NeuroImage 84 (2014) 962–970

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Mapping hemispheric symmetries, relative asymmetries, and absolute asymmetries underlying the auditory laterality effect

René Westerhausen [a,b,*], Kristiina Kompus [a], Kenneth Hugdahl [a,b,c]

[a] Department of Biological and Medical Psychology, University of Bergen, Norway
[b] Division of Psychiatry, Haukeland University Hospital, Bergen, Norway
[c] Department of Radiology, Haukeland University Hospital, Bergen, Norway

ARTICLE INFO

Article history:
Accepted 30 September 2013
Available online 10 October 2013

Keywords:
Dichotic listening
Hemispheric asymmetry
Speech perception
Planum temporale

ABSTRACT

Functional hemispheric differences for speech and language processing have been traditionally studied by using verbal dichotic-listening paradigms. The commonly observed right-ear preference for the report of dichotically presented syllables is taken to reflect the left hemispheric dominance for speech processing. However, the results of recent functional imaging studies also show that both hemispheres – not only the left – are engaged by dichotic listening, suggesting a more complex relationship between behavioral laterality and functional hemispheric activation asymmetries. In order to more closely examine the hemispheric differences underlying dichotic-listening performance, we report an analysis of functional magnetic resonance imaging (fMRI) data of 104 right-handed subjects, for the first time combining an interhemispheric difference and conjunction analysis. This approach allowed for a distinction of homotopic brain regions which showed symmetrical (i.e., brain region significantly activated in both hemispheres and no activation difference between the hemispheres), relative asymmetrical (i.e., activated in both hemispheres but significantly stronger in one than the other hemisphere), and absolute asymmetrical activation patterns (i.e., activated only in one hemisphere and this activation is significantly stronger than in the other hemisphere). Symmetrical activation was found in large clusters encompassing temporal, parietal, inferior frontal, and medial superior frontal regions. Relative and absolute left-ward asymmetries were found in the posterior superior temporal gyrus, located adjacent to symmetrically activated areas, and creating a lateral–medial gradient from symmetrical towards absolute asymmetrical activation within the peri-Sylvian region. Absolute leftward asymmetry was also found in the post-central and medial superior frontal gyri, while rightward asymmetries were found in middle temporal and middle frontal gyri. We conclude that dichotic listening engages a bihemispheric cortical network, showing a symmetrical and mostly leftward asymmetrical pattern. The here obtained functional (a)symmetry map might serve as a basis for future studies which – by studying the relevance of the here identified regions – clarify the relationship between behavioral laterality measures and hemispheric asymmetry.

Introduction

Functional differences between the two cerebral hemispheres represent a basic characteristic of the human brain (Hervé et al., 2013). In healthy participants these differences have been traditionally studied using behavioral paradigms which are constructed to selectively assess the processing abilities of each hemisphere. One of the most frequently used paradigms is dichotic listening, which is commonly used to behaviorally assess hemispheric asymmetries for speech and language processing (Bryden, 1963; Hugdahl, 2011; Kimura, 1961, 2011). The paradigm typically consists of the presentation of two slightly differing verbal stimuli (such as consonant–vowel syllables), whereby one stimulus is presented to the left ear and the other one is simultaneously presented to the right ear. Instructed to report the syllable that was perceived best, participants more often report the right- than the left-ear stimulus. This behavioral auditory laterality effect is widely accepted to be a non-invasive indicator of left-hemispheric dominance for speech and language processing (e.g., Della Penna et al., 2007; Kimura, 1967; Tervaniemi and Hugdahl, 2003; Toga and Thompson, 2003); an interpretation which has been validated in studies on patients with hemispheric or callosal lesions (e.g., Eslinger and Damasio, 1988; Hugdahl and Wester, 1992; Pollmann et al., 2002; Spierer et al., 2007) as well as in clinical studies using the invasive sodium-amytal procedure (e.g., Hugdahl et al., 1997; Kimura, 1961; Zatorre, 1989).

At the same time, functional neuroimaging studies in healthy participants also indicate that the task is more complex since both hemispheres are usually reported to be significantly activated when performing a dichotic-listening task. More specifically, bilateral frontal and temporal brain regions are found to be activated, irrespective of whether the dichotic-listening condition was contrasted with silence (e.g., Dos Santos Sequeira et al., 2010; Stefanatos et al., 2008; van den Noort et al., 2008), binaural verbal (e.g., Jäncke and Shah, 2002;

* Corresponding author at: University of Bergen, Department of Biological and Medical Psychology, Jonas Lies vei 91, 5009 Bergen, Norway.
E-mail address: rene.westerhausen@psybp.uib.no (R. Westerhausen).

1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.09.074

Lipschutz et al., 2002; Thomsen et al., 2004), or non-verbal control condition (e.g., Hugdahl et al., 1999). However, significant activation of both hemispheres does not exclude that one hemisphere is more strongly activated than the other, i.e. showing a relative asymmetrical activation pattern. To date, no study has systematically analyzed both symmetries as well as relative and absolute asymmetries in brain activation in response to the dichotic-listening paradigm. This would allow distinguishing between symmetrically engaged brain networks that possibly are responsible for processing of basic acoustic features of the stimulus and response execution, and asymmetrically engaged brain areas that are possibly responsible for the observed behavioral laterality effects.

Although functional imaging allows to directly assess hemispheric asymmetries (e.g., Badzakova-Trajkov et al., 2010; Josse et al., 2008; Kompus et al., 2011; Pujol et al., 1999; Westerhausen et al., 2006), some important issues need to be considered when conducting the asymmetry analysis. As pointed out frequently, demonstrating that a brain region in one hemisphere is significantly engaged while its contralateral counterpart is not, provides only insufficient evidence for hemispheric asymmetry (e.g., Friston, 2003; Liégeois et al., 2002; or for a more general discussion see Nieuwenhuis et al., 2011). Rather, it could be the case that the activation differences in both hemispheres are of more or less of same magnitude, but just above the statistical threshold in one hemisphere and just below the threshold in the other. Likewise, showing that both hemispheres are significantly activated does not exclude that there is an asymmetry in the magnitude of the activation between the hemispheres. Thus, a direct inter-hemispheric comparison of the activation is required in order to test for hemispheric asymmetries. Testing for inter-hemispheric differences alone ignores the level of activation within each hemisphere, and only when supplemented with further analyses, regions that show absolute and relative asymmetry, respectively, can be distinguished. Here, absolute asymmetry is defined as a significant inter-hemispheric difference together with the task-related contrast only being significant in one of the two compared regions. In case of a relative asymmetry both homologue regions show a significant effect but one is activated significantly stronger than the other (for overview see Table 1).

We report an analysis of a large-scale fMRI study on 104 participants, for the first time combining an interhemispheric asymmetry and conjunction analysis to assess symmetries as well as relative and absolute asymmetries during dichotic listening. For this purpose, the paradigm was implemented as closely matching to the standard version of the paradigm as it is typically used in behavioral laterality studies in many research laboratories and clinical units (Hugdahl, 2003; Hugdahl et al., 2009). This approach enabled us to study functional hemispheric symmetries and asymmetries that parallel behavioral auditory laterality measures.

Material and method

Participants

The sample consisted of 104 healthy, right-handed participants between 18 and 45 years old (mean: 28.5 ± 7.2 years), of whom 49 were females and 55 were males. The data of six additionally recruited left-handed subjects was excluded in order to increase the homogeneity of the sample, whereby handedness was verified with a Norwegian version of the Raczkowski's questionnaire (Raczkowski et al., 1974). All participants were native Norwegian speakers and had no psychiatric or neurological history. Furthermore, auditory testing was performed prior to inclusion to assure sufficient hearing acuity (i.e. an auditory threshold not higher than 20 dB and no inter-aural threshold difference of more than 15 dB, as assessed for test tones with the frequencies of 500, 1000, 2000, and 4000 Hz). The data collection took place between 2005 and 2010 at the University of Bergen, Norway, using the same experimental design and imaging protocol for all participants. Data from this database has been analyzed previously, however, focusing on the attentional modulation in the so called "forced attention" conditions of the paradigm (see below; Kompus et al., 2012) and sex differences (Hirnstein et al., 2013b) so the analysis reported here presents novel results. All participants gave written informed consent for participation.

Stimulus material, experimental paradigm, and procedure

The experimental procedure represents an fMRI-adaptation of the Bergen dichotic-listening test (Hugdahl, 2003; Hugdahl and Andersson, 1986; Hugdahl et al., 2009). A basic set of six consonant–vowel syllables (/ba/,/da/,/ga/,/pa/,/ta/, and/ka/) served as stimulus material, which were recordings of a native, male Norwegian speaker and were spoken with constant intensity and intonation. Mean stimulus duration ranged from 350 to 450 ms depending on the differences in the voice-onset time representing the distinction of voiced and unvoiced syllables. By combining (unidentical) syllables to stimulus pairs (e.g., /ba/ presented to the left and /da /presented to the right ear), 30 dichotic stimuli were created, whereby the two syllables of each pair were temporally aligned so that the initial energy release of the consonant segment coincided in the left- and right-ear channels.

Following an fMRI block-design, the paradigm consisted of nine task and nine (interleaved) rest blocks each containing ten presentations of dichotic stimulus pairs. During the first three blocks the participants were asked to report, after each stimulus presentation, which syllable they heard best or most clearly, a condition usually referred to as non-forced (NF) attention condition (Hugdahl and Andersson, 1986). In the remaining six blocks the subjects were instructed to selectively attend to one ear, and only report the syllable presented to the indicated ear. In three of the blocks the attentional focus was directed to the left, and in the other three to the right ear. Since for the present analysis we were only interested in the basic, "bottom-up" hemispheric asymmetry effect, only the data of the three NF blocks and the first three rest blocks was submitted for further analysis (for results regarding the forced attention conditions see Kompus et al., 2012).

After performing hearing test and filling out the questionnaires, and before entering the MR scanner, participants were required to perform five practice trials of the NF condition in order to familiarize them with stimulus material and experimental procedure. Inside the MR scanner, instructions were presented via goggles mounted onto the head-coil. The instructions consisted of a brief statement about what to do in the upcoming block, replaced after 2500 ms by a fixation cross. In case of the here relevant NF and rest blocks, the instruction was to report the syllable which was heard the best, or to relax, respectively. Stimulus administration and its synchronization with the MR image acquisition was controlled by E-Prime software. Stimulus presentation was done via headphones, and responses were given orally during a "silent gap" between two MR volume acquisitions created by the applied sparse-sampling imaging technique (see below). The responses were recorded with an mp3-recorder connected to an MR-compatible microphone. After the experiment, individual recordings were "offline" coded and the percentage of correctly reported syllables was determined separately for left- (LE) and right-ear (RE) stimuli. For further analyses a behavioral laterality index (LI) was calculated

Table 1
Possible outcomes of the combined inter-hemispheric difference and conjunction analysis.

		Inter-hemispheric difference analysis (LH ≠ RH)	
		Significant	Non-significant[a]
Inter-hemispheric conjunction analysis (LH ∩ RH)	Significant	Relative asymmetry	(Positive) symmetry
	Non-significant[a]	Absolute symmetry	Negative Symmetry

Note: LH/RH = left and right hemisphere, respectively.
[a] The conclusions are only warranted assuming that the "non-significant" comparison has sufficient power to interpret the null hypothesis (see text).