1

Introduction

> *Once the emperor Hui Tsung was enjoying the sight of a lichee tree laden with fruit before the palace when a peacock approached the tree, and he summoned his artists at once to make a picture. They produced a magnificent painting of the peacock with its right foot poised to take a step on a flower-bed: but to their surprise the emperor shook his head over it. A few days later when he asked if they had discovered their mistake, they had no answer ready. Then Hui Tsung told them: 'A peacock always raises its left foot first to climb.'*
>
> Cheng Chen-To, Chang Heng and Hsu Pang-Ta (1957)

Summary

Once thought to be unique to the human brain, lateralization of structure and behaviour is now known to be widespread in vertebrates and, furthermore, it has a similar plan of organization in the different species. This chapter introduces the basic pattern of lateralization of vertebrate species and does so in a historical context to highlight the fact that, until some 20 years ago, it was widely and incorrectly assumed that having a lateralized brain was a mark of the cognitive superiority of humans. It also introduces some of the new evidence showing the presence of lateralization in invertebrate species.

1.1 Introduction

It is difficult to understand why incorrect ideas in science sometimes establish such deep roots that it is very difficult to eradicate them. Paul Broca, the French physician and anthropologist, is numbered among the founders of research on brain asymmetry. Discussing left–right differences in the brain, in 1865 he wrote, 'there is a less but still very evident degree of dysymmetry in the great apes' (Broca, 1865, p. 527). Judging from the excerpt above on the emperor and the peacock (see also Humphrey, 1998) and from notes on foot preferences in

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parrots (Harris, 1989), the existence of asymmetry in the behaviour of animals had been acknowledged for a very long time, but outside academic circles. Until relatively recent years, however, textbooks of neuroscience and psychology referred to brain asymmetry as a uniquely human attribute, linked to superior cognitive abilities of our species and, in particular, to language.

Maybe this omission should be considered a late outcome of a mistaken concept of evolution based on the ancient idea of *Scala Naturae* (see Hodos and Campbell, 1969). Yet, even assuming that certain phenomena such as the handedness so conspicuous in human behaviour were not so clear in other animals (dismissing for the moment that this could have been simply because other species do not have or do not use appendages in any way similar to that of humans), the raw facts of anatomy should have been difficult to dismiss. Consider the evidence for anatomical asymmetries at the level of the midbrain or diencephalon (which we shall discuss in detail in Chapters 3 and 5). Diencephalic asymmetries were common knowledge among neuroanatomists at the beginning of last century (see Braitenberg and Kemali, 1970). For instance, habenular asymmetries, referring to a collection of cells in the dorsal thalamus of the brain, had been observed in the most primitive living vertebrates, the jawless fish (Cyclostomes), e.g. the lamprey (see Braitenberg and Kemali, 1970). However, any mention of these asymmetries subsequently disappeared from anatomy textbooks, and they have been re-discovered only

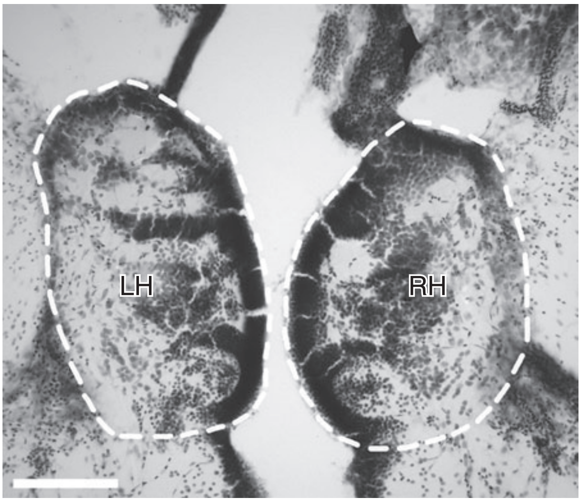

Figure 1.1 Habenular asymmetry in the convict cichlid fish. Brightfield microphotograph of a coronal section through the habenula of a female convict cichlid (*Amatitlania nigrofasciata*). In this individual, the left habenula is 28.01% larger in volume than the right (calculated by measuring areas on many sections). The laterality index is –0.123. Scale bar = 200 μm. Microphotograph courtesy of Professors Peter L. Hurd and Cristian Gutierrez.

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recently. An example is shown in Figure 1.1, which depicts habenular asymmetry in the convict cichlid fish *Amatitlania nigrofasciata*, where the left habenula is larger than the right (Gutiérrez-Ibánezfoun *et al*., 2011).

Turning from brain structure to function, we must wait until the late 1970s or early 1980s for the first evidence of functional lateralization of the animal brain. Perhaps as an illustration of the operating of the Zeitgeist, more or less simultaneously Fernando Nottebohm (1971, 1977) reported asymmetrical control of song production in two species of songbird; Lesley Rogers (Rogers and Anson, 1979) reported functional asymmetries in domestic chicks; and Victor Denenberg (1981) reported asymmetries in rats. The techniques used to reveal these asymmetries were severing of nerves that control singing, injection of a pharmacological agent into one or the other hemisphere of the brain and placement of unilateral lesions on the left or right side.

Nottebohm's findings were probably the most well known outside the realms of neurobiologists specializing in avian and rodent anatomy and behaviour, because they seemed to provide a direct link to lateralization of language in the human brain (see Chapter 5). Cutting of the branch of the left hypoglossal nerve, which innervates the muscles on the left side of the syrinx, the organ producing song in birds, severely impairs the bird's ability to produce song, whereas lesions of the equivalent nerve on the right side have no effect on song. Similar results are produced by lesions of the left, but not the right, higher vocal centres in the brain (Nottebohm *et al*., 1976; Nottebohm, 1977, 1980).

More recent research has confirmed these findings, although species differences seem to exist (Schmidt *et al*., 2004). Moreover, hemispheric specialization has been observed for perception, rather than production, of song by passerine birds. George *et al*. (2004) recorded neuronal responses in the primary auditory area of the songbird brain, the Field L complex, to species-specific and artificial sounds in both awake and anaesthetized male starlings (*Sturnus vulgaris*). They found significantly more responsive neurons in the right hemisphere than in the left hemisphere of awake birds, and this difference was significantly reduced in anaesthetized birds. Clear hemispheric specialization towards categories of behaviorally relevant stimuli and precise parameters of these stimuli were found in awake birds: the right hemisphere responded most strongly to species-specific sounds, particularly to familiar vocalizations and bird's own individual-specific whistles, and the left hemisphere responded to unfamiliar individual-specific songs. When the birds were anaesthetized, the left hemisphere responded more than the right to artificial, non-specific stimuli. Furthermore, it is known that songbirds are able to discriminate between their own song and the songs of conspecifics. Using functional magnetic resonance imaging (fMRI), Poirier *et al*. (2009) showed that this selectivity is present at midbrain level in adult male zebra finches (*Taenopygia guttata*) and lateralized towards the right side.

It has been argued that control of speech in humans is made possible by two distinct mechanisms: a feedback control mechanism, by which speech

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production is monitored during speaking and any deviation from the expected signal is corrected on the basis of auditory information, and a feed-forward control mechanism, by which speech is produced on the basis of previously learned commands, without reliance on incoming sensory information (Guenther, 2006). Tourville *et al.* (2008) suggested that, while the left lateralization of speech production deduced from studies using lesions would reflect left lateralization of the feed-forward control system, right lateralization of the auditory feedback control would explain the importance of the right hemisphere observed in numerous aspects of speech production, such as self-recognition processes (Fu *et al.*, 2006). The latter seem to be lateralized to the right hemisphere in both the auditory (Rosa *et al.*, 2008) and the visual modality (Keenan *et al.*, 2001). It is possible that the right lateralization to discriminate between the bird's own song and other conspecific songs, as found in zebra finches (see above), is due to a right lateralization of the auditory feedback control system, suggesting important anatomical and functional similarities between birds and humans.

Discovery of lateralization in domestic chickens (Rogers and Anson, 1979) is interesting because, in contrast to other examples, such asymmetry was not actively searched for but rather observed serendipitously. The same was the case in later research on domestic chicks: for example, lateralization of imprinting memory constituted a nuisance for research on the biological bases of memory.[1]

Intracranial injection of substances that interfere with memory consolidation was used widely as a tool for investigation of memory consolidation and the domestic chick as an animal model for such research (see for reviews Andrew, 1991b). At the time it was implicitly assumed that the site of the injection, to the left or to the right hemisphere, would be immaterial. Lesley Rogers, however, proved for the first time that injecting cycloheximide (an inhibitor of protein synthesis) into the chick's left hemisphere produced distinct effects on visual discrimination learning and auditory habituation that were absent when the injection was performed in the right hemisphere (Rogers and Anson, 1979).

In a similar vein, in the early 1970s a research group formed by the ethologist Patrick Bateson, the anatomist and neurobiologist Gabiel Horn and the neurochemist Steven Rose started to use the phenomenon of filial imprinting (a process by which young precocial, nidifugous birds come to recognize their mother and social partners by being exposed to them briefly) in the domestic chick as a model-system for investigation of the biological bases of memory (Horn *et al.*, 1973). After identification of a plausible area of the brain as a putative candidate

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[1] A remarkable comment by neurochemist Steven Rose on Sir John Eccles's claims about lateralization in humans may serve as advice to those who, with little mastering of biological literature, would still argue about human uniqueness as to brain asymmetry: 'But if Eccles did turn out to be right, and functional lateralization is the key to possession of a soul, then any of my chicks would have as good claims as Sir John to possessing one' (Rose, 1992, p. 249). Eccles could be excused at the time, but more recent epigones cannot be so.

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for the site of storage of imprinting memories, the intermediate medial mesopallium (IMM, an associative area of the chick forebrain), researchers started a series of control experiments to disentangle specific effects of learning from non-specific brain activation related to sensory and motor activity associated with exposure to the imprinting stimulus. The assumption was that imprinting processes in the left or the right hemisphere would be the same. However, results from sequential lesioning experiments at various times after imprinting and analyses of plastic changes at the synapses soon revealed an unexpected pattern of lateralization. Evidence suggested that both the right and the left IMM act as short-term memory stores, but only the left IMM is used as a long-term store (Cipolla-Neto *et al.*, 1982). The right IMM is crucial in establishing another store, somewhere outside the IMM region, referred to as S′. The right IMM passes information on to S′ over a period of several hours. It has been suggested that passing of the memory from the right IMM 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 IMM (see Horn, 1985, 2004).

Another experimental paradigm mostly used in research on the biological aspects of memory formation is the so-called passive avoidance learning (PAL) task, originally introduced by Cherkin (1969) to test chicks. The standard version of the task involves the presentation of a coloured (e.g. red) bead, at which chicks will readily peck, coated with a bitter-tasting substance. After this training, chicks will subsequently avoid pecking at a bead of similar colour and size (but not at a bead of a different colour, e.g. blue) (Lössner and Rose, 1983). Long-lasting learning occurs after a single and sharply timed experience (pecking the bitter bead), enabling scientists to study the time course of memory formation with great precision. The formation of a memory of the PAL task occurs over the course of hours, with a range of well-documented biochemical, physiological and morphological changes occurring mainly in the intermediate medial mesopallium, but also in structures such as the medial striatum, StM (Rose, 2000). In the hours following training the memory trace becomes fragmented and redistributed in different structures. In particular, circuits in the IMM might retain some aspects of the memory trace (e.g. the colour of the bead), whereas other aspects (e.g. the size and shape of the bead) might be encoded by the StM (Rose, 2000). The changes observed at different levels in chick's forebrain, after the training experience, are associated with different memory phases (short-term, intermediate-term and long-term memory), defined on the basis of sharply timed on/offsets of sensitivity to different amnesic agents and memory loss at specific times after training (e.g. Gibbs *et al.*, 2003), as well as brief enhancements of memory recall (Andrew, 2002a).

While studying the time course of memory formation, the presence of structural and functional lateralization was noticed. Evidence seemed to indicate that the memory for the standard PAL task forms mainly in the left hemisphere. A seminal finding was that bilateral or left, but not right, lesions of the mesopallium made before training resulted in interference with acquisition of the task (Patterson *et al.*, 1990). Moreover, unilateral injections of the amnesic agents used to determine memory phases revealed that, in most cases, the timing of the effects of left hemisphere injections was identical with that of bilateral injections (Gibbs *et al.*, 2003). The trace encoded by the left hemisphere is, therefore, considered to be largely responsible for subsequent performance and for the processes involved in the phases of memory formation, since injections of amnesic agents into the right hemisphere are usually ineffective (Gibbs *et al.*, 2003). In particular, a crucial left hemispheric involvement might be prevalent in the earlier stages of memory formation, with participation of the right hemisphere in later encoding (e.g. Rickard and Gibbs, 2003a, 2003b), such as during the intermediate-term memory phase (Gibbs *et al.*, 2003). This is also consistent with biochemical evidence showing that the memory trace appears to consolidate first in the left mesopallium and then in the right (Sandi *et al.*, 1993).

The involvement of the right hemisphere in intermediate-term memory (manifested in a transitory susceptibility to amnesic agents during that phase) suggested that there is normally an interaction between left and right hemispheres at this stage (even though the left hemisphere seems to be still the dominant one). A putative function of this sort of interaction would be that of establishing linkages between the memory traces held in the two hemispheres, each encoding different aspects of the same experience (Andrew, 1997, 1999). Thus, the successful consolidation of memory traces would depend on the integration of information about the learning task encoded in both hemispheres. When the trace of the right hemisphere is degraded, due to the effect of amnesic agents, the interaction between the two hemispheres leads to a decrease of performance.

The predominant role of the left hemisphere in memory formation for the standard PAL task is likely to be due to its importance for the control of motor ‘manipulative’ responses towards objects, including those performed with the chick’s beak (Andrew *et al.*, 2000). In addition, the left hemisphere has a role in the discrimination of local, specific cues associated with a target (such as the colour of the bitter-tasting bead that allows the chick to tell it apart from a neutral bead; see Vallortigara *et al.*, 1996; Tommasi and Vallortigara, 2001). Whereas the information stored by the left hemisphere is about the properties of objects to be manipulated, the detailed representation encoded in the right hemisphere involves mainly elements such as position and spatial context (as will be discussed in the next sections).

The possibility of establishing use of the chick as an ideal experimental model for the study of brain lateralization was then complemented by the first experimental evidence of visual lateralization in an intact non-human animal. This was shown by Richard Andrew using temporary occlusion of either the left or right eye (Andrew *et al.*, 1982; Figure 1.2), which takes advantage of the virtually complete decussation (crossing over the midline) of optic nerve fibres at the optic chiasma in birds with laterally placed eyes.

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Figure 1.2 Monocular testing. A chick wearing an eye-patch for behavioural tests of brain lateralization. Photograph courtesy of Dr Cinzia Chiandetti, laboratory of Professor Giorgio Vallortigara.

Andrew *et al.* (1982) showed that the right eye was better at discriminating visual stimuli, such as grains from pebbles, and that the left was more reactive to emotionally charged stimuli (note that this result is consistent with the findings of Rogers and Anson, 1979). Charles Hamilton, a former pupil of Nobel Prize winner for research on split-brain patients (Roger Sperry), commented: ‘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). The results were duplicated and extended to several other species, and the basic pattern of hemispheric specialization confirmed (reviewed by Vallortigara, 2000; Rogers, 2002a; Rogers and Andrew, 2002).

The field of research on lateralization in animal models is nowadays huge and rapidly expanding. Although studies of lateralization in non-human species is clearly at odds with the idea that cerebral asymmetry is a unique characteristic of humans, there could be specifically human abilities that are also lateralized (for example this is likely to be the case in aspects of language). However, although evidence of lateralization in non-human animals is now penetrating into textbooks (e.g. Breedlove *et al.*, 2010), we are not persuaded that neuroscientists have a clear perception of how widespread it is in non-human species. The reason is that the literature reporting lateralization is sparsely distributed in a variety of journals, mostly of ethology, behavioural biology and animal neuroscience. This state of affairs provided an impetus for writing this book.

The aim of the book and of this first chapter in particular is not to provide the reader with an exhaustive review of the evidence for animal asymmetries in brain and behaviour, because several specialized reviews cover this (Rogers, 2002a; Rogers and Andrew, 2002; Vallortigara and Rogers, 2005; Vallortigara *et al*., 2011). Here we want to provide a general overview of research on animal lateralization, showing the variety of species, methods and findings currently available, and trying to make a little sense of it.

1.2 Handedness and other motor asymmetries

The most notable example of lateralization in humans is right-handedness, and given that both language and right-handedness are functions of the left hemisphere (e.g. Santrock, 2008), it has been argued that they could be in some way linked (e.g. Broca, 1865; Hellige, 1993a, 1993b). Humans exhibit 90% right-handedness (McManus, 2002) and within this population approximately 95% of individuals have language-processing regions situated in the left hemisphere of the brain (Lurito and Dzemidzic, 2001). However, the nature of the link between right-handedness and language is hotly debated (Corballis, 2002, 2003; Vauclair, 2004).

It has long been denied that non-human animals show differences in the use of their limbs in any way comparable to human handedness, and early research on great apes, our closest relatives, seemed to confirm this view. Historically, with only one exception (Boleda *et al*., 1975), results suggested that great apes did not express a right-hand population bias similar to humans (e.g. Finch, 1941; Marchant and Steklis, 1986). However, this view has been completely changed by a re-analysis of the data on hand preferences in primates by MacNeilage *et al*. (1987) and more recent systematic investigations with large sample sizes. Right-hand biases in great apes have been reported in captive chimpanzees (*Pan troglodytes*), related to complex manual tasks such as bimanual feeding, coordinated bimanual actions, bipedal reaching and throwing (for reviews, see Hopkins 2006, 2007), and in captive gorillas (*Gorilla gorilla*) (Byrne and Byrne, 1991; Meguerditchian *et al*., 2010a) for bimanual coordinated actions. Criticisms were raised about these initial reports, arguing that they were based on single laboratory samples (reviewed by McGrew and Marchant, 1997; Papademetriou *et al*., 2005), or on methodological and theoretical grounds (McGrew and Marchant, 1997; Palmer, 2002, 2003) and the suggestion that apes' exposure to human culture might have induced a bias of hand use in manual actions (e.g. McGrew and Marchant, 1997). However, such criticisms appear to be untenable since new data in support of a right-hand bias continues to mount from an increasing number of great ape species for a range of manual actions (e.g. Hopkins *et al*., 2004; Llorente *et al*., 2009; Meguerditchian *et al*., 2010a, 2010b; Llorente *et al*., 2011) across both captive and wild settings (Lonsdorf and Hopkins, 2005;

Llorente *et al.* 2011). Moreover, the controversy concerning whether handedness is observed only in apes in captivity, and therefore is possibly an artefact of apes imitating the right-handedness of their human caretakers, was dissolved recently by a large meta-analysis of studies on 1524 great apes, which revealed that right-handedness in chimpanzees and bonobos manifests itself irrespective of rearing conditions (Hopkins, 2006).

It has been argued, however, that the departure from a random distribution in these animal populations is typically small, compared with handedness in humans. The ratio of right- to left-handed chimpanzees is about 2:1 or 3:1 (in the case of gesturing and throwing), which is lower than most reports of handedness in various human cultures (Annett, 2006). This argument, however, should be taken with caution. Although right-handedness in humans appears to be a robust and universal finding (Perelle and Ehrman, 1994; Raymond and Pontier, 2004) the evidence that supports a 90% right-handed and 10% left-handed population split is mainly derived from self-report questionnaires in literate populations (e.g. Oldfield, 1971; Hardyck *et al.*, 1975; McManus, 1981). Although questionnaires rely primarily on measures of precision tool use, handedness patterns become more complex when a more ethological range of factors is considered, and right-handedness can then vary between 70 and 90% (Annett, 2002). Marchant *et al.* (1995) tracked naturalistic handedness across three different pre-literate populations and noted that, while there was an overall consistent but rather weak right-hand dominance (about 45:55 for left:right), individuals were mixed-handed for all actions across a comprehensive range of ethological measures with the exception of tool use, which was distinctly right-handed. Further studies in traditional cultures have shown that the percentage of left-handedness fluctuates widely (3–27%) (Faurie and Raymond, 2005; see Chapter 2). Most important, it should be considered that 70% of left-handers still exhibit a left hemisphere dominance for language functions (e.g. Knecht *et al.*, 2000), thus calling into question that a bias in handedness represents a reliable marker of hemispheric specialization for language. Vauclair and Meguerditchian (2008) argued that the dominant hand for manual gesture may constitute a more accurate marker of language lateralized hemisphere.

Therefore, it remains to be seen whether the distribution of handedness differs between apes and humans and, if it does, whether it reflects the emergence of socio-cultural evolution or alterations in the genome between great apes and humans. The fact that the distribution of preferences in limb use in other species may conform to or be even stronger than that of humans would argue against the second possibility. 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 (Rogers, 1980; Harris, 1989; Rogers and Workman, 1993).

Neuroanatomical studies have indicated that all four species of great apes display regions of the brain homologous to the speech and language areas in the human brain – Broca's area (Cantalupo *et al*., 2003) and Wernicke's area (Spocter *et al*., 2010) – and they are larger in the left than in the right hemisphere (see Figure 3.6). In chimpanzees a leftward bias in cortical gyrification is present in right-handed animals, whereas it is absent in non-right-handed animals (Hopkins *et al*., 2007). In the primary motor cortex of chimpanzees a higher neuronal density of layer II/III cells on the left side has been documented (Sherwood *et al*., 2007).

Interestingly, measures of unimanual actions directed towards target objects (animate: self, social partner; inanimate: object, environment, enclosure) in semi-naturalistic conditions revealed in both gorillas (Forrester *et al*., 2011) and chimpanzees (Forrester *et al*., 2012) a significant right-hand bias for actions directed towards inanimate targets and no significant preference for use of the left or right hand for actions directed towards animate targets. The results may reflect the differential processing capabilities of the left and right hemispheres, as influenced by the emotive (animate) and/or functional (inanimate) characteristics of the target, respectively. Forrester and colleagues speculate that right-handed hierarchical object manipulation may have served as a precursor to modern human language skills. In great apes, communicative gestures may represent an evolutionary step towards language skills, extending the left hemisphere's specialized processing derived from tool use.

Evidence of handedness is also apparent in monkeys, as first determined by MacNeilage *et al.* (1987). Similar to chimpanzees (and humans), some species of monkeys show evidence of only individual-level handedness in simple behavioural tasks (e.g. marmosets; Hook and Rogers, 2008) but some species are lateralized at the population level in more complex tasks (Fagot and Vauclair, 1991). Baboons prefer to use the left hand during fine motor-spatial tasks such as object alignment, haptic discrimination, catching live fish or joystick manipulation, but prefer to use the right hand when they have to extract food from a narrow tube or gesture towards other monkeys (e.g. Meguerditchian and Vauclair, 2006). Humans also seem to be better at fine adjustments and haptic discrimination with the left hand (e.g. Fagot *et al*., 1997) and at fine motor tasks and gesturing with the right hand. As in the case of chimpanzees, a link between hand preference and structural brain asymmetry has been reported in monkeys (see for example in marmosets, Gorrie *et al*., 2008).

In non-primate mammals it was also once believed that limb preferences existed only at the individual but not population level (Figure 1.3 – the former referring to the case in which individuals are lateralized but with a 50:50 distribution of left- and right-hand biased individuals; the latter to the case in which the majority of the individuals in the population shows preference in a particular direction, e.g. right-hand bias in humans; see Chapter 2). However, more recent work has proved that this is not true: large samples of inbred mice