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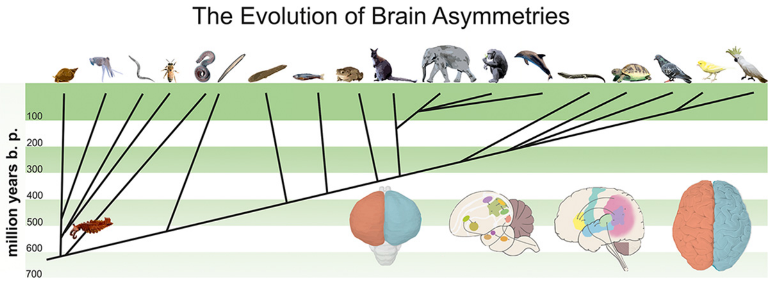
BRAIN LATERALIZATION: A COMPARATIVE PERSPECTIVE

GRAPHICAL ABSTRACT



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KEYWORDS

birds; cerebral asymmetry; commissures; evolution; language; nodal; zebrafish

CLINICAL HIGHLIGHTS

Brain asymmetries are key components of sensory, cognitive, and motor systems of humans and other animals. This review tracks their development from embryological asymmetries of genetic expression patterns up to left-right differences of neural networks in adults. These insights are crucial to understand pathologies of the lateralized human brain.

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BRAIN LATERALIZATION: A COMPARATIVE PERSPECTIVE

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Güntürkün O, Ströckens F, Ocklenburg S. Brain Lateralization: A Comparative Perspective. *Physiol Rev* 100: 1019–1063, 2020. Published April 1, 2020; doi:10.1152/physrev.00006.2019.—Comparative studies on brain asymmetry date back to the 19th century but then largely disappeared due to the assumption that lateralization is uniquely human. Since the reemergence of this field in the 1970s, we learned that left-right differences of brain and behavior exist throughout the animal kingdom and pay off in terms of sensory, cognitive, and motor efficiency. Ontogenetically, lateralization starts in many species with asymmetrical expression patterns of genes within the Nodal cascade that set up the scene for later complex interactions of genetic, environmental, and epigenetic factors. These take effect during different time points of ontogeny and create asymmetries of neural networks in diverse species. As a result, depending on task demands, left- or right-hemispheric loops of feedforward or feedback projections are then activated and can temporarily dominate a neural process. In addition, asymmetries of commissural transfer can shape lateralized processes in each hemisphere. It is still unclear if interhemispheric interactions depend on an inhibition/excitation dichotomy or instead adjust the contralateral temporal neural structure to delay the other hemisphere or synchronize with it during joint action. As outlined in our review, novel animal models and approaches could be established in the last decades, and they already produced a substantial increase of knowledge. Since there is practically no realm of human perception, cognition, emotion, or action that is not affected by our lateralized neural organization, insights from these comparative studies are crucial to understand the functions and pathologies of our asymmetric brain.

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Brain asymmetries are key components of sensory, cognitive, and motor systems of humans and other animals. This review tracks their development from embryological asymmetries of genetic expression patterns up to left-right differences of neural networks in adults. These insights are crucial to understand pathologies of the lateralized human brain.

I. INTRODUCTION: HISTORY OF COMPARATIVE RESEARCH ON LATERALIZATION

A. Broca's Discovery and Its Consequences

On Thursday, June 15, 1865, the young physician Pierre Paul Broca (1824–1880) delivered his paper on the seat of the faculty of spoken language to the Société d'anthropologie in Paris (60). His presentation summarized his work of the last five years in which he first analyzed speech deficits of patients to then meticulously reconstruct the damaged parts of their brains. His paper ended with the famous statement "Nous parlons avec l'hémisphère gauche" ("We speak with the left hemisphere," Broca, 1865, p. 384). The insights provided on this afternoon forever demolished two central scientific dogmata of 19th century, made Broca immortal, and marked the onset of cerebral asymmetry research. But the scientific events that unfolded around this time in France are not only a testimony of the past, but are responsible for the century-long neglect of the comparative perspective of brain asymmetries, the limited number of animal models in this field, and our consequential lack of in-depth knowledge on the neurobiological foundations of cerebral left-right differences.

B. Scientific Dogmata that Blocked the Path

The most important neuroscientific dispute of the first half of the 19th century concerned the question whether the cortex can be subdivided into functional entities or is organized as a holistic structure in which each part serves all mental functions (204). The person who strongly advocated a functional topography of the cortex was Franz Joseph Gall (1758–1828), a German neuroanatomist who fascinated lay people throughout Europe but was dismissed as a charlatan by his fellow scientists. Gall had observed that several colleagues with high verbosity and an excellent memory for text passages had protuberant and baggy eyes. Being an excellent neuroanatomist, he knew that large individual differences of brain shape and size exist. Thus he assumed that these people had especially enlarged retro- and supraorbital cortical areas that pushed the eyeballs to the front and down. From this hypothesis it was only a small step to conclude that the seat of language faculties had to be located in the frontal lobes in an area surrounding the eye sockets. Consequently, he thought that we should be able to discover the seat of further functions by tracking bulging spots on the uneven surface of the cortex of people with exaggerated mental abilities or characters. Gall further assumed that it would suffice to analyze the landscape of the skull since it should reflect the shape of the underlying cortex (153). Armed with this theory, he analyzed the heads of great poets, spirituals leaders, cruel murderers, and many more to come up with the cortical localization of 26 mental faculties like vanity, courage, mercy, etc. Accompanied by his assistant Johann Spurzheim, a servant, two monkeys, numerous skulls, and colored plaster casts, he then started on a hugely successful tour through the public lecture halls of Europe and convinced many people of his idea of "phrenology" (277). Scientists of his time, however, were outraged by his poor conclusions and soon (and since then) phrenology became a catchword for a sloppy way to map cortical functions. This quick and negative response made it later difficult to realize that Gall could have been right, but for the wrong reasons.

The main counterargument to Gall was put forward by the young anatomist Marie-Jean-Pierre Flourens (1794–1867) who conducted careful lesion experiments with pigeons and many more animal species. After ablating diverse regions of the forebrain of his subjects, he concluded that no specific function was lost, irrespective of where a small lesion was placed. If the lesions grew larger, however, the animals increasingly lost their abilities to sense or to initiate movements by their own will. But when nudged, they still were able to walk a few steps or fly a short path without any problem (135). Flourens concluded that the cerebral hemisphere must be the area where all senses are integrated and from where higher mental functions emerge. These hemispheres were, however, not arranged as a map of separate functions but as holistic chambers where all processes intertwine.

Parallel to Flourens, François Magendie (1783–1855) also had conducted animal experiments to reveal organizational principles of the central nervous system. During experiments with dogs, he thereby discovered the different functions of the dorsal and ventral horns of the spinal cord (300). Later on, he also studied motor functions of the cerebellum and the basal ganglia (301, 302). Additionally, other early animal researchers discovered that the cerebellum was a key structure in the production of organized movement patterns (135, 416). However, all of these discoveries on functional topographies were related to subcortical structures. The key concern of scientists of the early 19th century, however, was the cortex. And here, the conclusion of Flourens that no cortical functional subdivisions exist was readily accepted by the majority of scientists, and soon the holistic functional nature of the cortex became a scientific dogma.

Clinical scientists, however, objected. One of them was Jean-Baptiste Bouillaud (1796–1881) who later on became president of the French Académie de Médecine. Bouillaud argued that clinicians often observe specific motor or sensory deficits in patients with circumscribed brain lesions. So, there must be a cortical functional map. Although Bouillaud was fully aware how much the ideas of Gall were dismissed in the scientific community, he defended the idea of the frontal seat of language based on large numbers of carefully conducted patient studies (45). Several colleagues countered Bouillaud's arguments by reporting a phasic patient with lesions in temporal or parietal areas or cases with frontal lesions without language problems (277). One core problem of this time was a lack of awareness that expressive and receptive language problems should be distinguished and are differently localized. Only much later, Carl Wernicke (1884–1905) could clarify this issue by disambiguating between what is now called Wernicke's and Broca's area (506). A further problem was the unawareness of language asymmetry. As reconstructed a century later, most of the reports on negative cases that were thrown against Bouillaud had had right hemisphere lesions (32).

The second, equally important dogma of this time relates to the belief that healthy organisms have symmetrical organs. This assumption was forcefully established by Marie François Xavier Bichat (1771–1802) who became a tragic and at the same time towering figure in the medical sciences. When just in his mid 20s, Bichat became aware that he soon would die of tuberculosis. As a consequence, he started to work at a frantic pace to finalize his monumental book on the physiological studies of life and death (36). Tragically, Bichat did not die from tuberculosis but from a sepsis that resulted from an autopsy that he had conducted during this period. Using the argument of homeostasis of all physiological functions and their redundant circuits, Bichat concluded that the symmetry of all bodily organs is the core principle of life since this ensures that they can reciprocally supplement each other. His core example for symmetry was the human brain. He described it as perfectly symmetrical in all of its entities. Also the uneven parts like the corpus callosum were described by him as symmetrically embedded into the telencephalic tissue. Obviously, Bichat was well aware of the existence of handedness, but he saw this as a mere social habit since the arms and hands of people were, in his view, perfectly symmetrical.

Bichat's legacy was extremely influential and even affected the interpretation of studies on face asymmetries up the first half of the 20th century (179). However, scientists had nevertheless collected comparative evidence against Bichat's dogma in the period before Broca. Already in 1820, Gottfried Reinhold Treviranus (1776–1837, **FIGURE 1*A***) described for the first time conspicuous asymmetries of the human cortex: "Humans have multitude and deep convolutions that are asymmetrically organized in the two hemispheres. This is different from the cortex of monkeys" (470).

Similarly, Magendie (302) discussed just 4 years later in his comparative account on the brain that cortical folding patterns are asymmetrically organized and that it would be interesting to know if these individual morphological dispositions are related to the idiosyncrasies of the mind. Soon thereafter, these ideas became grounded on further solid evidence. In 1839, François Leurat and Louis Pierre Gratiolet (**FIGURE 1*B***) published a ground-breaking comparative book on the organization of the cortex of mammals including humans (286, 287). The authors aimed for a reconstruction of the evolution of cognition as remodeled from comparative analyses of the cortical organization. Based on a much larger database, Leurat and Gratiolet verified the observations of Treviranus that the cortical folding pattern became more irregular and increasingly asymmetric with phylogenetic proximity to humans. In addition, the authors observed that in primates the left cortex developed faster than the right. It was especially Louis Pierre Gratiolet (1815–1865) (**FIGURE 1*B***) who repeatedly stressed that it is the left frontal cortex that is in advance [an idea that is disputed today (80)]. This finding was later discussed as a causal ontogenetic explanation for asymmetries like handedness or language (204, 310). The conclusion of the sum of these findings was radical: while asymmetries had always been seen as evidence for pathology and malfunction (220, 294, 343), comparative evidence suggested that it was a hallmark of cognitive advance and reached its apex in humans. This conclusion became increasingly important after Broca's discoveries on language asymmetry. In short, they implied that asymmetries of brain and function are either unique to humans or were at least most advanced in our

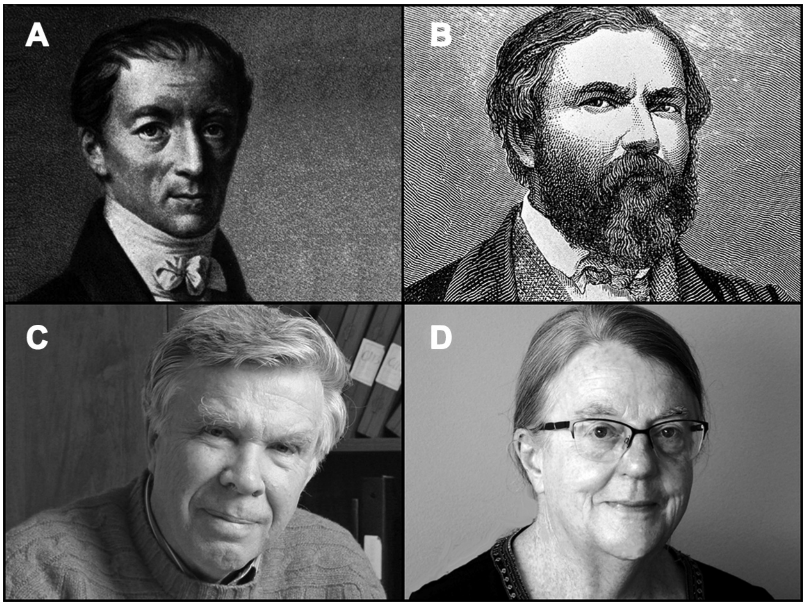


FIGURE 1. Pioneers of comparative cerebral asymmetry research of the 19th and the 20th century. *A*: Gottfried Reinhold Treviranus (1776–1837) was a German medical physician and scientist who coined the term *life sciences*. He was the first to describe the asymmetries of the cortical folding pattern and observed that asymmetry seemed to increase with phylogenetic proximity to humans. *B*: Louis Pierre Gratiolet (1815–1865) was a French anatomist and zoologist who published together with François Leurat a ground-breaking book on the pattern of the cortex, thereby confirming Treviranus' observations. Subsequently, he demonstrated that the left hemisphere develops faster and speculated about functional left-right differences that could result from this ontogenetic difference. (Photo courtesy of Wellcome Collection, CC BY 4.0.) *C*: Fernando Nottebohm (1940) is an Argentinian/American neuroscientist who discovered fundamental principles of the song system in songbirds like its ontogenetic learning principles, the relevant neural pathways, adult neurogenesis, and its motor asymmetry. (Photo courtesy of Zach Veilleux, The Rockefeller University.) *D*: Lesley Rogers (1943) is an Australian neuroscientist who discovered functional brain asymmetries in chicks and several further species. She also revealed the environmental and hormonal components that shape cerebral asymmetries in early ontogeny in birds. (Photo courtesy of Lesley Rogers and Gisela Kaplan.)

species. This conclusion importantly slowed down progress in comparative asymmetry research and resulted in a century-long absence of animal models for left-right differences of the brain.

C. 1865–1990s: Broca's Discovery and the Belief of Human Uniqueness

In 1861, at the hospital Bicètre of Paris, Pierre Paul Broca analyzed a patient named Leborgne who only could utter a few words but was able to understand spoken questions. When Leborgne died a few days later, Broca conducted the autopsy and revealed a lesion in the third part of the inferior frontal gyrus of the left hemisphere. He presented this case at the Société d'anthropologie to support Bouillaud's claim of the frontal seat of language (58). Soon, Broca encountered another patient with similar language problems, and this autopsy also revealed a lesion at the identical location. Broca was tantalized by the identity of the two lesion locations but was too cautious to make a point out of it. Instead, he again referred in an overall way to the frontal lobes as being relevant for language processes (57). Broca now started to collect further evidence from his own ward or from the literature (59). Then, in 1865, he presented a large number of meticulously analyzed cases to the members of the Société d'anthropologie (60). All of them had lesions in a cortical region that now bears his name and all suffered from severe deficits in speech production. Different from other scientists of his time, Broca carefully avoided to assume that the third component of the inferior frontal gyrus on the left hemisphere was the "seat of language" since these patients could understand language but had lost their ability to produce it. In a single step, Broca demolished the dogmata of the holistic and of the symmetrical brain.

After these events, it was only a small logical step to ask if similar properties exist in non-human animals. Since Broca had discovered language asymmetry in humans, numerous scientists started to search for similar left-right differences in animals in the subsequent years. The problem was an obvious one: many animals communicate but only humans have language. However, parrots can at least learn to copy human speech. Otto Kalischer (1869–1942) bought 60 parrots from a colonial store in Berlin and taught these birds to utter typical human phrases. Subsequently, he lesioned different parts of their brains uni- or bilaterally. Indeed, some lesions affected the vocalization of the animals, but there was no systematic hemispheric asymmetry visible (255). For a very long time, this was the end of an animal-research-based search for vocalization asymmetries at the functional level.

At the anatomical level, several neuroanatomists started to look for cortical asymmetries that resemble the human condition. As mentioned above, Leurat and Gratiolet had already reported some minor cortical asymmetries in different mammalian species (286, 287). Further reports followed like that of Cunningham (92) and Henschen (221) who observed that the anteroposterior extent of the cortex of several ape and monkey species is larger on the left. Cunningham (1892) also observed that similar to humans, the posterior angle of the Sylvian fissure shows a conspicuous left-right difference (92). Ingalls (1914) (244) conducted an anatomical survey in different monkey species and reported visible differences in the cortical organization that surrounded the Sylvian fissure. None of these descriptions on cortical asymmetries in non-human primates stirred major scientific interest. Since all discovered left-right differences were rather small and since no behavioral correlate could be found, they bolstered the view of Leurat and Gratiolet that a strongly lateralized brain is a defining feature of humans and that asymmetries in non-human primates constitute weaker, less advanced forms of lateralization.

This view slowly started to vanish in the second half of the 20th century when the first behavioral evidence on behavioral communication asymmetries in non-human primates was collected. Dewson (1977) (108) demonstrated that in macaques lesions of the left temporal cortex reduced the ability to discriminate auditory input, while the effect of right-temporal lesions were minor. Moving a step further, Petersen et al. (1978) (368) showed that communicative auditory signals are better discriminated with the right than with the left ear. At the same time, interest on anatomical asymmetries in non-human primates went through a revival. LeMay and Geschwind (1975) (281) measured the height of the posterior end point of the Sylvian fissure in the brains of 30 monkeys from 8 different species including capuchin monkeys, howler monkeys, spider monkeys, baboons, macaques, black apes, leaf monkeys, and proboscis monkeys. They also measured the height of the posterior end point of the Sylvian fissure in the brains of 39 apes from 5 different species, including gibbons, siamangs, orangutans, chimpanzees, and gorillas. They found that in monkeys and lesser apes, asymmetries were quite uncommon, with only 3 of 41 brains showing a rightward asymmetry of the Sylvian fissure. In contrast, out of 28 great ape brains, 17 showed a significant asymmetry, with 16 of these brains having a higher right Sylvian fissure. Similar findings were subsequently reported from different laboratories (125, 216, 433).

Yeni-Komshian and Benson (1976) (522) analyzed the length of the Sylvian fissure in chimpanzees and demonstrated that in the brains of 20 of 25 chimps, the fissure was longer on the left. A similar analysis of 25 macaque brains evinced no such asymmetry. Beheim-Schwarzbach (1975) (29) compared the cytoarchitectonic organization of the dorsal surface of the temporal lobe of a person who could speak 100 languages with that of a chimpanzee. She demonstrated that the inter-species differences were smaller than the interhemispheric ones since in both species the left cytoarchitectonic organization was far more complex. Overall, these data make it likely that functional and anatomical asymmetries of communicative systems occur in the family of Hominidae, to which both apes and humans belong (374).

Scientists of the 19th and early 20th century were well aware that the most glaring example of human lateralization was handedness. Although no proper neural correlate could be discovered, it was nevertheless tempting to look out for comparisons in non-human animals. Because reaching and scratching movements are easy to observe and quantify, most studies reported these simple behavioral bouts. However, these authors ignored that in humans simple reaching elicits only small handedness effects, not comparable to what can be seen for complex fine motor tasks like writing (308).

The first such systematic observation was conducted by Ogle (1871) (362), who observed 86 parrots in the zoo of London and reported that nearly three-fourths of them had a left foot preference while holding or rotating a food item. Unfortunately, Ogle (362) did not provide any information on the observed species, reducing the impact of his observation. Of even lesser scientific value was the report of Thomas Dwight who made similar observations in the same zoological garden (115). He stated, “I had satisfied myself that every parrot had a favorite side.”

Unfortunately, he then continued, “. . . I have forgotten which side was used the most” (1891, S. 466; cited from Ref. 205).

The first well-documented scientific study on parrot footedness was published by Friedman and Davies (1938) (149) and later by Rogers (1980) (402) who revealed a significant left-footed population level asymmetry for food holding in 14 and a right-footed asymmetry in only 2 parrot species. Similarly, significant left-footedness was also reported in goldfinches in a task in which they had to manipulate flaps to obtain a food reward (113). For rodents, the first pawedness study was conducted by Tsai and Maurer (1930) (471), shortly thereafter followed by a similar study by Peterson (1934) (369). Both papers described a mild preference for the right paw during reaching. In mice, Collins (1985) (83) observed that most individuals evinced paw preferences during a reaching task, but the overall number of left- and right-pawed animals was about equal. Thus mice showed individual level asymmetry (half of the population uses the left paw, while other half prefers the right), while rats demonstrate a mild population level asymmetry (a majority of individuals prefers one paw).

Apes are the closest relatives of humans. Early reports revealed a pattern comparable to rodents with no clear-cut population level asymmetry (124, 130, 175, 207, 292, 392, 490, 523). All of these studies suffered from a very small sample size and were thus seriously underpowered. However, also studies with sample sizes of more than 40 individuals did not observe a different pattern (15, 56, 128). Studies with macaques were partly conducted with a higher number of individuals. Itani et al. (1963) (245) observed food reaching behavior in 394 monkeys and observed a right hand preference in 118 (30.0%) and a left hand preference in 149 (37.8%); 127 (32.2%) evinced no individual asymmetries. Subsequent studies using a reaching task evinced similar conclusions (279, 503). Hörster and Ettlinger (1985) (234) trained 237 macaques in a tactile discrimination task and observed which hand the animals used. Overall, 77 (32.5%) animals were right-handed and 78 (32.9%) were left-handed, while 82 (34.6%) used both hands about equally. In total, these studies studied 886 macaques. Obviously, each study varied from the other. What did not vary, though, was that left-handed, right-handed, and ambidextrous animals had proportions of about one-third each. These results were sobering. Consequently, Richard Jung’s skeptical phrase provides a concise summary of its time: “Thus, I think that we must distinguish between the preference for one hand in animals, and the dominance of one side of the brain in man. As I said, no evidence whatsoever has been presented that cerebral dominance really occurs in monkeys” (253).

To summarize, despite several attempts, the discovery of human brain asymmetry was not followed by a surge of similar findings in non-human animals. Four major reasons seem to be responsible for an absence of such a development. First, the legacy of Leurat and Gratiolet sketched a theoretical frame in which asymmetries were mainly tied to the human brain and were, if at all, only expected in lesser magnitude in non-human primates. Second, human asymmetries were seen as related to language and handedness, two behavioral systems that have no counterpart in the animal world. There is no doubt that language is unique, but so is also our extraordinary dexterity that grants our ability to write, draw, and manipulate minute technical systems. Third, the limited left-right differences that had been discovered in primates were not convincing enough to establish an animal model of brain asymmetry. The same applied to the results in rodents. The findings in birds were stronger but went unnoticed by most scientists. Fourth, beginning in the 1960s, new theories started to dominate asymmetry research that regarded laterality as the result of the mutation of a single gene that occurred in the lineage to *Homo sapiens* (11, 13, 14, 91, 320). According to these theories, population level asymmetries of a neural function should not exist in non-human animals. The combination of these factors resulted in the strange fact that about a century had to pass after Broca’s major discovery until scientists realized that asymmetries of brain and function are a widespread property of the animal kingdom.

D. The Current View in Brief

One hundred five years after Broca's publication on language asymmetry, Fernando Nottebohm (**FIGURE 1*C***) published a seminal paper in which he described the ontogenetic events during song learning in chaffinches (345). He outlined that these birds go through processes that strongly resemble language learning in human infants. Most importantly for asymmetry research, he also described the results of unilaterally transecting the nervus glossopharyngeus pars tracheosyringealis that connects the brain stem motor areas with the syrinx, the functional equivalent to the mammalian larynx. Transecting this nerve on the right resulted in the loss of ~10% of the syllables. The same surgery on the left rendered the animal practically mute. Nottebohm (1977) (346) described canaries after left-sided nerve transection as behaving like an opera singer in a silent movie. The canary goes through all the movements of singing without any sound being heard. Since a short while after these reports the central neural components of the song system could be identified (see sect. V*A*), the avian song system became a classic animal model for vocalization learning and population level asymmetry.

Towards the end of the 1970s, Lesley Rogers (**FIGURE 1*D***) discovered that the left hemisphere of 2-day-old chicks dominates the ability of the animals to learn a visual discrimination task (406). In the subsequent years, Lesley Rogers and her colleagues were also able to discover both the ontogenetic events with which this asymmetry is established as well as the critical neural pathways that are responsible for lateralized behavior (4, 403, 411). As a consequence, visual asymmetries in birds like chicks and pigeons became an established animal model to disentangle the lateralized perceptual, cognitive, ontogenetic, and neurobiological fundaments of left-right differences (see sect. II). These discoveries in songbirds and chicks slowly turned the tide. Increasingly, novel kinds of non-human animal asymmetries were described and animal models that enable the analyses of brain asymmetries from genes to behavior could be established (see **FIGURE 2**). This paper will now first illustrate some principles that can be learned from these diverse findings before dwelling in detail about the insights generated by the main animal models.

1. Behavioral asymmetries can be traced back 500 million years

Babcock and Robison (1989) (21) analyzed bite marks on the rear of Cambrian trilobites that showed signs of post-attack healing. They found that two-thirds of the animals wore right-sided bite marks, while the rest evinced left-sided or bilateral wounds. At around that time it became likely that a large predator called Anomalocaris regularly preyed on trilobites by using its pair of spiny frontal limbs (97, 98, 509). According to fossil reconstructions, Anomalocaris possibly attacked a trilobite by biting its right rear end, used its left limb to keep the trilobite in position while repeatedly flexing with its right limb its victim up and down until the cuticle cracked in the vicinity of the mouth of Anomalocaris (339). If this reconstruction holds, the hunting strategy of Anomalocaris would be the first known example of "handedness" and could be traced back more than 500 million years. Thus lateralization is very likely not a recent evolutionary feature but about as old as the evolution of animals.

2. Vertebrate handedness has no common ancestor

Ströckens et al. (2013) (452) conducted a cladistic analysis on the large number of publications on the preponderance of one fin, paw, hand, or foot during all kinds of unimanual activities in 119 different vertebrate species. About two-thirds of the recorded species evinced some form of preference and were found throughout all vertebrate classes. Although possibly a publication bias exists, it still holds that limb preferences at the individual or the population level are widespread among vertebrates. Most importantly, this motor bias seems to have evolved in the many distantly related species all over the vertebrate tree. This makes common ancestry of the trait extremely unlikely and rather supports the idea of parallel evolution. This conclusion is supported by research on bipedal and quadrupedal marsupials (169). While the former often display a pronounced population level forelimb preference, the latter ones often show weak or no sidedness. This difference cannot be explained by phylogenetic relations, but seems to be shaped by local ecological adaptations that characterize what the animals do with their hands. While the upright posture of bipedal marsupials enables them to make use of their hands for manipulation of branches and leaves, this is hardly possible for quadrupeds that need all four extremities to walk. As a consequence, bipedal species develop pronounced population level handedness, while quadrupedal species have hardly any. Thus strong handedness does not depend on the phylogenetic proximity to humans, but on the local adaptation of a species to an ecosystem where it benefits from fine manipulation. These results make it understandable why species like humans and some parrots with their need and their ability for exquisite fine manipulation have developed strong and population level limb preferences.

3. The presence of asymmetry does not depend on brain size

Ringo et al. (1994) (395) published a landmark study in which they hypothesized that the large size of the human brain in conjunction with the average slow conduction time of the corpus callosum would prohibit multiple interhemispheric interactions during stimulus processing. As a result, time-critical tasks might be processed in one hemisphere, resulting in pronounced asymmetries. This prediction would imply that the probability to establish neural and functional left-right differences should be a function of

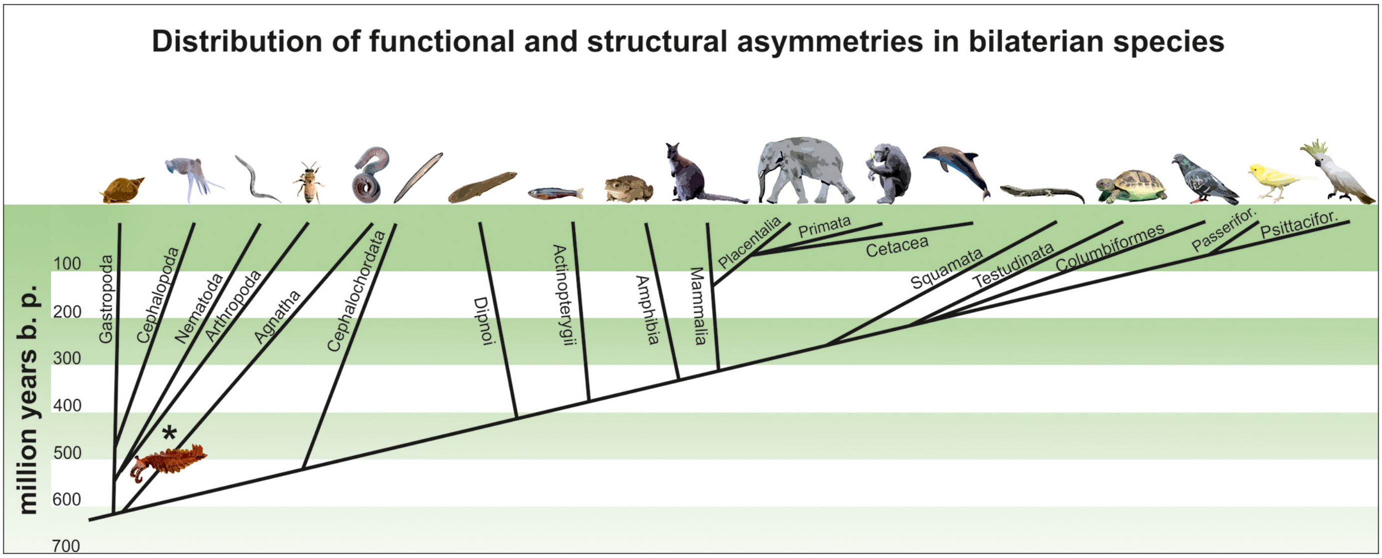


FIGURE 2. The phylogeny of asymmetry. A cladogram-based depiction of lateralized species that represent major taxa of the animal phylum. From *left* to *right*: lateralized mating in pond snail (*Lymnaea stagnalis*) (101) (Photo courtesy of Wolfgang Gessl.), visual asymmetries in cuttlefish (*Sepia officinalis*) (428) (Photo courtesy of Sebastian Niedlich.), asymmetry in the nervous system and lateralized behavior in the nematode (*Caenorhabditis elegans*) (227) (Photo courtesy of Judith Kimble.), asymmetry of olfaction in honey bees (*Apis mellifera*) (393) (Photo courtesy of Entomology, CSIRO, CC BY 3.0.), handed curling in hagfish (*Eptatretus stoutii*) (327) (Photo courtesy of Douglas Fudge and Andreas Zommers.), mouth asymmetry in lancelets (*Branchiostoma lanceolatum*) (445) (Photo courtesy of Hans Hillewaert, CC BY-SA 4.0.), lateralized predator avoidance in Australian lungfish (*Neoceratodus forsteri*) (291) (Photo courtesy of Russell Bicknell, thanks to University of New England (Armidale, NSW, Australia) Natural History collection, specimen UNE.NHM.Z 271.], asymmetrical organization of flight/fight responses in zebrafish (*Danio rerio*) (81) (Photo courtesy of Cherus, CC BY-SA 3.0.), right-pawedness in toads (*Bufo bufo*) (38) (Photo courtesy of Armin Kübelbeck, CC BY-SA.), handedness in red-necked wallabies (*Notamacropus rufogriseus*) (167) (Photo courtesy of Neil Turner, CC BY-SA 2.0.), forefoot preference in Asian elephants (*Elephas maximus*) (257) (Photo courtesy of Christian Zacke, CC BY-SA 3.0.), handedness in the food-tube task in chimpanzees (*Pan troglodytes*) (231), visual asymmetry in dolphins (*Tursiops truncatus*) (518) (Photo couretsy of Nataša Stuper, CC BY 2.0.), lateralized eye preference for monitoring and escape behavior in the common wall lizard (*Podarcis muralis*) (43), asymmetrical visual responses to mirrors in tortoises (*Testudo hermanni*) (446) (Photo courtesy of Richard Mayer CC-BY-SA-3.0-migrated.), lateralized visually guided foraging in pigeons (*Columba livia*) (188) (Photo courtesy of Lewis Hulbert, CC BY-SA 4.0.), asymmetrical song control in canaries (*Serinus canaria*) (346) (Photo courtesy of David Stang, CC BY-SA 4.0.), and left-footedness in sulfur crested cockatoos (*Cacatua galerita*) (402). Anomalocaris (*) is depicted on the line to modern arthropods, ~500 million years before present (21) (Photo courtesy of Matteo De Stefano, MUSE - Science Museum of Trento. CC BY-SA 3.0.). It possibly represents the oldest evidence for behavioral asymmetry.

brain size with its peak in large brained animals like humans, pinnipeds, elephants, and cetaceans. While indeed there is evidence for hemispheric asymmetries in all of these groups of animals (47, 256, 257, 518), there is similar evidence from small vertebrates (462, 492).

Importantly, also invertebrates like *Caenorhabditis elegans* (227) (see also sect. IIIA), slugs (317) and various insect species (140, 142, 144, 393) show hemispheric asymmetries. In addition, pronounced asymmetries in vertebrate species also occur without a corpus callosum as shown in marsupials (167, 168, 481) and various non-mammalian vertebrates (354, 413, 486). While there is no doubt that the corpus callosum is a critical structure for mammalian lateralization, the argument of a commissural time constraint as the main evolutionary selection pressure for the occurrence of brain asymmetries seems not to be valid.

4. Human language asymmetry has ancient mammalian predecessors

A cladistic analysis of vocal asymmetries in vertebrates revealed that a left-hemispheric dominance for the reception and production of species-specific vocal communication seems to be typical for mammals across five orders (361). These findings have important implications for recent theories on the phylogeny of human language lateralization (88, 278). These scholars formulated the "From Hand to Mouth" theory according to which the superiority of the left hemisphere for language is a consequence of human right-handedness for gesturing. Although indeed great apes gesture much more often with the right hand (231), the left-hemispheric communication superiority is also evident in animals like mice, rats, gerbils, dogs, sea lions, and horses that do not gesture and might not even show a right limb preference (361, 452). Thus a broader comparative framing supports the idea that we inherited a left-hemispheric superiority for conspecific vocalization from our mammalian ancestors and then modified this common lopsided mammalian pattern into our unique language system (see sect. V*A* for a detailed discussion of hemispheric asymmetries in neural systems for vocalizations).

E. Evolutionary Advantages of Hemispheric Asymmetries

If lateralization is so widespread in so many species that live in so many different ecosystems, it possibly provides an important fitness benefit. Several studies indeed suggest that this is the case, as long as the efficacy of the lateralized system itself is tested (190). For example, pigeons with pronounced asymmetry for visual object recognition find more grains that are scattered among pebbles (184). Similarly, chimps with stronger individual hand preferences catch more termites with their probing tools (319), and humans with pronounced language asymmetry have higher scores in their verbal IQ (122) and read better (78). A large-scale dichotic listening study in more than 1,800 participants also found that both strong left- and strong right-hemispheric asymmetry in the dichotic listening task for language lateralization were related to better task performance (225).

What are the mechanisms that link asymmetry to performance? There are possibly three such mechanisms. First, if an animal mainly uses one limb or one side of its sensory systems to interact with the environment, the hemisphere contralateral to the preferred side will go through life-long perceptual or motor learning. Thereby, sensory discrimination ability and motor efficacy will increase unilaterally. For example, black-winged stilts mainly use their right eye for predatory pecking. Consequently, pecks with their right eye are more successful (494). Similarly, when locusts have to walk past a gap, they usually preferentially use the right or the left leg. Individuals with a strong preference for one leg are more successful (31). Thus a small advantage of one extremity, combined with lateralized practice, will increase performance and an even higher likelihood that this side is used.

Second, increased training with the perceptual or motor system of one side results in shorter reaction times (177, 484), an advantage that enables survival when having to act fast to predators or food (479). This effect is also observed in countless visual half-field studies with human subjects when tested with material that activates lateralized sensory or cognitive processes (356, 496).

Third, if two complementary neural processes are computed in parallel in the two hemispheres, cognitive redundancy is reduced and overall efficacy is increased. Indeed, when lateralized and nonlateralized chicks perform a task in which they have to quickly search for grains scattered among pebbles and in parallel monitor birds of prey that occasionally fly overhead, the lateralized individuals perform both tasks at a higher level. The nonlateralized birds perform poorly, since they sometimes don't spot the predator and when seeing it often mistake grits for grain (414). These and further evidence in other species (93) make it likely that hemispheric asymmetry enables parallel processing of complementary information within the two hemispheres (see **FIGURE 3**).

All of these benefits can be reaped by an individual which shows lateralization for a given process like, e.g., object manipulation. If this would be the sole advantage of asymmetries, we could expect that ~50% of the human population is left-handed while the remaining 50% consists of right-handers. But this is obviously not the case. Instead, ~90% of the human population is right-handed. Similar, but less pronounced, population level asymmetry has also been found for language, spatial orientation, and many more aspects of human left-right differences (463). When hemispheric asymmetries in non-human animals are analyzed, many of the discovered examples also show population level asymmetries (143). Thus, from an evolutionary point of view, population level asymmetries require an explanation that goes beyond the three benefits listed above, since these three do not require that the majority of a population is skewed unto the same direction.

Vallortigara and Rogers (2005) (485) proposed that population level asymmetries are related to the diverse aspects of social interactions of lateralized species. According to their view, the evolution of cerebral lateralization possibly proceeded in two steps. In step one, individual level asymmetries were selected because this neural organization provides perceptual, cognitive, and motor advantages. However, for animals that live in groups like, e.g., fish that swim in shoals, there is a further factor that affects their lateralization. When this school is attacked by a predator, individuals can benefit from a dilution effect by all turning into the same direction. Thus aligning in turning preferences with the others can save lives and is therefore selected (37, 483). However, when predators learn about turning preferences of this species, they can anticipate in which direction to swim to catch the most. In this case, a minority with a different turning preference might have better chances for survival. Using game-theoretical modeling, Ghirlanda and Vallortigara (2004) (166) suggested that such a scenario would indeed produce a population level asymmetry for the majority of individuals, and a reversed asymmetry in a minority.

More recently, Ghirlanda et al. (2009) (165) extended this view by proposing an intraspecies evolutionary stable strategy that posits that population level asymmetries can arise by a balance between competitive interactions at the antag-

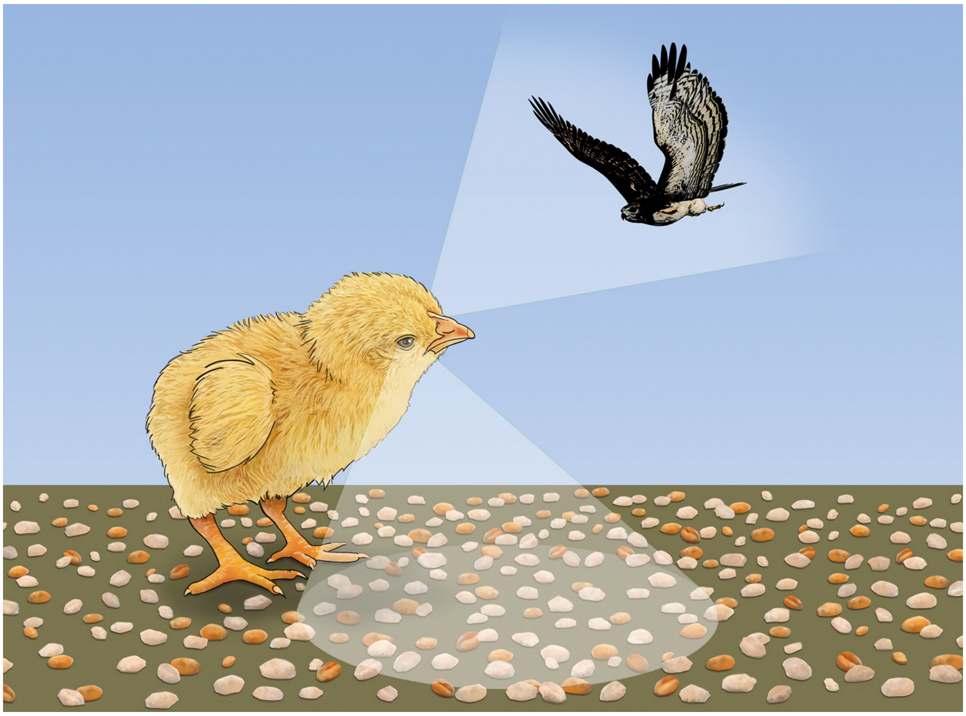


FIGURE 3. Asymmetry pays. Brain lateralization in domestic chicks is associated with an advanced ability to perform two tasks in parallel. In this study chicks had to find grains among pebbles and were simultaneously forced to be vigilant for birds of prey. Lateralized birds could do this well, while nonlateralized ones failed. [Based on Rogers et al. (414).]

onistic level and cooperative interactions at the synergistic level. The first would produce a minority with an atypical lateralization, e.g., left-handers that are successful in competitive sports like boxing (193) or fencing (206). In contrast, the second form of interaction would result in a majority with an identical side preference, e.g., as has been shown for gesturing during auditory signaling in apes (382).

F. Outline of the Review

In this section, we summarized the history of comparative lateralization research from its roots in the 19th century, focusing almost exclusively on humans, up to modern time studies identifying behavioral and brain asymmetries in hundreds of different vertebrate and even invertebrate species. Given that hemispheric asymmetries provide distinct advantages for the individual or even the whole population, it is likely that future studies will identify even more species with lateralized nervous systems and behavior. In the following sections of this review, we would like, however, to focus on a few, well-investigated examples of brain lateralization. In the second section of this review, we will use the examples of the zebrafish, the pigeon, and the nematode *C. elegans* to discuss the question of how brain asymmetries emerge during ontogenesis. In the third section, we will highlight different perceptual and motor asymmetries using mostly studies on bird species as examples. The fourth section deals with asymmetrical organized networks in the brain, with humans and pigeons as prime examples. In the fifth and last section, we will focus on language lateralization and lateralization in emotional processing based on studies on humans, songbirds, and non-human primates.

G. Interim Summary Section I

- Comparative anatomical studies in the first half of the 19th century suggested that cortical asymmetries in non-human primates were subtle while those in humans were pronounced. After Broca's discovery, mainly primates were anatomically analyzed for cortical asymmetries in the area of the human language system. In parallel, behavioral studies on handedness were conducted in primates and rodents. All discovered left-right differences were rather small, bolstering the view that left-right differences are a hallmark of our species' cognitive advance and our phylogenetic uniqueness. Consequently, it was assumed that animal models for asymmetries could not exist.
- It took about a century until, beginning with the 1970s, pronounced population level asymmetries of the avian song and visual system were discovered. These studies could also uncover neuroanatomical and ontogenetic left-right differences. Thus neurobiological details of lateralized systems could be studied for the first time.
- Today, left-right differences of various behavioral, genetic, or neural systems are known in close to 200 species, reaching from worm to human. Cladistic studies show that lateralized systems evolved multiple times, depending on local ecological pressures. The presence of asymmetries does not depend on brain type or size, nor on the presence or absence of the corpus callosum.
- Asymmetries are beneficial by *1*) increasing perceptual or motor abilities through life-long training of one hemisphere, *2*) decreasing reaction time and increasing

speed of this trained side, and *3*) parallel processing of complementary cognitive processes in the two hemispheres.

- Population level asymmetries where a majority is skewed to one and a minority to the other side might constitute an evolutionary stable strategy between circumstances in which being part of a majority or of a minority can produce complementary gains.
- Animal models enable the reconstruction of the phylogenetic past of asymmetries. But they also help to understand the ontogenetic events that cause the emergence of lateralized system during ontogeny. These relevant genetic, environmental, and epigenetic factors will be outlined in the next section.

II. HOW ASYMMETRIES EMERGE

A. Development of Neuroanatomical Asymmetries in the Zebrafish

As we have shown, brain asymmetries are a widespread feature in the animal kingdom and have clear evolutionary advantages. But how do they emerge during ontogeny? Early research on this topic suggested a monocausal, single-gene explanation for the emergence of handedness in humans (12, 321). In contrast to this view, today it is clear that a single genetic factor is insufficient to explain the ontogenetic development of any lateralized function (190). Instead, it is likely a mixture of several different genetic, environmental, and epigenetic factors that causes the emergence of asymmetries in a developing vertebrate embryo or insect larva. To make the story even more complicated, these three factors often interact with each other on many different levels, enhancing, muting, or altering their respective effects.

Probably the most widely used model species to investigate how genetic influences shape a lateralized phenotype is the zebrafish (*Danio rerio*). In these small tropical fishes, the pineal complex and the habenular complex within the epithalamus are strongly asymmetric. The pineal complex, consisting of the pineal and parapineal organ, is a unilateral structure, which is situated on the left side in ~90% of all wild-type zebrafish (94). The habenula of zebrafish consists of three subnuclei: the ventral, the lateral dorsal, and the medial dorsal habenula. While the ventral habenula is similar in size and projection pattern on both sides, the dorsal habenular subnuclei differ massively between the hemispheres. On the left side, the lateral dorsal habenular nucleus is significantly larger, contains more neurons, and in contrast to its counterpart on the right side receives input from the unilateral photosensitive parapineal organ. However, in the right habenular complex, the medial dorsal habenula is larger, contains more neurons, and receives predominantly input from the olfactory bulb (6, 240, 326, 419) **(FIGURE 4)**.

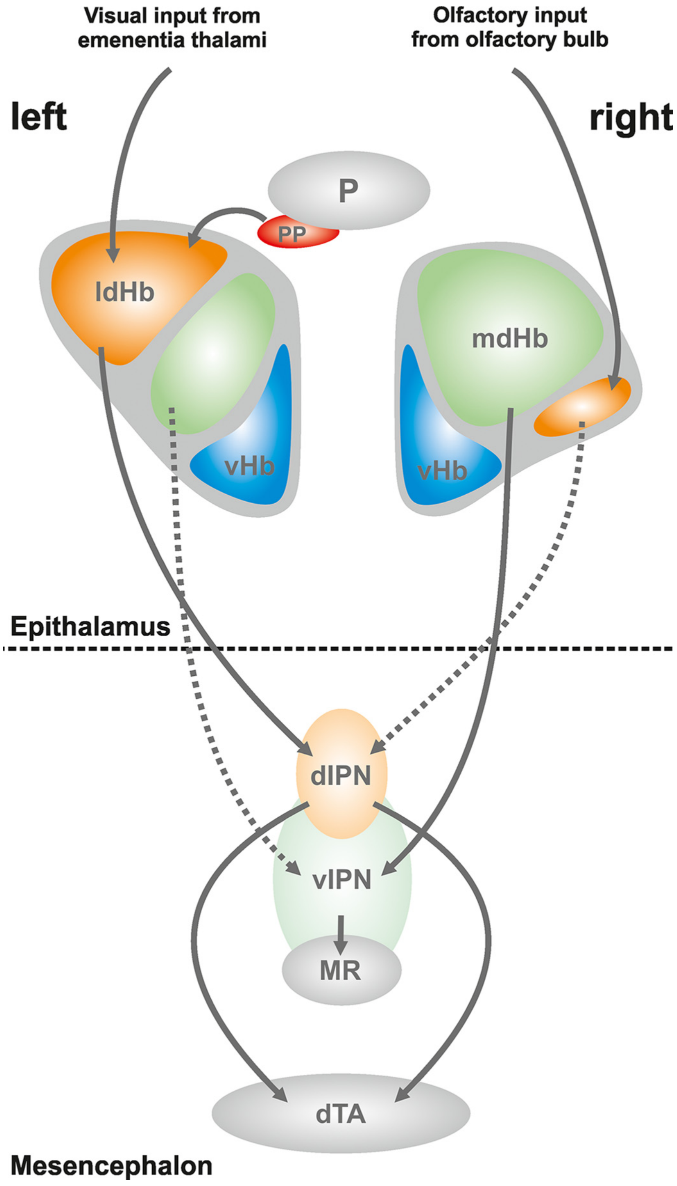


FIGURE 4. Asymmetries in the zebrafish epithalamus. Due to asymmetric genetic cascades during development (see text), the parapineal and the habenular complex in zebrafish are asymmetrically organized. The photosensitive parapineal (PP), associated to the pineal complex (P), is situated in most zebrafish on the left side and only projects to the left habenula. Furthermore, only the left habenula receives visual input from the emenentia thalami, while only the right habenula receives olfactory information by fibers from the olfactory bulb. Also, the size and neuron numbers of habenular subnuclei differ between left and right. The lateral dorsal habenular nucleus (ldHb) is significantly larger on the left, while the medial dorsal habenular nucleus (mdHB) is larger on the right side. The ventral habenular nucleus (vHb) does not differ in size between left and right side. These differences in size also cause an asymmetry in fiber projections onto nuclei within the mesencephalon. The dorsal nucleus interpeduncularis (IPN) predominately receives input from the left ldHb, while the ventral IPN is mostly targeted by fibers from the right mdHB. Dorsal and ventral IPN possess distinct efferents to the median raphe (MR) and the dorsal tegmental area (dTA), which are crucial for emotionally guided behavior. It is thus likely that habenular asymmetries have an effect on such behaviors (see text). [Modified from Güntürkün and Ocklenburg (190).]

Furthermore, only the left dorsal habenula receives visual input from a specific subset of retinal ganglion cells over the eminentia thalami (526). These gross differences in size and afferents are also reflected in lateralized habenular functions. While neurons in the left habenula mostly respond to light stimuli, neurons in the right habenula fire mostly in response to olfactory cues (111, 526). The size asymmetry of the dorsal habenular nuclei has also an effect on downstream areas. The lateral dorsal habenula projects to the dorsal component of the mesencephalic nucleus interpeduncularis (IPN), while the medial dorsal habenula projects to the ventral part of this nucleus. Since the lateral dorsal habenula is larger on the left side, the dorsal IPN predominately receives input from the left habenula, while the ventral IPN is mostly targeted by fibers from the right habenula (6). This projection asymmetry is likely to affect zebrafish behavior. Ventral and dorsal IPN possess distinct projections to the dorsal tegmental area and the median raphe nuclei, two areas with a high relevance for emotional behaviors. Thus it is not surprising that manipulation of the lateralized lateral or medial dorsal habenular nuclei also have distinct effects on behaviors like fear responses, anxiety, or social aggression (81, 112, 123). Habenular asymmetries in zebrafish have also been shown to affect functional hemispheric asymmetries. As outlined above, the pineal complex is usually located to the left side in wild-type fish. The migration of the pineal complex to the left side occurs early in development and induces the above-mentioned asymmetries in fiber projections (94). In a study that compared zebrafish with normal leftward pineal complex positioning to zebrafish with atypical rightward pineal complex positioning, several changes in functional hemispheric asymmetries were observed (94). Three motor laterality tests were conducted (eye preference for viewing own reflection, eye use in predator inspection, rotational preference), and zebrafish with their pineal complex on the right side were found to show significant differences to animals with the typical leftward positioning of the pineal complex in all three tests. However, the evidence for a reversal of behavioral asymmetries in zebrafish with atypical anatomical asymmetries is somewhat mixed, as a study in fsi zebrafish found a reversal of laterality only for a subset of behavioral responses (26).

B. How Genetic Factors Shape Anatomical Asymmetries

Over the last two decades, a plethora of studies have shown how genetic factors shape habenular and pineal complex asymmetries in the developing zebrafish larva. Among others, the Fgf, the Nodal, the Notch, and the Wnt/β-catenin signaling pathway seem to be crucial for this development (190, 240). In wild-type zebrafish embryos, Fgf signaling in the developing epithalamus occurs mostly symmetrical and leads to the before mentioned habenular asymmetries as well as to the left-sided position of the pineal organ in most fish. However, in zebrafish mutants in which Fgf signaling is impaired, the parapineal and the habenula develop symmetrically. Implantation of an Fgf8 bead in embryos of this mutant restores parapineal asymmetry, suggesting a symmetry breaking effect of Fgf signaling (390). However, the Fgf pathway does not seem to control the side of lateralization. This control is exerted by Nodal signaling, which almost exclusively occurs in the left but not in the right epithalamus in wild-type zebrafish larvae (85). In zebrafish lacking Nodal signaling, parapineal cells migrate towards Fgf sources, irrespective of where the sources have been placed. When Nodal signaling is intact, parapineal cells migrate mostly to the left side. In such a case, the exact location of the natural or artificially placed Fgf signal does not seem to play a role anymore (390). Thus Fgf signaling seems to be crucial to induce habenular asymmetries in zebrafish while lateralized Nodal signaling determines the direction of the asymmetry.

This obviously leads to the question why Nodal signaling in the epithalamus is lateralized during embryonic development. The lateralized epithalamic Nodal signaling is dependent on a general lateralization of Nodal signaling in the lateral plate mesoderm (LPM) to the left side in the developing zebrafish embryo (70, 296). This lateralization in turn is based on an event called "Nodal flow," which seems to be conserved in many, but not all vertebrate species (for birds, see Ref. 174). "Nodal flow" seems to be critical for the establishment of left-right asymmetries of inner organs like heart, stomach, pancreas, or spleen asymmetries (121, 226, 344, 364, 444). After establishment of the dorsal-ventral and anterior-posterior axis during early development, embryos of several vertebrate species form a fluid-filled node or organ (see **FIGURE 5*A***). This organ is called ventral node in mammals, Kupffer's vesicle in fish species like zebrafish, or in some species simply left-right organizer (120, 344, 444). The inner surface of this node is lined with cells bearing cilia, protruding into the fluid-filled chamber. These hairlike organelles have the ability to beat, causing a rotational movement around their basis (see **FIGURE 5*B***). However, due to their protein and cytoskeletal structure, these rotations can only occur in one direction, causing a weak fluid movement at the surface of or in the node (120, 342, 365). It has been suggested that this flow either transports a so far unknown morphogen or a morphogen-filled vesicle to the left side of the node. Alternatively, the flow itself could be detected by sensory cilia (22, 344).

Although the exact mechanism still needs to be clarified, it has been shown in both mice and zebrafish that the flow causes a stronger calcium influx in the cells on the left than on the right side of the node (273, 318). Furthermore, the flow causes a higher expression of Nodal in cells surrounding the node on the left side (55). Subsequently, these events lead to an activation of the Nodal signaling cascade in the

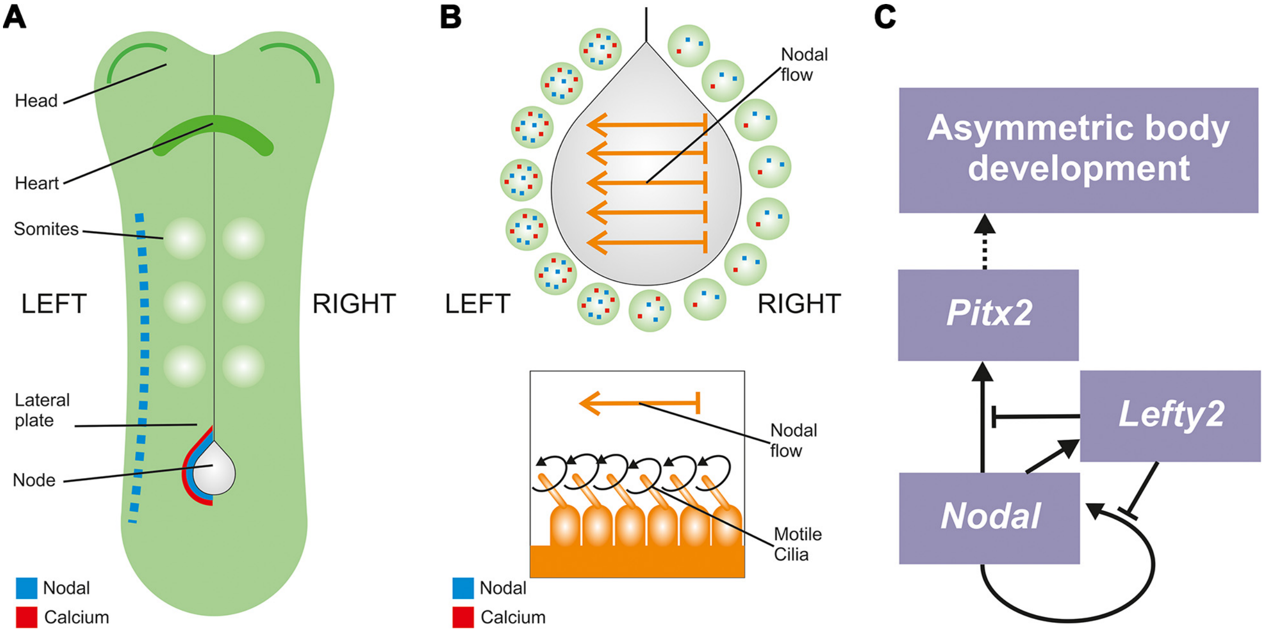


FIGURE 5. The role of cilia function for the emergence of hemispheric asymmetries. *A*: a schematic embryo showing asymmetric expression of Nodal on the left side. *B*: the inner surface of the node is lined with cells bearing cilia, protruding into the fluid-filled chamber. These motilic cilia have the ability to beat, causing a rotational movement around their basis, resulting in a leftward flow that leads to stronger calcium influx in the cells on the left than on the right side of the node as well as higher expression of Nodal in cells surrounding the node on the left side. *C*: the Nodal signaling cascade leads to asymmetric body development.

left but not the right LPM, observable by higher expression levels of the gene *Nodal* itself but also of genes of the Nodal signaling cascade like *southpaw*, *Lefty2*, or *Pitx2* (see **FIGURE 5*C***). This asymmetric expression in the left LPM also affects gene expression in the right LPM. Upregulation of Nodal in the left LPM results in a higher expression of Lefty2, which inhibits diffusion of Nodal to the right side. This further reduces the already lower levels of Nodal in the right LPM and prevents the expression of Pitx2, which is also dependent on Nodal presence (324). Thus Pitx2 is only expressed on the left side and seems to be responsible for establishing the inner organ asymmetry (293). Artificial changes in expression of these genes in the LPM alter the positioning of inner organs and prevent the establishment of a normal asymmetry pattern [e.g., Lefty2 (324), Pitx2 (420); reviewed in Ref. 344]. Also, changes of the "Nodal flow" within the node disrupt the normal asymmetry pattern of the inner organs (342, 364).

At this stage, also the before-mentioned Notch and Wnt/β-catenin signaling pathways come into play. Disruption of both pathways (and the before-mentioned Fgf pathway) can impair node formation and cilia structure (316), effecting the characteristics of the "Nodal flow." As an example, zebrafish mutants with a disrupted Notch pathway display shorter cilia and a reduced flow in their Kupffer's vesicle, leading to an impaired asymmetry of the gut (297).

Coming back to habenular asymmetries in zebrafish: the direction of habenular asymmetries is dependent on lateralized Nodal signaling in the developing epithalamus, which in turn is dependent on lateralized activation of the Nodal pathway in the LPM, which is, as we just described, dependent on a functioning "Nodal flow." A disruption of the "Nodal flow" would thus also disrupt habenular asymmetries, showing the importance of this event even for neuronal and possibly behavioral asymmetries. These examples, however, only represent an aspect of the role these four signaling pathways play for asymmetry induction. Given their central role during embryogenesis, it is very likely that they also affect asymmetry formation in other ways. For example, both Notch and Wnt signaling are required for the asymmetric distribution of dorsal habenular cells (240), which is in addition to the role Notch and Wnt take during ciliogenesis.

Given this well-studied example, it is appealing to connect and explain all neuronal or behavioral asymmetries to these genetically controlled events. However, unfortunately, this is not possible. For the most prominent behavioral lateralization in humans, handedness, a twin study showed that genetic effects could only account for 25% of the variance of handedness in twins, while the remaining 75% would have to be explained by other factors (322). This study is supported by a recent meta-analysis investigating the relationship between handedness and early life factors as well as genotype in more than 500,000 individuals (103). The analysis revealed only a very weak heritability for left-handedness (4.35%) and identified factors like birth weight, location of birth, sex, or occurrence of breastfeeding to affect handedness. A number of genes, including *PCSK6*, *LRRTM1* (18, 52, 53, 139, 422), and the microtubule-associated gene *MAP2* (103a, 510), have been associated with human handedness. However, genetic variation within these genes cannot fully account for occurrence and distribution of handedness in the population. Interestingly, *PCSK6* is involved in the Nodal cascade (435), possibly indicating that human handedness is not totally independent from the mechanisms described before.

C. Role of Environmental Factors for the Ontogenesis of Hemispheric Asymmetries

Aside from genetic factors, the development of brain asymmetries has often been linked to environmental factors. Although there are a couple of examples from humans like the before-mentioned relation of handedness to early life factors (103), culture (389), or early visual experience of the hands (351), one of the best examples for the role of environmental stimuli on asymmetry formation comes from birds. Both adult pigeons (*Columba livia*) and chicken hatchlings (*Gallus domesticus*) display behavioral asymmetries for a variety of visual tasks including for example discrimination of fine details (178, 306, 404), spatial navigation (334, 384, 468, 469, 480), categorization (519), or social cognition (96, 482).

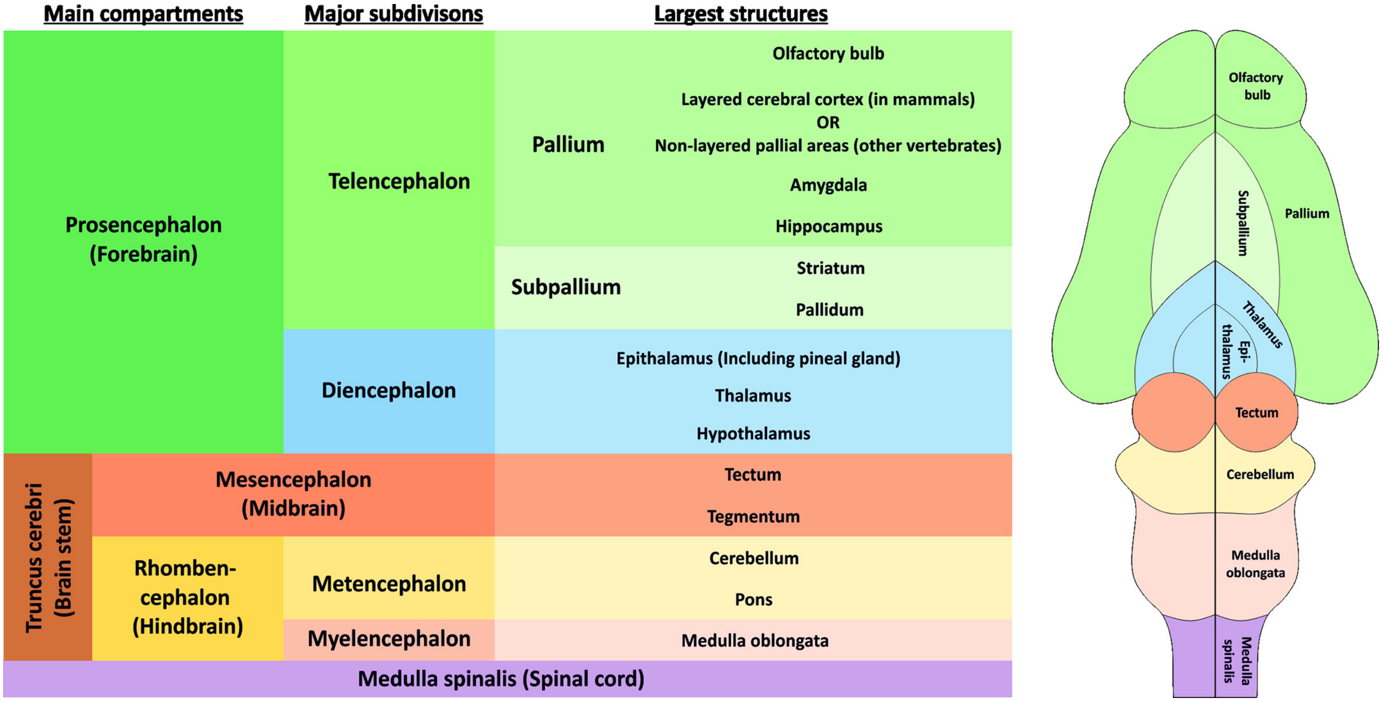
These asymmetries are not limited to behavior, but are also evident in the underlying neuronal networks. Even though one could assume that these behavioral asymmetries are caused by left-right differences of the sensory organs, it is not the peripheral visual system constituted by retinal cells and their fibers projecting over the optic nerves that show an asymmetry. Instead, mesencephalic (pigeon) or diencephalic (pigeon, chicken) visual relay areas show asymmetries in projection strength or differences in cell size between left and right side (180, 187, 304, 305, 407, 451). As an example, in pigeons, the right mesencephalic tectum opticum (homologue to the superior colliculus in mammals) exhibits larger neuron somata in the deeper layers 13–15 and sends more efferents to the contralateral diencephalic nucleus rotundus than the optic tectum on the left side (187, 305) (**FIGURES 6** and **7*A***). Since relay areas like the nucleus rotundus are critical in gating sensory input to the telencephalon, said asymmetries likely cause differences in the amount and quality of information available to each forebrain hemisphere (307).

In both pigeons and chickens, behavioral as well as anatomical asymmetries are triggered by the environmental factor light. During embryonic development, both bird species take an asymmetrical position inside the egg in which the right eye is pointed towards the translucent eggshell, while the left eye is occluded by the embryo's body (270). While the positioning of the body is very likely controlled by genetic cascades (possibly even the same as described for the zebrafish), the induction of the described visual asymmetries is induced by the stronger light stimulation of the right eye. Several experiments have shown that dark incubation of pigeon or chicken eggs prevents formation of visual asymmetries (145, 305, 403, 442). In addition, blocking visual stimulation of the right eye by an opaque patch before hatch in chickens (411) or after hatch in pigeons (304) reverses both anatomical and behavioral asymmetries. However, even the emergence of asymmetries in the visual systems of pigeons and chicken cannot be explained by a single environmental factor alone. Recent studies in pigeons have shown that distinct visual advantages of the right hemisphere (e.g., attentional bias) develop in the absence of light and are thus seemingly not reliant on an environmental factor but might be genetically or epigenetically predetermined (283, 284). Moreover, in chicks, it has been shown that some forms of lateralization (e.g., the preference of which eye is kept open during sleep) can develop even in the absence of light stimulation (315). Moreover, it has been shown that in chicks, the effect of light stimulation is modulated by the time window in which dark incubation occurs (76, 77).

D. Potential Impact of Epigenetic Factors on Hemispheric Asymmetries

The last aspect affecting the emergence of brain asymmetries we would like to discuss here are epigenetic factors. The role of epigenetic factors moved only very recently into the scope of lateralization researchers and was mainly driven by an apparent paradox in handedness research. Family research revealed the heritability of handedness to be between 0.39 and 0.66 (289, 396), with the handedness of the parents being a strong predictor for the handedness of the offspring (321). However, as we have mentioned above, identified genetic factors are not sufficient to explain the heritability of handedness. One could assume now that it is either explicit instruction by the parents or implicit role model learning that which shapes handedness in their children. The problem is that strength of lateralization in stepparents is unrelated to their children's handedness (224), devaluating the effect of education on handedness. Moreover, handedness in adoptive parents is unrelated to children's handedness (71). A solution to this heritability problem could be epigenetic effects (427). Epigenetic mechanisms alter the expression of genes without altering their nucleotide sequence and can thus lead to phenotypic changes (75). Since epigenetic DNA modifications can be inherited to the next generation, they could shape handedness without changes in the genotype. Although there are currently very few studies investigating the effect of epigenetic factors on brain asymmetries, the few studies published indicate that these factors might indeed play an important role (see BOX 1 for more details on epigenetic mechanisms).

Two recent studies (276, 426) investigated DNA methylation, a form of epigenetic DNA modification, of the *LRRTM1* and *NEUROD6* genes and found a relation



Main compartments		Major subdivisons		Largest structures
Prosencephalon (Forebrain)		Telencephalon	Pallium	Olfactory bulb Layered cerebral cortex (in mammals) OR Non-layered pallial areas (other vertebrates) Amygdala Hippocampus
			Subpallium	Striatum Pallidum
		Diencephalon		Epithalamus (Including pineal gland) Thalamus Hypothalamus
Truncus cerebri (Brain stem)	Mesencephalon (Midbrain)			Tectum Tegmentum
	Rhomben-cephalon (Hindbrain)	Metencephalon		Cerebellum Pons
		Myelencephalon		Medulla oblongata
Medulla spinalis (Spinal cord)				

FIGURE 6. Subdivisions of the vertebrate brain. The classification into separate regions and their nomenclature is based on sequential steps during the embryonic development of the brain, which are more or less identical within all vertebrate species. During early embryonic development, the neural tube at the rostral pole of the embryo forms three vesicular structures named prosencephalon (forebrain), mesencephalon (midbrain), and rhombencephalon (hindbrain). Both the prosencephalon and the rhombencephalon split up into two further vesicles, constituting together with the mesencephalon the 5 major subdivisions of any vertebrate brain: *1*) telencephalon, *2*) diencephalon, *3*) mesencephalon, *4*) metencephalon, and *5*) myelencephalon. The remaining neural tube develops into the spinal cord (medulla spinalis). Each subdivision develops into further structures of which we only listed the largest and most important ones. These structures can differ massively in shape and size between different vertebrate species. The brain on the left side is thus only a schematic of the vertebrate brain bauplan and does not represent a specific vertebrate species. Note that the pallium would normally cover the subpallium as well as parts of the diencephalon. We removed these pallial parts to make the underlying structures visible. Furthermore, the tegmentum and the pons are covered by the tectum and the cerebellum, respectively, and are thus not visible in our figure (181, 337, 457).

between handedness and the strength of methylation of these genes. Furthermore, an anatomical study discovered a profound asymmetry in the DNA methylation pattern in the spinal cord of human embryos, which could be related to developing motor asymmetries like handedness (359).

Besides human data, the only evidence for a role of epigenetic factors on the emergence of lateralized functions stems from research on the nematode *C. elegans*. *C. elegans* displays a well-studied asymmetry in chemotactic sensory system (456), which we discuss in more detail in section III*A* of this review. This asymmetry is based on a lateralized distribution of sensory neurons with different chemoreceptive properties. These different chemoreceptive properties and with them said asymmetry are primed very early during ontogeny in progenitors of these neurons by microRNA (miRNA). miRNA expression in the progenitor cell of the left-sided neuron, but not of the right-sided neuron, causes a change in chromatin configuration. This change is inherited over several cell generations finally allowing a boost of lsy-6 gene expression in the mother cell of the sensory neuron on the left, but not on the right side, which decides the fate of the neuron (82). This example shows impressively how an asymmetry can be inherited over multiple (cell) generations without the need of changing the genotype.

E. Hormones Can Shape Hemispheric Asymmetries

At the end of this section, we would like to briefly discuss a factor that is likely not initially triggering hemispheric asymmetries, but has been shown to be able to profoundly shape them. In addition to their effects on the reproductive system, sex hormones have been shown to effect brain physiology and cognitive functions (196). This also seems to hold true for hemispheric asymmetries. During the menstrual cycle in women, levels of the sex hormones estradiol and progesterone fluctuate, depending on cycle phase (210). Several studies have shown that the lateralized behavior in

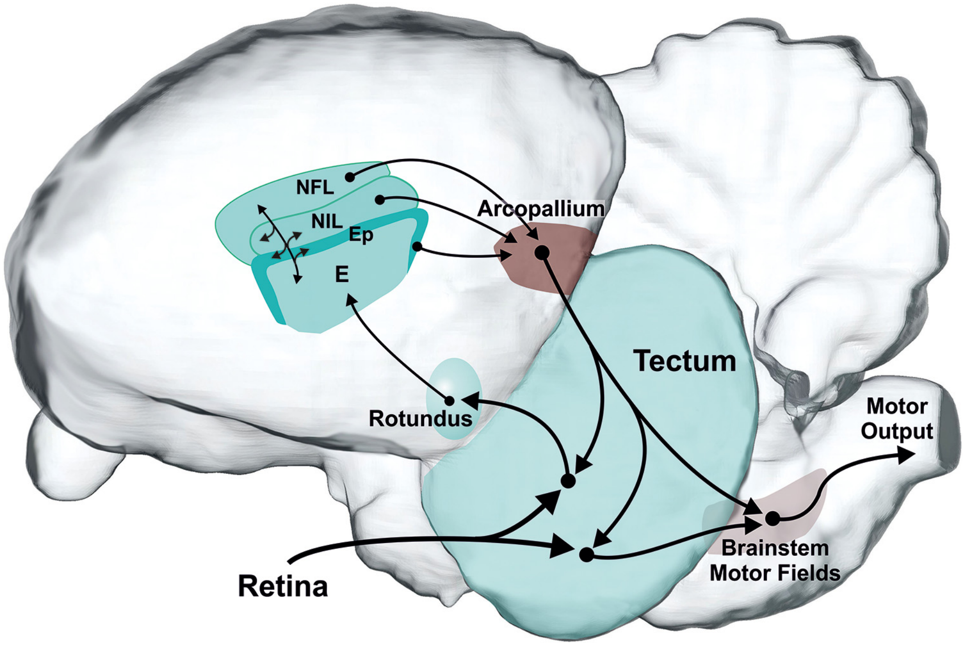


FIGURE 7. Sagittal view of the tectofugal pathway in pigeons. This system starts with the projection of retinal ganglion cells to the contralateral tectum. Tectal neurons project to the thalamic n. rotundus. From there, projection leads to the telencephalic entopallium (E), which then has cascades of reciprocal projections to several surrounding visual associative areas [perientopallial belt (Ep), nidopallium intermedium laterale (NIL), nidopallium frontolaterale (NFL)]. These areas then project to the arcopallium, a sensorimotor structure. Descending projections to the tectum close this tectofugal loop. However, both the tectum and the arcopallium also project to diverse brain stem motor fields that control various movement patterns. [Glass brain from Güntürkün et al. (192), with permission from Springer Nature.]

paradigms like figure recognition, spatial attention tasks, or the dichotic listening task (28, 209, 332, 399) change dependent on cycle phase and hormone levels. Neuroimaging studies confirmed these findings, showing a change in hemispheric asymmetries depending on menstrual cycle phase (466, 505). It was thus suggested that estradiol and progesterone influence the degree of lateralization most likely by influencing the transfer or information between the two hemispheres (210, 211). Furthermore, several studies showed that prenatal and pubertal testosterone levels can influence the strength of brain asymmetries like language lateralization, asymmetries in mental rotation, or dichotic listening tasks (30, 299, 329).

Effects of testosterone during critical developmental periods were also observed in several animals. As an example, in male chicken, injections of testosterone shortly after hatch prevents or reverses establishment of the visual discrimination asymmetries described above (524). An effect of testosterone on brain lateralization was also shown in rats (418) and gulls (377). Several theories have been brought forward to explain how testosterone influences the development of hemispheric asymmetries (161–163, 275, 514). However, a recent meta-analysis revealed that none of these theories is sufficiently supported by empirical evidence and that therefore more empirical studies on the subject are needed (370).

Taken together, in this section we tried to show that the emergence of neuronal and behavioral asymmetries is affected by many genetic, environmental, and epigenetic factors that can take action during different time points of ontogenesis. Most of these factors act during embryonic development, but some, for example, cultural effects on handedness in humans, also shape asymmetries well after birth. In addition, although some aspects of asymmetry emergence in some species is very well understood (e.g., symmetry breaking events in zebrafish), we still do not fully understand any of the chain of events leading from an initial symmetry breaking process to a behavioral lateralization in an adult animal.

F. Interim Summary Section II

- The emergence of asymmetries is likely dependent on a mixture of genetic, environmental, and epigenetic factors, which take effect during different time points of ontogenesis.
- In zebrafish, asymmetric expression of genes within the Nodal cascade during early embryonic development triggers left-right differentiation of the inner organs and set up the scene for later developing asymmetry in the habenular complex.
- This expression asymmetry is in turn triggered by an asymmetric fluid flow (the “Nodal flow”) caused by cilia only rotating in one direction.

BOX 1. Epigenetic mechanisms

Epigenetic mechanisms can alter gene expression without changing the DNA sequence itself (7, 75, 213, 491). Effects caused by epigenetic changes can be inherited mitotically (within a somatic cell lineage) or meiotically (from parents to their offspring) and can thus alter the phenotype of a cell or species population trans-generationally. The currently best investigated epigenetic mechanisms are DNA methylation, histone modification, and effects of noncoding RNAs. DNA methylation describes the addition of methyl groups to the cytosine bases within the DNA. These methyl groups can prevent binding of transcription factors or other DNA binding factors and thus inhibit transcription of a gene. Histone modification also alters gene transcription but relies on a different mechanism. Within the nucleus of a cell, the majority of DNA is wound around complexes of proteins called histones. Before transcription, the DNA needs to be "unwinded" to allow transcription factors access. Histones can be modified by the addition of acetyl groups or ubiquitin. This alters the DNA unwinding process and thus effects gene transcription. Noncoding RNAs are RNA fragments that are not translated into proteins (e.g., siRNA, microRNA, lncRNA). These RNA fragments can interact with mRNAs to repress their translation into proteins. Transgenerational inheritance based on these mechanisms has been well documented in bacteria, plants, and nematodes. However, in mammalian and likely also other vertebrate species, the majority of epigenetic marks are erased from the parental gametes and reset after fertilization. A specific challenge in epigenetic studies in human volunteers is the fact that DNA methylation (the most commonly investigated epigenetic process in human volunteers) is to some extent tissue-specific. As acquisition of brain tissue is limited to post mortem studies, researchers typically use blood, saliva, or buccal tissue as surrogate tissues in human in vivo epigenetics studies. While the correlations between DNA methylation in brain tissue and these surrogate tissue has been shown to be high for average methylation across the methylome (saliva-brain correlation: $r = 0.90$; blood-brain correlation: $r = 0.86$; buccal-brain correlation: $r = 0.85$) (54), correlations for specific loci within the genome can be substantially lower. Thus methylation in peripheral tissue needs to be interpreted as a marker for similar processes in neuronal tissue, not as a causal agent by itself.

- Studies in humans and the nematode *C. elegans* have shown that epigenetic factors like DNA methylation or miRNA might act as a mechanism to inherit asymmetries on an individual or cell level.
- In chicken and pigeons, visual asymmetries are shaped by an asymmetrical stimulation of the right eye by the environmental factor light during embryonic development, caused by an asymmetrical body posture of the embryo within the egg.
- Changes of sex hormones during development or sex hormone fluctuations during the menstrual cycle can change the degree of hemispheric asymmetries.
- These events alter the interactions between sensory and motor pathways in lateralized ways, as will be outlined in the next section.

III. THE LATERALIZED BRAIN IN ACTION: FROM SENSORY INPUT TO MOTOR OUTPUT

A. Asymmetries Start Early

The last section outlined that asymmetries of brain and behavior are molded into their adult form by various factors that reach from genes to environment. Most importantly, these processes modify many structures of the nervous system in lateralized ways. Some of these neural structures belong to the various sensory pathways. So, do asymmetries already start at the very beginning of perception or do they emerge at later stages of cognitive, affective, and motor processing? A strong argument against a sensory origin of lateralization would be the need to have a complete and thus symmetric organization of perceptual representation. For example, information from both visual fields are equally important for the organism's response to the environment since relevant cues can occur on both sides with equal probability. In contrast to this assumption, recent comparative research has brought forward convincing evidence that various hemispheric asymmetries of sensory information processing stream can be demonstrated in a large number of systems and species (401).

One prominent example is the simple nervous system of the nematode *C. elegans* that contains just 302 neurons, arranged in an essentially invariant structure (508). Two-thirds of these neurons are arranged as bilaterally symmetrical pairs, while one-third are located on or close to the midline (227). Interestingly, some pairs of structurally symmetric neurons in the chemosensory system show pronounced functional asymmetries. Chemotaxis, i.e., the movement of *C. elegans* in response to chemical stimuli, is controlled by a pair of neurons, the left-sided ASEL, and the right-sided ASER. ASEL is stimulated by increases, while ASER is activated by decreases in NaCl concentration (456). These asymmetries in sensory processing also extend to the behavioral level, as unilateral activation experiments indicated that activation of ASEL promotes forward locomotion of the nematode, while activation of ASER promotes direction changes (456). In principle, it can be argued that C. elegans and its nervous system is so small that stimuli cannot be represented in a topographical manner anyways. This argument is increasingly difficult to uphold with the following examples.

Animals with much larger nervous systems like some insect species evince asymmetries in processing of olfactory information like honeybees *Apis mellifera* (8, 141, 282, 393), the bumblebee *Bombus terrestris* (9), and fruit flies *Drosophila melanogaster* (114). The same is true for the auditory sense in the Australian bushcricket *Requena verticalis* (24). Outside of the Insecta class, sensory asymmetries have also been reported in the visual system of *Octopus vulgaris* (64, 65).

Given the widespread occurrence of neural asymmetries in sensory systems of invertebrates, it comes as no surprise that sensory hemispheric asymmetries have also been reported in several non-human vertebrate species (see **FIGURE 6** for an overview about major parts of the vertebrate brain discussed in the following sections).

One example is the organization of the visual system in pigeons (Columba livia) (190, 306, 477). For example, Yamazaki et al. (519) used a visual categorization paradigm in which pigeons had to categorize pictures of humans and were tested binocularly or monocularly (left or right eye) on the learned as well as on novel transfer stimuli. Their findings suggested that visual categorization in the left hemisphere of pigeons is focused on local features, while visual categorization in the right hemisphere is relying on stimulus configuration.

In the auditory domain, research on hemispheric asymmetries has for example been conducted in the zebra finch (*Taeniopygia guttata*). Research focusing on the auditory perception of birdsong in this species revealed that male zebra finches show hemispheric asymmetries in spectral and temporal domain processing of perceived songs (492). The study showed that songs with reduced spectral but normal temporal information elicited greater left-hemispheric activity in the auditory forebrain than unaltered songs. This is similar to what has been reported in human speech areas (see below).

For the haptic modality, the tufted capuchin monkey (*Cebus apella*) was shown to be more accurate in a haptic discrimination task when using the left compared with the right hand (447). Hemispheric asymmetries have also been reported for the chemical senses (taste and olfaction) in non-human vertebrates, e.g., dogs. Siniscalchi et al. (439) used a paradigm in which dogs had to sniff human or canine olfactory stimuli that were collected while the animals experienced different emotional events. They found that dogs used their right nostril to sniff canine olfactory stimuli collected in emotionally negative situations. In contrast, they prevalently used their left nostril to sniff human odors collected during emotionally negative situations. These findings led the authors to conclude that conspecific and heterospecific emotional olfactory stimuli are processed using different sensory pathways. The taste sense is closely related to olfaction, and similarly, hemispheric asymmetries have been shown to be relevant for this sense in non-human vertebrates. For example, in the rat, the anterior insular cortex serves as the primary taste cortex, and biochemical lateralization within this brain area is related to novel taste learning (243). The authors compared the levels of the activity regulated cytoskeleton associated protein (Arc)/Arg3.1 in the insular cortex of rats following the presentation of familiar or novel tastes. They found strong individual level lateralization of Arc/Arg3.1 protein levels after novel taste learning, with about half of the animals showing strong leftward and the other half strong rightward lateralization. No lateralization was observed after familiar taste learning, implying a specific role of lateralization for novel taste learning.

Comparable findings also exist for human subjects with respect to several sensory modalities (49). For vision, the most well-known example of hemispheric asymmetries in sensory processing comes from experiments with the classic Navon figures where the observer sees different patterns, depending on a local or gloval perceptual strategy (338). Here, the left hemisphere shows a dominance for the processing of local stimulus features, while the right hemisphere shows a dominance for the processing of global stimulus features (218, 489). In the auditory modality, pronounced hemispheric asymmetries for the processing of spectral and temporal characteristics of a sound have been reported (429). Here, it was shown that the left planum temporale, containing Wernicke's area, is sensitive to temporal sound variations, while its right-hemispheric homologue is sensitive to spectral sound variations. A different kind of evidence for the impact of the physical format of language stimuli on asymmetries comes from a study in which native speakers of Turkish whistle language were tested in a dichotic listening paradigm with the same syllables in articulated and whistled form. While classic articulated syllables caused the expected right-ear advantage, the whistled syllables were picked by both ears equally (185).

For the haptic modality, it has been reported that the left hemisphere shows an advantage for tactual simultaneous judgements (341). Similarly, a left hemisphere advantage has been reported for dichhaptic test in which participants had to simultaneously discriminate shapes with their two hands (48).

As for non-human vertebrates, lateralization has also been reported for the chemical senses (olfaction and taste) in humans. For olfaction, a dominance of the right hemisphere, particularly the right orbitofrontal cortex, has been reported for odor recall (50, 51). For taste, Faurion et al. (126) conducted an functional magnetic resonance imaging (fMRI) study in which brain activation was measured while various tastes were used to bilaterally stimulate the tongue in left- and right-handed subjects. Gustatory stimulation led to activation in the insula and perisylvan cortex. Interestingly, activation in the superior insula was mostly bilateral, while the inferior insula showed a strongly asymmetric activation pattern. In this area, left-handed subjects showed largely right hemisphere activation, while right-handed subjects showed largely left hemisphere activation.

Taken together, hemispheric asymmetries are a key feature of sensory processing and have been demonstrated across the animal kingdom. This does, however, not necessarily imply that asymmetrical processes indeed start at the level of perception and then proceed in feedforward manner towards associative and motor areas. It is also conceivable that feedback projections from associative areas could asymmetrically increase otherwise symmetrical sensory processes in a top-down manner. Indeed, there is support for this assumption from research on human language asymmetry (507, 515).

So, what comes first, perceptual asymmetries that cause left-right differences in feedforward manner or cognitive asymmetries that induce lateralized activity patterns in sensory areas by feedback projections? Are studies with animal models able to solve this conundrum? As will be shown in the following, they can at least add new evidence for the assumption that both left-right differences of bottom-up and top-down circuits exist and that these are inextricably intertwined during stimulus processing. To discuss this, we will first outline some basic aspects of the pigeons' visual system (see also sect. II).

Structural and behavioral asymmetries were investigated in the visual system of both chicken (*Gallus gallus*) and pigeons (*Columba livia*) (4, 187, 307, 411, 451). Both show different projection asymmetries in their ascending visual pathways. While pigeons predominantly evince asymmetries in the tectofugal pathway, chickens predominantly show asymmetries in the thalamofugal system (105–107, 407). Unfortunately, none of these anatomical or behavioral studies can properly disambiguate the individual contribution of feedforward and feedback projections for the emergence of left-right differences. For this, we need electrophysiological data that can resolve input-output relations with extremely high time resolution. Since such kinds of studies using single unit recordings were only conducted in pigeons, we will in the following concentrate on the tectofugal pathway in this species.

B. Lateralized Visual Feedforward and Feedback Circuits in Pigeons

Visual input reaches the bird forebrain by the tectofugal and the thalamofugal systems, two parallel ascending pathways that are homologous to the extrageniculocortical and geniculocortical systems of mammals, respectively (333). In pigeons, the tectofugal system is the most important pathway for visually guided behavior. It ascends from the retina to the contralateral optic tectum, from there bilaterally to the thalamic nucleus rotundus and thence to the ipsilateral entopallium in the telencephalon (see **FIGURE 7**). Any lesion along this pathway causes major deficits of visuoperceptual and visuocognitive functions (184). The thalamofugal system ascends along the thalamic nucleus geniculatus lateralis to a telencephalic structure called "wulst" (307). Lesions of this system create much subtler deficits (74, 186).

Within the tectofugal pathway, already the first central structures show morphological and neurochemical asymmetries. As briefly mentioned in section II, both the optic tectum, the nucleus rotundus, and the associated nucleus subpretectalis have larger somata at the visual input level on the left (145, 180, 304, 305). Soma size correlates with the extent of the dendritic arbor (212, 363, 528). Thus structural asymmetries that occur at brain stem and thalamic level of a sensory system make it likely that bottom-up signals are processed in a lateralized manner. Indeed, it was demonstrated that single units coding for ascending feedforward information within the nucleus rotundus show clearly different response patterns between left and right (136, 137).

But rotundal neurons also integrate lateralized feedback signals from the telencephalon that are relayed via the optic tectum (303). Folta et al. (136) and Freund et al. (146) could reveal a lateralized mechanism by which visually driven left rotundal neurons were significantly modulated by descending signals from the visual wulst, while single units in the right rotundus were hardly modified by top-down signals at all (see **FIGURE 7*A***). This implies that only left-sided thalamic neurons receive feedback from higher visual areas. This left-right difference could modify feedforward visual input to the left hemisphere by experience-based telencephalic feedback. Since single neurons in associative areas of the pigeon forebrain are partly tuned to functional or perceptual categories (19, 189, 264, 267), this feedback could selectively increase the activity level of those thalamic neurons that process category-relevant visual stimuli. Such a left-sided top-down control of the thalamic visual nucleus of the tectofugal pathway could be a key mechanism to enable the left-hemispheric superiority in the discrimination and categorization of visual patterns (180, 190, 519).

Indeed, several studies with human subjects could also reveal that asymmetrical cortical top-down signals are able to modify activity patterns of downstream structures during categorization of various stimulus types (10, 90). This left-right difference in top-down control seems to result from the learning of features that are diagnostic for a category and that are subsequently preactivated in downstream sensory areas (436, 474). At the cellular level, the results in pigeons reveal that similar processes could also occur already at thalamic level and may modify hemispheric left-right differences of stimulus categorization.

The nucleus rotundus projects ipsilaterally to the telencephalic entopallium. Verhaal et al. (495) recorded single- and multi-unit responses from the left and right entopallium while the animals were working on a color discrimination. Similar to what has been described by Colombo et al. (84), the authors observed a strong initial phasic burst of entopallial neurons after perceiving the rewarded color. This burst, however, was only discernable on the left side, possibly due to a recruitment of a large number of left entopallial neurons that initially responded to the relevant cue (see **FIGURE 8*A***). Such a brisk and unilateral avalanche of entopallial neurons could ensure a higher level of recruitment of downstream left-hemispheric associative and motor structures, thereby enforcing a primarily left hemisphere-based visually guided behavior. Indeed, in meta-control experiments, where one hemisphere takes charge of response selection, it is mostly the left hemisphere of pigeons that dominates response patterns (146, 475).

Entopallial neurons project via several visual-associative areas to the arcopallium, a heterogeneous area that functionally corresponds to mammalian premotor areas (222, 431). The arcopallium has descending projections to the optic tectum and to motor areas of the brain stem (219, 511). In addition, the arcopallium is the most important hub for interhemispheric crosstalk via the anterior commissure (285). To reveal the mechanisms of asymmetrical coding within the arcopallium and between the hemispheres, Xiao and Güntürkün (517) recorded single units from the left and the right arcopallium while the pigeons were working on a color discrimination task. The authors discovered that asymmetries of arcopallial functions were due to two key mechanisms. First, a significantly larger number of left compared with right arcopallial neurons were recruited by the rewarded stimulus. Second, left arcopallial neurons did not react faster to the conditioned stimulus, but were quicker in triggering the appropriate response. Thus the left hemisphere had a clear time-advantage with respect to reaction time. Possibly, these two effects are causally related. When a large group of left arcopallial cells are activated, they will also activate a large proportion of brain stem pre/motor neurons on the left side, thereby triggering a fast behavioral response and gaining control over the movement patterns of the animal.

FIGURE 7*B* provides a hypothetical explanation of how this evidence could be integrated into a mechanistic hypothesis. Our model rests on the experimental observation that small populations of neurons in the avian visual associative areas code for all kinds of features that are part of different visual categories (19, 267, 449). These associative areas are, among others, also connected with the visual wulst (431). If some visual features correlate with the delivery of reward, the wulst could activate those rotundal neurons that process such visual features via its descending tecto-rotundal pathway. Thus, if a stimulus with these features is seen by the bird, activity patterns of left-sided rotundal neurons will be amplified (see legend to **FIGURE 7*B***). As a consequence, left-sided rotundal projections to the entopallium could activate a burst firing mode that then ignites a large number of left hemisphere arcopallial cells. These arcopallial sensorimotor neurons would then have a time-advantage in activating the various brain stem motor nuclei. As a result, feature-based learning of visual categories could be acquired faster by the left hemisphere, and this hemisphere would gain control over the behavior of the animal during such kinds of discrimination tasks. This idea is depicted as loops of bold arrows in the left hemisphere of **FIGURE 7*B***.

At this point, it is important to emphasize that both avian hemispheres make their unique contribution to visual categorization. While pigeons and chicken reach higher speed and accuracy during color or pattern discrimination with their right eye/left hemisphere (383, 405, 478, 519), the left eye/right hemisphere is superior when configurational or emotionally charged stimuli are to be distinguished (421, 484). Thus our model does not impose an overall hemispheric dominance, but assumes that hemisphere-specific circuits can dynamically switch back and forth between left and right, while processing specific cues.

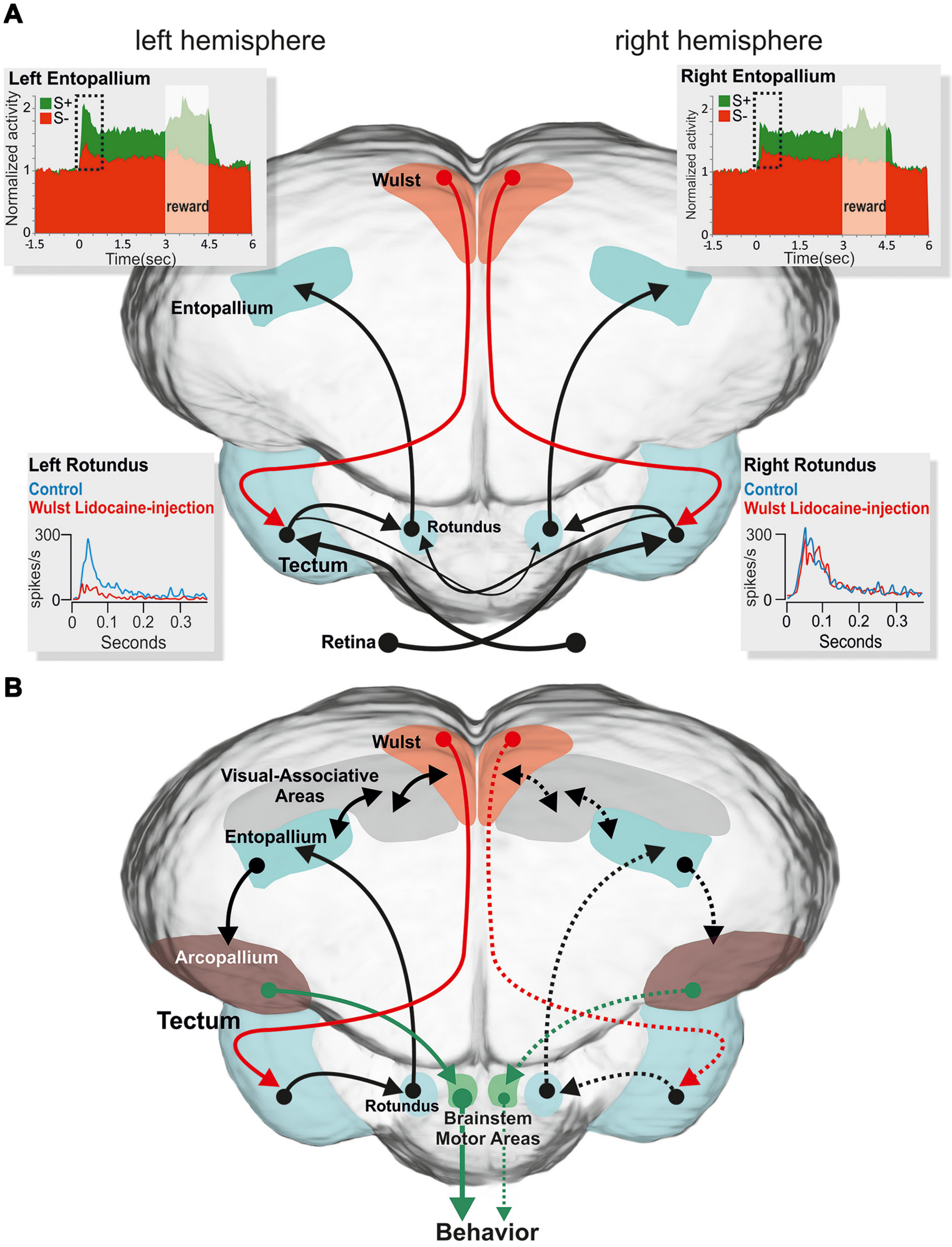
C. Interim Summary Section III

- A large number of animals show asymmetries of sensory processing. At least for animals with more complex nervous systems, these findings do not necessarily imply that asymmetries actually start at perceptual level, since they could also be the result of lateralized feedback projections from higher areas.
- Anatomical studies with birds show that already sensory processing areas at brain stem and thalamic level display morphological asymmetries. These observations make it likely that at least some of the observed left-right differences originate from perceptual analyses.
- Single unit recording studies in pigeons reveal an intricate lateralized interaction between telencephalic and thalamic structures. Thus feedforward and feedback projections seem to be intertwined, making a clear-cut distinction between asymmetries of bottom-up and top-down projections futile.
- At least in this animal model it is conceivable that depending on task-demands, left- or right-hemispheric loops of feedforward or feedback projections could be activated and would temporarily dominate the behavior of the bird.
- All of these events require networks that display characteristic left-right differences. This will be the topic of the next section.

IV. HEMISPHERIC ASYMMETRIES IN BRAIN CONNECTIVITY

A. Biased Connections: White Matter Tracts Are Lateralized in System-Specific Ways

The two hemispheres of the vertebrate brain are not working in isolation from each other, as they are connected by several interhemispheric fiber systems, so-called commissures. Commissures exchange neural information between the left and the right side of the brain (1). In placental mammals, the largest commissure is the corpus callosum (109, 415). In humans, it has ~200 million mostly myelinated fibers and is crucial for the integration of sensory and motor information between the hemispheres (2, 132). For comparison, in rhesus monkeys it has ~56 million fibers on average (271). While only placental mammals have a corpus callosum, other axonal connections between the two halves of the brain integrate information in the brains of nonplacental mammals and nonmammalian vertebrates (454). For example, in birds, the commissura anterior is the main connection between the two hemispheres (285). Importantly, research in split-brain patients (157, 159, 380), healthy human volunteers (349, 514), and comparative



studies between species (372) suggest that commissures are essential for the emergence of functional hemispheric asymmetries.

Here, two possible pathways have been suggested (89, 430, 488). On the one hand, commissural exchange of neural information could enhance functional hemispheric asymmetries if the dominant hemisphere inhibits the nondominant side. On the other hand, excitatory exchange of information could also reduce hemispheric asymmetries by equalizing information levels between the hemispheres. This twofold impact of interhemispheric transfer of neural information on the contralateral hemisphere is supported by neuropharmacological research. For the corpus callosum, it has been shown that most of its axons are glutamatergic and thus excitatory (488). However, most of these axons target inhibitory interneurons, therefore potentially inhibiting the contralateral hemisphere.

Based on these findings, both excitatory and inhibitory models for the function of the corpus callosum for the emergence of hemispheric asymmetries in the human brain have been suggested (40). According to the excitatory model suggested by Ringo et al. (395), functional hemispheric asymmetries arise due to the conduction delay during interhemispheric information transfer. If the conduction delay is longer, the brain is more likely to perform time-sensitive processes in one hemisphere to ensure fast behavioral output, leading to stronger hemispheric asymmetries. Support for this model for example came from a dichotic listening study that showed that language lateralization was less pronounced in participants with a larger corpus callosum (521). On the other hand, studies with small-brained animals with pronounced asymmetries are difficult to reconcile with this account (see sect. I).

In contrast to excitatory models, inhibitory models assume that excitation in the dominant hemisphere leads to inhibition of homotopic areas in the nondominant hemisphere via the corpus callosum (86, 87). Thus a smaller corpus callosum would be related to reduced functional lateralization which has been supported by neuroimaging studies on language lateralization (252, 386).

Thus both excitatory and inhibitory models for the function of commissures for the emergence of functional hemispheric asymmetries have been supported by some empirical evidence. This led van der Knaap and van der Ham (488) to conclude that both functional relationships can be observed in the corpus callosum. Thus the exact functional relationship of the corpus callosum depends on the subsegment of the corpus callosum, the involved fibers, and the targeted interneurons and brain areas in the contralateral hemisphere.

As the assessment of all of these factors with a decent temporal resolution in vivo is almost impossible in humans, comparative research in animal model species is essential. Xiao and Güntürkün (517) recorded single units from the arcopallium of pigeons while the animals were working on a color discrimination task. Arcopallial neurons constitute the majority of fibers of the commissura anterior and project to the contralateral side in homotopic fashion. To reveal the function of these commissural fibers, the authors temporarily inactivated the right or left arcopallium with lidocaine during the task, while simultaneously recording from the contralateral non-anesthetized arcopallium. Anesthetizing the visually dominant left arcopallium drastically increased the variance of spike times of neurons on the subdominant side. Thus silencing the dominant hemisphere neither decreased or increased the activity patterns on the subdominant side in an overall fashion. Instead, it turned out that the temporal structure of right arcopallial cellular responses was mostly controlled by the left side. This is only possible if both excitation and inhibition had taken place during normal performance, since left-sided lidocaine injections accelerated some right hemisphere neurons, while slowing down others. Indeed, Ünver et al. (476) transected the commissura anterior in pigeons and tested the animals before and after commissurotomy in a

FIGURE 8. *A*: frontal view of the tectofugal pathway. The wulst, a visual telencephalic structure of the thalamofugal pathway, projects via the tectum to the nucleus rotundus and thereby modifies tectofugal activity patterns. The insets on the left and the right lower corner show results of studies from Folta et al. (136) and Freund et al. (146). Both could show that light stimulation to the eye evoked a strong activation in the contralateral rotundus (blue spike activity patterns, depicted as control). Lidocaine injection into the left wulst caused a local anesthesia, reduced top-down input from the ipsilateral wulst to the tecto-rotundal projection, and diminished light-evoked activation in the left rotundus (red spike activity pattern, depicted as lidocaine injection). No such effect was discernable for the right side. The insets on top left and top right depict results from entopallium recordings (495). The red areas depict the activity pattern of entopallial neurons to the non-rewarded color (S-), while the green areas show activity to the rewarded one (S+). The broken rectangle shows the initial burst of left entopallial neurons to the S+. Such a burst is lacking on the right side. *B*: a hypothetical view on the activity patterns during a task in which a pigeon conducts a visual feature categorization task. Visual priors established during past category learning events in the telencephalon can modify via the left hemisphere wulst → tectum → rotundus pathway visual processes of the rotundus. As a result, neural activity patterns that code relevant feature properties are enhanced, resulting in a strong initial activation of the left entopallium when the relevant stimulus is perceived. Consequently, brain stem motor areas that code for approach or pecking are activated via the entopallium → arcopallium → brain stem pathway on the left. Processes in the right half brain (dotted arrows) might be similar, when configuration-based categorization tasks are conducted by the animal. See text for further details. [Glass brain from Güntürkün et al. (192), with permission from Springer Nature.]

meta-control task. This task was chosen since it depends on interhemispheric interactions to gain control on the other side. As expected, the transection of the commissura anterior revealed that meta-control is modified by interhemispheric transmission, although it does not seem to depend on it. If the mechanism discovered in the commissura anterior of pigeons would also apply to the corpus callosum of mammals, it would give both hemispheres the ability to either delay the other side when competing or to recruit neural resources of the other hemisphere for joint action. Thus the findings of Xiao and Güntürkün (517) contradict the assumption that the dominant hemisphere simply inhibits or excites the subdominant one in an overall fashion.

B. Lateralized Commissures in Humans and Birds

Could these findings also shed light on the commissural mechanisms of functional asymmetries in humans? Little is known about the human commissura anterior, but the human corpus callosum is a key structure for the emergence and maintenance of brain asymmetries (158). In humans, the corpus callosum itself is not a perfectly symmetric structure, but shows structural asymmetries that also affect interhemispheric transfer (313). Based on fiber tractography, the corpus callosum has been subdivided into five different vertical segments (228), and it has been shown that these subsegments show different structural asymmetries. Surface-based analysis of fMRI data revealed that the thickness of the corpus callosum showed significant rightward asymmetries for the anterior midbody and anterior third that were particularly pronounced in male subjects (298). The other three comparisons (posterior midbody, isthmus, splenium) did not show significant structural asymmetries. The authors concluded that these findings reflect a more diffuse organization of the corpus callosum in the vertical dimension in the right hemisphere than in the left hemisphere. A more recent study comparing structural asymmetries in the corpus callosum between male adolescents with autism and healthy controls found that autistic subjects showed stronger rightward asymmetry than controls in the posterior and anterior midbody (134). Interestingly, the authors also reported that in healthy controls the asymmetry index for the posterior midbody showed a significant positive correlation with handedness, indicating that rightward asymmetry in this segment of the corpus callosum was associated with a rightward shift in handedness. A nonsignificant trend into the same direction was also observed for the anterior midbody. This association between structural hemispheric asymmetries in the corpus callosum and handedness, a behavioral marker of functional hemispheric asymmetry in the motor system, indicates a potential functional role of callosal asymmetries for functional lateralization.

In addition to structural asymmetries in the corpus callosum, several studies have reported functional asymmetries in interhemispheric transfer of neuronal information. Both reaction time and electroencephalography (EEG) studies have shown that transport of neuronal information from the left to the right hemisphere is not identical to transport of neuronal information from the right to the left hemisphere (312). A meta-analysis of 16 behavioral studies using the Poffenberger paradigm (see BOX 2) revealed that interhemispheric transfer from the right hemisphere (left visual field stimulus presentation) to the left hemisphere (right hand motor response) was 3.3 ms faster than from the left hemisphere to the right hemisphere (314).

Marzi et al. (314) concluded that this asymmetry of interhemispheric transfer time of visuomotor information reflects a functional asymmetry of callosal transfer (also see

BOX 2. Commonly used behavioral laterality paradigms in human subjects

Dichotic listening paradigm: One of the most commonly used tests to determine language lateralization on the behavioral level. In this task, pairs of auditory stimuli (e.g., two consonant-vowel syllables like /DA/ and /GA/) are presented to the participant simultaneously via headphones, one to each ear. Participants have to indicate which syllable they heard best. Typically, participants report more of those syllables that had been presented to the right ear than those presented to the left ear, a phenomenon termed the right ear-advantage. The right ear-advantage is thought to reflect left-hemispheric language lateralization.

Divided visual field paradigm: In this family of tasks, participants are seated in front of a computer monitor and asked to focus on a fixation cross that is presented in the center of the screen. A stimulus is then presented very briefly on either the left or the right side of the fixation cross, and the participant is asked to respond to this stimulus. Due to the anatomical organization of the visual system, stimuli on the left side of the fixation cross are processed in the right hemisphere and vice versa. The divided visual field paradigm utilizes this principle to test whether one hemisphere is more efficient in processing a specific type of stimuli (e.g., words, faces, or emotional pictures) than the other.

Poffenberger task: A simple reaction time task that is used to measure the time the corpus callosum needs to transfer neuronal information from one hemisphere to the other. Participants are presented with simple visual stimuli (e.g., white circles) that are shown in the left or right visual half field. They have to react to these stimuli by pressing a button using either the left or the right hand. There are two types of trials. On "uncrossed" trials, the brain areas that perceive the visual information and the motor areas controlling the reacting hand are in the same hemisphere. Thus no transfer of neural information over the corpus callosum needs to take place before a reaction can be conducted. On "crossed" trials, the brain areas that perceive the visual information and the motor areas controlling the reacting hand are in different hemispheres. Thus information transfer over the corpus callosum is needed before a reaction can be conducted. Typically, reactions on "crossed" trials take longer than those on "uncrossed" trials. By comparing the reaction times on the two types of trials, interhemispheric transfer time can be estimated.

Ref. 54). Faster right-to-left than left-to-right interhemispheric transfer of neuronal information was also confirmed by a meta-analysis of 18 early EEG studies that measured interhemispheric transfer times using the P1 or N1 event-related potential (ERP) component after visual stimulation (61). This finding was in general replicated by subsequent studies in healthy subjects (25, 254, 274, 311), but seems to be affected by neurodevelopmental disorders. For example, a clinical study found that while healthy controls showed the expected right-to-left faster left-to-right effects, no such asymmetry was observed in subjects with attention-deficit hyperactivity disorder (417). In addition to neurodevelopmental disorders, handedness (247, 340) and eye dominance (73) have been shown to affect asymmetries in interhemispheric transfer.

Interhemispheric transfer asymmetries have been shown to interact with functional hemispheric asymmetries for the stimulus material (348). In this study, participants performed a matching-to-sample task with either laterally presented words (left-hemispheric advantage) or square wave gratings of spatial frequencies (right-hemisphere advantage), and participants had to react with either their left or their right hand. The authors found that for the spatial stimuli, interhemispheric transfer time was faster for left-to-right than for right-to-left. In contrast, for verbal stimuli, interhemispheric transfer time was faster for right-to-left than for left-to-right. Thus interhemispheric transfer time was shorter when information was transferred from the nondominant to the dominant hemisphere for a specific task. A subsequent ERP study using a letter-matching task instead of the traditional Poffenberger paradigm also confirmed faster right-to-left transmission of verbal information (328).

These data make it likely that the emergence of asymmetries is related to a dual coding of left-right differences. Thus lateralization cannot be explained entirely by the anatomical differences between left and right since a second, more dynamic component exists that is able to modulate neural processes between the hemispheres in an asymmetrical manner (306). This "dual coding" aspect is also visible in birds. If the posterior and the tectal midbrain commissures, which connect the optic tecta of both half brains, are transected, visual lateralization reverses to a left eye dominance, and this reversal is proportional to the number of transected fibers (182). If hemispheric asymmetry can be reversed by midbrain commissurotomy, it is likely that this asymmetry was maintained previously, at least partly, by an asymmetrical interaction between the optic tecta which are of primarily inhibitory nature (197, 398). Keysers et al. (260) tested this hypothesis by recording visually evoked field potentials from right or left intratectal electrodes plus an electrical stimulation of the contralateral tectum. They discovered that the left tectum was able to modify the light-evoked field potential of the right tectum to a larger extent than vice versa. This lateralized interhemispheric interaction could thus constitute an important "dynamic" component of asymmetric visual processing.

Since visual asymmetry in chicken depends less on the tectofugal but more on the thalamofugal pathway (see sect. II), their organization seems to be different. Their midbrain tectal and posterior commissural was shown to suppress lateralization for visually guided pecking (366).

C. Network Asymmetries

While the corpus callosum is an important structure for the emergence of hemispheric asymmetries, it is not the only white matter structure in the brain that affects functional lateralization. Recent research suggests that functional asymmetries are affected by both inter- and intrahemispheric projections (353).

Asymmetrical organization of intrahemispheric neuronal projections is a basic principle of nervous system organization in vertebrates and has been reported in both humans (473) and a multitude of non-human animal species across all major classes. These species include the Southern flounder (*Paralichthys lethostigma*) (269), the frog (*Rana esculenta*) (176), the slide-blotched lizard (*Uta stansburiana*) (119), the chicken (*Gallus gallus domesticus*) (261), the bottlenose dolphin (*Tursiops truncatus*) (516), the cat (*Felis silvestris catus*) (95), the rat (*Rattus rattus*) (434), and the chimpanzee (*Pan troglodytes*) (68), just to name a few examples.

In humans, a recent diffusion tensor imaging (DTI) and graph theory (see BOX 3 for commonly used neuroscientific techniques in human subjects) study aimed to determine the structural network properties of the two hemispheres revealed that the right hemisphere had greater intrahemispheric global efficiency and more interhemispheric interconnections than the left hemisphere (246). The left hemisphere showed a reversed pattern, with more intrahemispheric local connections, particularly in brain regions relevant for language and fine motor coordination.

In accordance with these findings, a subsequent graph theory study reported that left-hemispheric structural networks show increased network efficiency in brain areas related to language and motor coordination (66). In contrast, within right-hemispheric networks, efficiency was increased in brain areas relevant for visuospatial attention and memory. This is in line with the finding of a relative rightward lateralization of some of the cortical networks involved in attention (27). Interestingly, left-right asymmetries in structural white matter networks are reflected by differences in lateralization of functional networks. A recent fMRI resting state connectivity anal-

BOX 3. Commonly used neuroscientific techniques in humans

fMRI (functional magnetic resonance imaging): fMRI is a functional neuroimaging technique that uses magnetic fields to estimate brain activity by measuring blood oxygenation in the brain. Participants are scanned in an MRI scanner. When neurons in a specific brain area are active, blood flow to that brain area increases. Therefore, blood oxygenation can be used as a proxy for brain activity during a specific task a participant performs in the MRI scanner.

Resting state fMRI: Resting state fMRI is a specific form of fMRI in which the participants does not perform any task in the scanner, but rest in the scanner. By analyzing which brain areas are active together in resting state, brain networks can be identified.

PET (positron emission tomography): In PET studies, participants are injected with a radioactive compound, which is taken up by the brain and other organs. The speed of uptake is related to the compound properties and the metabolic activity of the organ. In many PET studies, radioactively labeled glucose is used, which accumulates in activated brain areas due to their higher metabolic rate. The radioactivity can be localized and measured by a scanner and is used as a proxy for brain activity.

DTI (diffusion tensor imaging): DTI is a MRI technique that measures water diffusion in brain tissue to generate images of brain structure. It is mostly used to visualize white matter.

Fiber tractography: A computational method to analyze DTI data. Fiber tractography is based on the fact that white matter tracts in the brain hinder the diffusion of water molecules. Therefore, they are more likely to move along the white tract than against it. Using this principle, 3-dimensional reconstructions of white matter tracts such as the corpus callosum can be created.

Graph theory: A computational method to analyze DTI data. Graph theory allows the measurement of the efficiency of white matter networks by estimating the extent to which a specific fiber tract contributes to information exchange.

NODDI (neurite orientation dispersion and density imaging): A diffusion MRI technique based on DTI that allows the measurement of the density and dispersion of axons and dendrites in the brain.

EEG (electroencephalography): EEG is an electrophysiological method that allows the measurement of electrical brain activity using electrodes that are placed on the participant's head.

ERP (event-related potential): A method to analyze EEG data. By repeatedly measuring electrical brain activity in response to a stimulus and averaging these signals, typical brain waves following the administration of specific stimuli can be identified.

ysis found that the left hemisphere showed more intrahemispheric connections than the right, particularly in brain regions related to language and fine motor coordination (172). In contrast, right-hemispheric brain regions involved in visuospatial and attentional processing showed more interhemispheric connections than the respective left-hemispheric brain regions. Importantly, the degree of rightward or leftward network lateralization selectively predicted behavioral measures of left- and right-dominant cognitive functions. While the degree of left-hemispheric lateralization predicted verbal ability, right-hemispheric lateralization predicted visuospatial ability.

A relevance of left-right differences in connectivity for behavioral lateralization has also been shown by DTI studies relating structural left-right asymmetries in individual intrahemispheric white matter pathways to behavior (see **FIGURE 9**).

For example, both macro- and microstructure of the arcuate fasciculus, which interconnects various language related human cortex centers from primary sensory auditory to motor speech areas ipsilaterally, show pronounced leftward asymmetries (63, 350, 385, 461). Several authors have linked these structural asymmetries in the arcuate fasciculus to functional lateralization in the language domain. For example, arcuate fasciculus laterality significantly predicted leftward language-related activation asymmetries in preadolescent children during fMRI (448). Similar results have also been obtained in adult participants (248, 357, 378, 385, 497). A comparative DTI study in humans, chimpanzees, and macaque monkeys (394) also found that leftward lateralization of the arcuate fasciculus seems to be a typical feature of the human brain that is not observed in other primates. While all human brains in the study showed terminations of the arcuate fasciculus in the middle temporal gyrus, only one chimpanzee brain and no macaque brain showed arcuate fasciculus terminations in this area. Interestingly, the terminations of the arcuate fasciculus in the middle temporal gyrus in humans showed strong leftward lateralization. As the middle temporal gyrus has been linked to language processing (387), this human-typical asymmetry of the arcuate fasciculus might be related to the evolution of language.

A link between structural white matter asymmetries and functional language lateralization has also been shown for the uncinate fasciculus, a lateral association tract that connects the anterior temporal lobe with the orbitofrontal cortex (467). Functionally, the uncinate fasciculus has been ascribed linguistic, socio-emotional, and memory functions (498a). Recently, the volume of the left uncinate fasciculus was shown to be positively correlated with leftward language asymmetry, as assessed with the dichotic listening task (358).

An association between white matter asymmetries and behavioral asymmetries has also been shown in chimpanzees (233). Here, the author conducted MRI in chimpanzees and found significant leftward asymmetries in 4 of 10 brain regions. Interestingly, depending on their sex, right-handed animals showed significantly greater leftward asymmetries than non–right-handed animals in several of these brain areas. Thus white matter asymmetries are associated with behavioral motor preferences in chimpanzees.

In addition to this evidence for a link between leftward structural intrahemispheric white matter asymmetries and left-dominant functional asymmetry, a DTI tractography

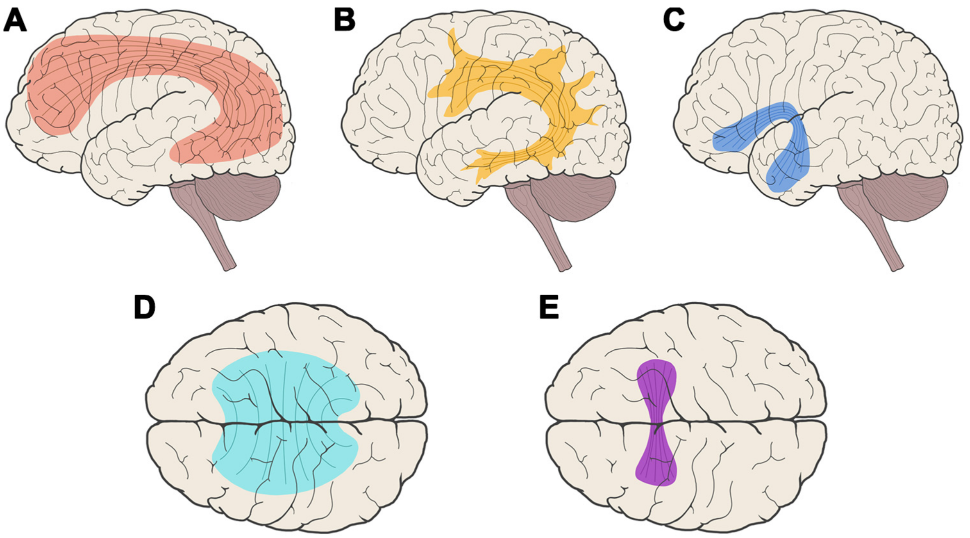


FIGURE 9. Schematic depiction of the principal white matter tracts in the human brain. *A*: superior longitudinal fasciculus. *B*: arcuate fasciculus. *C*: uncinate fasciculus. *D*: corpus callosum. *E*: anterior commissure.

study on the superior longitudinal fasciculus (SLF) provided evidence for a relevance of rightward structural intrahemispheric white matter asymmetries for right hemisphere dominant cognitive functions (465). The SLF consists of three subsegments: SLF I, SLF II, and SLF III. Greater rightward tract volume asymmetry in the SLF II was correlated with stronger rightward functional hemispheric asymmetry for visuo-spatial attention, as measured with the line bisection task (251).

A recent comparative neuroimaging study in humans and chimpanzees (214) also showed that the SLF as a whole showed a significant right lateralization in both species. When the three subsegments where analyzed differentially, it was shown that in chimpanzees SLF I showed a significant rightward lateralization, while SLF II and SLF III did not. In contrast, humans showed a significant rightward lateralization for SLF III, a nonsignificant trend for SLF II, and no lateralization in SLF I. Also, SLF III showed more prefrontal connectivity in humans than in chimpanzees. Thus, while the overall right lateralization of the SLF seems to be an evolutionary conserved feature across humans and chimpanzees, the specific asymmetries of the three SLF segments underwent selection towards greater rightward lateralization of SLF III and away from lateralization of SLF I during human evolution.

Also, birds show pronounced asymmetries of long white matter tracts and commissures. In pigeons, the tectofugal pathways ascend from the tectum to the rotundus and then to the entopallium in the telencephalon (**FIGURE 6**). A critical component of this system is the bilateral projection from each tectum to the ipsi- and contralateral nucleus rotundus. The majority of tectal projections of both half brains ascend ipsilaterally onto the nucleus rotundus, while a subpopulation projects to the contralateral side. This contralateral tectorotundal projection is asymmetrically organized with more fibers crossing from the right tectum to the left rotundus than from the left tectum to the right rotundus (187) (**FIGURE 7*A***). Thus, while each rotundus receives bilateral tectal input, the left nucleus rotundus integrates proportionally more tectal fibers and could thus represent both visual fields to a larger extent. Indeed, behavioral studies could demonstrate enhanced bilateral processing in the left hemisphere (477). Thus the ascending tectofugal pathway displays a neuronal organization that creates an asymmetrical representation of the visual scene at forebrain level.

Further evidence for a link between structural asymmetries in neuronal projections and functional hemispheric asymmetries is provided by research in the zebrafish (*Danio rerio*). The zebrafish, a widely used model species in genetic research, shows pronounced structural asymmetries in the epithalamus, the dorsal part of the diencephalon (see sect. II and **FIGURE 2** for a detailed explanation). Together with its associated projection fibers, the epithalamus forms a system that links the ventral midbrain to the forebrain of zebrafish (397). Interestingly, both parts of epithalamus show pronounced structural asymmetries in their fiber projections. As described above, the pineal complex shows a striking structural asymmetry as it is situated on the left side of the brain in wild-type fish. Moreover, its projections are also lateralized, as it projects to the lateral subnucleus of the left but not the right dorsal habenula (155). The habenular nuclei are bilaterally innervated by the anterior pallium, but there is a subset of olfactory bulb fibers that selectively innervates only the right habenula (326). Interestingly, asymmetries in zebrafish projections have been shown to affect behavior. For example, the dorsal habenulo-interpeduncular pathway has been shown to be involved in the fish resuming locomotor activity after freezing following a negative stimulus like electric shock. If the left habenular efferents to interpeduncular pathway were severed, fish showed prolonged freezing behavior, while severing the right habenular efferents to interpeduncular pathway did not affect freezing and fish rapidly resumed swimming after shock (112).

Taken together, there is clear evidence for the existence of structural hemispheric asymmetries in neuronal projection pathways in several vertebrate species. Moreover, these structural white matter asymmetries are likely to be one of the factors that influence functional hemispheric asymmetries.

D. Interim Summary Section IV

- Interhemispheric transfer of neural information can have either inhibitory or excitatory effects on the contralateral hemisphere. Both have been suggested to affect functional hemispheric asymmetries.
- A recent single unit recording study in pigeons challenges the notion that commissural interactions just inhibit or excite the contralateral hemisphere. Instead, commissural interactions could modify the temporal structure of the contralateral hemispheric activity patterns, thereby either delaying the side or synchronizing with it during joint action.
- Asymmetries of white matter pathways are evident both on the level of networks, and single tracts like the arcuate fasciculus have been shown to affect functional hemispheric asymmetries. Comparative research shows that asymmetries of neuronal projections are a general organizational feature of the vertebrate brain.
- Studies in birds also stress the notion of a dual coding of cerebral asymmetries. Thereby, static coding refers to structural white matter asymmetries of long-distance intrahemispheric or commissural projections. They are assumed to persist for the entire life time. The second, dynamic aspect of coding are left-right differences of short-term interactions via commissural systems. The combined action of these two processes creates the moment-to-moment gestalt of lateralized cognition and behavior.
- Communication by language or song is possibly the most thoroughly analyzed example for the dynamic structure of brain asymmetry. This will be outlined in the next section.

V. ASYMMETRIES IN EMOTIONAL AND COGNITIVE SYSTEMS

A. Speech and Song: A Mechanistic View on Asymmetries in Human Language, Primate Vocalization, and Avian Song

Spoken language is a unique trait of humans and is thus considered a hallmark of human evolution (34, 379). While most species capable of conspecific vocalization only possess the means to communicate a very limited amount of messages (e.g., emotional state), humans can use language to basically communicate about any concept (131). As we have described in section I, it was likely this uniqueness of human language that made scientists falsely believe that hemispheric asymmetries are unique to humans. Although no other species on this planet displays conspecific vocalization equal in complexity to human language, birds of the passerine order evolved a communication system which resembles spoken human language in a number of key features: bird song (131, 379). Like human language, bird song consists of discrete elements, which can be combined to increasingly complex sequences in a hierarchical fashion following specific syntactic rules (35). Furthermore, passerines, like humans, are vocal learners being able to learn new vocalizations by imitating and learning from conspecifics, a trait shared only by very few vertebrate species (379). Most importantly for the topic of this review though, Like the human language system, the passerine song system shows several forms of lateralization that could be crucial for the understanding of the functionality and evolution of lateralized brain functions (361). In this section, we briefly summarize the neuroanatomical basis of human language (with a small excursion to non-human primate vocalization) and bird song, including their lateralization, and show how similar these systems and partly their asymmetries are despite a separate evolution for ~300 mya and a differentially organized pallium (191, 250).

As we have described in the first section of this review, early anatomical studies in the 19th century revealed a leftward lateralization of language production (58) and decoding (506). The involved areas, named Broca's and Wernicke's area after their discoverers, are key components in a frontotemporal cortical network, required for the perception, comprehension, and production of speech. This speech network is located in the left hemisphere in ~90–95% of all right-handed humans (69, 265). While lesions in Broca's area in the posterior inferior frontal gyrus impair the ability to speak (but not to comprehend), lesions in Wernicke's area in the superior temporal gyrus can massively affect language comprehension but leaves speech production mostly unaffected (16, 367).

However, language asymmetries cannot simply be attributed to hemispheric asymmetries in these two areas but to profound differences between left and right hemisphere in the larger language network (170, 331, 355). In addition to Broca's and Wernicke's areas, the language network contains mainly the primary and secondary auditory cortex in the temporal lobe and the posterior speech area surrounding Wernicke's area (reviewed in detail in Ref. 148). fMRI studies have shown that these networks are asymmetrically activated during language production (23) and perception (357). Although networks were active in both hemispheres, the activation of the left network was stronger in most participants. Schönwiesner et al. (429) could also show functional differences between left and right hemisphere in language processing. While the left hemisphere seems to be more activated in response to temporal variations (e.g., sounds per time unit) of language stimuli, the right hemisphere responds stronger to spectral (e.g., pitch) variations. This fits nicely with data showing that the right hemisphere is important for understanding prosody or intonation of language [both highly dependent on pitch and tone (133, 290)]. Since music relies strongly on pitch variations, it is not surprising that several studies found also a higher activation of the right hemisphere when participants were listening to music (237, 525). In contrast, the left hemisphere is predominantly active during processing of syntactic and semantic information, which is highly dependent on temporal features (147, 453). Furthermore, lateralization of the language system could also be observed on the behavioral level. Studies employing the dichotic listening task in which two similar sounding syllables are presented simultaneously to right and left ear revealed that most participants reported the syllable presented to right ear, indicating a left-hemispheric advantage in syllable detection (235, 236, 238, 263, 360, 463). Left-hemispheric advantages for speech can also be observed in visual half-field tasks. Stimuli presented in the right visual half field which is mostly analyzed in left hemisphere are named faster than stimuli occurring in the left visual half field, processed by the right hemisphere (46, 118, 239, 487).

In addition to these functional asymmetries, left-hemispheric language networks and their right-hemispheric homologues also differ in their neuroanatomical structure. Early studies showed that language-relevant areas are often larger in the left than in the right hemisphere (151, 152). As an example, the planum temporale in the posterior temporal lobe constitutes major parts of Wernicke's area. Many studies have shown that this area is larger in the left hemisphere, in extreme cases up to 10 times, rendering it one of the most pronounced structural asymmetries in the human brain (164, 258).

In addition to these gross anatomical differences, studies could, for example, show asymmetries in cell size (242) and cortical column (241) in Wernicke's area or larger spacing between neuron clusters in the left superior temporal gyrus (154). In addition to these neuronal or gray matter asymmetries, differences between the left and right language system are also evident on a connectivity or white matter level. Catani et al. (72) used diffusion tensor imaging to investigate connectivity in the language system. They found that in ~62% of all participants a direct connection between Broca's and Wernicke's area (or their right-hemispheric counterparts) via the arcuate fasciculus is only present on the left side. In contrast, an indirect connection between the two areas over the posterior speech area was present in both hemispheres. Interestingly, the degree of lateralization in the direct connection was negatively correlated with verbal recall performance, suggesting an advantage of more symmetrically organized brains for this task. In a recent neuroimaging study, Ocklenburg et al. (352) used NODDI (neurite orientation dispersion and density imaging), which allows in vivo measurement of neurite density and microstructure in combination with EEG. They could show a higher density of dendrites and axons in the left posterior temporal lobe which was associated with faster processing of speech stimuli.

Taken together, there is a multitude of functional and structural asymmetries in the human language system. Whether they are an evolutionary new feature in humans or have been developed from hemispheric asymmetries in more basic communication systems can only be distinguished by comparative research in non-human animals. Naturally, communication asymmetries have therefore been investigated in our closest relatives, non-human primates. Functional and anatomical data from apes and monkeys allow some valuable insights into the evolution of language asymmetries. Apes and monkeys do not possess human-like language, but they use a varied set of conspecific vocalizations to communicate. Behavioral studies in Japanese macaques (368) and marmosets (230), PET studies in rhesus macaques (376) and chimpanzees (460), and an fMRI study in rhesus macaques (432) have shown that like in humans the left hemisphere is more active during perception and production of these vocalizations. Also on the anatomical level, there are surprising similarities in the asymmetrical patterns between humans and non-human primates. In chimpanzees, bonobos, and gorillas, parts of the inferior frontal gyrus (constituting Broca's area in humans) are larger on the left than on the right side (68), resembling the situation in humans. Also the planum temporale has been shown to be larger on the left side in chimpanzees, again reflecting the human pattern (156, 232). Recently, a leftward asymmetry of the planum temporale has also been shown in the olive baboon (*Papio anubis*), a non-hominid primate (309). Despite the lack of language in non-human primates, these data make it very likely that the asymmetry in the neuroanatomical substrate underlying language and a general lateralization of conspecific vocalization developed already in a common ancestor of men, apes, and monkeys and is by no means a trait unique to humans (361).

But what about animal species more distantly related to humans? As we have outlined before, complex conspecific vocalization systems including the ability of vocal imitation and learning are very rare in the animal kingdom. Only songbirds, parrots, hummingbirds, and several marine mammals seem to share this faculty with humans (41). While data on asymmetries of the vocalization system (or even on the system itself) are rather rare in the latter three, a compelling amount of data have been collected proving that the song system in passerine species is, like the language system in humans, lateralized. Due to their differently organized forebrain (birds lack a cortex but instead possess a nuclear organized pallium, Ref. 183), also their vocalization system appears rather different from the human case at first glance. However, there are some similarities. In song birds, auditory information from the inner ear is relayed over several brain stem nuclei and the thalamus to the primary auditory area of the avian pallium, the field L complex (41, 191). The field L complex projects to the associative auditory areas nidopallium caudomediale (NCM) and caudomedial mesopallium (CMM), which are key components for song perception, song recognition, and auditory memory (41, 160, 259, 323, 493) (see **FIGURE 10**).

Due to their functional similarities, NCM has been suggested to be the functional equivalent to Wernicke's area in humans (330). This auditory system is tightly interconnected with the so-called song system, comprising as core telencephalic components the pallial areas LMAN (see legend of **FIGURE 8** for full names), HVC, RA, and the striatal area X. These nuclei play crucial roles in song production, song learning, and song plasticity (110, 347, 423); for more details on the song system, see the reviews in References 41, 266. Since it plays a central role in song learning and production, HVC was suggested to be the analogous region to Broca's area in humans (330). Several studies in zebra finches (*Taeniopygia guttata*) but also other passerines have shown that the perception of song seems to be lateralized in the brain. Electrophysiological and fMRI studies in zebra finches revealed a stronger activation in the right than in the left NCM in response to song but also to other stimuli, with differences being most pronounced in response to conspecific or own song stimuli (371, 499). However, this pattern is not as robust as in humans, with strength and side of lateralization being highly dependent on stimulus type, prior experience, and age. In zebra finches being deprived of songs from other individuals and instead listening to songs of another song bird for a couple of days, responses to conspecific songs are lateralized to the left NCM (520). In juvenile zebra finches, tutor song (a song from an individual from which the juvenile learned its vocalization repertoire, normally the father) but not songs from unfamiliar conspecifics cause a left-lateralized activation in NCM (330). The idea that NCM lateralization is dependent on stimulus type is supported by a recent fMRI study revealing a change in asymmetry when structural or temporal parameters of the song stimulus are changed with a clear right-hemispheric sensitivity to spectral changes (492). A study in juvenile zebra finches suggested that left-sided NCM lateralization in response to song might be triggered by early life experience. In this study, birds without any prior contact to song did not show an asymmetry in NCM activation in response to a first time song exposure. Interestingly, when these naive birds were stimulated with rhythmic noise or were kept silent, they displayed a more pronounced right-sided NCM activation (79).

Although some studies show a lateralization of the suggested Broca's area analogue HVC in response to song stimuli to the left side (330), a clear dominance of one hemisphere for conspecific vocalization like in humans has not been confirmed in zebra finches. Albeit early studies found stronger effects on song production after lesioning of the nerve controlling the right syrinx, the vocal organ of birds (513), more recent studies could

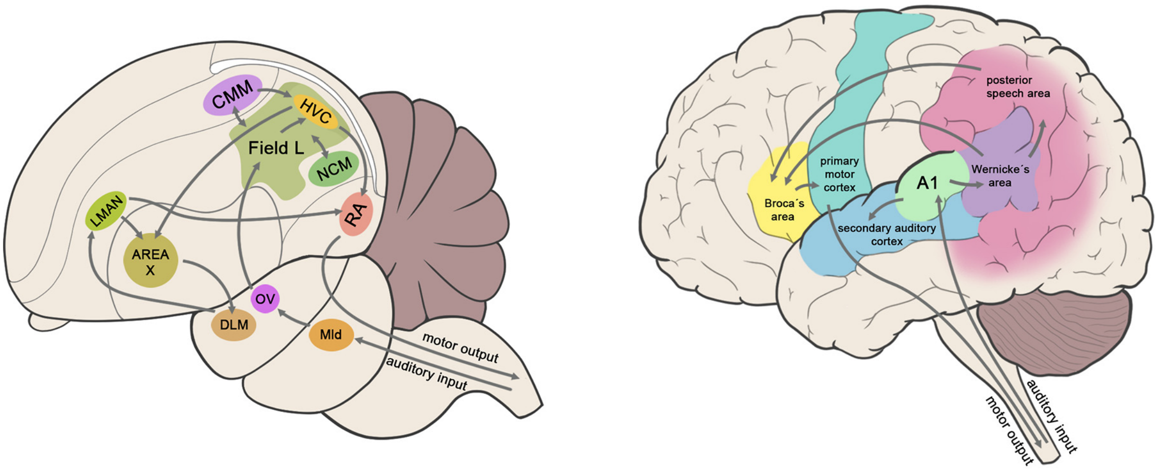


FIGURE 10. *Left*: schematic overview of the song system in zebra finches. Like for language in humans, the perception and production of song in zebra finches is controlled by a network of telencephalic areas. Even though birds do not possess a layered cortex but a nuclear organized pallium, functional properties of these areas are very similar to humans. Furthermore, key structures of this system like the nidopallium caudomediale (NCM, green), important for song perception, song recognition, and auditory memory, or the HVC (proper name, orange), critical for song learning and production, are to some extent functionally lateralized. See text for further information. For reasons of clarity, only the core nuclei of the song system have been depicted. CMM, caudomedial mesopallium; DLM, dorsal lateral nucleus; LMAN, lateral magnocellular nucleus of the anterior nidopallium; MLd, dorsal lateral nucleus of the mesencephalon; OV, nucleus ovoidalis; RA, robust nucleus of the arcopallium. *Right*: schematic overview of the language system in humans.

show that control of song production is likely shared between hemispheres. Within this process, HVC activation seems to switch rapidly between song production, with both sides composing individual parts or components of a song (295, 425, 502).

Even though the lateralization pattern of the song/language system is different in zebra finches and humans, there are still some interesting similarities. In both humans and zebra finches, specific aspects or qualities of auditory stimuli seem to be predominantly processed by one hemisphere. As we have described above, in humans the left hemisphere is more responsive to structural features of language like semantic or syntax information while the right hemisphere responds stronger to temporal features like prosody or intonation (17, 331, 375). In zebra finches, at least one study showed that the right hemisphere is more sensitive to general spectral changes, while several other studies reported differential lateralization patterns dependent on more specific stimulus types (e.g., own song, tutor song, rhythmic noise). The effect that experience during the juvenile stage can alter the direction or occurrence of vocalization asymmetries in zebra finches can also be seen in humans to some extent. Studies with congenital deaf participants showed a switch of the dominant hemisphere to the right side when presented with visual word perception task (458, 459). Moreover, an fMRI study in deaf participants also showed changes in lateralization of brain activation in the superior temporal gyrus, a brain area mostly involved in processing auditory input in hearing people (472). In contrast to hearing controls, deaf participants showed an increasing activation in the right superior temporal cortex during three decision making tasks, about the phonology and semantics of British Sign Language and the physical shape of objects. In the phonology task, deaf participants additionally showed a larger activation in the left superior temporal cortex. In addition, it has been shown that when participants learn a completely new tonal language, they at first show almost bilateral activation in the superior temporal gyrus. The more they get exposed to the new language, the more brain activation in the superior temporal gyrus becomes left-lateralized (373). Thus experience is a critical factor for leftward asymmetry of vocalization processing, not only in zebra finches but also in humans.

Concluding this paragraph, we would like to mention that also passerine species other than zebra finches, e.g., European starlings (*Sturnus vulgaris*; Ref. 102), canaries (*Serinus canaries*; Ref. 195), or Bengalese finches (*Lonchura striata domestica*; Ref. 527), possess asymmetries in their auditory and song system. However, these partly differ in side and strength from the zebra finch. Furthermore, few studies also reported evidence for a lateralization of conspecific vocalization for example in sea lions (*Zalophus californianus*) (47), mice (116), and maybe even fish (*Ictalurus punctatus*) (129). Due to the limited amount of space in this review, we will omit these data here and would refer the interested reader to the review on conspecific vocalization by Ocklenburg et al. (361).

B. Sadness and Hope: Brain Asymmetries in Emotional and Social Processing Across Vertebrates

Functional hemispheric asymmetries in emotion processing are one of the key topics in laterality research in humans, and several somewhat contradicting theoretical accounts have been brought forward to explain their emergence (104). Compared with other areas of laterality research, hemispheric asymmetries in emotion processing historically had a strong focus on research in humans and many theories have been built on data obtained in human subjects. This has several reasons. Up until the 1980s, it was widely believed that human handedness and other forms of functional hemispheric asymmetries were species-unique traits (504). This notion has been clearly refuted for limb preferences (452, 498) and functional lateralization of species-typical vocalizations (361) by a large number of studies in different non-human-animal species. However, the idea that only humans show emotional lateralization might have prevented researchers from investigating this feature in non-human animals on a large scale. Moreover, for lateralization of emotion, its assessment in non-human animals seems to be more complicated than for motor preferences like handedness. This is mainly because animals cannot communicate their emotions verbally, and assessing emotions often relies on self-report (e.g., when asking participants whether pictorial stimuli that were meant to induce certain emotion actually induced any emotions). Thankfully, in the last decade, a stronger focus on using developmental, neuroscientific, or observational techniques to assess hemispheric asymmetries of emotion processing in non-human animals emerged (280). These comparative studies are particularly important to determine evolutionary conserved patterns of emotional lateralization in humans and disambiguate between the different, sometimes contradicting, theoretical models for it.

Historically, the first two models for emotional laterality in humans that were proposed were the right hemisphere model and the valence model. The right hemisphere model assumes that the right hemisphere is dominant for processing of all types of positive and negative emotions. Emotional valence thus does not affect emotional lateralization. The idea that the right hemisphere plays an important role in emotion processing in humans has been supported by various empirical studies in both healthy subjects and different clinical populations. One of the lines of evidence supporting this idea comes from research in brain-damaged patients. For example, it has been shown that patients with left-hemispheric brain damage show a strong negative emotional reaction, an appropriate emotional reaction to a catastrophic event. In contrast, patients with right-hemispheric brain damage were emotionally indifferent, an inappropriate reaction to a catastrophic event such as suffering brain damage (150).

In healthy participants, several authors have used visual half-field experiments to investigate functional hemispheric asymmetries for the processing of emotional expressions of human faces (272, 288, 450). They consistently reported an advantage of the right hemisphere. Moreover, dichotic listening studies with emotional words in which participants were instructed to attend to the emotional content consistently showed a shift towards a left-ear advantage compared with verbal tasks, indicating a dominance of the right hemisphere for emotion processing (62, 171, 194). In addition to these behavioral studies, early neuroimaging studies have shown a right hemisphere superiority for the processing of acoustic emotion prosody (512) and attending to the emotional expression of a face (336). Complementing these studies in healthy volunteers, studies in neurological patients have shown that lesions in the right hemisphere are associated with larger impairments in the identification or discrimination of emotions than lesions in the left hemisphere (3, 44).

Evidence for the right hemisphere model of emotional lateralization also comes from comparative research. For example, in non-human primates, several studies investigated oro-facial asymmetries when animals produced emotional and nonemotional calls. The idea behind this is that the right hemisphere controls the muscles coordinating left hemiface movement so that a leftward asymmetry in oro-facial movements indicates a right-hemispheric asymmetry for communication of emotion. With the use of this paradigm, a right hemisphere specialization for facial emotion expression has been shown for chimpanzees (127), Olive baboons (501), and rhesus macaques (208).

In contrast to the right hemisphere model, the valence model of emotional lateralization assumes that emotional valence is critical for emotional lateralization in the sense that the right hemisphere is dominant for negative emotions and the left hemisphere is dominant for positive emotions (5, 217, 437). In general, the notion that only the right hemisphere is involved in emotional processing is strongly contradicted by recent neuroimaging studies. For example, a comprehensive meta-analysis of 54 fMRI and PET studies assessing lateralization of the amygdala, a central brain structure in emotion processing, during emotion processing actually found that the left amygdala actually was more often active during emotion processing than the right (20). Thus the idea that the left and the right hemisphere have differential roles in emotion processing is supported by the empirical evidence.

Early support for the notion that the left hemisphere is dominant for positive emotions and the right hemisphere is dominant for negative emotions was provided in a study using the Wada test, i.e., anesthesia of one hemisphere and subsequent assessment of behavioral reactions (464). Anesthesia of the right hemisphere and thus control of emotion by the left hemisphere led to euphoric, i.e., intensely positive, emotional states. In contrast, anesthesia of the left hemisphere and thus control of emotion by the right hemisphere led to catastrophic, i.e., intensely negative, emotional states. Further empirical support was provided by behavioral studies. For instance, a visual half-field study on discrimination of emotional face expressions found that participants were better when discriminating positive expressions with the left hemisphere and negative expressions with the right hemisphere (249). The most convincing body of evidence for the valence model comes from studies using EEG alpha asymmetries to gain an estimate of brain activity. In principle, it is assumed that the EEG alpha band reflects the absence of cognitive activity so that a leftward alpha asymmetry indicates greater right-hemispheric activation and vice versa (391, 443). Several studies have shown stronger left-hemispheric activation during processing of positive emotions and stronger right-hemispheric activation during processing of negative emotions (99, 117, 138, 500). However, evidence from functional neuroimaging studies is somewhat less supporting of the valence hypothesis. While some earlier fMRI studies supported the idea that overall brain activity is lateralized to the left hemisphere for positive stimuli and lateralized to the right for negative stimuli (67), more recent fMRI studies generally show more region-specific lateralization during emotion processing that is only partly in line with the valence model. For example, Bereha et al. (33) found that during positive stimulus processing there was significant leftward lateralization in brain activation in the medial prefrontal cortex, but also rightward lateralization of brain activation in the premotor cortex and the temporo-occipital junction. For negative stimulus processing, the authors reported that in line with the valence model, there was rightward lateralization of brain activation in the dorsolateral prefrontal cortex and in the temporo-parietal junction. However, in the amygdala, the uncus, and the middle temporal gyrus, there was significant leftward lateralization of brain activation.

Evidence supporting the valence model also comes from comparative studies specifically investigating both positively and negatively valenced emotions in the same species, e.g., in dogs (438). Dogs can express emotions by tail-wagging, and it has been shown that if a dog sees its owner (a situation with positive emotional valence), the animal shows more rightward tail-wagging, indicating more left-hemispheric brain activity (388). In the same study, seeing an unfamiliar dominant dog (a situation with negative emotional valence) leads to more leftward tail-wagging, indicating more right-hemispheric brain activation. In a later study, it was also shown that other dogs react to left- or rightward asymmetric tail-wagging (440). Dogs were shown videos of other dogs showing leftward or rightward tail-wagging. They showed higher cardiac activity and more anxious behavior when observing conspecifics that wagged their tails to the left, indicating negative emotional valence.

Moreover, a recent review integrating research on emotional lateralization in non-human animals also supported the valence model. Leliveld et al. (280) identified five major fields of research on emotional lateralization in animals. These include fear/anxiety, aggression, sex, responses to food rewards, and positive social interactions. Fear/anxiety has been investigated in studies on lateralization in escape behavior when an animal is facing a predator. For example, the common wall lizard (*Podarcis muralis*) has been proposed to have a left eye preference when inspecting predators, indicating right hemisphere dominance for this behavior (42). Aggression has for example be investigated in a study on aggressive courtship rejection in female striped plateau lizard (*Sceloporus virgatus*) that showed that females of this species showed a left eye/right hemisphere dominance for conspecific aggression towards male animals (223). Sex has for example been investigated in a study in sexually active male Mongolian gerbils (*Meriones unguiculatus*) that showed male courtship vocalizations were positively correlated with the volume of the left hypothalamic sexually dimorphic area, pars compacta (SDApc) nucleus, but not the right (229). Food reward has, for example, been investigated in a study on food smelling in dogs that showed a preference for the right nostril (controlled by the left hemisphere) when initially smelling new food odors (441). Positive social interactions have for example been investigated in a study in marmosets (*Callithrix jacchus*). These animals showed a right hemimouth/left hemisphere dominance for social contact calls (230). Importantly, Leliveld et al. (280) found that with the possible exception of fish, all classes of vertebrates (amphibians, reptilians, birds, and mammals) show a similar pattern of emotional lateralization that is largely in line with the valence model. While the right hemisphere is dominant for the processing of negative emotions such as fear and aggression, the left hemisphere is dominant for positive emotions such as those elicited by receiving a food reward. Recently, it was also shown that the red mason bee (*Osmia bicornis*) shows a rightward asymmetry for aggressive behavior (408). Moreover, the honeybee (*Apis mellifera*) shows leftward asymmetry for positive social contacts (409) and a rightward asymmetry to turn away from an alarm pheromone (412). Thus evidence in insects also supports the valence model.

In addition to the right hemisphere and the valence model, two newer models for emotional lateralization have been proposed in humans. These models make somewhat similar predictions but on different theoretical grounds. The motivational direction model (also sometimes called approach/avoidance model) assumes that in mammals, the left hemisphere is dominant for approach behavior and the right hemisphere is dominant for avoidance or withdrawal behavior (100, 201). Since most negative emotions like fear or disgust are linked to avoidance, and positive emotions like happiness are linked to approach, this model makes predictions that are largely in line with the valence model, with one important exception: anger is a negative emotion that is associated with approach-related behavior, e.g., moving towards an opponent to attack that person. Here, the valence model would predict right-hemispheric lateralization because anger is a negative emotion, but the motivational direction model would assume leftward lateralization because anger is approach-related. A number of EEG studies have specifically investigated this assumption and found greater left than right frontal cortical activity during anger, supporting the motivational direction model rather than the valence model (198, 200–203). When looking at the comparative lateralization of aggression data presented by Leliveld et al. (280), most Mammalian, reptilian, and amphibian species show a right hemisphere and only fishes show a left hemisphere bias. However, other authors also presented evidence for control of aggression in the right hemisphere in fish (39). Thus the comparative data would rather support the valence model than the motivational direction model. In Australian lungfish (*Neoceratodus forsteri*), predator escape responses are biased to the left side, indicating a right hemispheric dominance for avoidance behavior. In contrast, feeding behavior was lateralized to the right side, indicating a left-hemispheric dominance for approach behavior, as predicted by the motivational direction model (291).

A model that is conceptually similar to the motivational direction model is the "Behavioral Inhibition System and the Behavioral Activation System" (BIS/BAS) model. According to this model, the left hemisphere is dominant for behavioral activation while the right hemisphere is dominant for behavioral inhibition (455), which would also lead to left-hemispheric dominance for anger as opposed to other negative emotions. Like for the motivational direction model, there is EEG data supporting this model, e.g., it has been shown that individuals with greater behavioral activation system sensitivity show greater left-frontal activity (199).

Taken together, all four models for emotional lateralization are supported by some empirical evidence but also contradicted to some extent by other empirical evidence. For example, a recent study comparing the right hemisphere model, valence model, and motivational direction model for facial emotion processing came to the conclusion that the empirical data do not unequivocally support any of these three models (335). Therefore, it has been suggested that it might not be an optimal approach to pitting these hypotheses against each other, but that researchers should instead focus on identifying specific contributions of left- and right-hemispheric brain networks in specific situations involving emotions (262, 381). For example, one fMRI study using a chimeric faces task reported general activation of the posterior right hemisphere during non-conscious perception of emotional faces, regardless of the affective valence of these faces (262). This finding was in line with the right hemisphere model. However, the authors also reported valence-specific activations in bilateral anterior brain regions that were in line with the valence model. The authors concluded that the right hemisphere model and the valence model are not really in opposition to each other, but instead are both correct as they reflect two differentially lateralized brain networks within the complex distributed neural network controlling emotion processing. They suggested that one emotion network in the posterior right hemisphere is dominant for emotional perception in general, independent of valence. This system is interrelated with a second emotion network in the posterior left hemisphere that involves valence-specific activation of the orbitofrontal cortex and the ventral striatum. In line with this idea, other authors also suggested that the right hemisphere model and the valence model (or the motivational direction model) reflect different subsystems within a complex distributed emotion network (217, 381, 400, 424). Within this network, the right hemisphere model reflects activation of the right posterior cortex during emotion perception, while the valence model reflects valence specific activations associated with emotional experience that have been linked to the dorsolateral prefrontal cortex. In addition, it has been suggested that all of these models of emotional lateralization neglect an important aspect of emotion processing in the human brain: inhibitory executive control processes in the prefrontal cortex (173). This led to the development of the asymmetric inhibition model of emotional lateralization that specifically takes into account such emotion-cognition interactions.

Taken together, evidence in humans suggests that there are at least two differentially lateralized neural subsystems underlying emotion processing. One follows the prediction of the right hemisphere model and is mostly relevant for emotion perception, while the other follows the predictions of the valence model and is mostly related to the emotional experience. This second subsystem seems to be evolutionary conserved across vertebrates.

C. Interim Summary Section V

- In humans, production, perception, and comprehension of language is controlled by a fronto-temporal cortical network, which is in most humans lateralized to the left side. Broca's area (language production) and Wernicke's area (language comprehension) are the central components of this network.
- Although the left hemisphere shows a dominance for processing language, the right hemisphere contributes specific aspects to language (e.g., prosody). This difference is likely based on a general left hemispheric advantage to process temporal and a right hemispheric advantage to process structural features.
- Song of passerine birds shows many similarities to human language including similarities in the underlying neuronal structure. Like in humans, the perception and to some extent production of song are lateralized, although this lateralization seems to be more experience dependent.
- While research on emotional lateralization initially concentrated on humans, in the last decade, a stronger focus to development neuroscientific or observational techniques to assess hemispheric asymmetries of emotion processing in non-human animals led to an increase of comparative studies in this field.
- Several models have been brought forward for emotional lateralization. Among them are the right-hemisphere model that predicts that the right hemisphere is dominant for all emotions and the valence model that predicts that the right hemisphere is dominant for negative emotions while the left hemisphere is dominant for positive emotions. Both have been supported by empirical evidence.
- Comparative research indicated that most classes of non-human animals show a similar pattern of emotional lateralization that is largely in line with the valence model. While the right hemisphere is dominant for the processing of negative emotions such as fear and aggression, the left hemisphere is dominant for positive emotions such as those elicited by receiving a food reward.

VI. SUMMARY

After the discovery of the asymmetry of the human brain, more than a century had to pass until finally left-right differences of brain and behavior in other animals became a topic of detailed research. Within the short period since then, several animal models were established that increasingly enabled the reconstruction of the complex interactions between genes, environment, and epigenetic factors that shape the developing brain into its adult form. Now, with the help of these animal models, key frontiers should be tackled that are impossible to solve by studying human subjects only. One of these key challenges of the next decade will be the decoding of the molecular epigenetic processes that link environmental factors to changes in gene expression and finally to brain development. Most epigenetic processes like methylation of CpG islands in the DNA, histone modification, or posttranscriptional regulation by microRNAs are to some extent tissue-specific and time-sensitive. Therefore, comparative research in non-human model species is essential to gain an understanding of this crucial puzzle piece in the search for the determinants of asymmetry. A further area of future research should be the analysis of the dynamical interactions within asymmetrical neural networks since these dynamics determine the lateralized perceptual, cognitive, and motor functions of asymmetrical brains. A special subfield of this research agenda is the commissural interactions between hemispheres. Although we have solid evidence that they are of key importance for asymmetries, we know very little what is transferred between left and right and how that affects contralateral processes. Most importantly, we know that practically all pathologies of the mind go along with altered functional asymmetries. Animal models could help us in the future to understand why.

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