

Lateralization of Language

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Abstract and Keywords

It is intriguing that the two brain halves of the human brain look so similar, but are in fact quite different at the anatomical level, and even more so at the functional level. In particular, the highly frequent co-occurrence of right-handedness and left hemisphere dominance of language has led to an abundance of laterality research. This chapter discusses the most important recent finding on laterality (i.e., left or right hemisphere) and degree of hemispheric specialization for speech production, auditory speech processing, and reading. Following a descriptive overview of these three core sub-processes of language, the chapter summarizes possible influences on the lateralization of each, including anatomical, evolutionary, genetic, developmental, and experiential factors, as well as handedness and impairment. It will become clear that language is a heterogeneous cognitive function driven by a variety of underpinning origins. Next, the often-underestimated role of the right hemisphere for language is discussed with respect to prosody and metaphor comprehension, as well as individual differences in the lateralization of healthy and language-impaired brains. Finally, recent insights into the relationship between lateralized language and non-language functions are discussed, highlighting the unique contribution of lateralization research to the growing knowledge of general human brain mechanisms.

Keywords: laterality, hemispheric dominance, brain, handedness, speech production, auditory speech processing, reading

Introduction

THOUSANDS of researchers are accumulating knowledge concerning how language is processed in the human brain. It is such a fascinating topic because it is considered to be one of the traits that makes humans unique. Moreover, the specialization to one cerebral hemisphere is extraordinary: about 95% of right-handers and 75% of left-handers dominantly activate their left hemisphere (LH) during speech production, whereas the remainder of humans shows an atypical right hemispheric (RH) dominance or bilateral organization (Knecht et al., 2000). However, it is not the ability to communicate that differentiates

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humans from other animals, nor can language dominance be selectively attributed to humans. Vocal expressions and other communicative gestures are equally left lateralized in birds, mice, and nonhuman primates (Rogers & Andrews, 2002). It is the intriguing joint dominance of right-handedness and LH speech lateralization that has led to the abundance of language lateralization research in the human brain.

Let us introduce this chapter with the dominating question: Are handedness and language lateralization linked? This is an ongoing debate, but recent evidence points to an indirect relationship between these phenotypes. A common underlying origin was first suggested by the higher incidence of aphasia in right-handers than left-handers after unilateral LH brain damage (Benson & Geschwind, 1985; Hécaen & Sauguet, 1971). Evidence for an influence of handedness on language laterality was further provided by long-believed single-gene theories. For example, the right-shift gene theory posits that an RS + allele leads to right-handedness and LH language dominance, whereas an RS - allele randomly assigns handedness and language dominance. The combination of the two alleles most likely results in typical LH language dominant right-handers (Annett, 1998). Single-gene theories, however, have been refuted because evidence from most recent studies clearly shows that both handedness and language (p. 878) dominance are determined by multiple genes, with so far no candidate genes common to both functions (e.g., *LRRTM1* [Francks et al., 2007] and *PCSK6* [Brandler et al., 2013] for handedness, and *FOXP2* for language dominance [Ocklenburg et al., 2013; Pinel et al., 2012]). Still, the prevalence of LH language lateralization in right-handers compared to left-handers appears to be too high to be incidental. Differences in research approaches may explain why this puzzling coherence has not been unraveled yet. For example, evolutionary research suggests that the nature of manual actions must be taken into account. Language dominance may be linked to the lateralization of communicative gestures, but not to noncommunicative manual actions, such as grasping an object (Cochet, 2015). In language laterality research, however, handedness scores are often derived from the Edinburgh Handedness Inventory, asking manual preference for daily noncommunicative actions (Oldfield, 1971). Another possibility is that alternative measures of handedness, such as familial sinistrality, are more closely related to language lateralization. For example, having a left-handed first-degree relative reduced the surface area of the planum temporale in the LH up to 10%, independently of the individual's own handedness, in Tzourio-Mazoyer, Simon, et al. (2010). Finally, the degree, apart from direction, of handedness and language lateralization may also play a role in the link between both phenotypes (Mazoyer et al., 2014).

Despite the unclear role of handedness in language lateralization, left-handers are considered an interesting sample when studying cerebral asymmetries. It is wrong to take them as a homogeneous atypical group based on their handedness because the majority of them still show typical LH language dominance (see the following section), but some are RH language dominant. Their heterogeneity provides a unique perspective on how cognitive functions are related in healthy participants. If, for example, speech production shifts to the RH, related functions are expected to lateralize to the same atypical side in order to optimize information exchange, whereas unrelated functions reside in the contralateral hemisphere (Willems, Van der Haegen, Fisher, & Francks, 2014). Language laterality can

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be an ideal starting point to reveal interactions between cognitive functions such as cognitive control, memory, and so on, because it is the most well-documented lateralized function until now (Cai & Van der Haegen, 2015). Studies including left-handers with or without known atypical lateralization will therefore be extensively reviewed in this chapter, even though one should bear in mind that handedness correlates with language lateralization without revealing direct causes.

Lateralization research is, of course, far from limited to a comparison between right- and left-handers. A long history of research made clear that language lateralization is influenced by anatomical, evolutionary, genetic, developmental, and experiential factors, and impairment; some of these factors were already introduced earlier. We will briefly describe evolutionary and anatomical influences on language lateralization in general in this introduction. More detailed studies investigating the influence of these factors on language sub-processes will be discussed in further sections. Evolutionary, hemispheric specialization might have arisen when the cortex expanded and unilateral specialized regions became more advantageous than redundant processing of the same function in homologue areas in the LH and RH. In an increased brain volume, intra-hemispheric processing facilitates information exchange between connected brain (p. 879) regions. Moreover, lateralization increases brain capacity by creating cortical space available for other cognitive functions. In particular, the expansion of the frontal cortex in primates, housing Broca's area (involved in speech production), may have contributed to language asymmetry (Toga & Thompson, 2003; see also Corballis, 2009; Hopkins & Cantalupo, 2008). Anatomically, three remarkable asymmetries have consistently been observed. First, the so-called right frontal and left occipital petalias refer to the anterior extension of the RH beyond the LH and the occipital protrusion of the LH beyond the RH. In addition, RH frontal and LH occipital areas are wider. Second, the Sylvian fissure runs more anteriorly and steeper in the RH than LH. Third and presumably most important for language lateralization, the planum temporale is about 35% larger on the left side (Toga & Thompson, 2003; see also Hugdahl, 2011).

An important note is that so far, we have collapsed lateralization findings across language functions. A large part of the literature has indeed long treated language as one unitary function, mostly taking the asymmetry of speech production as an equivalent of language lateralization. It became clear, however, that language processing is much more complex: The focus of neurocognitive research has shifted from identifying individual neural nodes to structural and functional networks, and not all language sub-processes are lateralized to the same degree or even in the same direction. We will therefore review lateralization in more detail by discussing the sub-processes. We will first give an overview of the most important recent studies on the lateralization of speech production, auditory speech processing, and reading, as these are considered to be the three core sub-processes of language. We limit this chapter to higher-order processes, as the low-level stages of language in the primary auditory and visual cortex are not lateralized—with the exception of articulation, which is controlled by unilateral motor cortices. We also refer to other chapters for a more detailed overview of non-lateralized brain regions involved in these functions. For all three core sub-processes, we first describe the most important findings with

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respect to the direction and degree of lateralization, and thereafter summarize speculations on what might drive this lateralization based on the seven possibly influencing factors mentioned earlier. We then discuss the role of the RH, which has a pivotal role in the processing of prosody and metaphors, but also gains importance when language is impaired (e.g., in the case of dyslexia) or extended (e.g., in the case of bilingualism). Finally, the relationship between language lateralization and other asymmetric functions has become a hot topic in research, in line with the shift from individual neural nodes to highly interactive brain networks within and across domains. It will become clear that language lateralization can be a unique gateway to gain knowledge about how the human brain is organized.

Speech Production

In the nineteenth century, Marc Dax attributed speech production to the LH for the first time. Paul Broca published his seminal paper in 1865 stating that we speak with our left hemisphere, after observing a lesion to the third gyrus of the inferior frontal (p. 880) cortex in two severely speech-impaired patients (Broca, 1865; see Wilson, Chapter 2 in this volume). The lesioned region corresponded to what we still call Broca's area today, including the *pars opercularis* (approximately Brodmann area 44) and *pars triangularis* (approximately Brodmann area 45). Despite widely accepted insights that language is much more complex than speaking with Broca's area, activity in this region has long been equalized to language, in particular in the domain of laterality. Clinicians, for example, localize language most often in the LH because many patients are prevented from speaking when the LH is temporarily anesthetized by sodium amytal in the Wada test (Wada & Rasmussen, 1960). The preponderance of the LH in language received even stronger confirmation from research with split-brain patients, also in the 1960s (Gazzaniga, Bogen, & Sperry, 1962). These patients have their corpus callosum and anterior commissure severed in order to isolate intractable epileptic seizures in one hemisphere. They could not name an object held in their left hand, connected to the contralateral RH. This verified that the LH houses speech production, as it could not receive the necessary information via interhemispheric transfer (see Gazzaniga, 1975, 2005, for reviews). Remarkably, these findings were generalized as evidence for overall LH language dominance for decades. This is reflected in laterality assessments of more recent research: Many behavioral and neuroimaging paradigms are compared against outcomes of the Wada test (e.g., Binder et al., 1996; Hirata et al., 2010), or start from production when studying language lateralization, albeit with the notion that their results reflect speech production lateralization and not language lateralization as a whole (e.g., Abbott, Waites, Lillywhite, & Jackson, 2010).

Behaviorally, visual half-field tasks reveal an LH speech dominance when pictures presented in the right visual field are named faster than pictures in the left visual field because the partial crossing of optic fibers at the optic chiasm sends visual information to the contralateral hemisphere. Van der Haegen, Cai, Seurinck, and Brysbaert (2011) presented this behavioral approach as a screening method to identify (a) typically speech-lateralized participants. Their visual half-field picture-naming latencies correlated signifi-

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cantly ($r = 0.65$) with a functional magnetic resonance imaging (fMRI; see Heim & Specht, Chapter 4 in this volume) word-generation task in 50 left-handers with variable directions and degrees of lateralization. Neuroimaging techniques—and in particular fMRI because of its good spatial resolution—are today widely used to map brain regions involved in speech production and their lateralization. The verb-generation task (i.e., saying a verb associated with an object), word-generation task (i.e., generating a word starting with a target letter), and picture naming are most popular for speech-production lateralization. The results are often expressed in indices reflecting the direction and degree of lateralization, in line with the view that lateralization is graded and not absolute (Behrmann & Plaut, 2015), a notion that is not taken into account by the Wada test. The widely used toolbox by Wilke and Lidzba (2007), for example, compares the difference in neural activity between LH and RH homologue areas, thereby giving more weight to voxels activated at a higher activity level to avoid basing the indices on arbitrarily chosen statistical thresholds (see Seghier, 2008, for methodological issues in calculating lateralization indices). Early large-scale studies using word (p. 881) generation in fMRI (Pujol, Deus, Losilla, & Capdevila, 1999) or functional transcranial cerebral Doppler sonography (comparing blood flow velocity in the left and right middle cerebral arteries; Knecht et al., 2000) estimated LH speech dominance to be present in about 95% of right-handers but only 75% of left-handers, boosting the belief that handedness affects language lateralization. Mazoyer et al. (2014) scanned 297 healthy participants balanced for handedness during a sentence production task (i.e., silent sentence generation versus repetition of months of the year as overlearned sequence repetition). Lateralization indices based on individual contrast-activity maps (with most activity in the LH inferior frontal gyrus and lower part of the precentral gyrus, and RH activity at the junction of the middle and inferior temporal gyri in the occipital lobe) divided the participants into typical LH dominants (88% right-handers, 78% left-handers), atypical RH dominants (the remaining 7% left-handers), and participants with bilateral patterns (12% right-handers, 15% left-handers). Overall, these studies agree that the majority of participants produce speech dominantly with their LH, but left-handers have a higher incidence of atypical bilateral or RH dominance.

These laterality studies focused on Broca's area during speech production. Most lateralization indices were based on combined activity in the *pars opercularis* and *triangularis*. It should be noted that Broca is a large region that can be divided into several sub-regions, for example six regions based on neurotransmitter receptor type (Amunts et al., 2010). It is not surprising, then, that it also turns out to be a heterogeneous area at the functional level, linked to semantic processing, syntactic processing, motor functions, music perception and execution, and so on (e.g., Fadiga, Craighero, & D'Ausilio, 2009) apart from phonological processing. It is thus important for researchers to specify on which regions their lateralization estimates were based. Speech production also activates a mosaic of cerebral regions outside Broca's area. Again, even though researchers are aware of this, individual indices should be reported separately for other speech production-related areas if we want to reach a complete image of lateralization. Indeed, the lack of reporting lateralization indices of sub-processes reflects the general duality between psycholinguistic-

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tics focusing on higher-order level processes (e.g., the *pars opercularis* and *triangularis* for word retrieval) and motor control neuroscientists investigating lower-level articulatory processes (e.g., pre- and post-central motor regions associated with mouth movements; Indefrey, 2011; Price, 2012), as highlighted by Poeppel, Emmorey, Hickok, and Pylkkänen (2012). Broca's area may indeed remain the most important region for speech production, and if all regions co-lateralize, a limitation to the classical *pars opercularis* and *triangularis* may not be problematic, but differences in the degree of lateralization may help explain relationships with other brain regions and possible causes of lateralization, which we will now discuss.

Anatomically, Broca's area has been found to be larger in the LH than RH, but this may mainly apply to Brodmann area 44 (*pars opercularis*). Amunts et al. (1999) divided Broca's area into 10 different regions based on cytoarchitectonic laminar patterns. Despite large between-participant differences, only area 44 showed a clear left asymmetry in all brains. The same authors later reported a significant lateralization of cholinergic M2 receptors in this area (Amunts et al., 2010). The relationship between (p. 882) functional and anatomical asymmetries remains puzzling, however. Keller et al. (2011) compared 15 healthy participants with a functional LH dominance during word generation with 10 RH dominants. Volume asymmetry of the insula could predict 87% LH and 90% RH functional dominance, and the termination of the right posterior Sylvian fissure lay more vertical in LH dominants, but planum temporale volume asymmetry had no predictive value. Even more surprisingly, gray matter asymmetry of Broca's area, considered as the core region activated during word generation, did not correlate with functional asymmetry. Likewise, Greve et al. (2013) found volume asymmetry differences in the insula in 34 LH speech-dominant and 21 RH speech-dominant left-handers identified by Van der Haegen et al. (2011), but not in the *pars opercularis/triangularis* (again, participants were strikingly divided into an LH- and an RH-dominant group based on their functional asymmetry in these regions), nor in the planum temporale or Heschl's gyrus. Exploratory surface-based analysis did find small differences in the posterior temporal gyrus (overlapping with planum temporale) and the ventral occipito-temporal region involved in reading.

Evolution is a second factor that has been related to speech lateralization. It has been theorized that language evolved from manual gestures. The main argument is found in the similar location of Broca's area in humans and the F5-area in monkeys, housing the mirror-neuron system. Mirror-neurons respond to both the execution of manual actions and the perception of the same movements, such as reaching and grasping. This created the possibility to imitate, and from there, more complex movements such as speech articulation could evolve, leading to communication via speech (Rizzolatti & Arbib, 1998). Bipedalism and more complex hand movements in tool use further contributed to the evolution of complex human communication with, for example, syntax (Corballis, 2003; see Vingerhoets et al., 2013, for a correlated lateralization pattern between tool use pantomiming and speech production). It is the vocal mechanism in Broca's area that would have led to unilaterality, as articulation does not require bilateral control, even though this view has not fully been accepted yet because asymmetric speech perception may

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have evolved first; the vocal tract used for articulation developed in *Homo sapiens* 170,000 years ago, whereas left lateralization of Broca's area was already reported for *Homo habilis* nearly two million years ago (Corballis, 2003). In this light, it would be useful to dissociate sub-regions of Broca involved in manual gestures related to communicative from non-communicative actions.

With respect to development, studies examining the lateralization of speech in young infants are sparse but seem to agree that strong LH frontal lateralization during expressive language (e.g., verb generation, verbal fluency) is already present in children between the ages of 3 and 18 years (e.g., Holland et al., 2007; Paquette et al., 2015; Sowman, Crain, Harrison & Johnson, 2014; see Minagawa & Cristia, Chapter 7 in this volume). Paquette et al. (2015) tested a sample with an age range between 3 and 30 years old with a near-infrared spectroscopy verbal fluency task in which participants had to sum up as many semantic category items as possible. Neural activity bilaterally increased with age in fronto-temporal language regions, but the degree of LH lateralization remained stable from infancy until young adulthood.

(p. 883) Investigating changes in laterality due to increased experience with speech is difficult, given the early use of expressive language in life. Inferior frontal activity has been observed during sign language by deaf participants, with minimal differences compared to normal hearing participants (e.g., Emmorey, Mehta, & Grabowski, 2007, using a positron emission tomography (PET) picture-naming task with face orientation as a control condition), pointing to an amodal expressive language by Broca's area and in line with previously described commonly developed neural networks for speech and gestures. Sign language does evoke more LH parietal activity, such as in the supramarginal gyrus linked to hand configuration and superior parietal lobule associated with proprioceptive monitoring of gestures (Emmorey et al., 2007). Allen, Emmorey, Bruss, and Damasio (2013) observed a larger volume of the *pars triangularis* in deaf signers compared to normal hearing signers and non-signers, along with increased gray matter volume in the visual calcarine sulcus, but no differences in lateralization. These results suggest that deaf signers have increased language areas bilaterally because of their highly demanding language system.

Finally, speech laterality explained by impairment brings us back to where we started this section, namely the observation of Paul Broca that the so-called motor aphasia in his right-handed patients was caused by an LH lesion in the inferior frontal gyrus (Broca, 1865). Later reports estimated aphasia due to unilateral LH lesions to occur in 60% of right-handers and 32% of left-handers, whereas right-hemispheric lesions led to aphasia in only 2% of right-handers but 24% of left-handers (Benson & Geschwind, 1985). Interestingly, the temporal cortices that are considered to contain the second most important areas for language were discovered in a similar way, namely by the observation of so-called sensory aphasia after an LH lesion in Wernicke's area, now known to be important for semantic auditory language processing.

Auditory Speech Processing

About one decade after Paul Broca published his seminal paper describing patients with speech problems as having motor aphasia, the German neurologist Carl Wernicke introduced the so-called sensory aphasia to refer to the syndrome of losing speech comprehension due to a lesion in the LH posterior temporal gyrus (Wernicke, 1874). In laterality research, auditory speech comprehension also seems to be considered as the second most important language sub-process, with speech being more often taken as an equivalent to general language lateralization (see Poeppel, Cogan, Davidesco, & Flinker, Chapter 26 in this volume). From an ontogenetic point of view, this is counterintuitive, as speech comprehension develops before speech, already in utero (Partanen et al., 2013). Some researchers do use auditory speech perception as a language laterality measurement, such as in the widely used behavioral dichotic listening task (Kimura, 1961). In this paradigm, participants are presented with auditory stimuli in both ears, often consonant-vowel syllables. The participant is asked to indicate which of two (p. 884) different input stimuli (s)he heard best. Reporting most signals from the right ear is seen as a marker of LH auditory speech dominance because of the preponderance of auditory pathways running from the ear to the contralateral auditory cortex—but note that in the auditory modality, ipsilateral connections are also highly present (Kimura, 1961). Hugdahl et al. (1997) found a right-ear advantage in 92% of right-handers who were LH (speech) dominant in the Wada-test. Tzourio-Mazoyer, Petit, et al. (2010) assessed language dominance, operationalized as story listening in the participants' mother tongue, versus an unknown foreign language in an fMRI study with 94 right-handers. LH asymmetry was found in the posterior superior temporal sulcus, the inferior frontal gyrus, and precentral gyrus, with a reduced lateralization degree in the presence of familial sinistrality, a smaller head size, and absence of strong manual preference.

Auditory speech recognition thus seems to lateralize to the LH. However, studies manipulating different components of speech comprehension point at two pathways. Bozic, Tyler, Ives, Randall, and Marslen-Wilson (2010) found bilateral fronto-temporal activity for the processing of general perceptual complexity and sound-to-meaning conversion during speech comprehension, whereas an LH inferior frontal asymmetry was only found when linguistic morpho-syntactic complexity of the auditory stimuli was increased. Hickok and Poeppel (2007; see also Hickok, Chapter 20 in this volume) described the auditory dual network in more detail. According to their theory, a ventral stream, including middle and posterior temporal cortices, connects acoustic signals to lexical meaning and is hence targeted by speech recognition tasks. In contrast, a dorsal stream running through the superior temporal sulcus bilaterally, a left part of the Sylvian fissure at the border of the parietal and temporal lobe, and left posterior frontal regions translate acoustic signals into articulatory codes and are activated during sub-lexical tasks such as syllable discrimination. Importantly, the ventral stream is bilaterally represented, which explains why speech comprehension is not necessarily devastated after unilateral damage, but it is the dorsal stream accounting for speech perception that is LH lateralized (Hickok & Poeppel, 2007). In addition to a ventral and dorsal stream, auditory speech processing has been

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thought to show time-related interhemispheric differences. The LH would be specialized in fast information processing, such as in the case of identifying rapidly changing sounds in speech, and the RH for slower spectral information that is required for prosodic analysis of a speech stream (Zatorre, Belin, & Penhune, 2002). Hickok and Poeppel (2007), in contrast, propose that the ventral stream integrates slow speech information in the RH, but fast information bilaterally (but see Scott & McGettigan, 2013). A review by Specht (2013), however, suggests that a more pronounced LH asymmetry is observed for lexico-semantic compared to auditory-phonetic processing and from posterior to anterior regions involved in speech processing showing that it is still under debate which aspects of speech processing are lateralized.

Comparing the degree of lateralization for speech production and comprehension might provide further insights, given their close functional relationship, especially in the dorsal stream. Tzourio-Mazoyer, Josse, Crivello, and Mazoyer (2004) found stronger functional asymmetries for production (verb generation) than comprehension (story p. 885 listening, both against rest) in a PET study. The weaker asymmetry during speech comprehension was mainly driven by the superior temporal gyri and Heschl's gyri. On the other hand, Häberling, Steinemann, and Corballis (2016) recently found no significant difference between three lateralization indices based on activity in the inferior frontal gyrus during verbal fluency word generation (against fixation) and the inferior frontal gyrus and middle/superior temporal gyrus during a synonym judgment comprehension task (against similarity of letter strings). It may be that the importance of lexico-semantic information in the visual synonym task boosted left lateralization, which again highlights that a variety of paradigms and especially control conditions can lead to different outcomes. Häberling et al. conclude that it makes sense for the fronto-temporal regions to tune their lateralization in order to optimize information exchange, and that the left lateralization of the dorsal stream introduced by Hickok and Poeppel (2007) uniquely adapted to vocalization in humans.

In sum, auditory speech processing is at least partly LH lateralized, but future research needs to clarify exactly which aspects are specialized to one hemisphere and whether this specialization is less extremely pronounced than speech production. We will now discuss studies providing information on the possible factors affecting laterality. First, Häberling et al. (2016) included an overrepresentation of left-handers to ensure sufficient variability in the lateralization indices and indeed found less asymmetry in this group. Van der Haegen, Westerhausen, Hugdahl, and Brysbaert (2013) pursued the left-handed approach more extremely and compared their atypically RH speech production lateralized left-handers (based on an fMRI verbal fluency word-generation task) with LH dominant left- and right-handers in a behavioral dichotic listening task. At the group level, RH speech dominants indeed turned out to have a left-ear advantage, whereas LH speech dominants had the expected right-ear advantage. At the individual level, however, the dichotic listening task showed variability in all groups. This can be due to more variability in a behavioral task, or an indication that speech perception in the case of syllable discrimination is more symmetric than speech production (Hickok & Poeppel, 2007). No effects of handedness

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were found when left-handers were considered as a homogenous group, which suggests the importance of their individual differences in hemispheric speech lateralization.

Evolutionary speculations on the development of auditory perception and comprehension go along with anatomical asymmetries. The planum temporale around the superior temporal gyrus, involved in imagining and hearing sounds (Price, 2012), is larger in the LH in humans (Geschwind & Levitsky, 1968) as well as chimpanzees (Hopkins, Marino, Rilling, & MacGregor, 1998), but not in rhesus monkeys and baboons (Wada, Clarke, & Hamm, 1975). These results point to the importance of leftward asymmetries in the planum temporale, which might be linked with some communicative functions (Corballis, 2009; Hopkins & Nir, 2010). Familial sinistrality affected the planum temporale in Tzourio-Mazoyer, Simon, et al. (2010): Having a left-handed relative decreased the surface size of the area by 10% and led to a larger gray matter volume, accompanied by a smaller leftward asymmetry. The size and gyrification pattern of Heschl's gyrus (belonging to the bilateral superior temporal gyri and involved in speech (p. 886) and non-speech sound processing; Price, 2012) also seems to play a role in establishing language lateralization. Marie et al. (2015) observed less duplications of Heschl's gyrus in the RH and a decreased LH asymmetry of the anterior gyrus of Heschl in left-handers. Tzourio-Mazoyer et al. (2014) linked the duplication and decrease in anatomical surface area of the anterior gyrus to a decrease in functional asymmetry in Heschl's gyrus during word-list listening. Leroy et al. (2015) reported a superior temporal asymmetrical pit that may be unique to humans, that is, more LH sulcal interruptions in a superior temporal sulcus region ventral to Heschl's gyrus, leading to a deeper structure in 95% of humans. This may be a precursor of human language lateralization as the asymmetry is present in healthy adults as well as infants, (a)typically lateralized speech dominants, left- and right-handers, and participants with *situs inversus*, autism spectrum disorder, Turner syndrome, or corpus callosum agenesis, but not in chimpanzees. A final anatomical asymmetry is found in the long-distance tracts of the arcuate fasciculus, connecting frontal and temporoparietal language areas such as Broca's area and Wernicke's, respectively. Its direct pathway (apart from the indirect pathway via the inferior parietal cortex) is LH lateralized in more than 80% of healthy participants (Catani et al., 2007). The structural asymmetry, however, seems to be independent from handedness and functional language lateralization as measured with a verbal fluency verb-generation task against tone listening (Vernooij et al., 2007). The recent diffusion tensor imaging study by Allendorfer et al. (2016) similarly reported no asymmetry differences for the pathway between left- and right-handers, even though left-handers as a group were less extremely LH lateralized in the functional verb-generation task. In contrast, Ocklenburg, Schlaffke, Hugdahl, and Westerhausen (2014) did find positive correlations between tract volume and fractional anisotropy of the LH arcuate fasciculus with the degree of right-ear advantage in a dichotic listening task.

Apart from evolutionary and anatomical insights, genetic studies are slowly adding information. With respect to speech perception, Ocklenburg et al. (2013) linked two polymorphisms of the *FOXP2* gene, rs2396753 and rs12533005, to the right-ear advantage in a dichotic listening task presenting consonant-vowel syllables to about 450 healthy participants. Variations in the *FOXP2* gene, however, also have been associated with language

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functions other than speech perception (e.g., reading ability; see discussion later in the chapter), and dichotic listening activates many brain regions such as the superior and middle temporal gyrus, pre- and post-central gyrus, supplementary motor area, and middle and superior frontal gyrus (Van den Noort, Specht, Rimol, Ersland, & Hugdahl, 2008). As mentioned by the authors themselves, it remains unclear how exactly molecular changes affect speech processing laterality.

Further, changes in auditory speech lateralization have been observed during development. Perani et al. (2011) found that perisylvian language areas in the inferior frontal and superior temporal cortices are already activated by 2-day-old babies listening to speech, but the auditory cortex showed RH dominance. LH speech perception was present in 3-month-old infants (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002), accompanied by a structural LH asymmetry of the arcuate fasciculus (Dubois et al., 2009). Another important difference compared to the adult language network pointed (p. 887) out by Perani et al. (2011) was the functional connectivity: Whereas most adults' fronto-temporal connections are strongest within the LH, 2-day-old babies mainly activated interhemispheric connections between LH and RH temporal regions. This preponderance of interhemispheric connectivity is still present by the age of 6 years (Friederici, Brauer, & Lohmann, 2011).

In deaf people (see also, in this volume, Newman, Chapter 14, and Corina & Lawyer, Chapter 16), the superior temporal gyrus reacts on visual motion stimuli and is more strongly connected to the calcarine fissure. This functional connectivity is positively correlated with the duration of wearing a hearing aid in hearing-impaired participants (Shiell, Shampoux, & Zatorre, 2014). With respect to the lateralization of a reorganized auditory cortex after unilateral deafness, Van der Haegen et al. (2016) found no difference in LH dominance for right-sided deaf participants who had profound hearing loss from birth during a semantic speech-listening task (i.e., judging whether or not a heard sentence refers to an animal against noise).

Reading

Reading (see Paz-Alonso, Oliver, Quiñones, & Carreiras, Chapter 24 in this volume), the third main subprocess of language, developed much later than speech production and comprehension in evolution. It originated about 6,000 years ago, even though being able to read was still rare only a century ago. Reading also develops last at the individual level, after extensive learning via instruction.

A region in the LH ventral occipito-temporal (vOT) sulcus has been identified as a crucial area and was consequently called the "visual word form area" (Cohen et al., 2000). Dehaene and colleagues argue that the area became specialized in a way of neuronal "recycling" (i.e., neurons were tuned to recognize visual words, but this evolved in an existing framework that was not genetically manipulated by learning to read). Plasticity could only occur within the existing constraints of the brain, and reading evokes most neural activity in the ventral visual cortex because of the close relationship to recognition

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of line junctions that form objects (see, e.g., Dehaene & Cohen, 2011, for a review). This area has, however, been shown to be activated by nonvisual stimuli as well, and interacts with top-down information coming from frontal phonological areas (Price & Devlin, 2011). The latter is especially interesting in light of lateralization. Seghier and Price (2011) found that the LH dominance of the vOT relative to pictures varied across three sub-regions of the area, mainly driven by decreased activity in the RH. Laterality indices of the posterior vOT were mostly influenced by RH reduction for letters and words relative to objects and nonobjects, indicating that this sub-region is related to visual attributes. The anterior vOT, on the other hand, was more activated by familiar (words and objects) than unfamiliar (Greek letters and nonobjects) stimuli and by a semantic task rather than reading aloud, suggesting that the lateralization of the anterior vOT is influenced by connections with frontal phonological and semantic (p. 888) regions. The middle vOT was affected by a mixture of visual and nonvisual factors. Inferior frontal regions already play a role in very early stages of visual word recognition. Cornelissen et al. (2009) did not find a significant time difference between the peak of the inferior frontal gyrus (after 130 ms) and the visual mid-fusiform gyrus (after 140 ms) in a passive word-viewing task. Words further elicited activity in the anterior and left posterior middle temporal gyrus, left superior temporal gyrus, and angular and supramarginal gyri. Co-lateralization of the inferior frontal gyrus during word generation and vOT during lexical decision was also found in left-handers with typical LH and atypical RH dominance (Cai, Lavidor, Brysbaert, Paulignan, & Nazir, 2008; Cai, Paulignan, Brysbaert, Ibarrola, & Nazir 2010; Van der Haegen, Cai, & Brysbaert, 2012). Pinel et al. (2014) compared reading (words versus scrambled stimuli) and auditory speech (native language sentences versus tone listening) lateralization in a one-back task. Participants with the strong leftward asymmetry in the middle superior temporal sulcus during speech processing also had a stronger LH lateralized vOT, driven by reduced RH activity, as in Seghier and Price (2011). These findings together reveal an influence from earlier developed functions such as speech production and comprehension on the recently developed reading skill. The vOT remains the most investigated region involved in visual word recognition, but it is clear that reading, as all cognitive functions, functionally relies upon a broader network, including frontal and temporal regions to support phonological and semantic processing. Richardson, Seghier, Leff, Thomas, and Price (2011) presented three possible reading routes connecting the posterior inferior occipital, posterior superior temporal gyrus, anterior superior temporal sulcus, and vOT region, with one pathway even running through the first three regions without involvement of the vOT. To our knowledge, no laterality differences have been reported for these routes.

Returning to our seven possible factors influencing laterality, we will now discuss evolutionary theories further than the previously mentioned neuronal recycling view, as reading is too recent and too unique for humans to speculate on parallel development of brain regions with nonhuman primates. Anatomically, two white-matter tracts end near the vOT: the inferior fronto-occipito fasciculus and the inferior longitudinal fasciculus running from the occipital lobe to anterior and medial temporal lobe. A third fasciculus, the vertical occipital fasciculus, runs from the lateral occipito-temporal sulcus to lateral oc-

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capital and inferior parietal lobes (Yeatman, Rauschecker, & Wandell, 2013; see Catani & Forkel, Chapter 9 in this volume). Again, different asymmetries of these pathways related to atypical (functional) lateralization have not yet been reported, to our knowledge. The only significant difference found was the more leftward/rightward gray matter volume asymmetry for speech LH and RH dominants, respectively, in Greve et al. (2013).

Pinel et al. (2012) scanned 94 healthy participants while they silently read sentences and linked the two single-nucleotide polymorphisms rs6980093 and rs7799109 in the *FOXP2* gene (associated with language impairment) to their functional LH lateralization of the frontal cortex, and rs17243157 variants in the *KIAA0319/TTRAP/THEM2* gene (associated with reading disabilities) to reduced LH asymmetry in the superior temporal (p. 889) sulcus. Other genetic influences on the lateralization of the vOT were found in Pinel et al. (2014), who tested monozygotic and dizygotic twins during their one-back visual task. Monozygotic twins showed intra-pair correlations as high as intra-participant correlations measuring replicability for LH vOT activity. The number of voxels activated above a $t > 1$ threshold was also more similar between monozygotic than dizygotic twins, suggesting that LH vOT activity is at least partly driven by genetic influences. This may be contradictory to the evolutionarily recent acquirement of the reading skill, but Pinel and colleagues conclude that this can be explained by the neural constraints in which the reading circuit developed. Genetic underpinnings of properties of the visual cortex to be able to recognize detailed information in central vision and connections to frontal and temporal regions may drive the heritability of the LH vOT activity.

To explore how the vOT evolves during learning to read in education, Ben-Shachar, Dougherty, Deutsch, and Wandell (2011) scanned children aged 7–12 four times in one year during an implicit reading task: Children were asked to indicate the color of a fixation mark that was presented together with word stimuli varying on visibility at four levels. Sensitivity to the word visibility was linked with better performance of overt speed reading and increased with age, especially in the LH posterior occipito-temporal sulcus nearby the vOT. The occipital V1 and posterior parietal cortex did not show such correlation, and remarkably neither did the RH occipito-temporal reading region. Thus, for developing perceptual expertise of words in a noisy context, the LH seems to play a more important role than the RH homologue area.

Dehaene, Cohen, Morais, and Kolinsky (2015) review how gaining reading experience by illiterates changes neural circuits. Not only letters, but also objects and faces, are better discriminated when acquiring reading, as reflected in an increase of activity in the early bilateral occipital regions (Dehaene et al., 2010). Moreover, the ventral visual pathway, including the vOT, becomes specialized for the script that is being trained, with a positive correlation between the amount of neural activity and reading speed (Dehaene et al., 2010). Learning an artificial language can even change the brain after a short training: Xue, Chen, Jing and Dong (2006) conducted two weeks of visual training and two weeks of phonological and semantic training with normal readers. Visual training decreased activity bilaterally in the fusiform cortex and LH inferior occipital cortex, whereas phonological training had the opposite effect. Semantic training affected the RH fusiform area

more. Reading acquisition further improves the processing of phonological representations; the vOT is activated by phonology only in literates (Dehaene et al., 2015). Perhaps the most striking change in terms of laterality is the influence that reading experience has on the lateralization of non-reading-related face recognition. The fusiform face area specialized for faces in the ventral visual cortex is reduced in the LH but enhanced in the RH when literacy increases (Dehaene et al., 2015). We will discuss the remarkable relationship between the laterality of word and face recognition in more detail in the following section.

Finally, reading impairment has been associated with differences in laterality. A meta-analysis of functional connectivity in dyslexic and control participants pointed at weaker LH connections between regions involved in visual and visuo-phonological processes, (p. 890) such as the LH inferotemporal region, fusiform gyri, inferior frontal, premotor and supramarginal cortices. In addition, dyslexics activated a dorsal fronto-parietal network less, including LH parietal and premotor cortices, associated with altered motor and visuospatial attention (Paulesu, Danelli, & Berlinger, 2014). Diffusion tensor imaging (see Catani & Forkel, Chapter 9 in this volume) studies generally found lower fractional anisotropy in white-matter tracts running through temporoparietal and frontal regions, especially in the LH arcuate fasciculus and corona radiata. Ventral tracts related to reading, such as the inferior longitudinal fasciculus and inferior fronto-occipital fasciculus, were less affected (see Vandermosten, Boets, Wouters & Ghesquière, 2012, for a review).

The Role of the Right Hemisphere in Language Processing

In contrast to the widely studied core sub-processes discussed earlier, the role of the RH receives much less attention in neuroscientific research. It is well-known, though, that the RH is active in several ways: (1) It plays a dominant role in some sub-processes such as prosody and metaphor comprehension (see, in this volume, Rapp, Chapter 28, and van Berkum, Chapter 29). (2) Neuroimaging has made clear that language lateralization in all functions is not absolute, processes are distributed across the hemisphere with a dominance in the LH for most language processes, and the RH can even be the dominant hemisphere in atypical left-handers. Moreover, individual differences are often explained by variations in RH activation. (3) Language impairments and mental disorders with a language component often increase the importance of the RH, as well as an extension of the language system, such as in the case of bilingualism. We will now discuss these three domains in more detail.

Prosody refers to either the variations in pitch and rhythm that form the emotional expression of the speaker, called emotional prosody, or the stress within sentences and words, called linguistic prosody. A meta-analysis by Belyk and Brown (2014) makes clear that the two types of prosody share many common brain regions, but are nevertheless distinct and differ in their lateralization. Pitch modulation is a common factor of both prosody types, leading to joint activation in the posterior superior temporal gyrus, with an

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RH dominance for emotional prosody and a more bilateral distribution for linguistic prosody. Common activity was also found in the RH supplementary motor area linked to speech production. A differentiation was found in the inferior frontal gyrus: evaluating affective cues in speech activates the pars orbitalis bilaterally (Brodmann area 47), a region connected to areas involved in experiencing and perceiving emotions, such as the amygdala, whereas linguistic prosody is more related with the bilateral pars opercularis (Brodmann area 44), which can be explained by its role in lexico-syntactic processing (Belyk & Brown, 2014). These meta-analytic results thus suggest RH involvement of (p. 891) auditory temporal regions and bilateral involvement of frontal regions irrespective of prosody type, in contrast to inconsistencies regarding lateralization in individual neuroimaging studies. For example, Witteman et al. (2014) found a right-ear advantage for both emotional and linguistic evaluation of dichotic listening stimuli associated with an early negativity event-related potential latency (see Leckey & Federmeier, Chapter 3 in this volume) in the contralateral hemisphere. In contrast, Wildgruber et al. (2005) did find functional asymmetries in an fMRI experiment in which participants were asked to either judge the emotions (basic emotions: anger, happiness, sadness, fear, and disgust) or linguistic content (i.e., reporting the first vowel following the first heard /a/) of sentences. Apart from common widespread bilateral activation, emotional judgment tapped into an RH network, including the posterior superior temporal sulcus, and dorsolateral and orbitobasal frontal cortices. The linguistic task made use of LH speech areas, such as the dorsolateral frontal cortex. These studies show a less consistent pattern than suggested in Belyk and Brown (2014), which could in part be explained by the different paradigms used.

A similar controversy of RH involvement probably depending on the type of task being used can be found in the literature on non-literal language comprehension, such as metaphor processing. Here again, the fronto-temporal language network is important with LH involvement in inferior, middle, and superior temporal gyri and the inferior frontal gyrus. Yang, Edens, Simpson, and Krawczyk (2009) reported that the amount of RH involvement mainly depends on the difficulty level of the sentences used, and not whether participants have to judge novel or known metaphors. Semantic judgments rely more on frontal areas, whereas imageability affected parietal regions such as the precuneus, but the laterality of these regions depended on the difficulty level of the stimuli.

This leads to the assumption that RH variations can generally explain individual differences in language laterality. Vigneau et al. (2011) evaluated the role of the RH in language tasks in a meta-analysis showing that LH activity occurred much more often in a unilateral fashion, whereas most RH peaks were observed in the case of bilateral peaks (i.e., in combination with LH activity in a homologue region). Phonological tasks activated RH auditory and motor areas (with the exception of only LH mouth-related activity and verbal working-memory tasks). Lexico-semantic tasks made use of RH frontal regions to support attentional and working-memory processes. During high-level sentence and text processing, the RH even had an exclusive role in temporal regions. Seghier, Kherif, Josse, and Price (2011) in addition highlighted that laterality differs across regions, confirming our general claim that language laterality should not be expressed in one unitary lateral-

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ization index. In Seghier et al. (2011), high LH angular gyrus activity was connected with low LH ventral precentral laterality. Even more interesting, interregional and inter-participant variability across 50 activated brain regions and 82 healthy participants performing a semantic word-matching task was mainly driven by differences in RH rather than LH activation. A dynamic causal modeling analysis of data from the same task revealed that the degree of LH laterality during word (p. 892) matching increased when the coupling from LH to RH dorsal frontal cortices decreased (Seghier, Josse, Leff, & Price, 2011).

If RH activity determines individual laterality patterns, can it also predict differences in performance? Van Ettinger-Veenstra et al. (2010) ran a dichotic listening task (taken as a general language laterality measure) and fMRI sentence completion task (i.e., complete the last word of a sentence versus the same sentences with asterisks replacing letters) to correlate their lateralization indices with performance on a wide variety of language tasks (e.g., sentence, text and metaphor comprehension, picture naming, and verbal fluency). Verbal fluency correlated positively with right-ear reports during dichotic listening, but overall, a decreased right-ear advantage led to better performance in almost all language assessment tasks. Rightward fMRI indices were also associated with better reading ability in the posterior temporal lobe and better comprehension scores in the inferior frontal cortex. On the other hand, Prat, Mason, and Just (2010) found increased RH frontal, temporal, and inferior occipital activity in participants with a smaller vocabulary size when they had to read more complex sentence pairs. This suggests that the RH is activated more if the participant experiences difficulties in language comprehension. Dehaene et al. (2010) reported increasing LH activity in the vOT with increasing literacy. Pinel et al. (2014) localized the vOT more anteriorly (associated with larger orthographic units) in participants who showed a smaller difference in reaction time when reading pseudo-words compared to words, but did not find differences in the amount of activity. Related to reading impairment, dyslexia was associated with less optimal connections between language areas in the LH only (Paulesu et al., 2014; Vandermosten et al., 2012). The different paradigms again impede straightforward conclusions about the relationship between the degree and direction of laterality, on the one hand, and language performance, on the other hand. Moreover, the functions tested in behavioral performance assessments are often different from those used to calculate the functional neural lateralization indices (see also Boles & Barth, 2011). One could speculate that, for example, RH activity increases when phonological, semantic, or reading processes become too difficult for the LH alone, and that language becomes more LH lateralized when performance increases because the RH is no longer needed. A similar idea was formulated by Prat et al. (2010) as the RH spillover hypothesis: that is, the RH contains coarser language abilities than the LH, but can take over if needed, for example, after a lesion or when the LH exceeds its capability during difficult tasks.

The dynamic role of the RH can be studied when existing knowledge is extended by learning a new language (see Green & Kroll, Chapter 11 in this volume). Xiang et al. (2015) collected longitudinal diffusion tensor imaging data from native German speakers following an intensive six-week Dutch course. They found that tracts between Brodmann area 6 and temporal regions, overlapping with the arcuate fasciculus, became more RH lateral-

ized in the beginning stages of the course but again turned into an LH dominance with better proficiency in their second language. It thus seems that structural connectivity is indeed reorganized to the RH when bilingualism challenges the language network, but then again becomes typically LH dominant when proficiency is high enough. In line with this point of view, Kepinska et al. (2017) also pointed out that (p. 893) fronto-parietal structural connectivity (right anterior segment of arcuate fasciculus) in the right hemisphere plays an important role in superior language learning, which might involve attentional processes and reasoning abilities. A functional increase has also been observed for bilinguals relative to monolinguals during native language picture naming and reading aloud in the LH dorsal precentral gyrus, *pars opercularis/triangularis*, superior temporal gyrus, and planum temporale (Parker Jones et al., 2012). Parker Jones and colleagues attributed this difference to a higher demand of word retrieval, articulation, and speech monitoring in bilinguals. A meta-analysis of behavioral lateralization tasks by Hull and Vaid (2007) pointed to the importance of taking age of acquisition into account: Early bilinguals who learned their second language before the age of 6 activated language areas more bilaterally, whereas later bilinguals were more LH dominant, especially when proficiency was low, English was the second language, and laterality was measured in a dichotic listening task. Learning a new language even influences brain areas recruited during native-language processing. Mei et al. (2014) trained Chinese speakers who had English as their second language with an artificial language based on Korean Hangul characters. The training focused on semantic learning, not just on acquiring visual-phonological correspondences. The results showed reduced LH activity in the *pars opercularis/triangularis*, and bilateral inferior temporal gyrus, fusiform gyrus, and inferior occipital gyrus while reading Chinese. The semantic training even influenced similar regions during English reading. In line with Xiang et al. (2015), the effects were strongest in the initial stages of the training and decreased with increasing proficiency. Finally, laterality differences in bilingualism depend on the similarity between the two acquired languages, usually tested in bilinguals with knowledge of alphabetical languages such as English and logographic languages such as Chinese and Japanese Kanji. English-Chinese bilinguals activate the RH posterior fusiform cortex more than English monolinguals, in a similar way as Chinese monolinguals show a more rightward lateralization during reading than English monolinguals (Mei et al., 2015). Koyama et al. (2014) drew similar conclusions from late bilinguals who were either native speakers of Japanese syllabic Kana and logographic Kanji languages and learned English, or native English speakers who mastered Japanese. A visual one-back reading task revealed less LH lateralization in the posterior lateral occipital region for logographic Kanji compared to syllabic Kana and alphabetic English, irrespective of the participant's first language. If the first and second language were non-logographic, no lateralization differences were found.

Finally, more RH activity has been associated with language-related areas in mental disorders. *FOXP2* polymorphisms, previously linked to reduced reading ability and dyslexia, were also associated with schizophrenia and autism spectrum disorder (Gong et al., 2004; Li et al., 2013). Schizophrenia patients in Bleich-Cohen et al. (2012) showed a reduced LH asymmetry and interhemispheric connectivity in the inferior frontal gyrus, an effect that

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was more pronounced with increasing severity of negative symptoms. Kleinmans, Müller, Cohen, and Courchesne (2008) found increased activity in RH frontal and superior temporal regions during verbal fluency word generation in participants with autism spectrum disorder, characterized by impairments in speech, (p. 894) syntax, and pragmatic knowledge compared to controls (see also Lindell & Hudry, 2013, for a review concluding that asymmetries become more atypical with increasing language impairments).

Language Laterality in Relation to Other Functions

It is clear from what we have discussed so far that all sub-processes of language can vary in their lateralization across individuals. This can be a fruitful starting point to gain knowledge about how the human brain is organized, both with respect to language and non-language functions (Cai & Van der Haegen, 2015). There are two dominant views on how functions are distributed across the RH or LH. The statistical independence view states that functions develop irrespective of how already established functions are organized. Alternatively, according to the competitive complementary hypothesis, cortical space is limited, and thus brain functions compete with each other for resources. The latter view makes clear that apart from the seven possible influences on laterality we reviewed per language sub-process (handedness, anatomy, evolution, genetics, development, experience, and impairment) there is an eighth possible factor: cooperative and competitive non-language functions (Behrmann & Plaut, 2013). Recent neuroimaging studies most extensively explored the relationship between reading and face recognition, and between speech production and visuospatial attention.

Behrmann and Plaut (2013) introduce three views on brain functioning: (1) the one-to-one vision in which one structure can be coupled with one cognitive function and vice versa; (2) the one-to-many vision in which a cognitive function triggers a network of structures and vice versa; (3) the many-to-many vision that integrates the first two perspectives and argues that structures and functions form distributed but interacting networks. Evidence for the many-to-many view can be found in the ventral visual cortex, where nodes are optimized for a specific visual category such as the vOT for words (Cohen et al., 2000) and the fusiform face area for faces (FFA; Kanwisher, McDermott, & Chun, 1997). At first sight, words and faces have more differences than commonalities. They both contain detailed information that has to be processed in central vision, but face recognition developed much earlier in evolution than reading and consists of coarser elements than the fine-grained line junctions in letters (Behrmann & Plaut, 2013). Statistical independence could argue that spatial frequencies pushed reading into the LH and faces into the RH, with the LH/RH being inherently more sensitive to high/low spatial frequencies, respectively (see Woodhead, Wise, Sereno, & Leech, 2011, who reported interhemispheric sensitivity to spatial frequencies; but see Ossowski & Behrmann, 2015, for evidence that LH high spatial frequency sensitivity was not found in pre-literate children, suggesting that the sensitivity is a consequence rather than cause of reading). Yet, interactions between

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reading and face recognition have been reported (p. 895) in several recent studies supporting the competitive hypothesis (Dehaene et al., 2010; Dundas, Plaut, & Behrmann, 2013, 2015; Cantlon, Pinel, Dehaene, & Pelphrey, 2011; Li et al., 2013). For example, Dundas et al. (2013) found a right/left visual field advantage for words and faces, respectively, but only in adults and not in children or adolescents. The younger participants showed only a right field advantage for words, with no visual field preference for faces. Face lateralization additionally correlated with reading performance. This could be explained from a developmental point of view that face recognition is bilaterally processed at first, but is then pushed into an RH dominance because words occupy overlapping neurons in the LH in order to optimize the connections with earlier LH lateralized fronto-temporal language regions (Dundas et al., 2013). Cantlon et al. (2011) found an LH occipito-temporal sensitivity to letters and digits, and an RH mid-fusiform dominance for faces in 4-year-old children in an fMRI study showing pictures of these visual categories and shoes. The early RH face dominance somewhat contradicts Dundas et al. (2013), who did not find a face lateralization before the mean adult age of 21, but more interestingly, Cantlon et al. (2011) add evidence for a competing view on word and face processing because children's behavioral symbol (i.e., letters and numbers together) matching scores correlated negatively with face-selective activity in the LH occipito-temporal region, whereas there was not even a correlation found with symbol neural activity itself in the same region. Similarly, behavioral face-matching accuracy was not associated with increased neural sensitivity for faces in the RH face-selective fusiform area, but with decreased activity for shoes, with no association with neural activity for symbols. Thus, visual areas generally seem to specialize by means of pruning away non-preferred categories, rather than favoring preferred categories. With respect to word and face lateralization in particular, an anti-correlation was found in the LH but not in the RH, even though the authors remark that this could be different in other stages of development. Looking at what atypical handedness could tell about this issue, no study to date has compared word and face lateralization in left-handers whose reading lateralization was clearly RH dominant, but Willems, Peelen, and Hagoort (2009) and Bukowski, Dricot, Hanseeuw, and Rossion (2013) found overall reduced RH face lateralization in the FFA of left-handers compared to right-handers. Dundas et al. (2015) confirmed this finding, together with LH word discrimination superiority for both right- and left-handers. In their study, more negative LH N170 event-related potential components (previously shown to distinguish orthographic from non-orthographic stimuli in the LH and sensitive to faces in the RH) during word presentations predicted a stronger amplitude for the N170 for faces and more RH behavioral asymmetries for faces. In the earlier discussed study by Pinel et al. (2014) using a one-back visual task with words and faces, among other visual categories and a speech-processing paradigm, different contributing factors to reading and face lateralization came forward: vOT activity showed significant intra-pair correlations for monozygotic twins but the FFA did not, suggesting that the vOT partially develops under genetic influences, whereas the FFA is more sensitive to environmental factors. RH FFA lateralization did not directly correlate with LH vOT lateralization, but was related to LH lateralization of the superior temporal sulcus during speech listening and reading skill, as operationalized by the (p. 896) additional time cost in naming pseudo-words compared to words. Fi-

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nally, Badzakova-Trajkov, Häberling, Roberts, and Corballis (2010) confirmed the correlation between RH face recognition and LH word generation, but were among the first to relate these two lateralized functions to another widely studied RH-dominant cognitive function: visuo-spatial attention.

According to Kosslyn (1987), visual attention to stimuli in the environment, like speech production, is unilaterally processed because rapid and precise actions are best coordinated by one control system. In addition, the control systems are best located in opposite hemispheres so that they do not interfere. This is in line with the competitive view in which functions can be crowded out, and in contrast with the statistical independence view in which lateralization of functions develop independently from each other. The 155 participants from Badzakova-Trajkov et al. (2010) did show a small but significant negative correlation between the verbal fluency word-generation task in frontal areas and the bisection task measuring visuospatial attention (i.e., judging whether a vertical line bisects a horizontal line versus indicating whether a vertical line is present in the control condition) in parietal areas. The bisection task was, however, the only task that did not elicit more atypical patterns in left-handers, and its lateralization did not correlate with RH face lateralization. We have argued before that an effect of handedness is not necessary to observe (a)typical lateralization patterns, and visuospatial attention has theoretically not been linked to face processing, but the relationship between speech production and visuospatial attention is indeed more mixed in the literature than the complementary lateralization patterns of reading and face recognition.

The first doubts about causal complementarity came from patient observations with a unilateral brain lesion. If speech and visuospatial attention indeed crowd each other out, then LH-damaged patients should have aphasia with spatial ability problems, and vice versa for RH-lesioned patients (Bryden, Hécaen, & DeAgostini, 1983). This, however, was not always the case: LH lesions led to aphasia, but also to spatial ability deficits or both, with a comparable picture for RH lesions. Zago et al. (2016) also found independence between lateralization indices of speech production (measured by contrasting sentence production based on a line drawing versus recalling the months of the year) and visuospatial attention (measured by line bisection versus fixation). At the group level, the 293 participants balanced for handedness mostly activated LH fronto-temporal language regions during speech production and RH frontal and posterior occipito-parietal-temporal regions during visuospatial attention, but a negative correlation was only found for left-handers with a strong manual preference. A clear interhemispheric distinction was reported by Cai, Van der Haegen, and Brysbaert (2013): All but one of 16 left-handers who were clearly LH lateralized for speech production (i.e., verbal fluency word generation versus non-word repetition) were RH lateralized for visuospatial attention (i.e., line bisection versus indicating whether a vertical line touched a horizontal line), and all 13 left-handers with clear RH speech dominance were LH dominant for visuospatial attention that elicited activation in the dorsal fronto-parietal attention pathway and inferior frontal regions.

(p. 897) Why is there agreement that reading and face recognition negatively correlate in line with a causal complementary view on brain functions, whereas speech production and visuospatial attention only seem to lateralize to the opposite hemisphere in extreme left-handers but support statistical independence in the remainder of the population? It could be that visuospatial attention tasks evoke less stable neural patterns than, for example, the verbal fluency task. Pernet et al. (2016) evaluated the between- and within-subject variance of a speech-production (verb generation triggering Broca's area) and landmark task (indicating which of two lines are smaller or larger, activating the intraparietal cortex) in order to estimate their reliability as clinical presurgical tools. A reliable paradigm should have higher consistency over two sessions tested within the same participant than at the group level, which was the case for word repetition but not for the landmark task. Another possible explanation for a stronger causal complementarity between reading and faces than between speech production and visuospatial attention is that the interplay between the function pairs is based on different underlying mechanisms. In the first pair, faces are presumably crowded out of the LH once the visual cortex needs to adapt to reading, which is preferably dominated by the LH to co-lateralize with earlier developed fronto-temporal language functions (Behrmann & Plaut, 2013). This is a competition for cortical space in homologue areas between an already established and newly developing cognitive function. Language and visuospatial attention, on the other hand, are more widespread throughout the cortex and are presumably separated because they each need a unilateral control system (Kosslyn, 1983). Petit et al. (2015) suggested another evolutionary explanation: In the sample studied by Zago et al. (2016), the dorso-parietal attention network was especially RH lateralized in strong left-handers, and even more so if they were right-eye sighted. Petit et al. argue that processing visuospatial control of the environment in the same hemisphere as their dominant hand may give these left-handers an advantage in, for example, interactive sports. It may thus be that visuospatial attention evolutionarily first lateralized to the RH because of functional advantages, and that language was then crowded out to the LH without having large overlapping neural populations that have to move for a competing function. Whatever reasons future studies will point out with respect to competitive or statistical independent relationships between functions, this overview makes clear that lateralization research, and in particular studies including atypically lateralized left-handers, can reveal interesting insights into brain mechanisms in general.

Conclusion

We can conclude from this chapter that language laterality gives unique information on how language and non-language functions are being processed in the human brain. It can be seen (前面刚用了 this overview made clear) that most language functions, such as speech production, auditory speech processing, and reading are dominantly (p. 898) processed in the LH in most humans, even though the degree of laterality can differ across functions and across individuals. Left-handers introduce more variability in the samples studied, leading to insights into mutual interactions when one factor such as speech production is atypically lateralized. Possible causes of an LH dominance have

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been proposed for each sub-process from studies reporting anatomical, evolutionary, genetic, developmental, experiential factors, and consequences of impaired functions and lesion studies in patients. We further discussed that the role of the RH within language remains underestimated, but prosody and metaphors are well-known to be dominated by the RH in most participants, and its importance to explain individual variability in healthy participants, dyslexia, and mental disorders such as autism spectrum disorder and schizophrenia is widely acknowledged. Recent laterality literature is dominated by neuroimaging studies mapping the direction and degree of lateralized functions, often (but far from always) reporting results of behavioral correlates that make it still unclear to what extent the lateralization of functions affects cognitive performance. It will thus be important to continue to combine different methodologies, while trying to optimize paradigms in order to facilitate the comparability across studies. Finally, language lateralization can be an ideal starting point to explore general brain mechanisms. We have discussed competitive complementarity between reading and face recognition, and, at least in strong or atypically lateralized left-handers, between speech production and visuospatial attention. From a wider perspective, future laterality studies can also reveal how the human brain works, beyond focusing on one or two cognitive functions. For example, Liu, Stuffelbeam, Sepulcre, Hedden, and Buckner (2009) identified four asymmetric networks during resting state activity that could roughly be related to regions involved in vision, internal thought, attention, and language. If these networks are indeed independent, with their own degree of inter-individual variability, then neuroscientists should not try to find one explanation (competitive complementarity or statistical independence) for the whole brain, but instead should investigate how and why separate clusters are grouped into networks underlying different functions, and how they are related to each other. One view on how the numerous and complex functions our brain houses can function so well together was given by Fedorenko and Thompson-Schill (2014). They argue that apart from a domain-general attention-related multiple demand network, the language network consists of functionally specialized core regions (i.e., regions that are consistently activated during language tasks and co-activate) and nonspecialized periphery regions (i.e., regions that are activated during language tasks, but can also co-activate with regions belonging to another specialized network depending on the current task). In this chapter, we have mainly focused on the core regions of language because we know most about the laterality of these regions, but future lateralization studies could test the view of Fedorenko and Thompson-Schill (2014), among other views on brain mechanisms, to further chart functional and anatomical asymmetries, starting from variations in language lateralization.

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