Speech dominance is a better predictor of functional brain asymmetry than handedness: A combined fMRI word generation and behavioral dichotic listening study

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Abstract

An unresolved issue in behavioral studies of hemispheric asymmetry is why both left-handers and right-handers show a right ear advantage at the group level. In the present study we screened left-handers for left- versus right-hemisphere speech dominance with fMRI by comparing right versus left hemisphere frontal lobe activity (in Broca's area) in a silent word generation task. A left hemisphere dominant right-handed control group was included as well. All participants took part in a dichotic listening task with consonant-vowel syllables. The results showed that left-handers and right-handers with left-hemisphere speech dominance showed a right ear advantage. However, the left-handers with right hemisphere speech dominance had a left ear advantage. Thus, at the group level the direction of the ear advantage in dichotic listening was predicted by language dominance but not by hand preference. At the individual level, the dichotic task we used showed more variability than the fMRI results. Further research will have to indicate whether this is a feature inherent to dichotic listening, or whether the variability is due to alternative explanations such as a more bilateral representation of speech perception compared to speech production.

Introduction

Hemispheric asymmetry is one of the fundamental principles of neuronal organization, with profound effects on motor, sensory, cognitive, and emotional processing (Hugdahl & Westerhausen, 2010). One of the most noticeable consequences of hemispheric asymmetry is handedness, with preference for right hand use in about 90-95% of the human population (Corballis, 2010; see also Annett, 2002; McManus, 2002). Another well-established finding is that about 95% of right-handers have language localized in the left hemisphere, as observed by using the sodium-amytal test (Wada & Rasmussen, 1960). This invasive test temporarily anaesthetizes one of the hemispheres. Then, speech production performance is evaluated for each hemisphere. A third fairly well established finding derived from haemodynamic neuroimaging (e.g., van den Noort, Specht, Rimol, Ersland & Hugdahl, 2008) and electrophysiology studies (e.g., Brancucci et al., 2004; 2005) is that the right ear advantage (REA) in dichotic listening is a marker of left hemisphere language dominance in right-handed individuals (see also Bryden, 1963; 1988; Kimura, 1961, 2011 for references to the original dichotic listening studies). In dichotic listening tasks, participants hear two auditory stimuli simultaneously, with one sound presented to each ear, and are asked to report which stimulus they heard first or best. Hugdahl, Carlsson, Uvebrant and Lundervold (1997) found that dichotic listening correctly identified 92% of right-handed patients as left-hemisphere dominant for language when the dichotic results were compared with a sodium-amytal investigation (see also Bethmann, Tempelmann, De Bleser, Scheich & Brechmann, 2007; who found similar percentages when using functional Magnetic Resonance Imaging [fMRI]).

Kimura (1967) suggested an anatomical model as explanation for the REA as a marker for left hemisphere language processing, or more precisely, as a marker for left temporal lobe speech sound perception (see also Pollmann, Maertens, von Cramon, Lepsien & Hugdahl, 2002; Pollmann, 2010). The model takes advantage of the preponderance of the contralateral auditory pathways from the ear to the brain. This favors the right ear in dichotic listening, because the independent, ipsilateral input from the left ear is blocked (see also Hari & Mäkelä, 1988; Pantev, Ross, Berg, Elbert & Rockstroh, 1998 for more recent validations of the anatomical model behind the REA). The Kimura (1967) model was further substantiated by anatomical studies which showed more grey matter volume in the left planum temporale area compared to the homologous right side area in about 70-80% of the population, albeit a weaker asymmetry for left-handers (Steinmetz, 1996). Given the strong correlation between scores on the dichotic listening task and performance on invasive sodium-amytal tests (or less invasive neuroimaging studies) in right-handers, and the observation that handedness is the most obvious sign of asymmetry of function (Corballis, 2010), it is surprising that dichotic listening does not distinguish right- from left-handers well when it comes to language asymmetry.

Data from the Bergen Dichotic Listening Database (see Hugdahl, 2003) reveal that both right- and left-handers across the entire life-span show a significant REA, with no significant difference between the groups (see e.g. Hirnstein, Westerhausen & Hugdahl, submitted; Hugdahl, 2003). The magnitude of the REA was somewhat reduced in left-handers, and the in-group variance was larger compared to right-handers, but the difference failed to reach significance despite the large number of participants involved (N > 1500). This is in line with the old dichotic listening studies where speech lateralization and not handedness seemed to be a better predictor of ear advantage in dichotic listening. For example, Bryden (1988) concluded from a review that

only 10 out of 18 studies found significant differences between right- and left-handers. Kimura (1961) similarly concluded that handedness was not a factor behind her dichotic listening results. In contrast, the reduced mean and greater variance did reach significance in the meta-analysis by Kim (1994), which means that precautions should be taken when drawing firm conclusions from the existing results. In addition, it should be noted that the results of Kimura (1961) and Bryden (1988), and the Kim (1994) analysis were based on studies published between 1965 and 1988, at a time when synchronization of stimulus onset between channels, and the overall quality of recordings and play-back equipment were crude and noisy, compared to current day technology. What may be of greater importance is that Sommer (2010) in a more recent meta-analysis of a total of 3,822 adults regarding sex and handedness differences (including dichotic listening studies) came to the same conclusion as Hugdahl (2003) that handedness did not lead to significant differences. The finding that both left- and right-handers show a REA in dichotic listening is surprising given that handedness has been used as an indirect measure of hemispheric functional asymmetries in previous studies (Corey, Hurley & Foundas, 2001; Jackson, 2008; McCormick, Witelson & Kingstone, 1990; Witelson & Nowakowski, 1991).

One solution to the puzzle could be that the number of left-handers with right-hemisphere dominance is too low to strongly affect the group mean. Traditionally, it has been assumed that 10 to maximally 30% of left-handers have right hemisphere language dominance (e.g. Knecht et al., 2000; Loring et al., 1990; Pujol, Deus, Losilla & Capdevila, 1999; Rasmussen & Milner, 1977; Van der Haegen, Cai, Seurinck & Brysbaert, 2011; Westerhausen et al., 2006). If the subgroup of left-handed students with clear right speech dominance is low and if the ear advantage of the other left-handers is comparable to that of right-handers, using handedness as an independent variable in studies of brain asymmetry would be of limited value (see Brysbaert,

1994, for a similar argumentation with respect to visual half-field [VHF] differences). To test this hypothesis, we compared groups of left-handers with known left and right hemisphere speech dominance to right-handers with left hemisphere speech dominance on a standard dichotic listening task. If the above reasoning is correct, we would expect no difference in ear advantage between left-dominant left-handers and right-handers, whereas there would be a clear difference with right-dominant left-handers (and right-dominant right-handers if we had been able to include them). Not including atypically lateralized subjects may have led to varying results in the past, because previous results could not determine whether weaker lateralization patterns were caused by deviating means and/or variances, or by smaller proportions of atypical laterality within the compared subgroups (McManus, 1983). Comparing sufficiently large samples of typically and atypically lateralized subjects was only made possible by investing heavily in the identification of the atypical group. We first screened 250 left-handers for atypical brain dominance by using behavioral picture and word naming VHF tasks (Van der Haegen et al., 2011; see also Van der Haegen, Cai & Brysbaert, 2012). Fifty of them were selected to take part in an fMRI silent word generation task (see also Hunter & Brysbaert, 2008; Knecht et al., 2000; Pujol et al., 1999). More specifically, we calculated a laterality index score on the basis of the fMRI brain activity in pars opercularis/BA44 and pars triangularis/BA45, known as Broca's area. A previous comparison with the WADA test has established the validity of the word generation task for speech dominance (Adcock, Wise, Oxbury, Oxbury & Matthews, 2003).

We asked all subjects who had participated in the study of Van der Haegen et al. (2011) to come back to the laboratory for a second time and undergo a dichotic listening test. A few extra left-handed subjects were added to the sample, together with a right-handed sample. These were assumed (and verified) to be left dominant.

Method

Participants

Fifty left-handed participants from the Van der Haegen et al. (2011) fMRI screening study were invited to come back for a second test. Thirty-one of the 50 left-handers (17 left-dominant, 14 right-dominant) were willing to take part in the current dichotic listening study. Ten more left-handers were recruited to enlarge the sample to a total of 41 participants (32 females and 9 males). Mean age was 21.0 years, ranging from 18 to 32 years, SD: 2.9. In addition, 22 right-handers (17 females, 5 males; mean age: 21.7 years, ranging from 18 to 31 years, SD: 2.8) were recruited and scanned. Thus, the total number of participants that had been fMRI screened for hemispheric asymmetry for language was 63. The participants' lateral preferences were verified with the Edinburgh Handedness Inventory (Oldfield, 1971) and the questionnaire of Porac and Coren (1981) assessing eyedness, earedness and footedness. Scales ranged from -3 to -1 in case of left side preference, and from +1 to +3 in case of right side preference. Classifying a participant as left- or right-handed was based on their preference for writing and drawing only. If other actions were performed by the non-dominant hand (e.g. using scissors) the participant was not excluded to ensure large variability. The participants' mean questionnaire scores can be found in the Supplementary Materials. All participants declared to have normal or corrected-to-normal vision and no hearing impairments. Their native language was Dutch.

For the dichotic listening task, the fMRI-screened participants were divided into three groups according to handedness (as determined by the handedness questionnaire) and language dominance (as determined by the fMRI silent word generation task, see below). The three groups were: 25 left hemisphere dominant left-handers (LD_LHa; 19 females, 6 males; mean age: 20.7

years, SD: 2.9; mean handedness score: -2.2, SD: 1.1); 22 left hemisphere dominant right-handers (LD_RHa; 17 females, 5 males; mean age: 21.7 years, SD: 2.8; mean handedness score: 2.7, SD: 0.3), and 16 right hemisphere dominant left-handers (RD_LHa; 13 females, 3 males; Mean age: 21.5 years, SD: 2.9; mean handedness score: -2.4, SD: 0.8).

All participants fulfilled the conditions to be scanned and signed an informed consent form according to the guidelines of the Ethics Committee of the Ghent University Hospital.

fMRI silent word generation task

The silent word generation task used for the fMRI screening consisted of a standardized paradigm used in other studies to determine language dominance (e.g., Abbott, Waites, Lillywhite & Jackson, 2010; Badzakova-Trajkov, Haberling, Roberts & Corballis, 2010; Hunter & Brysbaert, 2008; Knecht et al., 1996). In this task, 10 different letters (b, d, k, l, m, n, p, r, s or t) are presented during 10 blocks of 15s duration for each block. Participants are asked to mentally generate as many words as possible beginning with the presented letter in 15 seconds. Neuronal activation during these 15s experimental blocks is contrasted with the corresponding activation during control blocks in which the Dutch non-word *baba* appears on the screen. Participants are then asked to mentally repeat the non-word during ten blocks of 15s. Experimental and control blocks were alternated with 20 more rest blocks of 15s each, indicated by a horizontal line at the screen center.

MR images were acquired on a 3-Tesla Siemens Trio MRI scanner (Siemens Medical Systems, Erlangen, Germany) with an 8-channel radiofrequency head coil. A high –resolution anatomical image was obtained using a T1-weighted 3D MPRAGE sequence (TR = 1550 ms, TE

= 2.39 ms, image matrix = 256 × 256, FOV = 220 mm, flip angle = 9°, voxel size = 0.9 × 0.9 ×

0.9 mm^3). Functional images were acquired using a T2*-weighted gradient-echo EPI sequence.

Forty axial slices covered the whole brain (TR = 2630 ms, TE = 35 ms, image matrix = 64 * 64,

FOV = 224 mm, flip angle = 80°, slice thickness = 3.0 mm, distance factor = 17%, voxel size =

3.5 * 3.5 * 3 mm^3). Analysis of the fMRI silent word generation data was performed using the

SPM5 software (Wellcome Trust Centre for Neuroimaging, London, UK). The first four acquired

image volumes were discarded in order to obtain a magnetic equilibrium. Data pre-processing

included the following steps: (1) slice time correction to correct for the interleaved image

acquisition; (2) realignment using rigid body transformations to correct for movement artifacts;

(3) co-registration of the anatomical image to mean functional image; (4) normalization to the

Montreal Neurological Institute (MNI) T1 template; and (5) spatial smoothing with an isotropic 8

mm full width at half-maximum Gaussian Kernel. Data were analyzed by using a boxcar function

convolved with a haemodynamic reponse function (Friston, Jezzard & Turner, 1994) in a general

linear model (GLM). Experimental word generation blocks were contrasted against control non-

word repetition blocks.

Lateralization indices (LIs) were calculated for the fMRI data on the basis of the brain

activation in the pars opercularis (approximately Brodmann Area, [BA] 44) and the pars

triangularis (approximately BA 45) according to the AAL template (Tzourio-Mazoyer et al.,

2002). Together, these regions are generally considered as Broca's area. We used the LI toolbox

1.02 provided by Wilke and Lidzba (2007) to obtain robust LIs that are not contaminated by

statistical voxel outliers (see also Seghier, 2008 for methodological considerations when

calculating LIs). In brief, 20 equally sized steps from 0 to the maximum t-value were taken as

thresholds in both the left and right hemispheric BA 44 and BA 45. A hundred resamples were generated at each level by a bootstrapping mechanism (resample ratio k = 0.25). The central 50% of the 10,000 possible LI combinations were then used to calculate a weighted mean LI with a higher weight assigned to higher thresholds. The LI thus reflects a normalized difference of activated voxels in left and right Broca's area. More details can be found in Wilke and Schmithorst (2006) and Van der Haegen et al. (2011). The resulting fMRI LI ranged from -1 (complete right lateralization) to +1 (complete left lateralization). We used 0.60 as an absolute cut-off LI value and the factor handedness to classify our participants into the three groups described above.

The 25 left-handed participants belonging to the LD_LHa group all had an LI value above the cut-off value +.60 (Range: 0.60 – 0.91, Mean: 0.77, SD: 0.09); (2) The 22 right-handed participants forming the LD_RHa group also all had LI above +0.60 (Range: 0.64 – 0.95, Mean: 0.81, SD: 0.10); (3) The remaining 16 left-handed participants from the RD_LHa group showed atypical right language dominance with LI values below -0.60 (Range: -0.62 – -0.93, Mean: -0.81, SD: 0.11)[1]. Thus, the lateralization of the groups clearly differed in direction of asymmetry, but not in degree of lateralization [$F(2,60) = 1.19$, $p = .31$, partial $\eta^2 = 0.04$, based on the absolute LI values].

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[1] None of the scanned right-handers had an LI below -0.60; We did not recruit right-dominant right-handers given the very low incidence of this group in the population (Knecht et al., 2000). Also note that we did not include subjects with a bilateral activation pattern in fMRI (LIs between -0.60 and +0.60) in the current study in order to disentangle handedness and speech dominance in the DL performances in clearly lateralized subjects.

**Dichotic listening (DL) speech perception task**

The DL task followed the standard procedure used at the University of Bergen, Norway (e.g., Hugdahl, 2003). CV syllables consisted of one of the six stop consonants /b/, /d/, /g/, /p/, /t/ or /k/, combined with the vowel /a/. Thirty-six stimulus-pairs such as /ba/-/da/, /ga/-/pa/, etc., were formed whereby one of the syllables was presented to the right, and the other one simultaneously to the left ear. Thirty of the 36 stimulus pairs were dichotic, i.e. the syllable presented to the right and left ear were different, and served as basis for the laterality analysis. The 6 homonym pairs were used to confirm that the subject was able to discriminate the syllables. The stimuli were recorded by a male native Dutch speaker. Each pair was temporally aligned to ensure equal onset of the vocalization of the initial consonant.

The length of the CV syllable-pairs was around 350 ms, and they were presented with an inter-stimulus interval of 4000 ms. Participants were asked to listen to the sounds and to report the syllable they heard best, first, or most clearly. The participants were told that it could seem as if there were two sounds at the same time, but that they could only give one response at each trial. Stimuli were presented through headphones by means of the E-Prime 2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA). The percentage of correctly identified left- and right-ear syllables was recorded and used as dependent variable in the statistical analysis

Analysis of the dichotic listening data consisted of comparing the response accuracies to stimuli presented in the right and the left ear, respectively. The DL scores were subjected to a factorial analysis of variance (ANOVA) with the between subjects factor Laterality Groups (three levels, LD_LHa, LD_RHa, and RD_LHa) and the within subject factor Ear of presentation (left/right). In order to compare the absolute magnitude of the ear advantages in the three groups,

a one-way ANOVA was performed based on the absolute DL laterality index scores, disregarding the direction of the ear advantage (right [REA] or left ear advantage [LEA]). The DL scores were converted to a similar laterality index score as for the fMRI data based on the formula: (RE-LE)*100/(RE+LE) (Hugdahl & Andersson, 1986) where RE = correct right ear reports, LE = correct left ear reports.

Figure 1 shows a scatter-plot of the fMRI and DL individual values.
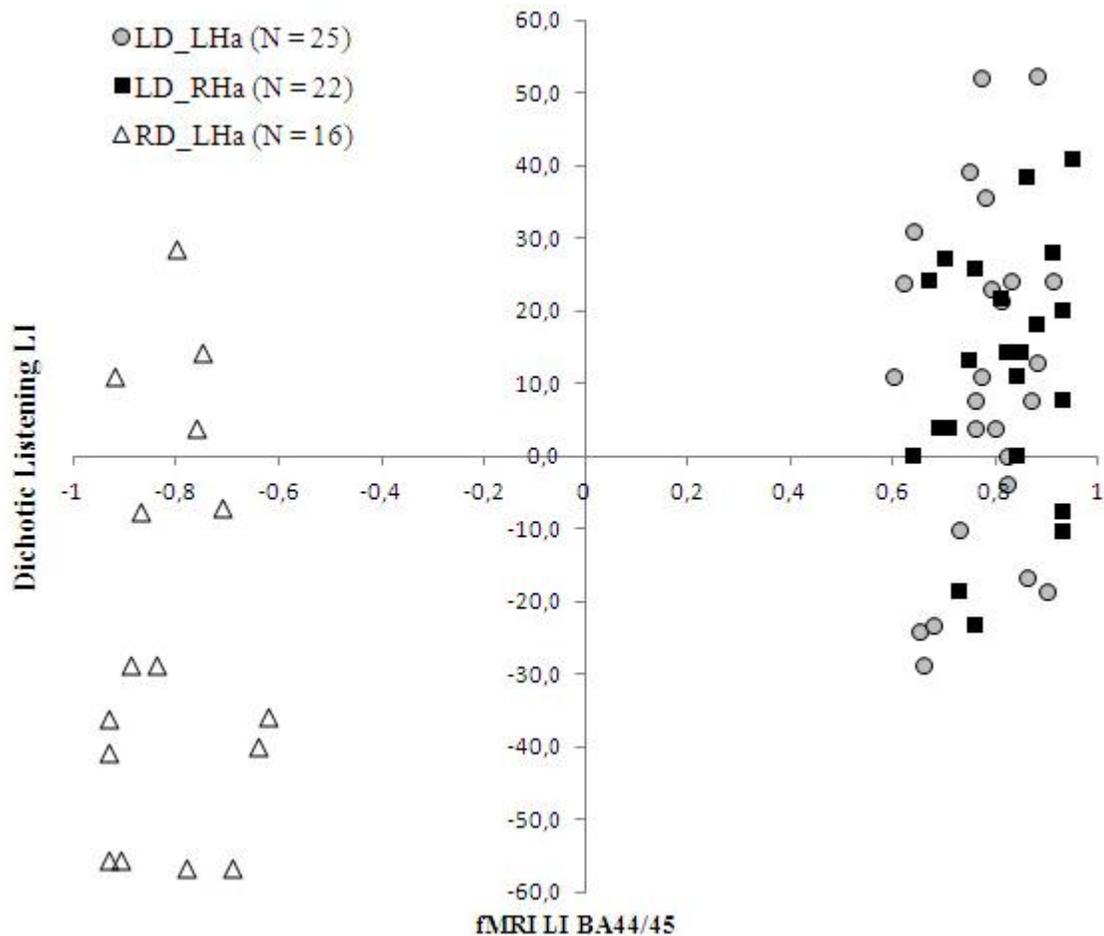
Figure 1. Comparison of individual laterality indices (LIs) calculated from activity in Brodmann area's 44 and 45 in the fMRI silent word generation task (x-axis) and percentage difference score between the two ears in the dichotic listening task (y-axis).

Results

A repeated measures ANOVA based on the DL scores showed a statistically significant interaction between laterality group and ear [$F(2,60) = 14.14$, $p < .001$, partial $\eta^2 = 0.32$]. Pairwise comparisons revealed a statistically significant REA for both the LD_LHa [$t(24) = 2.24$, $p < .05$] and the LD_RHa group [$t(21) = 3.12$, $p < .01$], and a significant LEA (meaning more correct reports from the left ear) for the RD_LHa group [$t(15) = -3.40$, $p < .01$]. There was no significant main effect of ear [$F < 1$], indicating that there was no overall ear advantage when averaging over the three groups. The main effect of laterality group was also not significant [$F < 1$], indicating that the groups did not differ in overall level of accuracy. Figure 2 shows the mean percentages of correctly reported syllables in the DL task.

	LD_LHa	LD_RHa	RD_LHa
Left Ear	32,2	32,3	44,8
Right Ear	39,4	40,5	27,8
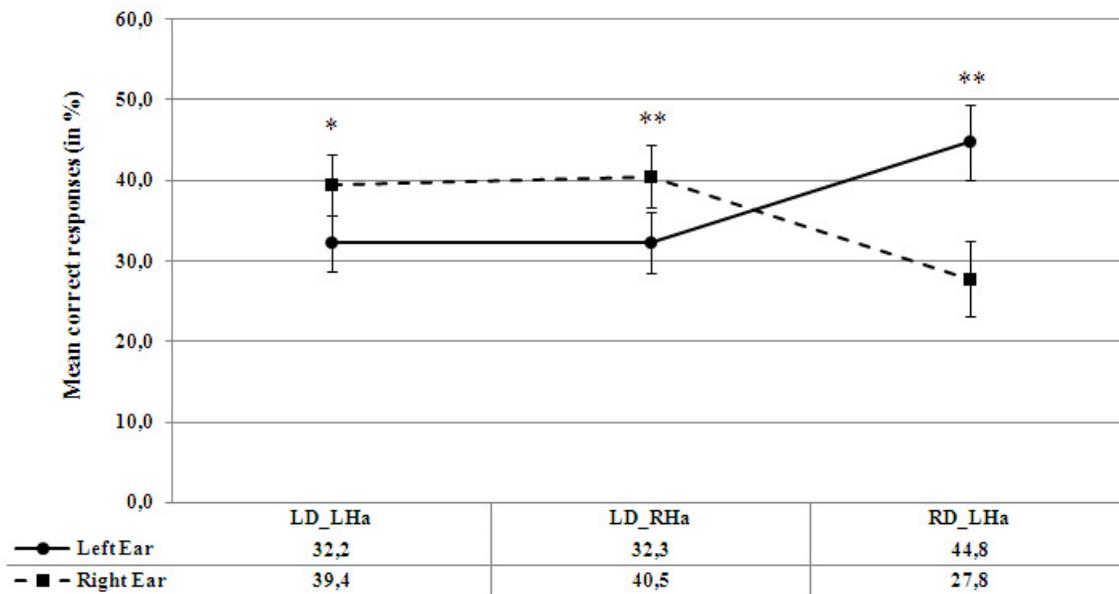
Figure 2. Percentage correct responses and 95% confidence intervals for the left and right ear dichotic listening scores, observed for the left lateralized left-handers (LD_LHa), left lateralized right-handers (LD_RHa) and right lateralized left-handers (RD_LHa). * = $p < .05$; ** = $p < .01$

Figure 2 indicates that the REA is equivalent for the two left hemisphere dominant groups, but that the LEA in the right hemisphere dominant group is about twice the magnitude (disregarding the direction of the ear advantage) of the REA in the other two groups.   At the same time, the variability in the left-handed groups was larger, in particular for the RD group (Mean ± SD in DL LI scores: LD_RHa = 11.52 ± 17.0, LD_LHa = 10.43 ± 22.8, RD_LHa = -24.41 ± 28.0). To assess whether the LEA in the RD_LHa group was significantly larger than the REA in the two LD groups, we ran a one-way ANOVA with the reversed LI values for the RD_LHa group (i.e. their values were multiplied by -1 to make them comparable to the LH dominants while keeping the variability present in the group). The ANOVA did not return a significant difference between the groups [$F(2,60) = 2.16$, $p = .12$, partial $\eta^2 = 0.07$], suggesting that the apparent, larger LEA for the RD_LHa group could be due to chance. The RD_LHa group did not differ significantly from the LD_LHa [$t(39) = -1.75$, $p = .09$] or the LD_RHa group [$t(22.9) = -1.64$, $p = .12$].

Discussion

The aim of the present study was to use a fMRI silent word generation task to classify left-handers into left and right hemisphere speech dominant sub-groups, in addition to a right-handed left hemisphere speech dominant group and to use this classification to compare the three groups on a non-invasive behavioral measure of hemispheric asymmetry, as obtained with dichotic listening. The expectation was that the right-handed group would show a statistically significant right ear advantage (REA), i.e. more correct reports from the right ear, with the same outcome for the left-handed left hemisphere dominant sub-group, while the right hemisphere dominant subgroup would show a statistically significant left ear advantage (LEA).

The results, shown in Figure 2, confirmed the predictions, with statistically significant REAs for the right-handed and left-handed left hemisphere dominant groups, and a LEA for the right hemisphere dominant left-handed group. Handedness did not influence the ear advantage within the LH dominants; The DL results only changed significantly when speech dominance shifted to the right hemisphere. Thus, the results confirmed that not taking into account language dominance is the most likely explanation why previously dichotic listening studies did not find significant differences with regard to the overall direction of the ear advantage between right- and left-handers (e.g. Hugdahl 2003; Jäncke, 1992; Jäncke & Shah, 2002; Peters & McGrory, 1987, see also McManus, 1983, who already stated than not only means and variances should be taken into account, but also the proportion of sub-types). . If more dichotic listening studies include atypically lateralized subjects in their sample, it would be interesting for future research to model how many subjects should be included to obtain a significant effect of language dominance.

The present results show that splitting the left-handers into left- and right hemisphere dominant subgroups reveals different directions of the ear advantage. As such, the present findings support the conclusion reached by Kimura in her 1983 study of aphasia incidence in left- and right-handed stroke patients. After reviewing the data from a large sample of patients she concluded that aphasia after left hemisphere stroke was no less observed in left- than in right-handers, and that *"on the whole, the findings suggest a negligible role of the right-hemisphere in speech function in most left-handers who do not have early left-hemisphere damage"* (p. 147). Moreover, the present results are in agreement with invasive studies using the sodium-amytal procedure which have shown that about 92-95% of right-handers with left-hemisphere language also have a REA on the dichotic listening task (e.g. Hugdahl et al., 1997).

Our data indicate that handedness cannot be considered as a parameter in itself that will affect measures of laterality, but that it requires a further sub-classification according to functional laterality measures (see also Brysbaert, 1994). Previous laterality studies also illustrate the need to differentiate sub-groups of left-handers. Vingerhoets et al. (2012, in press) for example, could relate the lateralization of tool use to speech dominance but not to handedness. They only observed marginal differences between the cortical activation pattern of left- and right-handers during a tool use pantomiming task (i.e. most LH activity in dorsolateral prefrontal, premotor and posterior parietal regions, but reduced LH activity for left-handers in the parietal lobule), but a completely reversed pattern when comparing LH and RH speech dominant left-handers (i.e. the ventral and dorsal premotor cortex, dorsolateral prefrontal cortex, posterior parietal cortex and supplementary motor area were lateralized to the same side in a word generation and tool use task). The coherence between speech and praxis lateralization would have been masked if the left-handers had consisted of an unselected group with predominantly left language dominance. The differentiation of sub-groups of left-handers with left versus right hemisphere language dominance could also explain the divergent findings of previous laterality studies such as the structural asymmetry of the planum temporale area in the superior temporal gyrus. While some studies have reported reduced leftward asymmetry of the planum temporale area in left-handers (Steinmetz, Volkmann, Jäncke & Freund, 1991), others have failed to find a reduction of the asymmetry in adextrals (Foundas, Leonard & Hanna-Pladdy, 2002). Including handedness as an indirect measure of functional language lateralization has led to inconsistent results in this research field: The asymmetry was probably reduced in a sample of left-handers with a larger proportion of right hemisphere speech dominant individuals, while it was equal or nearly equal to the asymmetry seen in right-handers in a sample with a larger proportion of left

hemisphere speech dominant individuals. Research about the influence of an asymmetrical planum temporale on language lateralization was further complicated by unclear definitions of the anatomical borders of the area (Jansen et al., 2010).

A look at Figure 2 suggests that the LEA in the right dominant group is almost twice as large as the REA in the right-handed and the left-handed left-hemisphere dominant groups. At the same time, the variability in this group is larger. Because the difference was not significant in an ANOVA with reversed scores for the right dominant group, at present there is no need to interpret it, although it may be interesting to keep it into account in case it would be replicated in future studies.

The association between the laterality index in a speech production task (silent word generation) and the laterality index in a speech perception task (dichotic listening) further testifies to the tendency of both functions to be co-lateralized (see Cai, Lavidor, Brysbaert, Paulignan & Nazir, 2008; Cai, Paulignan, Brysbaert, Ibarrola & Nazir, 2010; Van der Haegen et al., 2011 for similar findings with the VHF task). This makes sense, as one cannot easily imagine an evolutionary advantage in having language perception in one hemisphere and language production in the other hemisphere. Efficient language production without equally efficient language perception would put the organism at a disadvantage when it comes to communication with others. Having both functions in the same hemisphere reduces time costs that would be created if information has to be transferred for the integration of production and perception processes. We would therefore like to argue that by having shown that laterality for language perception follows laterality for language production in both left- and right-handers strengthens the evolutionary explanation of hemispheric asymmetry.

At the same time the association between dichotic listening and speech laterality is far from perfect, as can be seen in Figure 1. Even though the DL task is quite effective at the group level, there is quite some variability at the individual level, since DL and fMRI correlated moderately and classifications were correct for only 77% of the participants with an absolute DL LI-value above 10. There could be several explanations for this imperfect correlation. First, speech perception, or more specifically phoneme recognition, may be less lateralized than speech production and may therefore produce more individual variability (see Van der Haegen et al., 2011, for comparable findings with the VHF task). Note that variability for speech production was reduced in our sample as participants were first selected on the basis of a clear positive or negative speech LI. We did not identify a sufficiently large sample with bilateral speech production LIs (i.e. values between -0.60 and +0.60) to investigate what happens with speech perception if production, generally known as the most lateralized human function (Kosslyn, 1987), is not clearly dominated by one hemisphere. In contrast, performance on the DL task was not used as a selection criterion making the range of possible outcomes wider.

A second possible reason why speech production and perception do not perfectly co-lateralize is that our DL task did not include enough trials to have reliable data at the individual level. Speaks, Niccum and Carney (1982) found a split-half reliability of +0.90 when the LI was based on six runs of 30 CV-syllable pairs rather than the 36 trials included in our task. On the other hand, Voyer (1998) reported reliability coefficients of up to +0.91 in his overall review of dichotic CV-syllable paradigms.

Finally, a minority of the population may have crossed fronto-temporal lateralization patterns, similar to the finding reported by Van der Haegen et al. (2012) who found 3/55 cases

with speech production and word reading in opposite hemispheres. Given the larger variability in the left-handed groups, such crossed pattern may be more prevalent in these people than in their right-handed peers. This seems to be particularly true for the participants with atypical right hemisphere frontal speech dominance. It would be interesting to have a look at what consequences crossed lateralization patterns have on language processing. In the current study, 4/16 RH speech production dominants were LH dominant for speech perception, whereas 11/47 LH speech production dominants showed the reversed pattern (with three more subjects showing no clear ear advantage). We predict that they would be slower at tasks involving both speech production and perception (e.g. translating a spoken text as an interpreter) than participants processing both functions in the same hemisphere (i.e. when controlling for other confounding cognitive abilities).

In summary and conclusion, the present study has shown that left-handed individuals who have language in the right hemisphere differ on a dichotic listening task from their handedness peers who have language in the left hemisphere, and from right-handers who have language in the left hemisphere. Hemispheric asymmetry for language was determined by analyzing brain activation to a silent word generation fMRI task. The dichotic listening task was then applied, and correct scores from the right and left ear were calculated and subjected to an analysis of variance. It is concluded that studies of cerebral organization in right- and left-handers should take into account that only a small proportion of left-handers are right hemisphere speech dominant, considerably reducing the power of the design.

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