Introduction

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Interest in lateralization of function in a non-human vertebrate species was stimulated by Fernando Nottebohm's finding of differential effects on song production of sectioning the left and right tracheosyringeal nerves supplying the musculature of the avian syrinx (Nottebohm, 1971). He found that, in the canary, severing the left nerve impairs singing, whereas severing the right nerve has no effect on song. Within the next decade, such lateralization of song control had been traced to centres in the forebrain (Nottebohm, Stokes and Leonard, 1976), and Victor Denenberg and colleagues had discovered lateralization in the rat brain for control of activity and emotional responses (Denenberg et al., 1978; Denenberg, 1981). The latter had also been reported by Bianki, whose work received less recognition in the Western world largely because he was based in Russia (in translation Bianki, 1988). Also, in the next decade, lateralization for visual responding had been discovered in the domestic chicken brain, shown first by unilateral treatment of the forebrain hemispheres with either cycloheximide (Rogers and Anson, 1979) or glutamate (Howard, Rogers and Boura, 1980). Treatment of the left hemisphere led to a set of behavioural changes that differed from those resulting from the same treatment of the right hemisphere. Later it was found that the behavioural lateralization in the chick was matched by asymmetry in the visual projections from the thalamus to the Wulst region of the forebrain (Rogers and Sink, 1988) and that glutamate treatment of the Wulst reveals lateralization by stimulating neural transmission in the Wulst (Rogers and Hambley, 1982) and enhancing the growth of visual projections unilaterally (Khyentse and Rogers, 1997).

Knowledge of lateralization in these species became a basis for a series of in-depth studies. This development was greatly assisted by the recognition that lateralization in birds, and in other species with optic nerve fibres completely crossed at the chiasma, can be revealed by testing the animals monocularly (Mench and Andrew, 1986). Not only did the technique of monocular testing to reveal lateralization simplify the procedure for revealing lateralization, but it also met ethical guidelines for research more adequately, and so laid the basis for investigating lateralization in species living in their natural environment. Once it was clear that chicks tested using the right eye performed very differently from those using the left eye (Andrew, 1983; Rogers, Zappia and Bullock, 1985), it was a logical step to assume that animals with eyes placed laterally on the sides of their head would respond differently to stimuli detected on their left and right sides (Andrew and Dharmaretnam, 1991) and, in other cases, choose to view particular stimuli with either their left or right eye. First demonstrated clearly in the chick (Andrew and Dharmaretnam, 1993), eye preferences for viewing can be measured without a great deal of difficulty and can now be applied to study of animals in the wild.

The study of lateralization has so expanded over the last two decades that it is no longer seen merely as an interesting idiosyncrasy of a few species (admittedly including our own), but instead as a key property of most or all vertebrates. Until recently, investigation of lateralization in species other than humans was neglected, largely because of the widespread notion that lateralization was unique to humans. Indeed, so long as lateralization was seen as intimately linked to tool use, consciousness and language, no other conclusion was possible. It is now obvious that this earlier assumption was incorrect. Some researchers, while recognizing the existence of lateralization in nonhuman species, then developed the idea that human uniqueness resided in the fact that humans are more lateralized than all other species (Corballis, 1991). This too is incorrect, as many examples in various chapters of this book show. Not only is lateralization common in vertebrates, but there also appears to be a common pattern of lateralization that evolved at least as early as fish, which has been retained amongst all of the major groups of vertebrates.

At a statistical level there are two kinds of lateralization. One is present in individuals within a population but is inconsistent between individuals, so that there is no overall bias in the population (or species) as a whole. Handedness in rats and mice is the best known example of this kind of lateralization: half of a population is left-handed for retrieving food and the other half is right-handed (Collins, 1985). The other kind of lateralization is present at the population level as well as in individuals. In this case, the majority of individuals are lateralized in the same direction so that a frequency histogram for the population is skewed to the right or left side of the no-preference value. Lateralization for control of activity or emotional responses in rats fits this kind of distribution. It also shows that, within one species (rats in this case), there may be lateralization of both the first and second kinds depending on the behaviour scored.

Different kinds of lateralization occur at different levels of neural organization. To use the example of rats again, there are cortical lateralizations, occurring at both the individual and population levels, and also lateralizations occurring at hypothalamic level (Nordeen and Yahr, 1982). It is likely that the presence of different types of lateralization at different levels of neural organization explains why individual-level and population-level lateralization can coexist in the same species. Learning and individual experience may also modulate lateralization at different levels of neural organization.

The book is divided into four parts. The first part considers the evolution of lateralization of the type present at the population level and, in so doing, traces it back to the primitive chordates. Remarkably, it seems the basic pattern of lateralization that first evolved has been retained by fish, amphibians, birds and mammals, even primates. The resilience of this basic pattern suggests that it confers an advantage to the individual and to the population. Possible advantages, as well as disadvantages, of being lateralized are, therefore, discussed.

The second part discusses development of lateralization and how shifts in which hemisphere is in control at different ages determine transitions in behaviour as development takes place. The effect of early visual experience before and after hatching on lateralization is discussed and so is maternal influence on the development of hand preferences in primates. The role of the corpus callosum is important in the lateralization of the mammalian brain, and one chapter discusses its development and the influence of sex hormones on its development.

Cognition and lateralization form the basis of Part Three. The basic pattern of lateralization, it seems, is common to the visual, auditory and olfactory senses. The eventual evolution of language and its lateralization deserves reconsideration on this basis. Moreover, lateralized responding of primates to vocalizations and asymmetry of facial muscle movement in primates when communicating by facial expressions have allowed the identification of precursors to lateralization in humans. In addition, this section presents evidence for unexpected cognitive abilities of young chicks and relates them to hemispheric specialization.

Finally, in Part Four, lateralization of memory processes, both biological and behavioural, is discussed. Using the young chick as a model, a large number of studies have revealed neurochemical asymmetries in different regions of the forebrain. These are related to specialized use of the hemispheres in memory formation and recall.

Many chapters mention lateralization in humans, in comparison to lateralization in animals. Thus, the evolution of hemispheric specialization in humans is considered in a number of contexts and placed within the broader scheme of comparative vertebrate lateralization.

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Part One

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1

How Ancient is Brain Lateralization?

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1.1. Introduction

This chapter is devoted to discussion of the evolution of lateralization. We have limited ourselves to vertebrates, and concentrated in particular on the so-called lower vertebrates (i.e. fishes, amphibians and reptiles). We think that we should declare our position from the start: we believe that, in its basic and fundamental form, lateralization among higher vertebrates (i.e. birds and mammals) is a phenomenon of homology (i.e. that it has been inherited from a common ancestor). We also believe that important clues to the evolution of lateralization can be obtained by investigation of extant vertebrate forms, particularly fish, which are likely to come closest to retaining the original conditions under which lateralization probably first appeared in early chordates.

1.2. A Brief History of the Comparative Study of Lateralization

The discovery of functional brain lateralization in the human being is associated with the classical observations by Broca in 1861 and, more recently, its study received renewed impetus from the work carried out on split brain patients by Sperry and his associates in the 1960s.

Interestingly, for a very long time it was maintained that there were no anatomical data that could be associated with functional asymmetries in humans (von Bonin, 1962). The first contrary evidence came in 1968, when Geschwind and Levitsky reported that the planum temporale, which is part of Wernicke's area, is larger in the left than in the right hemisphere. Thus, in humans, observations on functional asymmetries preceded evidence of structural asymmetries. Quite the opposite occurred for research on non-human animals, though the story is less widely known.

The existence of structural asymmetries in the brain (particularly the diencephalon) of vertebrates was common knowledge among neuroanatomists at the beginning of the century (see Braitenberg and Kemali, 1970; Harris, Guglielmotti and Bentivoglio, 1996). For instance, Gierse (1904, quoted in Shanklin, 1935) reported the right habenular nucleus to be larger than the left one in the fish *Cyclothone acclinidens*; Johnston (1902) and Roethig (1923, quoted by Frontera, 1952) reported a vastly preponderant right habenulo-peduncolar tract in the lamprey Petromyzon. All of this very early evidence of animal lateralization came from lower vertebrates.

Subsequently any mention of these anatomical asymmetries disappeared from textbooks (see Braitenberg and Kemali, 1970) and apparently nobody searched for evidence of functional asymmetries in fishes, amphibians and reptiles for a very long period of time.

In the 1970s and early 1980s, came the results of Fernando Nottebohm with songbirds (Nottebohm, 1971, 1977; Nottebohm et al., 1990) and those of Lesley Rogers (Rogers and Anson, 1979) and Richard Andrew (Andrew, Mench and Rainey, 1982) with chickens, demonstrating both structural and functional lateralization in the avian brain (see also Andrew, 1983, 1988, 1991). At the same time Victor Denenberg (Denenberg et al., 1978) and Stanley Glick (Glick and Ross, 1981) reported lateralization in rodents; Denenberg also provided the very first comprehensive review of the subject (Denenberg, 1981), which was instrumental in producing a cascade of data from a variety of avian and mammalian species, summarized by Bradshaw and Rogers (1993).

We return at this point to cold-blooded vertebrates and the associated evolutionary issue: did brain lateralization evolve independently in birds and mammals by sheer coincidence? It is perhaps possible that, in the course of evolutionary history, similar solutions have been independently provided to similar problems in phylogenetically disparate species. Note that lineages of the amniote groups separated about 300 million years ago from the ancestral 'stem reptiles'. Alternatively, it is possible that lateralization in birds and mammals was inherited from common ancestors.

If two species with a common phylogenetic history exhibit structurally similar traits, we call such traits homologous (Campbell, 1988); if two species lack a common phylogenetic history but exhibit structurally similar traits, we call such traits homoplasic (Hodos, 1988). Homoplasy results because even distantly related species may evolve the same solution, selected from a limited set of possible adaptive solutions to the same environmental problem. 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 find out what these forces might have been. If cerebral asymmetries of birds and mammals are homologous, we should find widespread traces of lateralization among current living fishes, amphibians and reptiles. In order to make an argument for homology, therefore, it is crucial for lateralization among lower vertebrates to be a widespread phenomenon. We therefore start with a short review of the current evidence for lateralization among fishes, reptiles and amphibians. More detailed reviews are given by Bisazza, Rogers and Vallortigara (1998) and Vallortigara, Rogers and Bisazza (1999).

1.3. Evidence for Lateralization in Fish, Amphibian and Reptilian Species

Table 1.1 summarizes the current evidence for lateralization (both functional and structural) in lower vertebrates. This is discussed under three headings: anatomical, motor and sensory asymmetries. Such subdivisions and terminology are simply based on convenience and do not necessarily correspond with any important theoretical issue. We discuss first asymmetries that are present at the population level (see Section 1.5 for a discussion of asymmetries at the individual level).

1.3.1. Anatomical Asymmetries

Left–right asymmetries in brain anatomy are ubiquitous in lower vertebrates. The habenular nuclei, located in the anterior dorsal diencephalon, behind the epiphysis (pineal gland), on either side of the third ventricle, are markedly asymmetrical in size in cyclostomes (lampreys and hagfish), sharks, and some teleost fish and amphibians (reviewed in Walker, 1980; Bradshaw and Rogers, 1993). Braitenberg and Kemali (1970) reported marked differences between the right and left habenular nuclei in a frog (*Rana esculenta*), newt (*Triturus cristatus*) and eel (*Anguilla anguilla*). In all three species the left habenula was found to be more lobate than its right counterpart. In the frog, the asymmetry is particularly striking because the left habenula consists of two distinct nuclei, whereas the right habenula has a single nucleus only. An asymmetry similar to that described by Braitenberg and Kemali in *Rana esculenta* has been reported in *Rana temporaria* by Morgan, O'Donnell and Oliver (1973). These authors also reported that tadpoles and young frogs are asymmetrical as well. The left nucleus is partially divided by a vertical septum, lacks cells adjoining the third ventricle along part of its length and

Table 1.1. *Evidence for brain asymmetries in cold-blooded vertebrates. Reference to studies where laterality has been shown only at the individual level is underlined*

	Type of asymmetry		
Species	Sensory	Motor	Anatomical
Chordata			
Amphioxus			Kappers et al. (1936); Young (1962)
Jawless fish			
Petromyzon			Braitenberg and Kemali (1970);
Myxine glutinosa			Braitenberg and Kemali (1970)
Cartilaginous fish			
Sharks			Kappers et al. (1936)
Bony fish			
Gambusia holbrooki	Bisazza and Vallortigara (1997); Bisazza, Pignatti, and Vallortigara (1997a, b); Bisazza and Vallortigara (1997); Bisazza et al. (1998); Bisazza, De Santi and Vallortigara (1999); Bisazza, Facchin, and Vallortigara, (2000); Sovrano et al. (1999); De Santi et al. (2001)	Bisazza and Vallortigara (1996); Bisazza, Pignatti, Vallortigara (1997a); Bisazza et al. (1998)	
Gambusia nicaraguensis	Bisazza, Pignatti, and Vallortigara (1997a)		
Girardinus falcatus	Bisazza, Pignatti, and Vallortigara (1997b); Bisazza et al. (1998); Facchin, Bisazza and Vallortigara (1999); Bisazza et al. (2000); Bisazza, Facchin and Vallortigara (2000)	Cantalupo, Bisazza and Vallortigara (1995); Bisazza et al. (1998).	