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## Laterality: Asymmetries of Body, Brain and Cognition

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### Lateralisation of conspecific vocalisation in non-human vertebrates

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## Lateralisation of conspecific vocalisation in non-human vertebrates

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Lateralisation of conspecific vocalisation has been observed in several vertebrate species. In the present article we review the results of behavioural and neuroanatomical studies investigating this feature. By employing cladographic comparisons we identify those vertebrate orders in which evidence for or against lateralisation of production and perception of conspecific vocalisation has been reported, and those orders in which further research is necessary. The analysis shows that there is evidence for lateralisation of conspecific vocalisation in several mammalian orders (e.g., Primates) and also evidence for lateralisation of conspecific vocalisation in some avian species (e.g., within the Passeriformes order). While the primate data in particular suggest that human language lateralisation could have resulted from an inherited dominance of the left hemisphere for those neural properties of language that are shared with the sensory or motor aspects of vocalisations in other vertebrate species, it becomes clear that this conclusion is presently supported by only sparse empirical evidence. The majority of vertebrate orders, especially among non-amniotes, still need to be explored.

**Keywords:** Functional cerebral asymmetries; Laterality; Language; Communication; Comparative neuroscience.

The processing of linguistic information requires the integration of a multitude of neural subsystems. These range from basic features such as the physical properties of speech sounds to more complex semantic or syntactic features and, finally, to the coordination of a widespread motor network (Holt & Lotto, 2010). Several but not all key subsystems of language

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display a left-hemispheric superiority (Corballis, 2009; Lindell, 2006). Early studies in brain-damaged patients have identified two regions in the left hemisphere that are essential for language production and perception. Damage to Broca's area, located in the left inferior frontal gyrus, leads to massive impairments in language production but not comprehension. The reverse pattern is observed after damage to Wernicke's area, located in the left posterior superior temporal gyrus. Lesions in this area lead to problems with language comprehension but more or less intact language production (Broca, 1861; Stowe, Haverkort & Zwarts, 2005; Wernicke, 1874). However, these findings do not imply that language production is solely controlled by Broca's area, while Wernicke's area is controlling the perception of language. Instead a more recent PET (positron emission tomography) study revealed that a fronto-temporal network including both the left inferior frontal gyrus and the posterior part of the left superior temporal cortex as well as the anterior part of the left inferior temporal gyrus is active during both language production and perception (Papathanassiou et al., 2000).

Apart from lesion studies, several other techniques have yielded evidence supporting the view that the left hemisphere is dominant for language production in most humans. The most reliable of these techniques is the so-called Wada Test (Baxendale, 2009), a clinical procedure that has been developed to determine the hemisphere dominant for language production prior to epilepsy surgery. To localise language production in surgery candidates, speech capability is assessed after anaesthesia of one hemisphere, with anaesthesia of the dominant hemisphere leading to severe speech impairments. A less invasive but still highly reliable method to determine which hemisphere is dominant for language production is fMRI (functional magnetic resonance imaging). For example, Badzakova-Trajkov, Häberling, Roberts, and Corballis (2010) measured asymmetrical brain activation induced by speech production using a word generation task. Overall, these authors found stronger left-hemispheric activations in the inferior frontal gyrus, the supplementary motor area, the precentral gyrus, and the superior and inferior parietal lobules as well as in the inferior occipital gyrus. Flöel, Buyx, Breitenstein, Lohmann, and Knecht (2005) used a similar word generation paradigm and found that 97% of the right-handed and 74% of the left-handed participants in their sample had a left-hemispheric dominance for language production.

In addition to these rather direct measures of asymmetrical brain activation, there are also behavioural asymmetries that are indirectly linked to hemispheric asymmetries. In most individuals the right side of the mouth is opened to a larger extent during speech production compared to the left side (Hausmann et al., 1998), and it has been suggested that this phenomenon is caused by a stronger contralateral activation of right-sided

lip opening muscles due to the left-hemispheric dominance for speech articulation (Graves, Landis, & Simpson, 1985).

Similar to language production asymmetry, language perception asymmetry can also be determined using fMRI (Bethman, Tempelmann, De Bleser, Scheich, & Brechmann, 2007; Corballis, 2009). In general, sentence processing leads to bilateral activation in the superior temporal gyri, including the primary auditory cortices (Friederici, Meyer, & von Cramon, 2000). Moreover, bilateral frontal activity is observed, with left-hemispheric activation being related to sequence formation and building structural, semantic and thematic associations, and activation in the right hemisphere being related to the processing of sentence melody (Friederici, 2002). Bethman et al. (2007) could show that 26 out of 30 participants showed left-hemispheric language perception asymmetry. Overall, greater left- than right-hemispheric activation during language perception was observed in four regions of interest including the inferior frontal sulcus, the inferior part of the inferior frontal gyrus, the posterior part of the superior temporal sulcus, and the ascending branch of the superior temporal sulcus (Bethman et al., 2007). A left-hemispheric dominance for language perception is also supported by several other lines of evidence, including EEG (electroencephalography) and MEG (magnetoencephalography) studies (Brancucci, 2010; Ocklenburg, Güntürkün, & Beste, 2011).

In addition to direct measures of hemispheric asymmetries in language perception, there are also behavioural asymmetry measures that are correlated with hemispheric asymmetries, such as the dichotic listening task (Tervaniemi & Hugdahl, 2003). In this widely used behavioural paradigm two different auditory stimuli (usually short consonant-vowel syllables like TA or DA) are presented at the same time, one to each ear. Participants have to indicate which syllable they recognised best. Typically, a clear right-ear advantage is observed, a fact that is interpreted as a behavioural measure for left-hemispheric dominance in language perception (Tervaniemi & Hugdahl, 2003; Ocklenburg, Arning, et al., 2011). This explanation is supported by high correlations between the results of the dichotic listening task and direct measures of hemispheric asymmetries obtained with different neuroimaging techniques (Della Penna et al., 2006; Jäncke, Buchanan, Lutz & Shah, 2001; Jäncke & Shah, 2002; Sandmann et al., 2007) or the Wada Test (Hugdahl, Carlsson, Uvebrant & Lundervold, 1997).

While both language production and perception tasks lead to activation of left-hemispheric fronto-temporal networks in most humans (Papathanasiou et al., 2000), there is evidence that hemispheric asymmetries for language production and perception can be dissociated to some extent. Tzourio-Mazoyer, Josse, Crivello, and Mazoyer (2004) measured regional cerebral blood flow while participants were either listening to stories or

generated verbs. Comparing the comprehension task to a rest condition, larger left-hemispheric activations were observed in the middle and inferior temporal gyri. Moreover, non-significant trends towards larger left-hemispheric activation were also observed in several different frontal regions, including the inferior frontal gyrus corresponding to Broca's region. When the word production task was compared to a rest condition, significantly larger left-hemispheric activations were also observed in the middle and inferior temporal gyri and additionally in the inferior frontal gyrus, the insula, the precentral gyrus, the supplementary motor area, and the inferior parietal lobe. Overall, the leftward activation asymmetry was stronger during the word production task than during the comprehension task. In addition to these differences in activation asymmetries during language production and comprehension, Tzourio-Mazoyer et al. (2004) also reported that one of their participants showed a left-hemispheric dominance during word production but a rightward asymmetry during the comprehension task. Similarly, Lee et al. (2008) reported that 4 out of 490 patients with intractable epilepsy who underwent the Wada Test showed hemispheric dissociations between an overt speech production and a speech comprehension task. Despite clear activation overlap between language production and perception, these findings show that hemispheric asymmetries during these tasks are, at least to some extent, functionally dissociable.

Thus, taken together, the experimental approaches to investigate language lateralisation can be subdivided into four different categories:

1. Direct measures of hemispheric asymmetries for language production.
2. Behavioural asymmetries indirectly linked to hemispheric asymmetries for language production.
3. Direct measures of hemispheric asymmetries for language perception.
4. Behavioural asymmetries indirectly linked to hemispheric asymmetries for language perception.

All of these measures point towards left-hemispheric language lateralisation, a phenomenon that was long thought to be uniquely human (Corballis, 1991). However, over the last decades this assumption has been challenged, since compelling evidence for lateralisation of conspecific vocalisations has also been reported for several non-human vertebrate species. The presence of asymmetrical properties for the production and/or perception of species-typical communications gives rise to two alternative possibilities: First, lateralised communicatory sound processing might have developed independently several times within the vertebrate subphylum. In this case human language asymmetry could be one of the independent developments and in this respect it would be unique. Second, such an asymmetry might have developed very early in evolutionary time, producing lateralised commu-

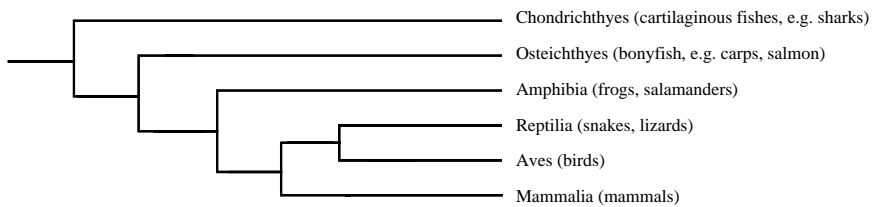
nication systems in downstream species. In this case human language asymmetry would have been inherited, at least in its basic lateralised properties. A comprehensive comparative cladistic analysis is needed in order to elucidate which of these possibilities is more likely. The present article therefore reviews the results of behavioural and neuroanatomical studies investigating communication asymmetries in production and perception. By employing cladographic comparisons, we identify those vertebrate orders for which evidence for or against lateralisation of conspecific vocalisation has been reported, and those orders for which further research is necessary (for an overview of vertebrate classes see Figure 1). We then evaluate these findings in order to identify the phylogenetic origins of a left-hemispheric bias in species-typical communication that could constitute the root of human language lateralisation.

## CHONDRICHTHYES

No research on lateralisation of vocalisation (or any other form of hemispheric lateralisation) has been conducted in Chondrichthyes (cartilaginous fishes, e.g., sharks).

## OSTEICHTHYES

Osteichthyes (bony fishes, e.g., herring) do not have a larynx or a syrinx. However, there are several species of bony fishes that have been reported to produce various sounds in reproductive or antagonistic social contexts (for an overview see Ladich, Collin, Moller, & Kapoor, 2006). For example, clownfish (*Amphiprion clarkii*) produce conspecific vocalisations by colliding their jaw teeth, with the jaws acting as sound radiators (Parmentier et al., 2007), while fawn cusk-eels (*Lepophidium profundorum*) use contractions of swim bladder muscles to produce sounds (Nguyen, Lin, Parmentier, & Fine, 2008). Similarly, the oyster toadfish (*Opsanus Tau*) produces different sounds by contracting specialised swimbladder muscles (Bass & Baker, 1991). Fine (1982) recorded and analysed three different types of these sounds and observed that they were produced by different contraction patterns of left and right muscles. Based on these non-experimental observations, Fine (1982) hypothesised that sound production in oyster toadfish could be lateralised. A morphological study in the three-spined toadfish (*Batrachomoeus trispinosus*), a species of toadfish that possesses a bilaterally divided swimbladder which is used for sound production, provides further support for this assumption. Rice and Bass (2009) could show that the left and right swimbladder in this species is asymmetrical in terms of length. In 15 out of 25 fish the left swimbladder was longer than the right, while in nine fish the



**Figure 1.** Cladographic overview of the vertebrate clade. Agnatha (jawless fish) and extinct orders are not shown.



reverse pattern was observed. Only one specimen had equal-sized left and right swimbladders. However, the behavioural consequences of this peripheral morphological asymmetry as well as its relation to hemispheric asymmetries remain unclear.

Fine et al. (1996) experimentally investigated lateralisation of sound production in the channel catfish (*Ictalurus punctatus*). These species produces a series of pulses presumably associated with social communication by rubbing a process on the first pectoral spine against the surface of a groove located in the pectoral girdle during fin abduction (Fine et al., 1996). Both fins can be used in this process, but out of the 20 fishes analysed by Fine et al. (1996), half showed a significant preference for one side. Interestingly, nine out of these ten animals showed a preference for the right fin, while only one preferred the left fin. Since most of the descending spinal tracts relevant for fin movement in teleost fish cross (Prasada Rao, Jadhao, & Sharma, 1987), this finding may be a first behavioural indicator for a left-hemispheric dominance in sound production in catfish. Clearly more research of the neuronal control of this behaviour is needed before any comparison with lateralisation of conspecific vocalisation in animals using vocal chords to produce sounds can be drawn. Nevertheless, these findings support the assumption that at least some species of bony fish show lateralisation of conspecific vocalisation.

## AMPHIBIA

The earliest vertebrates with vocal cords for which lateralisation of conspecific vocalisation has been investigated are Anurans. Several members of the order Anura produce highly complex communication calls (Kelley, 2004; Lardner & bin Lakim, 2002; Suthers et al., 2006). Evidence for a lateralisation of production of conspecific vocalisations in Anurans comes from a lesion study in the northern leopard frog (*Rana Pipens*) conducted by Bauer (1993). After baseline recording of the frogs' vocalisation patterns, the two experimental groups received knife cuts at the border of cerebellum and tectum either in the left or the right hemisphere. Both experimental groups showed less post-operative vocalisation than non-operated and sham-operated control groups. Moreover, there was a significantly higher reduction of vocalisation after a lesion in the left compared to the right hemisphere. However, since Bauer (1993) conducted the only published study on Anuran communication asymmetries so far, it is clear that more research is needed in this field. Independent replication in larger samples as well as in other frog or toad species would yield strong support for left-hemispheric dominance of production of conspecific vocalisations in early vertebrates.

## REPTILIA

In general there is compelling evidence for lateralisation of brain and behaviour in reptiles (for a comprehensive review see Bisazza, Rogers, & Vallortigara, 1998). For example, Stancher, Clara, Regolin, and Vallortigara (2006) reported a right-sided preference for the righting behaviour in the tortoise (*Testudo hermanni*), and Bonati, Csermely, López, and Martín (2010) found a rightward bias in the escape behaviour of the common wall lizard (*Podarcis muralis*). While at least some species of reptiles produce sounds that are related to social communication (Vergne, Avril, Martin, & Mathevon, 2007; Vergne, Pritz, & Mathevon, 2009; Manley & Kraus, 2010), there is as yet no research on whether this behaviour or its neural control is lateralised.

## AVES

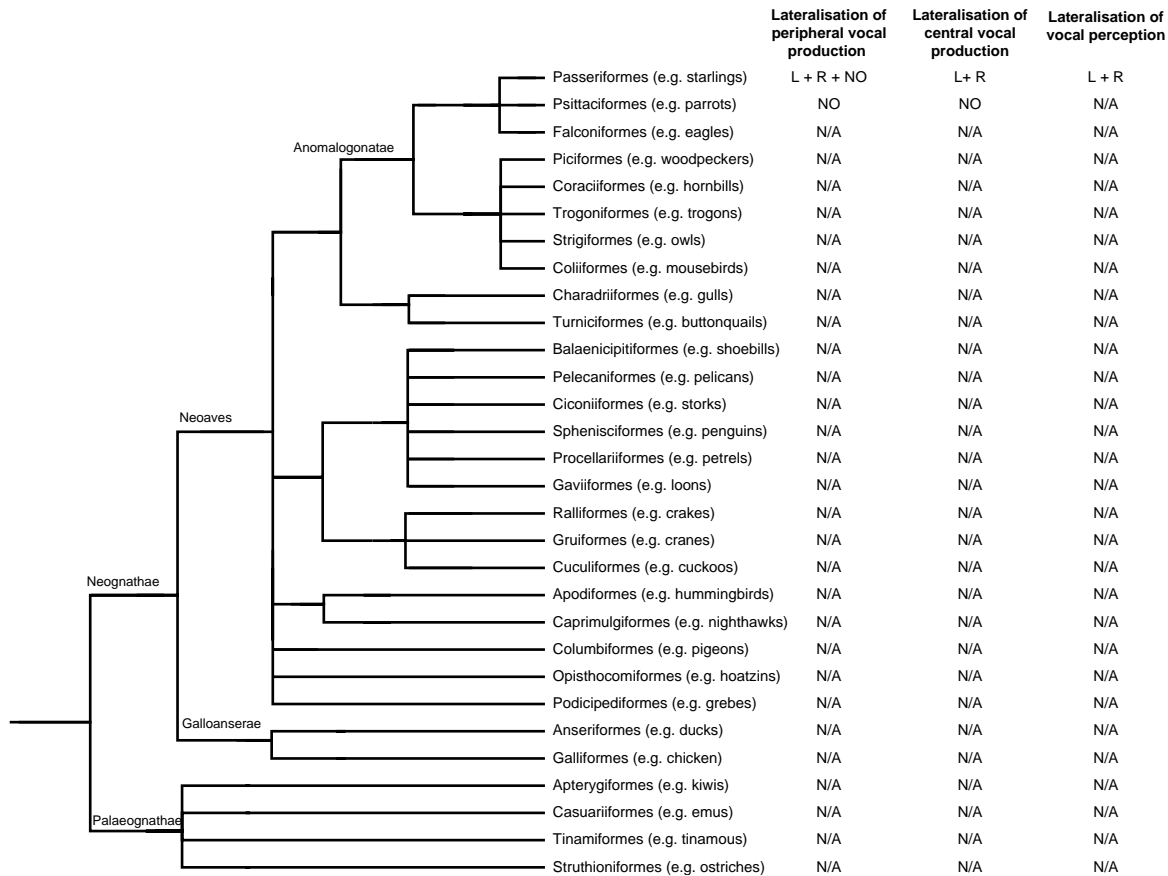
Apart from speech in humans, the Aves class possesses the most complex forms of vocalisation in the animal kingdom. Over the last decades various experiments have been performed to study behavioural as well as anatomical features of bird songs, rendering the avian song system a valid neurobiological model for species-specific communication, motor learning, plasticity processes, and vocalisation in general. In the following section we will review lateralisation patterns in conspecific vocalisations within the Aves clade (for an overview see Figure 2).

### Passeriformes

Most studies on vocalisation in birds have been conducted in the Passeriformes order, which is not surprising given that it contains the suborder of song birds. Male oscine birds use their song mainly for courtship and to mark their territory, while song of female birds is often less distinct (for review on behavioural function of bird vocalisation see Nowicki & Searcy, 2004).

Since the avian class diverged from the mammalian phylogenetic branch about 280 million years ago, bird brains differ to a high degree from those of mammals. Nonetheless, pallial and subpallial areas of the cerebrum are homologous, albeit differing in terms of a laminated organisation of the pallium (Jarvis et al., 2005). Within this framework the organisation of the oscine song system shows a high level of similarity to the organisation of neural speech structures in humans.

The song system consists of several telencephalic areas that project to brainstem nuclei controlling the syrinx (the sound-producing organ in birds). The system originates in the nucleus HVC (high vocal centre) of the



**Figure 2.** Cladogram of the Aves class based on genetic sequences, modified after Hackett et al. (2008). Only non-extinct orders are shown. Chart depicts whether lateralisation of conspecific central vocal production, peripheral vocal production, or vocal perception can be found within this order. L: left-directed lateralisation, R: right-directed lateralisation, NO: no lateralisation observed, N/A: no literature available.

forebrain, projecting to the robust nucleus of the arcopallium (RA). RA gives rise to fibres that run to nuclei innervating the respiratory system and to the tracheosyringeal part of the hypoglossal nucleus (XIIIts) that controls the ipsilateral syrinx. The connections of RA and XIIIts can either be predominantly ipsilaterally or bilaterally organised, depending highly on the species observed (Wild, Williams, & Suthers, 2000). The syrinx is a bipartite organ with a left and a right component, which can generate sound independently. During sound production, one or both syringeal halves can contribute to individual song syllables, while the respiratory system is tightly linked to syrinx activation gating airflow. Lesions in telencephalic areas of this pathway prevent the production of song-like syllables, whereas electric stimulation induces it (Farries 2001, 2004). Lesions to the hypoglossal nerve, which innervates the syrinx, reduce the amount of syllables or impair acoustic features of the song (Suthers, 1997). Apart from this song production pathway, a parallel frontal pathway subserves song learning. Based on anatomical, electrophysiological, and developmental data, it is assumed that HVC and RA function as an analogous structure to the mammalian motor or premotor cortex for vocalisation (for detailed reviews on these pathways and syringeal coordination, see Brainard, 2004; Farries, 2001, 2004; Goller & Cooper, 2004; Schmidt, 2008; Suthers, 1997).

Song perception in oscines starts with the auditory pathway that originates in the cochlear nuclei and runs over brainstem, midbrain, and thalamic nuclei to Field L in the forebrain. Field L is the equivalent to the primary auditory cortex in mammals. Within the forebrain the information is conveyed to higher auditory areas, like the Nidopallium caudomediale (NCM), which is specialised for vocal communication signals, as well as to the previously described song system (for a review see Knudsen & Gentner, 2010). Due to the differences in the amount of ipsi- and bilateral projections of RA to syringeal control nuclei in the brainstem between several bird species (Wild et al., 2000) and due to the fact that these projections have not been investigated yet in most of the remaining species, we will distinguish between three forms of lateralisation of vocalisation in the avian taxon:

1. Lateralisation of central vocal production, as shown by studies investigating forebrain structures by means of electrophysiology, fMRI, and behavioural assays.
2. Lateralisation of peripheral vocal production, including studies on syrinx functions like activation studies or lesioning of the syringeal nerve.
3. Lateralisation of vocal perception.

Several studies show that perception and central as well as peripheral production of vocalisation in song birds can be lateralised. However, other

studies could not reveal any song lateralisation. Overall, species differences seem to be of great importance. Zebra finches (*Taeniopygia guttata*) are possibly the most widespread model organism in birdsong research and seem to show a dominance of their right syrinx during song production (Williams, Cranel, Hale, Esposito, & Nottebohm, 1992; George, 2010). Floody and Arnold (1997) cut the nerve controlling the syrinx, finding stronger song impairment after right-sided than after left-sided lesions.

However, in a more recent study Goller and Cooper (2004) analysed the bronchial airflow gated through the syringeal halves during song production and found that syllables were composed by simultaneous and independent contributions of both sides of the syrinx. Furthermore, Long and Fee (2008) slowed activation of HVC-neurons by cooling and found no degradation but a stretching of the song. Song stretching induced by left HVC cooling was negatively correlated to song stretching by right HVC cooling and vice versa. Both studies assume that zebra finches neither exhibit a permanent central nor peripheral dominance, but a rapid switching between both hemispheres with both sides composing individual parts of a song. This assumption is supported by a study of Wang, Herbst, Keller, and Hahnloser (2008), in which left and right HVC were briefly stimulated at the beginning of the first note of a song motif. The authors found that the effectiveness of stimulation rapidly switched between hemispheres. Moreover, while stimulation was effective on one side, simultaneous stimulation on the contralateral side showed no effect. Taken together it seems more likely that vocal production in zebra finches is neither lateralised at central nor at peripheral level. Instead a steady interhemispheric switching with brainstem structures as a possible pacemaker seems more likely (Schmidt, 2008).

For song perception, electrophysiological recordings from forebrain areas (NCM) showed that zebra finches exhibit a stronger response to conspecific songs in the right hemisphere than in the left (Phan & Vicario, 2010). This asymmetry was modulated by sex and experience with species-specific calls, with a more pronounced asymmetry in male animals as well as in more experienced animals. Poirier, Boumans, Verhoye, Balthazart, and Van der Linden (2009) examined brain activation in zebra finches with fMRI and found stronger activation of auditory areas in the right compared to the left hemisphere to a bird's own song, a conspecific song, or a tutor song. These data imply that zebra finches possess a dominance of the right hemisphere for song perception. Comparable data for song perception can be found in European starlings (*Sturnus vulgaris*), which show stronger responses in right than in left HVC while listening to acoustic stimuli (George, Cousillas, Richard, & Hausberger, 2005). In line with more recent data in zebra finches, European starlings do not show a peripheral lateralisation in song production with regard to syrinx usage while producing a song (Uchida, Meyers, Cooper, & Goller, 2010). Evidence on central lateralisation is

missing in this species. Brown-headed cowbirds (*Molothrus ater*) express a minute dominance of the right syrinx during song production (Allan & Suthers, 1994), whereas data on song perception and central production are absent.

While the birds mentioned above exhibit a dominance of the right side either in peripheral song production or song perception, there are also data on left-sided lateralisation within the Passeriformes order. In an early study Greenspon and Stein (1983) injected testosterone in female canaries (*Serinus canarius*) to induce male singing behaviour. After successful treatment they lesioned either the left or right HVC and found a stronger song impairment after left-sided lesions. The same effect was found in male canaries, with left-sided HVC lesions being more severe than right sided (Halle, Gahr, & Kreutzer, 2003). Result of both studies suggests a left-sided central lateralisation of song production in canaries. Nottebohm (1976) showed that there is a left-sided dominance of the syrinx of canaries during song production, providing evidence for a left-sided peripheral lateralisation in this species as well. Unfortunately, data on lateralisation on song perception in canaries are missing altogether.

In Bengalese finches (*Lonchura striata var. domestica*), there is evidence for lateralisation of both central song production and song perception. Okanoya and Watanabe (1994) lesioned the HVC of these birds and found greater effects on song production after left-sided than after right-sided lesions. Moreover, after lesions of the left HVC, Bengalese finches needed significantly longer to learn new songs from conspecific birds than after lesions of the right HVC (Okanoya, Ikebuchi, Uno, & Watanabe 2001). The authors suggested that this might be due to a dominance of the left hemisphere regarding discrimination of conspecific songs. Data on peripheral production lateralisation are absent for Bengalese finches.

In the remaining Passeriformes order, only data on peripheral lateralisation of song control are available. Suthers and colleagues measured airflow and related song production in grey catbirds (*Dumetella carolinensis*) and brown thrashers (*Toxostoma rufum*) and found no dominance for any syrinx side during song production (Suthers, 1990; Suthers, Goller, & Hartley, 1994). However, there was a difference in frequency range, with the right syrinx producing a higher frequency range than the left syrinx.

Taken together, the results in the Passeriformes order are quite heterogeneous. There are data on central and peripheral lateralisation of song production as well as on lateralisation of song perception. Still, neither direction nor persistence of such lateralisation is stable. For peripheral song production there is evidence for a left (canary), a right (brown cowbird), or no dominance (starling, grey catbird, brown thrasher). For zebra finches, data are even contradictory within the species, although more recent studies with more modern techniques tend to find no lateralisation of peripheral

song production. The same ambiguity holds true for central song production. There is evidence for left-hemispheric dominance (canary) as well as evidence for no lateralisation (zebra finch). For song perception, evidence for both a right-sided dominance (zebra finch) as well as a left-sided dominance (canary) exists. Taken together, lateralisation of song production/perception in the Passeriformes order greatly depends on the observed species and to some extent also on the experimental technique used.

## Psittaciformes

Plenty of research on vocalisation in Psittaciformes has been done, mainly focusing on species like parrots that are able to imitate human speech. African grey parrots (*Psittacus erithacus*) in particular were the target of extensive research, highlighting almost every aspect of vocalisation starting from vocal learning to production and imitation of speech (for review see Pepperberg, 2010). Nonetheless, only little research on lateralisation of vocalisation in the Psittaciformes order has been published so far. One of the few studies was conducted in 1905 by Otto Kalischer who lesioned the lateral forebrain of Amazon parrots (*Amazona spec.*), probably hitting NLC and AAC, which are possibly comparable to HVC and RA in songbirds (Paton, Manogue, & Nottebohm, 1981), although Kalischer did not know this at this time point. He found that unilateral lesions did not have an effect on vocalisation. Only bilateral lesions led to a loss of vocalisation abilities. He concluded that vocalisation in parrots is not lateralised but equally distributed between the two hemispheres (Kalischer, 1905).

Apart from this historical study, Nottebohm (1976) denervated the syrinx of orange-winged Amazon parrots (*Amazona amazonica*) and found no differences between left and right denervations, attributing this to a bilateral innervation of the syrinx in parrots. Heaton, Farabaugh, and Brauth (1995) did the same experiments in budgerigars (*Melopsittacus undulates*), also finding no lateralisation at syrinx level. Snyder and Harris (1997) analysed individual footedness in African grey parrots (*Psittacus erithacus*) and correlated their findings with the amount of learned vocabulary. They found that right-footed animals showed a more extensive vocabulary than left-footed ones, and assumed motor lateralisation to be linked to a left-hemispheric dominance for cognitive functions. However, this finding does not provide direct evidence for a lateralisation of vocal perception or production. Taken together, Psittaciformes show lateralisation in neither central nor peripheral vocal production. Unfortunately, there are no direct data on perceptual lateralisation.

## Falconiformes

In the Falconiformes order only one study describing lateralisation in vocalisation perception exists. Palleroni and Hauser (2003) used the orienting-asymmetry paradigm (see Primates section) to test inexperienced and hunting experienced harpy eagles (*Harpia harpyja*). They found that inexperienced harpy eagles had a head-turning bias to the right side for conspecific calls only, whereas hunting experienced harpy eagles had a right-sided bias for conspecific calls and howlers of prey animals. Control sounds induced left turning behaviour.

## Other Anomalogonatae

For other Anomalogonatae there is almost no literature about conspecific vocalisation or lateralisation. In the Piciformes (woodpeckers), Coraciiformes (hornbills, rollers), Trogoniformes (trogons, quetzals), and Coliiformes (mousebirds) orders, research in this field has yet to be conducted. For Strigiformes, there are some data on conspecific vocalisation in owls. Apart from a few other studies, Roulin, Kölliker, and Richner (2000) examined vocalisation in owl hatchlings (*Tyto alba*) and found negotiations between the siblings for the next prey items delivered by the parents. However, studies on lateralisation in the Strigiformes order are also missing.

## Charadriiformes and Turniciformes

So far, no research on conspecific vocalisation or lateralisation has been conducted either in Charadriiformes (e.g., gulls and auks) or in Turniciformes (buttonquails).

## Ralliformes, Gruiformes, and Cuculiformes

In the Ralliformes (crakes), Gruiformes (cranes), and Cuculiformes (cuckoos) orders, literature for conspecific vocalisation is only available in Cuculiformes birds, while data on lateralisation is missing completely. Fuisz and de Kort (2007) analysed mating calls in the common cuckoo (*Cuculus canorus*) and showed host-specific components within these calls that are essential to find a matching reproduction mate.

## Apodiformes and Caprimulgiformes

Apodiformes (hummingbirds) show conspecific vocalisation. Clark and Feo (2010) investigated mating behaviour in two species of hummingbirds (*Calypte costae* and *Calypte anna*) and found that both species use vocal song and feather sound to communicate during courtship. Whether the



vocalisations are lateralised is unknown. No data on conspecific vocalisation or lateralisation are available for Caprimulgiformes (nighthawks).

## Columbiformes

Within the Columbiformes order most research has been done in pigeons (*Columba livia*). No data about lateralisation of vocalisation are present yet. Despite the lack of studies on vocal lateralisation in pigeons, many studies on visual asymmetries exist (Bingman, Siegel, Gagliardo, & Erichsen, 2006; Prior, Wiltschko, Stapput, Güntürkün, & Wiltschko, 2004; Stapput, Güntürkün, Hoffmann, Wiltschko, & Wiltschko, 2010; Valencia-Alfonso, Verhaal, & Güntürkün, 2009; von Fersen & Güntürkün, 1990). In contrast to pigeons, vocalisation in ring doves (*Streptopelia risoria* L.) was target of several studies ranging from biophysical properties of the specific “coo” sound (Elemans, Spierts, Hendriks, Schipper, & Müller 2006) to effects on ovulation during courtship (Erickson, 1986), although studies on lateralisation of vocalisation are not present.

## Other Neoaves

For the remaining neoaves orders, Balaenicipitiformes (shoebills), Pelecaniformes (pelicans, gannets), Ciconiiformes (storks, herons), Sphenisciformes (penguins), Procellariiformes (petrels, albatrosses), and Gaviiformes (loons), research on lateralisation of conspecific vocalisation has not been conducted yet. At least for gannets and penguins there is some literature on conspecific vocalisation. White, White, and Thorpe (1970) analysed calls of gannets (*Sula bassana*), which are able to recognise individual birds by their unique calls. This has also been observed in penguins (Aubin, 2004). Whether production or perception of these calls is lateralised is still unknown.

## Galloanserae

In the phylum Galloanserae, comprising the orders Galliformes (chicken, quails) and Anseriformes (ducks, geese), plenty of research on lateralisation has been done. In domestic chicken (*Gallus gallus*) lateralisation could be shown for social learning (Rosa Salva, Daisley, Regolin, & Vallortigara, 2010), visual discrimination tasks (Mench & Andrew, 1986) and olfaction (Vallortigara & Andrew, 1994). Furthermore, several studies indicate the existence of conspecific vocalisation in chicks. Evans and Evans (2007) investigated food calls in chicken and found that those food calls were used to provide information about the food location to other chicken nearby. Unfortunately there is as yet no evidence for a lateralisation of this vocalisation. Apart from the chicken, there is also some data regarding lateralisation in quails. Zucca and Sovrano (2008) showed that quails (*C.*

*coturnix* X *C. japonica*) use their left visual hemifield when approaching a companion and their right visual hemifield when approaching a stranger. Conspecific vocalisation in quails is well known (for a review see Mills, Crawford, Domjan, & Faure 1997), while it is unknown if this vocalisation is lateralised. For Anseriformes, data on lateralisation and conspecific vocalisation are very sparse. Gottlieb (1988) analysed the reactions of domestic mallard ducklings (*Anas platyrhynchos*) to parental calls and found that they were able to allocate those calls to individual adult ducks. Again data on lateralisation of this behaviour are missing.

### Palaeognathae

The superorder Palaeognathae represent the evolutionary most basal forms of all avian species and consists of mainly flightless birds like ostriches (Struthioniformes), kiwis (Apterygiformes), and emus (Casuariiformes), plus flying tinamous (Tinamiformes). Although vocalisation in these animals is known, only very few studies have been performed in this field so far, omitting information about lateralisation of vocalisation at all. In fact only one study describing the anatomy of the syrinx of ostriches (*Struthio camelus*) exists (Yildiz, Bahadır, & Akkoç, 2003), and neurobiological data regarding sound production are missing completely. For ostriches at least, there are some data showing lateralised behaviour. Baciadonna, Zucca, and Tommasi (2010) were able to show that ostriches show a population dominance of the right leg, which is comparable to other avian species. However, data for lateralised vocalisation are missing in the Palaeognathae phylum, and further research is needed in this field.

## MAMMALIA

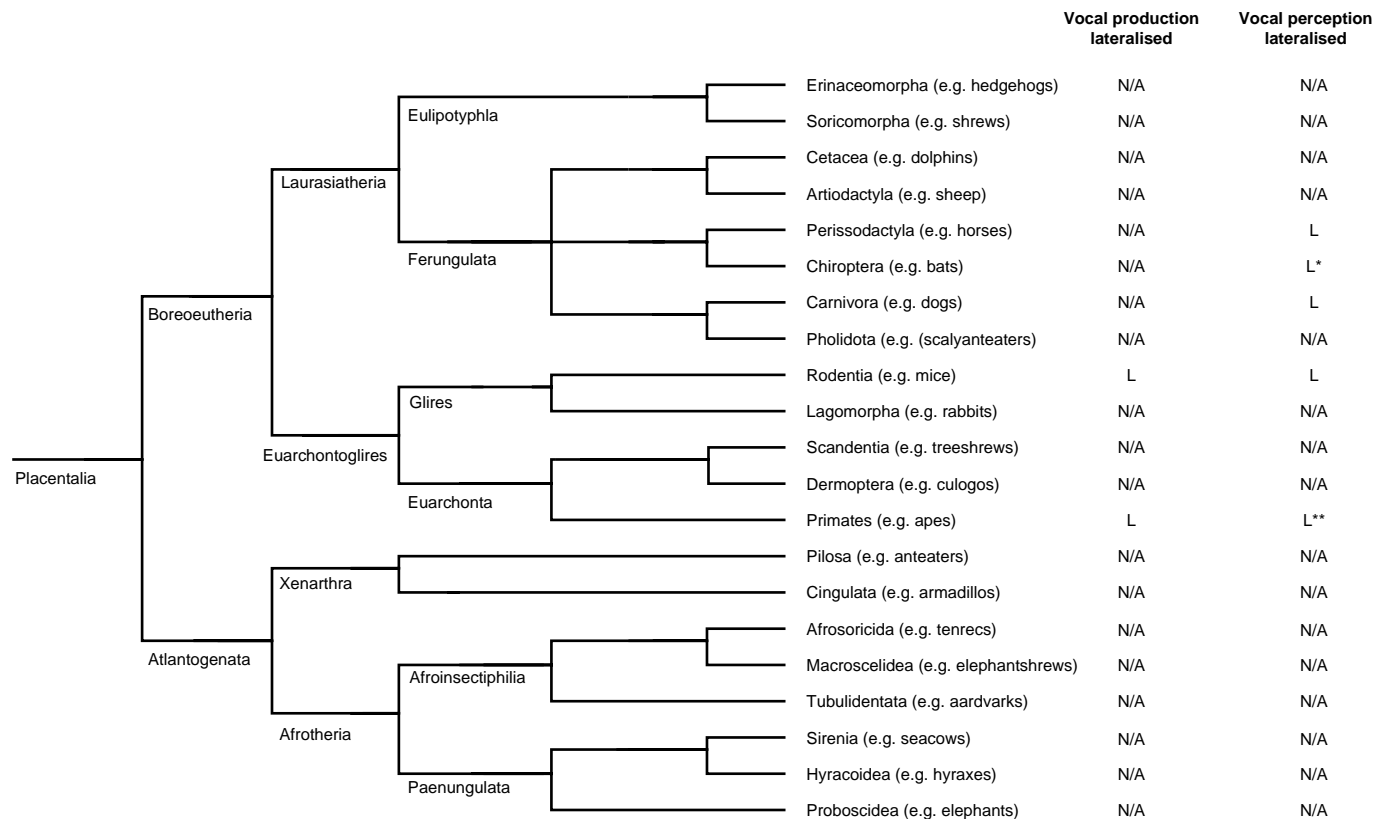
Evidence for a lateralisation of conspecific vocalisation has been found in several mammalian orders (see Figure 3 for an overview). In the following section we will review this evidence in detail.

### Erinaceomorpha and Soricomorpha

No research on lateralisation of vocalisation (or any other form of hemispheric lateralisation) has been conducted in the orders Erinaceomorpha (hedgehogs and gymnures) and Soricomorpha (shrews and moles).

### Cetacea

While there is evidence for a left-lateralisation of numerical abilities (Kilian, von Fersen, & Güntürkün, 2005) as well as visuo-spatial abilities (Kilian, von Fersen, & Güntürkün, 2000) in the bottlenose dolphin (*Tursiops*



**Figure 3.** Cladogram of the Eutheria phylum based on genetic sequences, modified after Murphy, Pringle, Crider, Springer, and Miller (2007). Only non-extinct orders are shown. Chart depicts whether lateralisation of conspecific vocal production or vocal perception can be found within this order. L: left-directed lateralisation, N/A: no literature available. \*Lateralisation only on individual level. \*\*One study in Barbary macaque reported no lateralisation.

*truncatus*), no research on lateralisation of vocalisation has yet been conducted in the order Cetacea (dolphins, porpoises and whales).

### Artiodactyla

While Versace, Morgante, Pulina, & Vallortigara (2007) reported evidence for a lateralisation of obstacle avoidance behaviour in sheep (*Ovis aries*), there is as yet no research on lateralisation of vocalisation in the even-toed ungulates (e.g., pigs, sheep, and others).

### Perissodactyla

In odd-toed ungulates, including horses, donkeys, zebras, tapirs, and rhinoceros, lateralisation of perception of conspecific vocalisation has been investigated in the horse (*Equus caballus*). Basile, Boivin, et al. (2009) tested the influence of the degree of familiarity on lateralisation of the response to conspecific whinnies using a behavioural paradigm in which the horses' ear movements towards the source of a conspecific whinny were assessed. They observed a clear left hemispheric preference for familiar neighbour calls, but no lateralisation for whinnies by other group members or strangers.

### Chiroptera

In bats, lateralisation of the neural base of auditory perception of conspecific vocalisation has been investigated in the moustached bat (*Pteronotus parnellii*). Sherwood, Raghanti, and Wenstrup (2005) performed a stereologic analysis of Nissl-stained cells in layer III of area DSCF in the auditory cortex of ten adult moustached bats, since this area contains neurons that are sensitive to temporal features of conspecific vocalisations. No population-level asymmetries in neuron or glial density as well as glial–neuron ratio or mean neuron volume were observed in this area. However, several individual bats had asymmetric neuron distributions in favour of either the right or the left hemisphere. These findings suggest that no general left-hemispheric dominance for auditory perception of conspecific vocalisation comparable to humans exists in bats; nevertheless lateralisation is present at an individual level. To further investigate this assumption, behavioural experiments directly investigating communicative behaviour in bats are clearly needed.

### Carnivora

In carnivorans hemispheric specialisation for processing different types of acoustic stimuli has been investigated in the dog (*Canis familiaris*). Siniscalchi, Quaranta, and Rogers (2008) tested the head-orienting response

in reaction to playbacks of a thunderstorm or to different types of species-typical vocalisations in a sample of 14 domestic dogs. They found that the dogs in their sample turned their head to the right side in response to conspecific vocalisations, indicating a left-hemispheric dominance for the processing of this type of acoustic stimuli, whereas a leftward turning bias was observed in response to the sound of the thunderstorm. Using a similar paradigm, Böye, Güntürkün, and Vauclair (2005) investigated lateralisation for the processing of conspecific vocalisation in infant, sub-adult, and adult sea lions (*Zalophus californianus*). They observed a right-sided turning bias to conspecific sound in sub-adult and adult, but not infant sea lions, yielding further evidence for a left hemisphere advantage for perception of species-typical vocalisation sounds in carnivores. No lateralisation was observed for processing of primate or bird calls.

### Pholidota

No research on lateralisation of vocalisation (or any other form of hemispheric lateralisation) has been conducted in scaly anteaters.

### Rodentia

Several species of rodents show a rich repertoire of social communicative sounds (e.g., Brudzynski, 2009; Suta, Popelár, & Syka, 2008). Ehret (1987) investigated lateralised recognition of the ultrasonic calls that are emitted by young house mice (*Mus musculus*) in order to evoke maternal caring. To this end, Ehret (1987) used a two-alternative choice test in which lactating female house mice had to decide between an artificial pup call and a neutral signal. When both ears were open or when only the left ear was plugged, the animals showed a clear preference for pup calls. However, when the right ear was plugged no significant preference difference between conspecific and neutral sounds was observed. These results suggest a left hemisphere advantage for perception of conspecific calls in mice. Interestingly, research in the Mongolian gerbil (*Meriones unguiculatus*) suggests a left hemisphere advantage not only for conspecific call recognition but also for production of vocalisations. Several studies found that in male and masculinised female gerbils, the number of neurons in and volume of the left sexually dimorphic area pars compacta, (SDApc) of the preoptic region correlates significantly with the rate of the courtship vocalisations (Holman, 1998; Holman & Hutchison, 1991, 1993; Holman & Janus, 1998; Holman & Rice, 1996). Another possibly relevant study on lateralisation of vocalisation in rodents has been conducted by Bianki and Snarskiĭ (1988) in rats (*Rattus norvegicus*). These authors recorded vocalisation to painful tail stimulation in animals with an intact brain as well as in animals with left- or right-hemispheric lesions, and

concluded that the left hemisphere is dominant for the control of pain vocalisations in rats.

## Lagomorpha

No research on lateralisation of vocalisation (or any other form of hemispheric lateralisation) has been conducted in rabbits and hares.

## Primates

In non-human members of the order Primates the most widely used behavioural paradigm to assess lateralisation of recognition of conspecific vocalisation is the orienting asymmetry paradigm (for a review and criticism, see Teufel, Ghazanfar, & Fischer, 2010). In this paradigm a loudspeaker is installed behind a food dispenser. Food is then offered, and when the animal is positioned with its back towards the loudspeaker and its head held straight forward, a species-specific call or a non-specific sound is presented. This procedure is repeated several times, and the number of right and left turns during the animals' orienting reaction towards the sound source is used as dependent variable (Teufel et al., 2010). While both auditory cortices receive input from both ears, it has been shown that each hemisphere predominantly receives projections from the contralateral ear (Tervaniemi & Hugdahl, 2003). Thus a right-sided head turn in the orientation-asymmetry paradigm (which brings the right ear closer to the sound source) is thought to reflect a left-hemispheric dominance for processing of conspecific calls, whereas a left-sided head turn is supposed to reflect a right-hemispheric dominance (Hauser & Andersson, 1994). The first study that applied the orienting-asymmetry paradigm was conducted by Hauser and Andersson (1994) in the rhesus macaque (*Macaca mulatta*). They reported that 61 of 80 adult animals showed a preference to turn towards the right side when conspecific vocalisations were presented. In contrast, a left-sided turning bias was observed when bird calls were presented. No asymmetries were observed in infant animals. Hauser and Andersson (1994) concluded that rhesus macaques have a left-hemispheric dominance for perception of conspecific vocalisations, and the finding of a right-sided turning bias towards conspecific calls in rhesus macaques has since been replicated by two other studies (Hauser, Agnetta, & Perez, 1998; Ghazanfar, Smith-Rohrberg, & Hauser, 2001). However, further studies applying the orienting-asymmetry paradigm in different primate species yielded much more inconsistent results regarding the direction of lateralisation for different types of conspecific calls (Basile, Lemasson, & Blois-Heulin, 2009; Leliveld, Scheumann, & Zimmermann, 2010; Scheumann & Zimmermann, 2008) with some studies finding a leftward turning bias towards conspecific calls (Gil-da-Costa &

Hauser, 2006; Lemasson et al., 2010) and one study in the Barbary macaque (*Macaca sylvanus*) reporting no turning asymmetry at all (Teufel, Hammerschmidt, & Fischer, 2007). Moreover, Fischer et al. (2009) did not find any relation between orienting bias in the orienting-asymmetry paradigm and speech-evoked activation in Broca's area in humans. Fischer et al. (2009) therefore concluded that orienting bias in humans does not directly reflect language perception asymmetries, but instead is influenced by several other factors including experience, attentional biases, and experimental conditions. These problems lead Teufel et al. (2010) to question the validity of the orienting-asymmetry paradigm. These authors concluded that more research of the underlying processes of turning asymmetries is needed before any conclusions can be drawn based on the results obtained with this paradigm. In addition to work with the orienting-asymmetry paradigm, there are several studies applying other—possibly more valid—measures to investigate lateralisation of conspecific vocalisation in primates.

Hook-Costigan and Rogers (1998) investigated whether the production of social contact calls in marmosets (*Callithrix jacchus*) is lateralised by determining the area of the left and right hemimouth during call production in eight animals. They found that the animals made a larger right than left hemimouth when making social contact calls, concluding that marmosets have a left-hemispheric dominance for the production of social communication. Petersen, Beecher, Zoloth, Moody, and Stebbins (1978) investigated lateralisation of perception of species-specific vocalisations in five Japanese macaques (*Macaca fuscata*) monkeys on a neural level. They trained the animals to discriminate communicatively relevant or irrelevant acoustic features in conspecific calls. All five animals showed a right ear advantage for discriminating the sounds with respect to communicatively relevant features, indicating a left-hemispheric dominance for the processing of communicatively significant sounds. For communicatively irrelevant features, the results of only two animals were reported. One of these animals showed a marked right-hemispheric dominance, whereas the other had a slight left-hemispheric dominance. The right ear / left hemisphere advantage for conspecific communication in Japanese macaques observed in this task was replicated in a later study by the same group (Petersen et al., 1984). Moreover, a left-hemispheric dominance for processing of communicative sounds in this species was also confirmed by two lesion studies. Heffner and Heffner (1984, 1986) trained Japanese macaques to discriminate between two types of species-specific coo vocalisations. They found that unilateral lesions to the left auditory cortex resulted in an impairment of vocalisation discrimination ability, whereas a lesion of the same area in the right hemisphere did not have this effect. A left-hemispheric dominance for processing of conspecific vocalisations in macaques was further confirmed by an imaging study in rhesus macaques (*Macaca mulatta*). Poremba et al.

(2004) measured local cerebral metabolic activity using PET while the macaques listened to species-specific vocalisations compared to other sounds. A greater activation in the left temporal pole was observed in response to conspecific calls as compared to other sounds.

Further evidence for a left-hemispheric dominance for processing of conspecific vocalisations is provided by work in the chimpanzee (*Pan troglodytes*). Gannon, Holloway, Broadfield, and Braun (1998) could show that, comparable to humans, chimpanzees have an anatomical asymmetry of the planum temporale, with the left planum being larger than the right in 17 out of 18 animals. Since the planum temporale constitutes parts of Wernicke's area in the human brain and is therefore critical for language processing, this anatomical asymmetry might be indicative of left-hemispheric dominance for the processing of species-specific vocalisation in chimpanzees. Moreover, it has also been shown that chimpanzees as well as bonobos (*Pan paniscus*) and gorillas (*Gorilla gorilla*) have a significantly larger left than right Brodmann area 44 (Cantalupo & Hopkins, 2001). This part of the inferior frontal gyrus constitutes parts of Broca's area, a region critical for speech production in humans. Interestingly this anatomical asymmetry is also linked to a functional asymmetry. Using PET, Tagliabattola, Russell, Schaeffer, and Hopkins (2008) could show a significant activation in the left inferior frontal gyrus during the production of species-specific vocalisations in chimpanzees. Taken together, there is compelling behavioural and anatomical evidence for lateralisation of conspecific communication in primates. In most, but not all, primate species, the left hemisphere is dominant for communication, a pattern that is generally comparable to the left-hemispheric language dominance in humans.

## Dermoptera and Scandentia

Together with primates, the orders Dermoptera (cologos) and Scandentia (treeshrews) constitute the clade Euarchonta, with cologos being identified as the closest living relatives of primates (Janecka et al., 2007). Given the abundance of evidence for a lateralisation of conspecific vocalisation in primates, one would expect similar findings in these genetically close orders. However, no research on lateralisation of vocalisation (or any other form of hemispheric lateralisation) has yet been conducted in Dermoptera and Scandentia.

## Magnorder Atlantogenata

In the Magnorder Atlantogenata, including the orders Pilosa (anteaters and sloths), Cingulata (armadillos), Afrosoricida (golden moles and tenrecs), Macroscelidea (elephant shrews), Tubulidentata (aardvarks), Sirenia (sea



cows), Hyracoidea (hyraxes), and Proboscidea (elephants) no research on lateralisation of vocalisation has yet been conducted.

## CONCLUSION

Despite the multitude of vertebrate orders in which no research on lateralisation of conspecific vocalisation has yet been conducted, some preliminary conclusions about the phylogenetic origins of human language lateralisation can be drawn from the present review. First, lateralisation of vocalisation is a widespread brain feature in communicating animals. While the results in amphibians and fishes should presently be considered with caution due to their scarceness and methodological constraints, we can safely say that there is convincing evidence for lateralisation of production and perception of conspecific vocalisation in several mammalian species, especially within the order of Primates. Moreover, there is evidence for lateralisation of conspecific vocalisation in some avian species (e.g., within the Passariformes order). The picture is not so clear regarding the direction of this asymmetry. Especially in birds, but also in some mammals, it is the right but not the left hemisphere that is dominant for conspecific vocalisation. In line with a model proposed by Gil-da-Costa and Hauser (2006), these findings may suggest that in the vertebrate evolution, lateralisation has been favoured as a neural feature that increases neural efficacy and therefore overall fitness (Vallortigara & Rogers, 2005). However, the direction of this asymmetry is more variable, possibly due to partly different genetic backgrounds and/or a stronger dependence on species-specific environmental or epigenetic factors.

With regard to the phylogenetic origins of human language lateralisation, the existence of similar hemispheric specialisations in several mammalian and some avian species may imply that human language lateralisation is not due to a dominance of the left hemisphere for executive functions involved in language processing. Rather it may be due to a dominance of the left hemisphere for those physical properties of language that are shared with vocalisations in other vertebrate species such as temporal or spectral characteristics (Böye et al., 2005). However, it becomes clear that this conclusion presently rests on only sparse empirical evidence, since the majority of vertebrate orders, especially among non-amniotes, still need to be explored.

## Outlook

When evaluating the evidence for lateralisation of conspecific vocalisation presented in this review, two main suggestions for further research in this field can be given. First, it is striking how few species have actually been

investigated with regard to this phenomenon. Despite the richness of communicative behaviour in fishes, lateralisation of conspecific vocalisation has been investigated in only two species. No research about this topic has been conducted in reptiles and only a single study in amphibians. Moreover, when evaluating the cladograms for birds and mammals it becomes clear that despite more or less compelling evidence for lateralisation of conspecific vocalisation in some orders (e.g., Passeriformes, Primates), we just do not know anything about communication asymmetries in the majority of avian or mammalian orders. Thus further research about lateralisation of conspecific vocalisation in all vertebrate orders that have not yet been investigated is necessary. In order to systematically investigate the question whether human asymmetry constitutes an independent development or is inherited, at least with regard to its basic lateralised properties, it is critical to investigate lateralisation of conspecific vocalisation in the remaining orders of the clade Euarchonta, which are Dermoptera (cologos) and Scandentia (threashrews). In a second step it would be interesting to investigate the Glires. In this clade evidence for a left-hemispheric dominance for conspecific calls has been shown in Rodentia, but as yet no research in on this topic has been conducted in Lagomorpha. In this order, for example, the pica (*Ochotona princeps*) has been shown to possess an extensive vocal repertoire in social situations and may therefore constitute an ideal model species (Connor & Whitworth, 1985). This approach would allow the determination of whether lateralisation of conspecific vocalisation is a common feature in all members of the superorder Euarchontoglires, which would be convincing evidence for the assumption that the basic lateralised properties of the human language system are indeed inherited.

Second, given the criticism that has been expressed regarding the validity of the orienting-asymmetry paradigm (Teufel et al., 2010), a widely used behavioural paradigm to assess lateralisation of conspecific vocalisation, more valid paradigms should be used and/or developed in communication asymmetry research. Apart from behavioural techniques, fMRI (e.g., Poirier et al., 2009) and PET (Poremba et al., 2004) have been proven to be powerful tools to investigate lateralisation of vocalisation. Ultimately these techniques may be particularly helpful in clarifying ambiguous behavioural results. While these techniques are well established in human research, there are still lots of non-primate animals in which they have not yet been applied. Due to the increased possibility of conducting fMRI and PET studies even in small animals, these techniques now offer the chance for tremendous insights into lateralised processing in the animal brain. Also, independent replication of existing findings in larger samples and the comparison of behavioural and neuroanatomical or imaging data in the same species would be of particular importance in this regard. Taking all this together, we would like to encourage researchers to conduct studies on lateralisation of conspecific

vocalisation in a wider variety of species with a wider variety of valid experimental paradigms. Only in doing so will it be possible to gain further insight into the background of human language asymmetry in vertebrate evolution.

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