Cerebral lateralization in animal species

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Summary

For a very long time, human cerebral asymmetries were thought to be unique. This view consequently requires that stable left-right differences of brain and behavior only emerged within the last few million years in the lineage leading to modern man. This assumption contrasts with a large number of recent reports on various asymmetries in animals. These data necessitate a completely new interpretation of the evolutionary events that resulted in the final pattern of human left-right differences of brain and behavior. This chapter attempts to provide an overview of animal asymmetries of handedness, spatial orientation, and communication. The aim of this review is twofold.

First, it will be shown that left-right differences are not only widespread among mammals but also among many other vertebrates. Thus, cerebral asymmetry is a ubiquitous phenomenon that possibly is not the exception but the rule. Second, the overview tries to reveal that in all three reviewed areas of asymmetry research the observations follow a consistent pattern. One aspect of this pattern is the fact that functional asymmetries mostly occur at the population level such that the majority of individuals are skewed into one direction. A further aspect of the consistent pattern becomes especially visible for asymmetries of communication: here, with few exceptions, a left hemispheric dominance can be seen that reaches from frog to man. Thus, not only cerebral asymmetry as such, but a certain pattern of left-right differences emerged during the evolution of vertebrates and is still visible in many species, including humans.

This overview makes it likely that cerebral asymmetries of anatomy and function have a history that stretches back at least several hundred million years. A brain architecture that is so old and can be found in so many different functional systems and forms of life must provide a solid selection advantage. The challenge of the future of the comparative analyses of asymmetry research will be to discover what this selection advantage is.

Introduction

Charles Darwin made a strong argument for continuity across species in both physical and psychological characteristics (Darwin, 1859; 1871). Around the same time, Pierre Paul Broca (1865) crucially advanced the principle of localization of function in the nervous system when he proposed that cerebral control for speech as well as for right-handedness lay in the left hemisphere. In combination, these two developments lent new significance to the possibility of animal laterality. Although both speech and handedness were seen as reaching their pinnacle of expression in humans, laterality itself ought not to be uniquely human. Thus, Broca (1877) assumed asymmetry to be possible in animals, noting that left-right differences of gyrification were very pronounced in man, but that "there is a less but still very evident degree of dysymmetry in the great apes" (p. 527) (Harris, 1989).

The general assumption of those times was that of a scala naturae – the natural staircase. Within this framework of thinking, evolution heads towards the more sophisticated, complex, intelligent, advanced representatives of the animal kingdom, leaving the clumsy previous forms behind. This long haul of nature finally culminates in humans. The less successful previous versions of life may survive in niches and can still be studied like specimens in a museum to testify to the inaptness of life before the arrival of Homo sapiens. Within this theoretical position, the presence of lateralized neural systems in humans makes cerebral asymmetries necessarily an advanced feature. According to the same logic, if non-human asymmetries exist, they...
should be less profound and may be present in chimpanzees, our closest relatives. Since apes don’t speak, only handedness remains as a tool to discover these lighter versions of left-right differences. As outlined below, the search for human-like handedness in apes was unsuccessful over a long period of time. The result of this frustrating search was the erroneous assumption that cerebral asymmetries must be a trait unique to humans. In bolder versions of this thought, asymmetries were even regarded as the critical evolutionary event that enabled us to achieve those cognitive abilities that truly separate us from the rest of life on our planet. In these theories that are still partly discussed today, the scala naturae persists.

The concept of the scala naturae is in its essence non-Darwinian and simply wrong (Hodos & Campbell, 1969). But as a consequence of this kind of thinking, studies on animal asymmetries halted for nearly a century, until the landmark paper of Nottebohm (1970) on song lateralization in chaffinches appeared. In 1985, Terry Robinson still soberly wrote: “With the exception of Nottebohm’s ... work on birdsong, research on behavioral and brain asymmetries in nonhuman animals is just in its infancy” (Robinson et al., 1985, p. 187). Now, about 20 years after this sentence, the situation radically differs. We can now overlook a rich tapestry of studies that more and more begin to create a larger picture (Vallortigara & Rogers, 2005). Obviously, it is not possible to review this whole field within a book chapter. For readers interested in further details, the book of Rogers and Andrew (2002) is an excellent choice. Given the limited space, I will concentrate on three topics, handedness, spatial orientation, and vocalization. For all three systems, we have detailed knowledge on the behavioral and neural asymmetries in humans. In the end I will try to capture the details into a wider framework of cerebral asymmetries in animals, including humans.

Handedness

John Daniel led a life full of luxury at the end of the British Empire. During parties at his home in 15 Sloane Street, London, he was known for his perfect manners; at 5 o’clock he never missed drinking a cup of tea and after dinner he always asked for a coffee. Apart from that he was known to be right-handed. This aspect of him was, probably, noted by his contemporaries only because John Daniel was not a human being but a gorilla (Güntürkün, 2002). The description of the life and death of John Daniel (Cunningham, 1921) is typical for a period of handedness research in animals that produced many anecdotes but fewer truly scientific papers. Additionally, since the preponderance of one hand, paw, or foot over the other during reaching or scratching is possibly the most easily observed aspect of laterality, most reports concentrated on these simple behavioral acts, ignoring that also in humans these behaviors produce, if at all, only a very mild handedness bias (Marchant et al., 1995). However, a large number of sophisticated studies and major meta-analyses have been meanwhile published on this subject. As will be shown in the next paragraphs, these studies testify that many animals have limb preferences that partly resemble human handedness.

Handedness in primates

Great apes

Chimpanzees and bonobos from the genus *Pan* are our closest relatives. The orang-utan (genus *Pongo*) and the gorilla (genus *Gorilla*) are more distantly related. This genetic proximity was the reason why the handedness of these animals was studied so often. However, decades of observations that produced dozens of papers could until recently not produce conclusive evidence. While all observations were able to reveal individual asymmetries (most animals prefer one hand but the number of left- and right-handed individuals is about equal), a population level asymmetry (most animals prefer the same hand) was often not observed. Examples of these kinds of data are the studies on simple reaching in chimps (*n* = 30; Finch, 1941) and gorillas (*n* = 31; Annett & Annett, 1991). A further battlefield has been the distinction of apes in captivity and those in the wild. While an overview of a large data set gave evidence for population-level right-handedness in chimpanzees (Hopkins & Cantalupo, 2005), data from
chimps in the wild were far less clear. Consequently, several authors argued that animals under captivity may copy the right-handedness of their caretakers, thus producing an arbitrary data pattern (McGrew & Marchant, 1997; Palmer, 2002). A third area of dispute is the behavior under study. In humans many activities with the hands involve simple behaviors such as picking or holding that do not show a pronounced right-sided bias (Marchant et al., 1995). Similarly, analyzing only these simple activities in great apes could result in an underestimation of a possibly existing population asymmetry. Fourth, handedness in humans is hereditary for direction and strength (Carter-Saltzman, 1980), while in mice it was found to be only genetically transmitted for strength (Collins, 1985).

A recent meta-analysis that involved reports on 1524 great apes could clarify a good part of these open questions (Hopkins, 2006). This analysis revealed that, overall, great apes show population-level right-handedness. However, there were two important caveats. First, there were clear species differences with chimpanzees and bonobos displaying a significant right-hand preference, while orang-utans and gorillas showed no population-level asymmetry. Second, the overall effect size was relatively small. This could explain why smaller samples from previous reports were usually unable to reveal population asymmetries. Importantly, both captive and wild great apes were significantly right-handed; although asymmetry was more pronounced in captive animals (see also Lonsdorf & Hopkins, 2005). Thus, in the genus *Pan*, population-level asymmetry of hand use is not as pronounced as in humans, but it exists and is not an effect of simply copying the behavioral patterns of caretakers.

The picture becomes more interesting when looking into the details. Usually, many simple behavioral patterns that can most easily be observed (e.g., hit, hold, scratch, pluck, touch, etc.) were not lateralized. Significant right-handed asymmetries were instead mostly evident in more complex and fine-tuned behaviors such as throwing, bimanual feeding, grooming, pulling food out of a tube, and gesturing (Fig. 2.1). Thus, the failure of many studies to find asymmetries of hand use was probably mostly due to an over-representation of simple behavioral units in the data sample. Additionally, both in chimpanzees and bonobos strength and direction of hand preferences seem to run in families (Hopkins, 2006).

The population-level right-handedness in chimpanzees is associated with brain asymmetries. Hopkins et al. (2007a) discovered that chimpanzees show a population level leftward bias of their cortical gyriﬁcation that is modulated by handedness. In right-handed individuals this gyriﬁcation is even more geared towards the left hemisphere, while no left-right differences in the extent of cortical folding are present in non-right-handed chimps. Sherwood et al. (2007) additionally analyzed the fine structure of the primary motor cortex of 18 chimpanzees tested on a coordinated bimanual task before death. They found a higher neuronal density of layer II/III cells on the left side. Interestingly, Hopkins et al. (2007b) additionally revealed that the asymmetries in the homologs to Broca's and Wernicke's areas are associated with tool use. These results go along with similar data in humans (Steinmetz et al., 1991) and may suggest that the neural substrate for tool use has served as a preadaptation for the evolution of language.
Monkeys

The situation in monkeys is probably comparable to that in great apes. In 1987 MacNeilage et al. published a target article in which they supposed that the early condition in the primate lineage consisted of a left-hand specialization for visually guided movements and a right-hand dominance for postural control and finer manipulation. In humans, they supposed, did the left-side reaching preference disappear while the right hand became dominant for all unimanual tasks. A few years later, Fagot and Vauclair (1991) published a new interpretation of the data from the literature and organized their review around the distinction between simple manual behaviors (picking, plucking, etc.) and more complex ones (adjusting an object into a frame, catching fish, etc.). Simple behaviors displayed individual- but no population-level asymmetry, while most of the more complicated ones evoked asymmetries at individual and population levels. When monkeys had to adjust their hand movements precisely to accomplish a fine-motor spatial task (object alignment in baboons: Fagot & Vauclair, 1988; haptic discrimination in rhesus macaques: Brown & Ettlinger, 1983; catching live goldfish in squirrel monkeys: King et al., 1987; manipulation of a joystick in baboons: Vauclair & Fagot, 1993) a left-hand preference emerged. However, when monkeys had to extract food from a narrow tube (capuchin monkey: Spinnozi et al., 1998; olive baboons: Vauclair et al., 2005) or were gesturing towards other monkeys (olive baboons: Meguerditchian & Vauclair, 2006) a strong right-hand prevalence was recorded. This is similar to humans who also are more adept in fine spatial adjustments or haptic discriminations with the left hand (Fagot et al., 1997), while being right-handed for: other fine-motor tasks or for gesturing (Kimura, 1973).

Non-primate mammals

The issue of pawedness is far less settled in non-primate mammals. Tsai and Maurer (1930) were probably the first to analyze pawedness in rats. They described that virtually all animals had a preferred side but that no population bias towards one side was discernible. Collins (1985) revealed a similar pattern in mice. Other studies using more sophisticated techniques, however, could observe a population level right-pawedness both in rats (Güven et al., 2003) and some strains of mice (Bianki, 1981; Maarouf et al., 1999). The relation of pawedness to brain asymmetries was mostly studied by studying depression, a potassium ion mediated self-propagating wave of cellular depolarization that is confined to a single hemisphere. Spreading depression of the left hemisphere is seen to result in larger motor decrements than that of the right hemisphere in mice (Bianki, 1981). Aydil and lioglu et al. (2000) could additionally reveal in dogs that paw preferences were significantly related to the size of the isthmus of the corpus callosum, a finding that resembles the human pattern described by Wieland (1985). The studies of Tan (1987) and Wells (2003) make it additionally clear that dogs have population-level asymmetries of paw use that is sex dependent and additionally correlates with immune measures (Quaranta et al., 2004). While males prefer the left paw, females go with the right.

Overall, several non-primate mammalian species have been shown to prefer one paw over the other in activities such as reaching or scratching. Different from the view prevailing in the 1980s (Walker, 1980), these issues of sidedness can not only be found at the individual but also at the population-level. The population level bias, however, is usually small.

Birds

Birds make counter-clockwise full body turns to escape the egg during hatching. The major force during this act is exerted by the right foot. Subsequent to hatching, domestic chicks, bobwhite, and Japanese quail chicks preferentially use the right foot to initiate ground scratching while searching for food (Rogers & Workman, 1993; Casey, 2005). Since ground scratching involves forceful behaviors, it is likely that the initially stronger foot is used. This population asymmetry of footedness persists into adulthood in several species of birds of prey that also have to strike by exerting strong forces (Csermely, 2004).

The situation is different for fine movement patterns. Friedman and Davies (1938) and Rogers (1980) revealed
a left-footed population asymmetry for food holding in 14, and a right-footed asymmetry in 2 Australian and South American parrot species. This result is reminiscent of an old report from Ogle (1871), who observed 86 parrots in the London Zoological Garden and reported that 63 of them preferred their left foot to hold and rotate a food item. Unfortunately, Ogle (1871) did not identify the species, such that his observation is of limited scientific value (Harris, 1989). Left-footedness was also observed for goldfinches when they are trained to manipulate doors to obtain a food reward (Dücker et al., 1986). A further point where birds need fine movement control is during landing. Consequently, Davies and Green (1991) showed pigeons to strongly prefer their left foot when landing from flight.

Absence of footedness in birds has been obtained when testing the animals in tasks where no naturally specialized movement pattern is involved. For example, individual- and population-level footedness is absent in pigeons and budgerigars for removing adhesive tapes from the beak (Güntürkün et al., 1988; Rogers & Workman, 1993).

Taken together, nearly two dozen avian species show a clear population asymmetry of footedness. The occurrence of this motor bias seems to depend on the need to either exert strong forces (right foot) or to use fine manipulations (left foot).

Amphibia

Some species of anurans use their front paws during feeding. Bisazza et al. (1997) used this behavioral pattern to test for pawedness by either wrapping a balloon around the head of the animals or by sticking a paper strip across the mouth. Toads of the species Bufo bufo tried to remove these objects preferentially with their right paws (Fig. 2.2), while no significant population level asymmetry was observed in Bufo viridis. A third anuran species tested, Bufo marinus, showed no population asymmetry in the balloon/paper-test but a population asymmetry for the right paw for righting when overturned on their back (Bisazza et al., 1996). Thus, population-level right-pawedness exists in some anuran species for some tasks.

Summary of handedness studies with animals

Studying handedness in humans, Healey et al. (1986) discovered two kinds of lateralized behavior that seem
to be controlled by different neural systems: (1) simple tasks such as reaching and carrying that require limited fine motor skills and have a relatively weak, or non-existent, lateralized bias at the individual or the population level, and (2) complex tasks such as throwing and writing that require considerably finer motor skills and have a relatively strong lateralized bias across the population. Summing up the evidence for limb dominances in animals it becomes evident that the distinction of Healey et al. (1986) describes not only the human condition but the pattern throughout the animal kingdom.

If species only use their extremities for locomotion or if they are tested with extremely simple tasks, only weak individual asymmetries without a population bias can be observed. The more demanding the motor output has to be, the more individual asymmetries with a clear population bias emerge. Presently it is unclear if there is a common motor theme that explains the different kinds of sidedness discovered in vertebrates. Equally likely, motor specialization could have independently evolved several times during evolution, such that, for example, the avian pattern has nothing in common with the primate condition.

Especially the need for fast, precise and strong actions (such as in striking or throwing) or fine and spatially guided manipulations (such as in pulling food out of crevices or in grooming) seems to promote the emergence of diverse hand or foot asymmetries. Within such a scenario, a species such as Homo sapiens naturally could not go without handedness including a clear population bias. If indeed the human condition does not differ in kind but only in quantity from the pattern of great apes, the question is, whether the extreme right-handedness of the human population is a true biological difference or the result of cultural evolution. Marchant et al. (1995) could not reveal much of an overall right-handed population bias when observing individuals of three preindustrial cultures. Right-handedness was only visible if the data pattern were analyzed for fine manipulations. Thus, it is in principle possible that cultural evolution created increasing demands for fine manipulation, thereby promoting right-handedness during ontogeny. By a snowballing effect that is also known from monkey hand use (Warren, 1977), increased right-hand use could have promoted the extreme right-sided population bias that characterizes Homo.

**Asymmetries for spatial orientation**

After Pierre Paul Broca (1865) published his landmark observations, the view of the major and the minor hemisphere was born. Since handedness and speech, the only known lateralized functions in those days, were both under left hemispheric control, Broca was interpreted as assuming a major role for this side of the brain. By default, the right hemisphere had to be the minor twin. According to Eling (1986), Broca himself was against such a view since he saw handedness and language as independent functions that were by chance both left-hemisphere based. But a lack of fluency in French prevented British, American, and German scientists reading Broca’s writings in the original, paving the way to the century-long misunderstanding of the left brain side being the major hemisphere.

In 1917, Riddoch described the case of a British Captain who was wounded by a bullet that destroyed his right hemisphere when trying to attack the Turkish lines at the battle of Gallipoli. “His ability to orientate in space things he sees quite well is almost entirely lost...” (Riddoch, 1917, S. 45). At the same time German scientists made identical observations on the other side of the front. “...so ist sogar die Vermutung möglich, daß rechtshirnige Herde bei den Störungen der Raumbildung ein Übergewicht haben”; *It is even possible to conceive a dominance of right brain lesions for malfunctions of space conception* (Pötzl, 1928, S. 267–268, Poppelreuter, 1917). Today a general right hemispheric superiority in spatial functions is firmly established (Hugdahl & Davidson, 2002). However, spatial cognition is, like language, a toolbox with diverse functions and it is important to differentiate these and then try to map them onto the hemispheres. Indeed, Kosslyn (1987) suggested a dissociation of two kinds of spatial representations: categorical and coordinate, the former being computed by the left and the latter by the right hemisphere. In addition, with practice, a “categorization” of the coordinate computation was assumed to appear. This basic dichotomy has been
expanded in the last years to cover further left and right hemispheric processes (Laeng et al., 2003). In the following, I will review studies with diverse animal species that make functional asymmetries for spatial cognition likely, although not necessarily revealing a pattern like that proposed by Kosslyn (1987).

**Mammals**

Only a few spatial laterality studies with non-human primates are available. Unfortunately, none of them has tested spatial orientation during navigation but concentrated on visual pattern discriminations that contain a spatial component. Jason et al. (1984) tested macaques in a discrimination task between two squares, one containing a centered, the other an off-centered dot of varied amplitude. Then the splenium was transected along with a unilateral ablation of the left or right occipital lobe. Only monkeys with a left lesion were unable to discriminate small eccentricities. Dépy et al. (1999) conducted a similar task with baboons and also found a left-hemisphere advantage. This is clearly different from the expected right-hemisphere advantage in a visuospatial task. However, the monkeys could also use a category-based strategy ("centered" vs. "non-centered"), which also in humans would result in a left-hemisphere advantage (Kosslyn, 1987). This is different for the studies of Hamilton and Vermeire (1986) and Vogels et al. (1994) who showed that monkeys were better with the left hemisphere in discriminating between lines differing in orientation. Here, the data are truly discrepant to comparable results with humans (Corballis et al., 2002). Within the framework of Kosslyn's theory, however, even these discrepant data between humans and monkeys can be reconciled if the vast differences in training time are considered. Usually, more than 1000 training trials were needed for the monkeys to meet the training criterion, while humans learned in less than 100 trials. The long training could facilitate categorical procedures for which the left hemisphere appears to be predominant. No study in humans has so far employed so many trials. The practice effect and its resulting hemispheric shift can be observed in some human studies after just a few dozen trials (e.g., Kosslyn et al., 1989). In macaques such a shift has also been demonstrated after extensive training (Doty et al., 1999).

A completely different approach was taken by different authors when using haptic exploration studies. For example, Agnès Lacroute gave capuchin monkeys sunflower seeds hidden in crevices of various objects that could not be seen but haptically explored. Humans are superior in exploring the spatial details of unseen objects with the left hand (Fagot et al., 1997). The same is true for capuchin (Lacroute & Fragaszy, 1996), spider (Laska, 1996), and rhesus monkeys (Fagot et al., 1991). Chimpanzees, however, depart from this result pattern and show higher performance measures with the right hand (Lacroute et al., 1999).

If rats are handled during the first weeks of life, a functional asymmetry in emotionality and spatial cognition emerges (Cowell et al., 1999). Handled rats have a tendency to first turn left when being placed in an open field (Sherman et al., 1980). This may indicate a right-hemispheric bias for spatial behavior, but it could also result from other lateralized processes. The experiment of Cowell et al. (1997) makes a spatial asymmetry more likely. Here, handled rats were tested in the Morris water maze with either the left or the right eye covered by a patch. Since more than 90% of the optic fibers cross at the optic chiasm in rats, most of the visual information from one eye crosses to the contralateral hemisphere. Cowell et al. (1997) discovered that male subjects with a right patch outperformed those with a patch on the left side. This result points to a right-hemispheric superiority of spatial navigation in male rats. For females, no clear left-right differences were discernable.

LaMendola and Bever (1997) showed that spatial navigation in rats is constituted by complementary specializations of both hemispheres. In their experiment they tested the effect of anesthetizing the left or the right whiskers. For rats, whiskers are an important source of information; they use whisker information to learn new pathways and to discriminate textures. By abolishing input from the left or the right whisker system it was shown that the left hemisphere of rats accesses a map-like representation during foraging, whereas the right hemisphere enables a rote path of a previously learned environment.
Section 1: Asymmetry, handedness and language lateralization

Birds

In birds, the optic nerves are nearly completely crossed. This anatomical condition enables the use of eye caps to study the performance of the animals with sight restricted to one eye, and so mainly the contralateral hemisphere. Different species of birds display right-eye (left-hemisphere) superiority during the discrimination of visual patterns (Güntürkün, 2002). In contrast to the left-hemispheric superiority in pattern learning, many studies could reveal a right-hemispheric advantage in spatial tasks. This was first shown by Rashid and Andrew (1989) who trained chicks to find food buried under sawdust at certain areas in an arena. When the chicks were tested monocularly, birds searched with their left eye in the critical areas, while those seeing with the right eye searched randomly.

The lateralized role of different spatial and non-spatial cues can be elegantly studied in food-storing birds during cache localization. Marsh tits store food in many caches, which they can retrieve days later with astounding accuracy (Shettleworth, 1990). To study lateralization of food storing and cache location under controlled conditions, Clayton and Krebs (1994) used a room with four feeders that were distinguishable by their location and by markings that made them visually unique. Birds tested with eye caps were given parts of a nut in one of these feeders and were then removed for five minutes. During this interval, the location of the correct feeder was swapped with an empty one so that spatial and object cues could be dissociated. Then the animals were allowed to re-enter and to retrieve the rest of the nut. With the left eye (right hemisphere), marsh tits searched at the correct spatial location, while they relied on object specific cues using the right eye (left hemisphere).

Vallortigara and colleagues were able to uncover further details of spatial cognitive asymmetry in chicks. First, chicks were trained to find food in the center of a square-shaped arena by ground-scratching under sawdust. The position of the food was indicated by two different cues. The first, was the geometric position of the arena center. The second, was that conspicuous landmarks were placed somewhere in the arena, or provided as panels hung to some of the walls. By changing the form or the size of the arena, geometric orientation (room shape) could be tested. By altering the position of the landmarks and panels, orientation according to visual objects could be analyzed. Both geometry and landmarks turn out to be utilized for spatial memory (Tommasi & Vallortigara, 2004; Gray et al., 2004) (Fig. 2.3). During geometric coding relations of objects (in this case the walls) have to be utilized. Landmark coding utilizes a conspicuous object and guides the search to a defined spot in space. Now let us consider what such studies on the asymmetry of these cognitive strategies have revealed in birds (see Vauclair et al. 2006 for a detailed review).

Geometric coding

Most studies reveal the relative predominance of the right hemisphere in utilizing the shape (geometry) of the environment (Kahn & Bingman, 2004; Vallortigara et al., 2004; but see Nardi & Bingman, 2007). If the size of the arena is altered (Tommasi & Vallortigara, 2001), or if object and geometric cues contradict each other (Vallortigara et al., 2004), chicks still search in the center with their left eye and therefore rely on room shape

Figure 2.3 Pigeon tested in a radial maze where object cues (colors of the food containers visible at the end of an arm) and spatial cues (position of the arms within the room) are tested simultaneously (from Prior & Güntürkün, 2001). The cardboard fit tree at the back serves as one of the distant cues that is used to properly orient in the room.
with their right hemisphere. If pigeons are tested in complex, very large-scale arenas, alterations of the position of diverse landmarks do not interfere with orientation as long as the animals are using the left eye, indicating also in pigeons a right-hemispheric geometric processing of major room cues (Prior et al., 2002). Hippocampal lesion studies in chicks reveal that encoding of global information actually occurs only in the right hippocampus (Tommasi et al., 2003; Kahn & Bingman, 2004). Since hippocampal lesions are known to interfere with homing performance (Bingman et al., 2003), it is possible that right hippocampal mechanisms aid homebound flights by using the relational position of stable and reliable spatial cues to construct a map-like representation (Vargas et al., 2004; Kahn & Bingman, 2004; but see Nardi & Bingman, 2007).

Landmark coding

Chicks (Vallortigara et al., 2004) as well as pigeons (Colombo & Broadbent, 2000; Prior & Güntürkün, 2001) can utilize various landmarks or other objects to guide their search for food. When geometric and landmark cues are brought into conflict, left-hemisphere chicks rely on landmarks (Tommasi & Vallortigara, 2001; Vallortigara et al., 2004). Similarly, right-eye pigeons significantly reduce their searching speed when major landmarks have been removed (Prior et al., 2002). Unilateral forebrain lesions reveal that landmark coding seems to be mainly a property of the left hemisphere (Tommasi et al., 2003; but see Nardi & Bingman, 2007). Although the hippocampus plays an important role in spatial navigation, birds are able to guide their search according to landmarks also without a functional hippocampus (Tommasi et al., 2003).

When pigeons home from a distant release site over known territory to the loft, they display a clear right-eye advantage (Ulrich et al., 1999), which does not seem to be due to a visual memory-based snapshot tracking that pursues visual features along their pre-learned route (Prior et al., 2004). Wiltschko et al. (2002) could also show a right-eye superiority in magnetic orientation in robins. In birds, magnetic compass orientation is based on infrarot light-dependent processes involving photon absorption to singlet-excited states that form radical pairs (Ritz et al., 2000).

As a result, a bird looking in different directions might “see” the magnetic field vector as a visual pattern on its retina that points into a constant direction. Thus, the magnetic field could be a true landmark that therefore is primarily analyzed by the visual system of the left hemisphere (Heyers et al., 2007).

Plasticity of cerebral asymmetries

In birds, the ontogenetic plasticity of visual asymmetry can easily be reconstructed. Embryos of virtually all avian species bend forward in the egg and keep their head turned to the right, so that the right eye is exposed to light that is shining through the translucent shell, while the left eye is occluded by the body. Since brooding parents regularly turn their eggs and often leave their nests for short time periods, the embryo’s right eye has a high probability to be stimulated by light before hatching (Buschmann et al., 2006). Thus, it is conceivable that asymmetry of light stimulation is the key event leading to visual lateralization. Indeed dark incubation of chick and pigeon eggs prevents the establishment of visual lateralization in discrimination tasks (Rogers, 1982; Skiba et al., 2002). It is even possible to reverse the direction of the behavioral and anatomical asymmetry by withdrawing the head of the chicken embryo from the egg before hatching, occluding the right eye and exposing the left to light (Rogers, 1990).

Since pigeons are altricial animals, the developmental plasticity of their visual pathways is prolonged and extends far into posthatching time (Manns & Güntürkün, 1997). Therefore covering the right eye of newly hatched pigeons for ten days reverses behavioral and anatomical asymmetries as tested up to three years later (Manns & Güntürkün, 1999). Thus, light stimulation asymmetry during a critical ontogenetic time span seems to be the trigger for avian visual asymmetry. Visual asymmetry in birds seems to be mediated through left-right differences in brightness between the eyes. These brightness differences are probably coded by mere activity differences between the left and right retinal ganglion cells since blocking retinal activity changes asymmetry (Prior et al., 2004). The differences in retinal activity are probably translated at a central level in a lateralized release of growth hormones (Manns et al., 2005).
These data reveal two different important aspects. First, the establishment of a functional asymmetry can proceed with the same principles of synaptic plasticity that are well known from other sensory or motor systems. Second, the key event of the avian visual asymmetry, namely the right turn of the head during embryogenesis, is mediated by mechanisms outside of the visual system. Thus, avian visual asymmetry results from an epigenetic event during ontogenesis.

Summary of spatial orientation studies with animals

The studies reviewed in this chapter show that the hemispheres of mammals and birds contribute differentially to spatial cognition, although both sides are to some degree able to utilize the strategy of the other. The situation in primates is rather patchy and less settled compared to birds. Several studies revealed a role of the left hemisphere in visual discriminations involving a spatial component. This is contrary to what would be expected from humans. However, the monkey data might reflect a left hemisphere categorical strategy that emerges after intensive training. Experiments with primates during haptic discriminations mostly indicate a right-hemispheric advantage in stereognosis. This resembles the human pattern. Also studies with rats point to a dominance of the right hemisphere in spatial navigation.

The experiments with bird species show that spatial navigation requires different computational strategies of the left and the right brain. The left hemisphere is mostly specialized to orient according to landmarks. The right hemisphere, on the other side, is able to utilize the shape of the room or the spatial relation of major objects to locate the goal. Both strategies work and probably both hemispheres complement each other during normal search bouts (Prior & Güntürkün, 2001) or non-spatial visual tasks (Yamazaki et al., 2007). But depending on certain circumstances, one strategy can be more useful than the other. In this case, we have to assume that a single hemisphere can temporarily be solely in charge of generating spatial orientation.

Asymmetries of communication

Soon after Broca’s seminal contributions, some authors wondered if animals might have an asymmetry resembling human speech. Obviously, only humans are able to speak, but most animals communicate and they might do so asymmetrically. Cunningham (1892) studied the Sylvian fissure in humans, apes, and monkeys and discovered similar left-right differences in all of them. Kalscher (1905) decided on a different approach. He taught 60 parrots phrases like “Eins zwei drei, Hurrat!” and then lesioned their left or right hemisphere. To his disappointment, lesion groups did not differ. Most of these initial attempts were soon forgotten and replaced by the assumption that cerebral asymmetries are uniquely human. Several generations later, studies on the asymmetry of non-human communication restarted after Nottebohm’s (1970) demonstration of song asymmetry in chaffinches. The following account gives an overview on the results gathered since then.

Mammals

Primates

Several lines of evidence make a left-hemispheric superiority in the analysis and production of species-specific vocalizations in primates likely. Petersen et al. (1978) tested the ability of Japanese macaques to discriminate a communicatively relevant acoustic feature of their “coo” sound. This is a brief, very tonal sound that occurs during affinitive, contact-seeking behavior. Several kinds of coo-sounds exist. The smooth early high variant is mostly produced by estrous females soliciting males, while the smooth late high variant is used by all individuals for general contact-seeking. Japanese macaques were significantly better in discriminating these two variants with their right ear. A left-ear advantage emerged when the animals had to discriminate pitch as an orthogonal (and non-communicative) feature of the same vocalizations. In other monkey species for which the coo-sound is not part of their species-specific communication, no asymmetry was present. The results of Heffner and Heffner...
(1984) support these results by showing that lesions of the left, but not the right, temporal lobe reduce the ability of Japanese macaques to discriminate coo-sounds. Similarly, Poremba et al. (2004) showed that the left, but not the right, pole of the dorsal temporal cortex increased its local cerebral metabolic activity when the animals were listening to macaque-specific calls.

Hauser and Andersson (1994) tested 80 adult free-ranging rhesus monkeys squatting in front of an apparatus where they could obtain food. Occasionally sounds of either their own species-specific repertoire or from turnstones, a local seabird, were played from the back. Sixty-one of the eighty animals turned their right ear towards the loudspeaker when hearing sounds from the own repertoire, but favored the left ear when listening to turnstones (Fig. 2.4a). Infants less than a year old displayed no asymmetry. A further piece of evidence for left-hemispheric communication asymmetries comes from studies in baboons. These animals quickly and repetitively rub or slap their hand on the ground to threaten or intimidate other individuals. Baboons never do so without a social partner. Meguerditchian and Vauclair (2006) showed that mainly the right hand is used for this activity, and that right-handedness increases when the animals signal towards other baboons instead of towards humans. However, not all primates tested up to now have displayed a left-hemispheric dominance for communicative sounds. Gil-da-Costa and Hauser (2006) showed that vervet monkeys display a left-ear (right-hemisphere) advantage for listening to species-specific vocalizations. Thus, an asymmetry of brain organization for communicative processes seems to be a general feature in primates, but not all species follow a left-hemispheric dominance.

The situation in chimpanzees is similar. Language-trained chimps only show a right visual field (left-hemisphere) advantage when being primed by a warning stimulus with a communicative meaning (Hopkins et al., 1992). Like humans, they also gesture more with the right hand (Hopkins et al., 2005) (Fig. 2.4b). This is especially evident when these gestures are accompanied by a vocalization. Even more interesting is the observation that the left inferior frontal gyrus (probably a homolog to Broca’s area) is enlarged in those individuals that reliably employ their right hand for gestures (Tagliatela et al., 2006). In chimpanzees, the equivalent of Wernicke’s area is larger on the left side (Gannon et al., 1998). The same is true for Broca’s area in chimpanzees, bonobos, and gorillas (Cantalupo & Hopkins, 2001). Thus, brain areas that in humans are lateralized and language related show morphological asymmetries in non-speaking species. This probably implies that human language asymmetry results from a precursor that already had anatomical and functional asymmetries related to communication in a broad sense.
Non-primate mammals

A left-hemispheric superiority for communication is no primate specificity. Mice decrease their reactions to pups’ ultrasound vocalizations when the right auditory meatus is closed (Ehret, 1987). Geissler and Ehret (2004) could show that the extent of activation of the auditory cortex of mice mothers listening to wriggling calls of mouse pups is larger on the left side. This difference was largely due to the labeling of an auditory association field that probably integrates call recognition with maternal responsiveness.

Bøye et al. (2005) tested Californian sea lions with an experimental approach as used in monkeys. When the animals were resting on a platform at the pool, conspecific or non-conspecific calls were delivered from behind. Adult, but not infant, sea lions consistently turned their heads to the right when hearing conspecific calls. Control sounds did not evoke any consistent bias. Taken together, a left-hemispheric superiority in the analysis of communicatory sounds seems to be present in many mammals and can be shown in representatives of primates, rodents, and pinnipeds.

Birds

The modern era of lateralization studies in animals started with the landmark paper of Nottebohm (1970) on the asymmetry of song production in chaffinches. Songbirds have to learn their song from adult conspecifics within a critical period in early ontogeny. The song is produced by the flow of air past the elastic membranes of the syrinx. In chaffinches normal song consists of a series of notes, some of which regularly are combined to form distinct syllables. Motor input to the syrinx is provided bilaterally by the hypoglossal nerve. If the left hypoglossal nerve is sectioned in adult chaffinches, 81% of song elements disappear or are produced in a highly altered way. Right transections produce effects only in 26% of the units (Nottebohm, 1970). This basic observation has been reproduced in canaries of the Waterschlager strain, Bengalese finches, as well as white-crowned, white-throated, and Java sparrows (Nottebohm & Nottebohm, 1976; Seller, 1979; Okanoya & Yoneda, 1995).

Lesions of central parts of the left forebrain song system disrupt singing much more than comparable lesions of the right side (Nottebohm et al., 1976). That this asymmetry is not only due to the production of song but also its perception has been shown by Okanoya et al. (2001). They trained Bengalese finches to discriminate songs of Bengalese and zebra finches. Subsequent lesions of the left-hemisphere song system had a higher impact on discrimination ability than right-sided lesions. However, courtship singing involves not only song but also display, and involves a visually guided interaction with the other bird. Consequently, George et al. (2006) discovered that male zebra finches had higher levels of activated immediate early genes on the left side of their visual tectofugal system when singing to a female companion. Additionally, the hypoglossal nucleus, which contains the motor neurons that innervate the syrinx, is larger on the left side in canaries (DeVoogd et al., 1991).

Up to now, the situation seems to indicate a straightforward pattern of left-hemisphere dominance for singing in song birds. Looking in greater detail, however, reveals a higher complexity. If not the Waterschlager strain of domestic canaries are chosen as experimental subjects but outbred strains from common canaries, no strong asymmetries are visible (Suthers et al., 2004). This is partly due to the specialization of the left and right halves of the syrinx to lower and higher frequencies, respectively. Since Waterschlager canaries specialize in low frequencies due to a hereditary hearing loss, they rely more on left syringeal song production (Suthers et al., 2004). Similarly, left- or right-sided lesions of the forebrain song system reduce the capacity to produce low or high frequencies, respectively (Halle et al., 2003).

Three conclusions can be drawn from these results. First, strain differences can importantly alter asymmetries. Second, part of the observed asymmetries in song production are due to simple peripheral factors in syrinx functions. Third, both left and right halves of the song system can specialize in different aspects of song production, although the contribution of the left side is still more important even in outbred common canaries.

This last conclusion does not fully apply to zebra finches. Here, lesions on the right side produce more pronounced asymmetries (Floody & Arnold, 1997), although both sides of the song system differentially
contribute to the final song pattern (Cynx et al., 1992). Similarly, left- and right-hemispheric song systems in starlings seem also to involve a specialization to long- or short-distance communication, respectively (George et al., 2005). Also non-songbirds show a left-hemispheric bias when being confronted with conspecific vocalizations. When captive juvenile harpy eagles, aerial predators in the neotropics, are given conspecific or other sounds, they only turn their head to the right when hearing conspecifics (Palleroni & Hauser, 2003).

**Amphibia**

Bauer (1993) induced vocalizations in northern leopard frogs by clapping the animals behind the forelimbs. Animals with lesions in the neural vocalization system on the left produced less vocalizations than those with equivalent lesions on the right side.

**Summary of studies on communication asymmetries in animals**

Experiments on asymmetries in the perception and production of communicatory signals cover a wide range of species from chimpanzees to frogs. With few exceptions, most of these studies show a predominance of left-hemispheric mechanisms. This goes along with anatomical brain asymmetries in neural systems. Additionally, in several studies, a larger number of right-sided gestures could be observed that accompany vocalizations. While this picture holds for most animals studied, a few species are less lateralized (common canary) or even show a reversed asymmetry (vervet monkey, zebra finch). Such a rather consistent pattern that reaches from man to frog is highly unlikely to occur by chance. Instead, it points to common heritage with a long history that possibly dates back several hundred million years. Although human language is unique, its asymmetry probably is not.

**Overall résumé**

1. Non-human animals have asymmetries of brain and behavior at the population level. This has been shown in c. 1000 scientific publications that were conducted on more than 50 different species. Human cerebral asymmetries with their typical population bias are in no way unique.

2. At least some of the asymmetries reviewed above show a rather consistent pattern. This is especially visible for communication asymmetries. With more caution, this is to some extent also true for handedness and spatial orientation. This distribution can be used to trace certain asymmetries back in time. If the left dominance for vocalization in frogs is included in such an analysis, communication/vocalization asymmetries with left-hemisphere dominance have a history of at least 350 million years (Carroll, 1988). If only mammalian and avian data are considered, their common history dates back to a time between 250 million and 200 million years. In any case, we as a species have inherited a pattern of cerebral asymmetries to then develop our species-typical mechanisms of language, manual control, etc. onto this asymmetrical fundament. Theories that assume that first a human-unique asymmetry pattern had to occur before we could develop our species-typical neural functions are certainly wrong, at least for the systems discussed.

3. There is no scala naturae of cerebral asymmetries. If it were to exist, we would expect apes to consistently show more clear-cut examples of functional and/or anatomical lateralizations than monkeys. Monkeys should be more asymmetric than non-primate mammals, and mammals should leave birds behind. This is not the case. The extent of population asymmetry in the preference of one limb over the other is larger in parrots than in apes. The data for communication asymmetries are equally compelling in birds and primates. The clearest evidences for asymmetries of spatial cognition do not come from chimpanzees but from domestic chicks and pigeons. The scala naturae is a pre-scientific, Aristotelian assumption. It has no place in today’s enquiries on the structure and evolution of cerebral asymmetries.
REFERENCES


