] and in manipulation by chimpanzees [54], but handedness varies between species of primates and, for example, orangutans show a left-hand preference to manipulated parts of their own faces, when cleaning the teeth, eyes of ears [88].

The criticism that the departure from an unlateralized 50:50 random distribution in these animal populations is typically small, compared to handedness in humans, has been questioned. Marchant et al. [67] showed that, when a wide range of everyday behavioural patterns of hand use in preliterate cultures was examined, the right handedness appeared to be consistent but rather weak (about 45:55 for left:right). The notable exception is hand preference in tool using, and particularly precision-gripping tool using and manipulative activities, which is markedly right-handed even in preliterate cultures. However, these specialised forms of hand use are not typical of the use of the limbs in most non-human species and there have been few studies of hand preferences in tool using by non-human animals.

As already mentioned, however, parrots and cockatoos that use their feet to manipulate food and objects with a high degree of sophistication have significant 'footedness' present at the population level with proportions similar to those of handedness of precision-gripping tool use in humans.

Another traditional criticism of the relevance of limb preference in animals to handedness in humans is that population limb preferences in animals are ''task-specific'' rather than ''true'' handedness, as in the case of humans [69]. But, again, the very existence of such a ''true handedness'' in humans is not clear cut. The ethological studies of Marchant et al. [67] show that humans are not as right-handed for *all* actions as it has long been assumed on the basis of the psychological literature.

When did limb preference evolve? Understanding the evolution of limb preference would be incomplete without an examination of the earliest tetrapods, the amphibians. Bisazza et al. [13] tested the common European toad *Bufo bufo*, using a task in which animals have to remove from the head an elastic balloon or a strip of paper. Results revealed a significant population preference for the use of the right forepaw to remove the balloon (59%) or the paper strip (55%). In another test, it was shown that the South American cane toad, *B. marinus*, uses the right forepaw preferentially (66%) to control rolling to an upright position after the body has been turned over and submerged in water. Simple explanations such as the claim that pawedness in toads merely reflects learning associated to emetic behaviour could be discarded. Naitoh and Wassersug [74] observed that the ingestion of toxic material by several species of frogs provokes vomiting, and in some cases the stomach itself is regurgitated. Before the prolapsed stomach is reswallowed, remaining vomitus is wiped from the gastric lining with the forepaw. These researchers suggested that a right forepaw preference in wiping tests might, therefore, have developed because asymmetric mesentery attachment causes the prolapsed stomach to hang to the right. However, Robins et al. [80] found that asymmetric use of the limbs also occurs for hindlimbs, which are not used in any wiping behaviour. Three species of toads (*B. marinus*, *B. viridis* and *B. bufo*) were overturned on a horizontal surface. In this condition the toad uses one of its hindlimbs actively to push against the substrate or throws a hindlimb across the body, thereby providing momentum for the righting response by displacing the body's centre of gravity. The other hindlimb assumes a more permissive role during this initial phase of the righting response. Owing to the operation of the hindlimbs, rotation of the pelvis and the pectoral girdle, and hence the involvement of the forepaws, is either secondary or incidental to the righting response. Both *B. marinus* and *B. bufo* toads revealed preferential right hindlimb use, whereas *B. viridis* revealed preferential left hindlimb use (interestingly, this species also showed a slight preference for left forepaw use in wiping tests [14]).

Handedness in toads is task- and species-specific, and its relation to anatomical asymmetries is still unclear. Asymmetries in the structure of the pectoral girdle have been reported [16,17] and they probably correlate with behavioural measures; however, they may be secondary to asymmetric contractions of the limb muscles rather than causing it.

Thus, 'handedness' in anuran amphibians clearly exists, with percentages of bias similar to those shown by, for instance, humans in the less 'manipulative' and demanding forms of manual activities [67]. Obviously, asymmetries in the use of the limbs by current living toads and by humans probably bear only weak relationships with each other: their functional significance in the two species are likely to be very different. It has been proved, however, that toads are also visually lateralized [108]. It cannot be excluded, therefore, that the roots of motor asymmetries can be traced back to even the early vertebrates.

6. Use of the eyes: from fish to humans (via toads and hens)

Recently, Corballis [27] suggested that cerebral asymmetry may have arisen from motoric rather than perceptual demands, on the grounds that there would be disadvantages in having a substantial degree of asymmetry in a perceptual system. The physical environment is in fact largely indifferent with respect to left and right (at least at the level which involves interactions with biological organisms); thus, a deficit on one side would leave the organism vulnerable to attack on that side, or unable to exploit prey appearing on one side. Moreover, predators might learn about systematic perceptual asymmetries in their prey and might exploit them. This would appear to be in agreement with data reported in the human neuropsychological literature: perceptual asymmetries are apparent only under extremely stringent (and unnatural) conditions, such as very brief presentations of stimuli (tachistoscopic viewing) or when there are competing inputs (dichotic listening). It appears that perceptual asymmetries in humans are seldom evident in normal everyday behaviour.

However, recent research on animal lateralization suggests that this just-so story could turn out to be incorrect. In fact, asymmetries in the use of the eyes seem to be ubiquitous among animals with laterally placed eyes. The first evidence came, once again, from birds. Dharmaretnam and Andrew [35] devised a method to study the lateral viewing of stimuli by chicks by allowing them to sit with their heads protruding through a hole in a wall and then, using videotaped recordings, they assessed each chick's pattern of fixation with the right or left eye. 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) with the left. More recent

work has confirmed that preferential eye use also occurs in adult hens [71]. Are these phenomena limited to the relatively restrained and unnatural conditions described in these experiments? They are not. It has been found, quite coincidentally by the way, that hens respond to playback of an aerial predator alarm call by turning their heads to one side to look up and they are more likely to use the left eye [37]. What is more interesting is that such perceptual asymmetries may influence motor behaviour, suggesting that the controversy about a perceptual or motoric origin of cerebral lateralization may be a matter of appearance rather than substance. For instance, Vallortigara et al. [106] studied detour behaviour in chicks faced with a barrier of vertical bars, behind which an imprinting object (a red ball) was located. Chicks showed a bias to detour the barrier on the left side, thus maintaining visual contact with the imprinting object using the lateral field of the right eye while circling around the barrier. When tested with a slightly novel version of the original imprinting object (i.e., a ball of a different colour), chicks showed a bias to detour the barrier on the right side, thus showing preferential left eye use. The same bias occurred when unfamiliar conspecifics were used as goal-objects. Results suggest 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 controlling the particular overt behaviour (see also Ref. [107]).

Research has shown that several species of fish show lateral asymmetries in detour behaviour very similar to those described here for the chick [9,10]. Male mosquitofish (*Gambusia holbrooki*) faced with an obstacle (a barrier of vertical bars) behind which a group of females was visible, preferentially circled around the obstacle in a leftward direction (thus maintaining fixation on the target with their right eye). The same bias was observed using a simulated predator (a fish lure used for open-sea fishing) as a target (that, in this species, induces detouring of the barrier to perform predator-inspection responses). The lateral asymmetry was task- and stimulus-dependent but, in each case, the bias was present at the group level. The asymmetry 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 using less attractive targets (i.e., a group of males or an empty environment). More recently, Bisazza et al. [12] have studied detour responses of the females of two species of poeciliid fish (*G. hoolbroki* and *Girardinus falcatus*) faced with a barrier of vertical bars through which conspecifics of different sex were visible (both species had already proved to show 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, whilst no bias was apparent in non-deprived females.

It may appear somewhat counter-intuitive that cerebral lateralization can impose differential use of the two eyes.

Biologically relevant stimuli would occur 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. This may be true for the initial detection of stimuli. However, it should be noted that sustained viewing in animals with eyes placed laterally is commonly monocular and therefore, after the initial detection and recognition, the choice of the right or left eye for viewing seems to be affected by lateralization of hemispheric function. The choice of right or left eye viewing would determine the type of visual analysis that follows. In fact, birds and fish may be able to bring into action the hemisphere most appropriate to particular conditions and to particular stimuli by using lateral fixation with the contralateral eye. Asymmetry in the visual projections to the hemispheres could underlie this eye/hemisphere bias.

Some mammals may show differential eye (and hemisphere) use also. White laboratory rats, for example, similar to birds, have eyes that are placed laterally and 95% of the fibers crossed over (see Ref. [20] for a review). Thus, direct monocular input is primarily to the opposite hemisphere. Consistent with this, rats tested monocularly can use spatial information to navigate in a maze provided that they are using the left eye (right hemisphere) but not when they are using the right eye [28]. Those mammals, including humans, with frontally placed eyes and accustomed to use obligatory conjugate eye movements to fixate stimuli of interest binocularly do not show any directly comparable phenomena. However, a lateralized mechanism somewhat similar to that observed in birds could be available to humans as well. The engagement of one or other hemisphere in verbal or spatial tasks is revealed by eye movements to the right or the left, provided that there are no external factors affecting gaze [49]. Also, direction of gaze to the left tends to promote analysis by right hemisphere strategies, while gaze to the right brings left hemisphere strategies into play [44]. Adjustment of head position and eye movements may thus play a similar role in mammals with frontal vision as does the choice for right or left lateral visual fields in birds.

Obviously, the complete decussation at the optic chiasma, in fish and birds (and also white rats), sets an initial eye bias on ascending inputs to the left and right sides of the brain but asymmetrical organization of the visual projections from the thalamus to the forebrain (see Section 4) ensures lateralized inputs to the higher visual centres. It should be noted that, even in mammals with incomplete decussation of optic fibres at the chiasma, 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, which cross to the contralateral hemisphere, are larger than those that arise from the lateral half of the retina and go to the ipsilateral hemisphere [15]. Fibers that cross the midline and go to the contralateral

hemisphere, therefore, conduct neural signals faster than the uncrossed fibers and they dominate the uncrossed fibers during binocular stimulation [77,109]. Consistent with this, eye preferences for viewing in both humans [1] and non-human primates [53,95] have been observed.

Perhaps the most notable demonstration of complementary eye use in a species with large binocular overlap was recently obtained with toads [108]. Prey catching behaviour was studied in three species of toads (the European green toad *B. viridis*, the European common toad *B. bufo*, and the cane toad, *B. marinus*, introduced to Australia) using a modification of the classic procedure known as the ''worm-test'' [38]. 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 was moving clockwise, and thus entered first the left and then the binocular field of vision, almost all of the tongue-strikes occurred in the right half of the binocular field. When the prey was moving anticlockwise, 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. Thus, it seems to be necessary for prey to enter the right half of the binocular visual field in order to evoke predatory behaviour. Initial detection in the left visual field does not allow the toad to show prey catching until the prey has moved into the right half of the binocular visual field. In contrast, initial detection of the prey in the right visual field allows the toad to orient towards and follow the prey and strike at it anywhere in the binocular field. Functionally, it is as if the toad shows a form of stimulus-specific visual 'hemineglect' in the left visual hemifield. Toads were also tested for agonistic behaviours in the form of tongue-strikes at competitors during feeding. Both *B. marinus* and *B. bufo* toads showed a population bias to strike with the tongue at other toads when these were occupying their left visual field [80].

A toad is more likely to attack prey to its right side (and ignore them on its left side) and to attack conspecifics to its left side (and ignore them on its right side). There is a striking similarity between the complementary behavioural lateralisations of toads described here and those found in 'higher' vertebrates. Use of the right eye in categorising food vs. non-food is well demonstrated in chicks [72] (and see Section 4) and in pigeons [48]. Also, chicks [93], lizards [29] and even baboons [25] are all more likely to attack conspecifics to their left sides. Therefore, despite substantial differences between species in the general structures of the brain and visual pathways, these particular functional specializations may be conserved throughout a wide evolutionary spectrum. Again, it is not the conservation of the direction per se that is crucial (i.e., left hemisphere for stimulus categorization and right hemisphere for attack and agonistic behaviours): we would not be surprised if some species had the opposite direction of lateralization, but we would be surprised if both of these functions are carried out in the *same* hemisphere.

7. When and why did brain lateralization arise?

At least some aspects of lateralization in tetrapods may have evolved from lateralization already present in fish. In organisms with laterally placed eyes and without bilateral input to both sides of the brain, dominance of one side of the brain for the controlling of responses would prevent the simultaneous initiation of incompatible responses to stimuli on both sides of the body. In organisms with a large area of binocular overlap, the same strategy could be maintained for stimuli perceived in the extreme lateral monocular fields, and which are likely to evoke turning. Control of a medial organ, such as the tongue, is constrained by the problem of avoiding the simultaneous initiation of incompatible turning/aiming responses to stimuli presented simultaneously on the left and right sides. In toads and frogs, for example, both prey catching and agonistic responses make use of a medial organ, the tongue. Frogs can select between prey objects seen initially in each monocular visual field, and it has been hypothesized that commissural pathways may play a critical role in inhibition of responses by one side of the brain [58].

When exactly did lateralization first evolve? Fossil records show that the most primitive chordates (calcichordates) were asymmetrical in the head region [59], and chordate ancestors at one time lay on the right side thereby receiving different sensory inputs through structures on the left and right sides of the body [60]. It is clear that lateralization of perceptual functions is ancient, first occurring probably just after the brain duplicated itself into two halves. We have discussed how there may be an advantage (possibly more than one) in having asymmetries between these two halves. It is perhaps less clear why asymmetries should manifest themselves at the *population* level. In the case of predation, a population bias for motor responses may be a disadvantage because predators could learn this bias and use it to their own advantage. In fact, organisms with asymmetries at the individual but not population level might be favored because they possess the computational advantages of having a lateralized brain but lack the disadvantages associated with predictable lateral biases (actually, the behaviour of an individual would be predictable under repeated trials, but not at first encounter on the basis of a general sampling of the individuals of the same species in the population). The explanation probably lies in the fact that in most circumstances the best for an individual depends on what is best for the majority of other individuals. In other words, sociality and gregarious behaviour could have provided the selective pressures to align the direction of the asymmetries in most individuals of a population. As the phylogenetic tree in Fig. 1 shows,

not all species are lateralized at the population level, but all species that show gregarious behaviour are lateralized at population level. Solitary species are more likely to show lateralization at the *individual* level. (The correlation is far from perfect, in that about 40% of the species classified as ''non-social'' exhibit lateralization at population level, but obviously social behaviour is a matter of degree rather than an all-or-none phenomenon.)

In schooling fish, a population bias for turning in the same direction may be an advantage because it would keep the school together, and this might outweigh the disadvantage of being predictable by predators. All of these considerations have interesting consequences that could be tested empirically. Furthermore, these issues provide a link between the fields of comparative neuroscience and evolutionary biology.

It is common for pairs of fish to leave their shoal in order to approach and inspect a potential predator [65,66]. In such cases, both fish shared the risk of being preyed upon, but not if one of the fish remains at a distance. The fish are thus believed to face a classical Prisoner's Dilemma in this situation, and predator-inspection behaviour has been used as a model to analyze the evolution of mutual cooperation among unrelated individuals. Milinski [73] 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 non-cooperative partner). Recently, Milinsky's original procedure was duplicated in order to check for the effects of positioning a mirror on either the left or the right side of the fish [8]. It was found that cooperative 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. hoolbroki*. (The effect cannot be due to asymmetries of the predator because control experiments with right–left inverted video images confirmed the asymmetry [8].) This demonstrates once again that in animals with laterally placed eyes the visual scenes seen on the right and left sides may evoke different types of social behaviour, as a result of differing modes of analysis of perceptual information carried out by the left and right sides of the brain. Moreover, it provides a striking demonstration of how perceptual (and consequently motor) asymmetries play a crucial role in everyday behaviour of biological organisms.

Population biases may also be important for other aspects of social behahaviour. Groups of young chicks with a population bias for visual lateralization (exposed to light before hatching) form more stable social hierarchies than groups of chicks without a population bias (incubated in the dark, see also Section 4) [91]. Environmental demands for interaction exploration vs. more cautious observation might also affect population biases for some forms of lateralization. We draw this inference from recent studies showing that right-handed primates exhibit more interactive exploration than left-handed ones (chimpanzees [55]; marmosets [22]). This relationship between hand preference and exploration may reflect a population bias for hemispheric specialization coupled with dominance of the hemisphere opposite to the preferred hand, at least in some contexts.

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