

Symmetry and asymmetry in the human brain

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Structural and functional asymmetry in the human brain and nervous system is reviewed in a historical perspective, focusing on the pioneering work of Broca, Wernicke, Sperry, and Geschwind. Structural and functional asymmetry is exemplified from work done in our laboratory on auditory laterality using an empirical procedure called *dichotic listening*. This also involves different ways of validating the dichotic listening procedure against both invasive and non-invasive techniques, including PET and fMRI blood flow recordings. A major argument is that the human brain shows a substantial interaction between structurally, or ‘bottom-up’ asymmetry and cognitively, or ‘top-down’ modulation, through a focus of attention to the right or left side in auditory space. These results open up a more dynamic and interactive view of functional brain asymmetry than the traditional static view that the brain is lateralized, or asymmetric, only for specific stimuli and stimulus properties.

Structural versus functional symmetry and asymmetry

In a neuroscience perspective, the concepts of symmetry and asymmetry are closely tied to the two hemispheres of the human brain (Figure 1), and the mirror symmetrical organization of the body along the vertical body axis, producing two mirror body halves. The two hands are also almost anatomically perfect mirror images of each other, but are clearly asymmetrical with regard to function or physiology. A clear majority of the population (~90%) prefers the right hand for manual activities, with superior fine motor control and motor strength.¹ Thus, the example with left- and right-handedness poses an important conceptual distinction between structural, or object, symmetry and functional, or activity-related, asymmetry. Two objects may show mirror symmetry with regard to shape and structure, although the functions of the two are clearly asymmetrical. A similar distinction applies to the two cerebral hemispheres, which at least on the surface

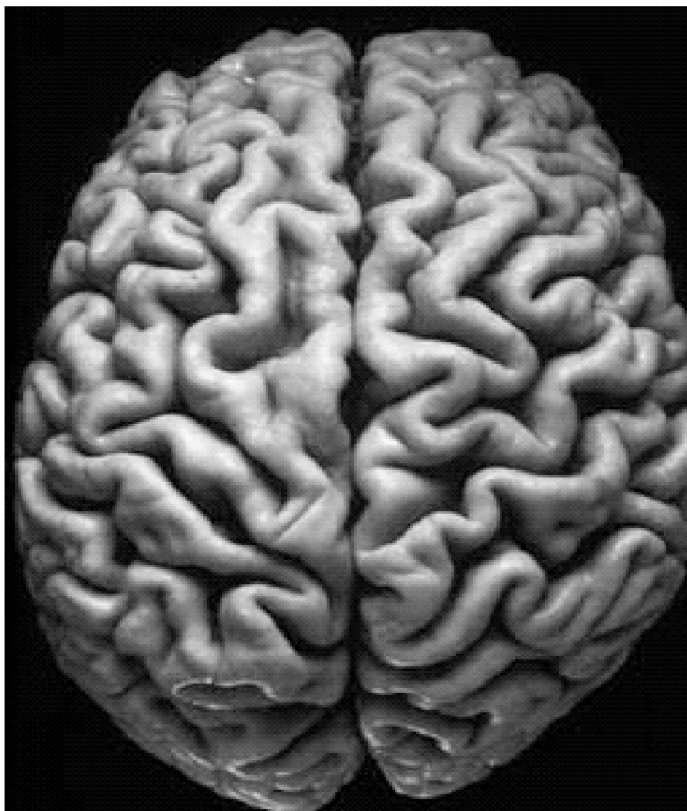


Figure 1. The human brain seen from above and behind. The most characteristic feature of the brain seen in this way is the longitudinal fissure that literally divides the brain into two halves, the right and left hemisphere, which are approximate mirror images of each other.

seems to be symmetrical mirror images, making up the left and right halves of the brain.

Language and the left side of the brain

It has been known for almost 150 years that the left hemispheres subserve language functions, while more recent research has pointed towards the right hemisphere as being specialized for processing of spatial relations and for emotional control.² Although asymmetry is the norm when it comes to functions of the brain and nervous system, the mind also strives for symmetry, and sometimes ‘symmetry breaking’ is an aversive state of mind, to be avoided. This can be exemplified in compulsive-obsessive disorders where breaking a symmetrical behavioural pattern produces anxiety and is a clinical syndrome that

seriously handicaps the patient. An obsessive-compulsive patient constructs a symmetrical inner world that should not be broken, and also shows stereotyped behaviour, e.g. only walking on left-right squares on the pavement. Thus, the distinction between structural and functional asymmetry is a key distinction when discussing symmetry and asymmetry in the brain and the nervous system.

The term asymmetry is often substituted for the term laterality when it comes to left–right differences in psychology and the neurosciences.³ However, while the term asymmetry can mean both structural and functional left–right dissimilarities, laterality is typically only used in relation to functional asymmetry.

The contributions of Broca and Wernicke

In 1864, the French neurologist Paul Broca made the observation that a patient with a vascular lesion that affected brain tissue in the middle frontal gyrus in the left hemisphere lost the ability to produce speech. This clinical syndrome later became known as Broca's, or expressive aphasia, indicating an inability to produce speech, while being able to understand when spoken to. Towards the end of 19th century another functional asymmetry was discovered, when the German neurologist Carl Wernicke made a similar observation, although in his case the patient, after a lesion to the left upper posterior part of the temporal lobe was unable to understand speech. This syndrome is known as Wernicke's, or receptive aphasia, i.e. the inability to understand when spoken to, although able to produce spontaneous speech.

Sperry's contribution

The original observations of different functional organization in the right and left hemispheres of the brain have been replicated and validated in numerous clinical and experimental studies. The most well-known example is perhaps the experimental series of studies carried out in the 1960–1970 by Roger Sperry and his colleagues.^{4–9} Sperry had the opportunity to test the functional specialization of the left and right hemispheres in patients with epilepsy who had undergone surgical cutting of the nerve fibres in the corpus callosum that connects the two cerebral hemispheres, in order to prevent an epileptic seizure spreading from one hemisphere to the other.

Sperry set up an ingenious, but quite simple experiment; a milk-glass screen was placed in front of the patient that covered most of the visual field (Figure 2). The patient was instructed to fixate his eyes on a centrally placed fixation point, while different words were briefly projected to the right or left of the fixation point from a slide projector placed behind the screen. When fixating in the middle of the visual field, any projection to the left of fixation will be passed to the right



Figure 2. The experimental set-up used by Sperry (e.g. Ref. 4) The patient had a screen in front of the eyes onto which words would be shown, either to the left or right of a fixation cross in the middle of the screen. On the table below the screen, hidden from view, several objects were placed, some of which matched the words seen on the screen. See text for further explanation. Adapted from Ref. 2.

hemisphere, and vice versa, because of the partial decussation of the visual fibres from the retina to the visual cortex in the occipital lobe. Thus, a patient with the left and right hemispheres disconnected from each other would act as if he had two brains that could not communicate with each other. On a table beneath the screen and in front of the patient, common objects (pencil, fork, apple, etc) were placed that corresponded to words being presented on the screen. The patient could however not see the objects but was capable of touching them with his right or left hand. When asked to report what they had seen on the screen the patients reported, to the surprise of everyone, that they had not seen anything when the words were projected in the left visual half-field, i.e. to the right hemisphere. There was however nothing wrong with their eyesight or any pathology related to the visual system. When the words were projected in the right visual half-field,

i.e. to the left hemisphere, the patients correctly reported the words shown. However, when asked to use his left hand, to pick up the corresponding item from the table, the patients invariably picked the item that corresponded to the word they reported having not seen. This remarkable outcome can only be explained as an example of the right hemisphere lacking the ability for expressive speech, thus when asked to report orally what had been shown on the left side of the screen, the left hemisphere reported accurately that it had not seen anything, while the mute right hemisphere could not respond. Since the left hand is controlled from the right hemisphere and vice versa, the right hemisphere was capable of directing the left hand to the corresponding item since it had seen and processed the word, but could not give an oral answer. This remarkable demonstration of functional asymmetry in the brain laid the ground for several decades of experimental and clinical research, still ongoing, to explore the asymmetrical functions of the cerebral hemispheres. Thus, when it comes to differences and similarities along the left–right dimension, the focus in the neurosciences has been on function rather structure, on asymmetry rather than symmetry.

Geschwind's contribution

In 1968, the American neurologists Norman Geschwind and W. Levitsky¹⁰ observed that a small triangularly shaped area, the *planum temporale*, in the upper posterior horizontal plane of the temporal lobes was clearly asymmetrical, with a larger area on the left than on the right side (Figure 3). The *planum temporale* overlaps to a large extent the classic Wernicke's area. Later studies have revealed that the grey matter volume is about 30–35% larger on the left side¹¹ with more widely spaced cellular columns, which implies greater connectivity per neuron on the left, compared with the right side. Axons in the left *planum temporale* are also more heavily myelinated, which could indicate increased transmission speed of the nerve impulse. *Planum temporale* asymmetry is observed only in primates and humans,¹² this could mean that the morphological differences in area size on the left and right side are not related to a corresponding functional asymmetry related to language, since chimpanzees show a similar asymmetry. On the other hand, it could mean that both humans and primates have both evolved the necessary structures for language development, but that something 'went wrong' for the primates along the evolutionary path in that they never developed language, although the *planum temporale* area was prepared for it.

The dichotic listening test of auditory laterality

We have further explored *planum temporale* asymmetry and functional differences between the two cerebral hemispheres in processing of simple speech

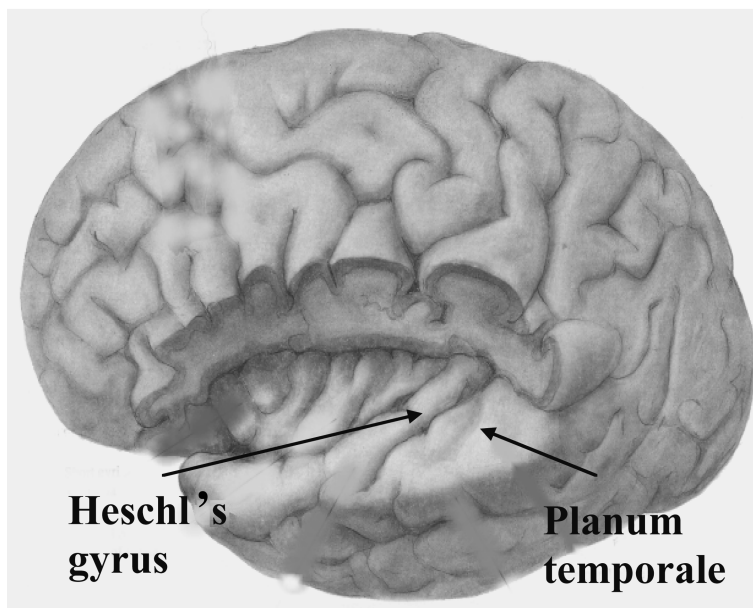


Figure 3. A drawing of the brain with a section of the upper posterior part of the left temporal lobe (and parts of the fronto-parietal area) removed, showing the characteristic landmarks of the Heschl's, or transverse, gyrus and the triangularly shaped area just behind the Heschl's gyrus, the *planum temporale* (adapted from Ref. 31). As mentioned in the text, the *planum temporale* extend a larger area in the left compared to the homologous area in the right hemisphere.

sounds, i.e. sounds that are phonetically relevant but semantically nonsensical. We have used as stimuli consonant-vowel syllables, like ba, da, ga, pa, ta, ka, that do not mean anything but are the building blocks for words and sentences. If the structural asymmetry observed for the *planum temporale* has any functional significance, one would expect that the perception and processing of speech sounds would predominantly occur in the left *planum*. One way to study this is to present consonant-vowel stimuli dichotically, i.e. two different syllables at the same time, one in each ear.^{3,13,14} Dichotic listening has been used in hundreds of research and clinical reports related to language processing, emotional arousal, hypnosis and altered states of consciousness, stroke patients, psychiatric disorders and child disorders, including dyslexia and congenital hemiplegia. Dichotic listening literally means presenting two auditory stimuli simultaneously, one in each ear, and the standard experiment requires that the subject report which of the two stimuli was perceived best. In our laboratory, we typically ask only for one response on each trial, although the subject sometimes may perceive that there

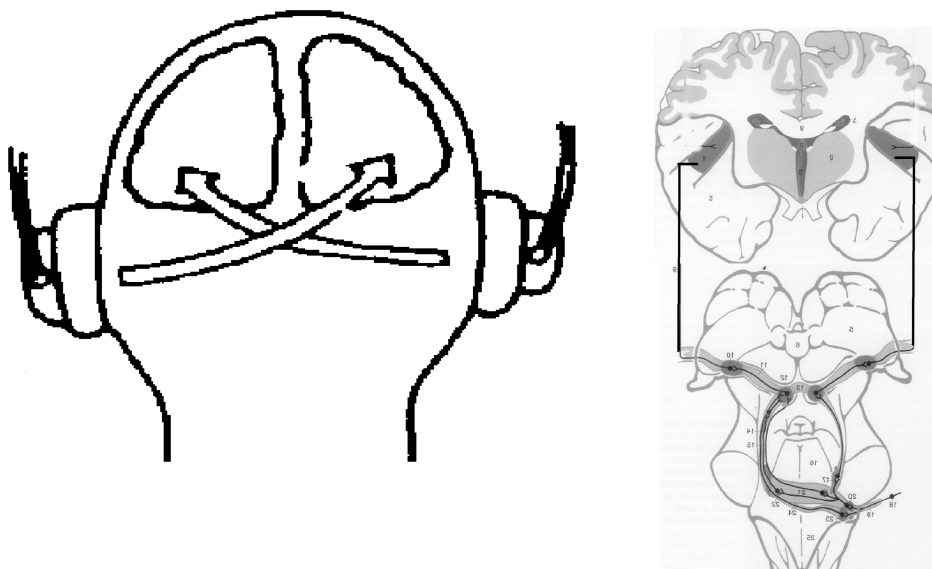


Figure 4. Basic outline of the dichotic listening situation. Dichotic presentation of the syllables /ba/ and /pa/. To the right is a schematic illustration of the auditory neural pathways from the inner ear to the Heschl's gyrus and *planum temporale* areas in the temporal lobe. The preponderance of the contralateral pathways will block the ipsilateral pathways. Thus, the right ear signal will primarily be projected to the left hemisphere, and the left ear signal will primarily be projected to the right hemisphere.

are two stimuli being presented on a trial (see Figure 4 for a schematic illustration of the dichotic listening situation).

If long series of CV-syllables are presented to the subject with the simple instruction to just report which sound they heard on each trial, one would expect that the results would, on average be equally from a left ear stimulus as for a right ear stimulus. This is, however, not what happens, typically there is a right-ear advantage (REA). According to Kimura,¹⁵ the REA is a consequence of the anatomy of the auditory projections from the cochlear nucleus in the ear to the primary auditory cortex in the temporal lobe, and of left hemisphere superiority for the processing of language related materials. The basic REA effect, as shown in Figure 5, was based on more than 1000 subjects, from the age of 8 to over 80, male and female, right- and left-handers.

The auditory system may conveniently be divided into five separate relay stations.^{16,17} An auditory stimulus activates neurons in the cochlear nucleus through the vestibulo-cochlear nerve, the ventral acoustic stria projects to the

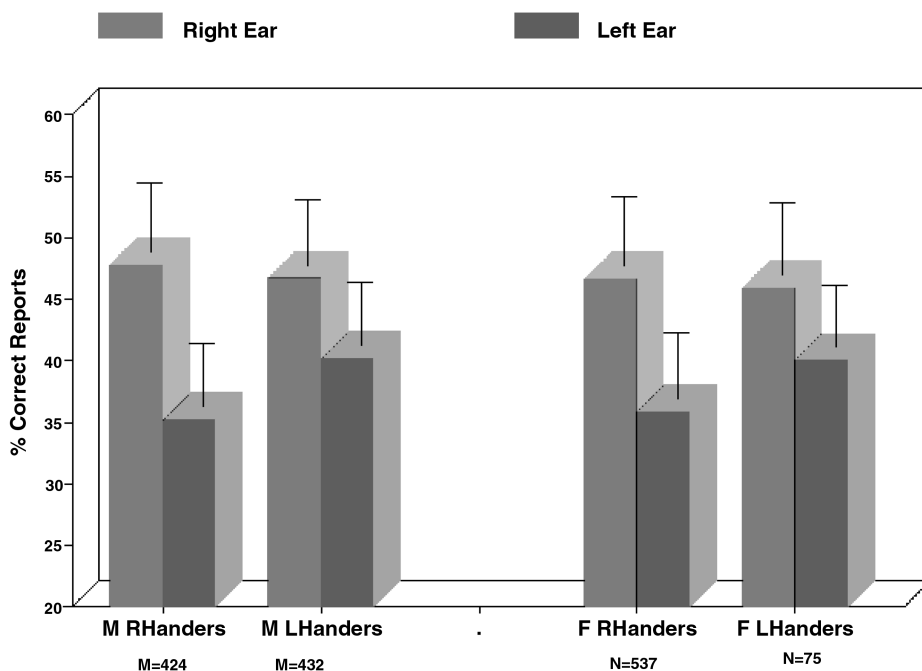


Figure 5. Percentage of correctly reported CV syllables presented in the right (light grey bars) and left (dark grey bars), separated for males (M) and females (F) and right-handers (RH) and left-handers (LH). The thin capped bars represent standard deviations for each group. The entire sample consists of over 1100 subjects. Note (a) the apparent right ear advantage (REA) in all groups, and (b) that the REA is reduced in the left-handed groups by the increase in correctly reported stimuli presented in the left ear for these groups.

second level, the superior olivary complex. From here, both inhibitory and excitatory impulses are projected within the lateral lemniscus to the dorsal and ventral nucleus of the lateral lemniscus, which make up the third-level relay station. Up to the level of the nuclei of the lateral lemniscus, the auditory system projects bilaterally. However, from the nuclei of the lateral lemniscus, projections are mainly contralateral, to the fourth relay station, the inferior colliculus in the tectum. The contralateral fibres innervate the medial geniculate body in the pulvinar thalamus, which is the fifth relay station, which sends axons to neurons in the auditory cortex in the posterior superior temporal gyrus.^{18,19} Thus, although auditory signals from one ear reach both auditory cortices in the temporal lobes, the contralateral projections are stronger and more preponderant. Although the input to the inferior colliculus follows ipsi- and contra-lateral pathways, the projection from the inferior colliculus is greater from the contralateral ear and will

favour representation of the contralateral ear in the auditory cortex (cf. Brodal¹⁶). The 'classic' model of dichotically produced brain asymmetry^{15,20,21} suggested that the REA is caused by several interacting factors. The auditory input to the contralateral hemisphere is more strongly represented in the brain, the left hemisphere (for right-handers) is specialized for language processing. Auditory information that is sent along the ipsilateral pathways is suppressed, or blocked, by the contralateral information and information that reaches the ipsilateral right hemisphere has to be transferred cross the corpus callosum to the left hemisphere language processing areas. Taking all of these steps together, the REA will thus reflect a left hemisphere language (speech) dominant hemisphere. This classic model was supported by the papers of Sparks and Geschwind,²⁰ and by Milner *et al.*²² These authors reported a complete, or near-complete extinction in the left ear channel in commissurotomy patients after dichotic presentations. The argument was that in order to report from the left ear, the signal had to travel from the right auditory cortex, via the corpus callosum, to the language dominant left region. Damage to the pathway anywhere along this route should consequently yield extinction of the left ear input. A similar argument was made that lesions in the left auditory region would produce a left ear extinction effect. By the same token, a left ear advantage (LEA) would typically indicate a right hemisphere processing dominance and a no ear advantage (NEA) would indicate a bilateral, or mixed, processing dominance. Unpublished data from our laboratory have shown that individuals with crossed laterality, i.e. crossed hand and eye preference, fail to demonstrate a significant REA in dichotic listening compared to individuals with non-crossed eye-hand laterality.

What is important when using the dichotic listening test is that any differences in hearing acuity between the ears in the subjects must be ruled out, as must differences in intensity or time deviations between the auditory channels. For these reasons, the stimuli are digitized and carefully sampled and analysed for simultaneous onset and equal sound intensity between the left and right channels before being played back to the subject. The subjects are also tested for differences between the ears in hearing acuity. A crucial question when both evaluating the classic structural model and when validating dichotic listening data is to what extent it can be shown that (a) dichotic listening correlates with other measures of brain laterality, and (b) it correlates with brain lesion data, that is, the extent to which dichotic listening performance can predict the side of lesion in brain damaged patients. Both of these questions will be addressed.

Wada-test validation

The standard validation procedure for dichotic listening has been the Wada-procedure²³ in epileptic patients undergoing surgery. The Wada test means that

a probe is placed into either the left or right femoral artery, and led up to the branching of the internal carotid artery into the middle and anterior cerebral arteries where a barbiturate (sodium amytal) is injected. This sedates the corresponding hemisphere for about 5–10 minutes, and the experimenter can then test for the presence of language (as well as other cognitive functions) in the sedated hemisphere. The procedure is replicated on the other hemisphere after a short resting period. In a recent study from our laboratory,²⁴ we compared dichotic listening performance in 13 subjects who had undergone Wada testing, knowing in advance on which side of the brain speech was located. All subjects had symptomatic epilepsy with partial seizures. The Wada-test results revealed that ten subjects had left hemisphere language, with three subjects having right hemisphere language. All three right hemisphere language subjects showed a left ear advantage (LEA) on the dichotic listening test, both pre- and post-operatively, with seven of the ten left hemisphere dominant subjects showing a right ear advantage (REA), pre-operatively, and eight postoperatively. Statistical discriminant analysis of dichotic listening performance led to correct classification according to the Wada-test results in 92.31% of all subjects. Thus, a quantitative classification procedure like discriminant analysis may be more sensitive when predicting hemisphere speech dominance from dichotic listening data than a qualitative procedure based on the ear advantage dichotomy, which typically has been used in the most other Wada-validation studies.

Brain imaging-validation

The Wada procedure has two disadvantages. First it is invasive, which means that only patients can be tested, no Wada tests are performed normal individuals. This leads to the second disadvantage, the experimenter is dealing with a damaged brain, which is compared with intact brains in healthy individuals. With the advent of the new haemodynamic imaging techniques of PET and fMRI²⁵ however, it is now possible to show localized changes in blood flow to a specific cognitive stimulus without using an invasive technique. The O¹⁵ PET technique was used by Hugdahl *et al.*²⁶ to monitor regional changes in blood flow to the left and right superior temporal gyrus and the *planum temporale* area in 12 healthy individuals. Blood flow change to both CV-syllables and short excerpts of musical instruments having the same duration and intensity as the CV-syllables was monitored. The procedure was slightly changed from the standard behavioural DL paradigm, one of the restrictions caused by the PET technique. The primary aim of the PET study was to record regional changes in the distribution of cerebral blood flow (CBF) to dichotically presented stimuli, to test the basic assumption of differential hemispheric involvement when stimuli presented to one ear dominates over that

presented to the other ear. All stimuli were 350 ms in duration with a 1000 ms inter-stimulus interval, and were presented in blocks of either CV-syllables or musical instruments pairs. Healthy subjects had to press a button whenever they detected a CV-syllable or a musical instrument target in a stream of CV- and musical instrument distractor stimuli. The CV-syllables and musical instruments target activated bilateral areas in the superior temporal gyri, mainly in the *planum temporale* area. However, there were significant interactions with regard to asymmetry of the magnitude of peak activation in the significant activation clusters. The CV-syllables resulted in greater neural activation in the left hemisphere while the musical instruments, resulted in greater neural activation in the right hemisphere. The changes in neural activation were closely mimicked by the performance data, which showed a right ear superiority in response accuracy for the CV-syllables, and a left ear superiority for the musical instruments. In addition to the temporal lobe activations, there were activation tendencies in the left inferior frontal lobe, right dorsolateral prefrontal cortex, left occipital lobe, and cerebellum. The PET data are seen in Figure 6. The PET results have later been confirmed in several fMRI studies from our laboratory.^{27,28}

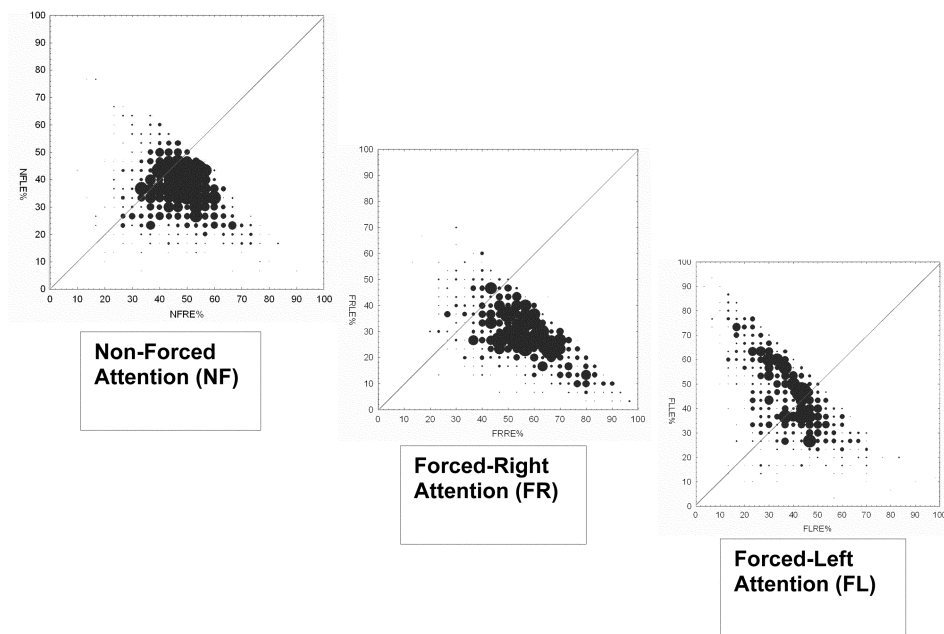


Figure 6. Mean percent correct reports from the right and left ears during divided attention (NF) and focused attention (FR and FL) with each individual plotted in the scatter plot. The diagonal line represents the 45-degree ‘symmetry line’, with individuals falling below the line showing a REA and individuals above the line showing a left ear advantage (LEA).

Bottom-up versus top-down information processing

A frequently used distinction in cognitive psychology and cognitive neuroscience is between bottom-up, or stimulus-driven information processing versus top-down, or instruction-driven information processing. Bottom-up means that the stream of processing is driven by the nature of the stimulus. Top-down means that the stream of processing is driven internally by the nature of the cognitive resources allocated to the task. Applied to hemisphere asymmetry, a bottom-up approach would mean that language stimuli would produce a left hemisphere response, while musical stimuli would produce a right hemisphere response.²⁹ A top-down approach would ask the question whether a bottom-up asymmetry effect could be modulated or switched through cognitive means. An example can clarify this. Suppose that the subjects in a dichotic listening experiment were instructed to pay attention and to report only from the right ear stimulus, ignoring anything they heard in the left ear. Would such an 'asymmetrical' allocation of cognitive resources in any way change the magnitude and/or the direction of the observed ear advantage? From a strict bottom-up perspective it should not affect the asymmetry or laterality effect caused by the phonetic characteristics of a CV-syllable. The REA would remain the same irrespective of attention directed towards the right or left ear. However, from a top-down perspective, allocation of attention to the right ear could be expected to increase the REA, while switching attention to the left ear could be expected to produce a smaller REA, or even a left ear advantage (LEA), despite the fact that the physical stimulus remains the same.^{3,30} From an ecological point of view, top-down modulation of a stimulus-driven laterality effect may have been instrumental for the evolution of language in humans. An example is the shifting of attention towards the speaker when we hear someone speaking to us. As soon as there are two or more sources speaking to us at the same time, speech perception would be chaotic if we did not have a 'filter' to zoom in on the relevant source and ignore the irrelevant source. There is no way the brain could sort out the different messages from different simultaneous sources merely from an analysis of the acoustic patterns of the sources. However, by switching attention between different persons talking to us at the same time, we can perfectly sort out who is saying what, without even moving our eyes or head towards the targeted source. Thus, an argument could be made that the development of certain cognitive abilities like attention and working memory may have been necessary precursors for the development of language and for the extraction of the phonetic code from an acoustic signal. We have tried to simulate the attention effect in speech perception by examining how the asymmetric ear advantage effect can be shifted between the right and left ears by instructing the subjects to focus attention, and report only from the right or left ears in the dichotic listening situation. The result is seen in Figure 6 (taken

Ref. 27). The data are plotted as scatter plots with percentage correct reports from the right ear along the ordinate, and percentage correct reports from the left ear along the abscissa, for the three attention conditions, non-forced, forced to the right ear, and forced to the left ear.

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interests are in brain asymmetry and laterality, both in basic and clinical research. He has contributed to the understanding of hemispheric asymmetry and language disorders in, for example, dyslexia, as well as contributing to studies of altered asymmetry in schizophrenia and other psychiatric disorders.

