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Investigating heritability of laterality and cognitive control in speech perception

Sebastian Ocklenburg [a,*], Felix Ströckens [a], Josef J. Bless [b], Kenneth Hugdahl [b,d], René Westerhausen [c], Martina Manns [a]

[a] Institute of Cognitive Neuroscience, Biopsychology, Ruhr-University Bochum, Germany
[b] Department of Biological and Medical Psychology, University of Bergen, Norway
[c] Department of Psychology, University of Oslo, Oslo, Norway
[d] NORMENT Center of Excellence, University of Bergen, Norway

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ABSTRACT

Several studies analyzing the ontogenetic origin of cerebral lateralization provide evidences for a genetic foundation of handedness in humans that is modulated by environmental influences. Since other forms of behavioral lateralization are less investigated, it is unclear as to how far different functions display similar heritability. But deeper knowledge is necessary to understand if and how developmental coupling of different functions is based on a shared genetic background or on the impact of environmental influences. Here, we investigated the heritability of language lateralization assessed with the dichotic listening task, as well as the heritability of cognitive control processes modulating performance in this task. Overall, 103 families consisting of both parents and offspring were tested with the non-forced, as well as the forced-right and forced-left condition of the forced attention dichotic listening task, implemented in the iDichotic smartphone app, developed at the University of Bergen, Norway. The results indicate that the typical right ear advantage in the dichotic listening task shows weak and non-significant heritability ($h^2 = 0.003$; $p = 0.98$). In contrast, cognitive factors, like attention focus (forced right condition: $h^2 = 0.36$; $p < 0.01$; forced left condition: $h^2 = 0.28$; $p < 0.05$) and cognitive control (Gain forced right: $h^2 = 0.39$; $p < 0.01$; Gain forced left: $h^2 = 0.49$; $p < 0.01$) showed stronger and significant heritability. These findings indicate a variable dependence of different aspects of a cognitive function on heritability and implicate a major contribution of non-genetic influences to individual language lateralization.

1. Introduction

One of the most controversial topics in laterality research is the question, to what extent functional hemispheric asymmetries are heritable (Collins, 1975; Francks et al., 2007; McManus, Davison, & Armour, 2013; Ocklenburg, Beste, Arning, Peterburs, & Güntürkün, 2014; Ocklenburg, Beste, & Güntürkün, 2013; Rentería, 2012). For handedness, evidence from adoption (Carter-Saltzman, 1980) and twin studies (Ooki, 2014) convincingly suggests that it is at least partly controlled by genetic factors. Interestingly, different aspects of handedness seem to have differential heritability, since Lien, Chen, Hsiao, and Tsuang (2015) found that degree of handedness showed higher heritability than a hand-preference index and direction of handedness. This suggests that different functional neuronal systems are involved in determining these aspects, all of them having their own gene-dependent pattern. To this respect, it would be useful to compare heritability of handedness with other lateralized functions to understand which aspects are most likely under genetic control and which are influenced by environmental factors. A shared genetic background may cause developmental coupling of different lateralized functions. Unfortunately, for all other forms of laterality (such as lateralization of language, emotion or spatial abilities), experimental evidence supporting or disproving a relation of children's and parent's left-right preferences is extremely scarce.

As a rare exception, Bryden (1975) published a study in which he used the dichotic listening task to investigate how language lateralization runs in families. Familial correlations in 49 families revealed somewhat puzzling results. While there was a significant positive correlation between the dichotic listening lateralization quotient (LQ) of mothers and offspring, no such relation was found

* Corresponding author at: Ruhr-Universität Bochum, Fakultät für Psychologie, Institut für Kognitive Neurowissenschaft, Abteilung Biopsychologie, Universitätsstraße 150, 44780 Bochum, Germany.

E-mail address: sebastian.ocklenburg@rub.de (S. Ocklenburg).

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between the LQs of fathers and offspring. Moreover, there was a stronger LQ correlation between the mother and father than between any parent and child, which is somewhat inexplicable. Also, there was a significant negative correlation between siblings, which would argue against genetic control of the trait. Bryden (1975) concluded that his dataset was too small to allow for definitive conclusions about the heritability of the trait and that further research on the topic was warranted. Unfortunately, in the decades after the publication of this paper no one followed up on this suggestion, with the exception of Somers et al. (2015) who recently performed a genetic linkage study in 355 subjects from 37 families. The estimated heritability of language lateralization measured with functional transcranial Doppler sonography during speech production was 31%, indicating moderate heritability of the trait. One factor that could explain the somewhat stronger heritability in the Somers et al. (2015) study compared to Bryden's (1975) work is the fact that Somers et al. (2015) investigated speech production, while the dichotic listening task used by Bryden (1975) targets speech perception. Moreover, performance in the dichotic listening task is not a 100% 'pure' measure of language lateralization. For example, Westerhausen, Passow, and Kompus (2013) showed that speech-related cognitive processes impact non-forced dichotic listening. One way of experimentally assessing the role of cognitive processes in the dichotic listening task is the forced-attention version (Hugdahl & Andersson, 1986; Hugdahl et al., 2009; Kompus et al., 2012). This version of the paradigm also includes two so called forced-attention conditions, one in which the subject is instructed to only attend to input from the left ear ('forced-left', FL) and one in which the subject is instructed to only attend to input from the right ear ('forced-right', FR), in addition to the classic, so called non-forced, NF condition with no instruction about attention focus. As suggested by Hugdahl et al. (2009), the FR condition taps the ability to shift attention when the bottom-up, non-instructed, and top-down, instructed processing strategies work synergistically, while the FL condition taps the ability for cognitive control, since the bottom-up and the top-down processing strategies are antagonistic, and induce a cognitive conflict situation. The forced-attention version of the task has recently been implemented in a smartphone app named 'iDichotic' (Bless et al., 2013, 2015), allowing for easier access to large samples of participants outside of traditional laboratory setting. Bless et al. (2013) recently evaluated the retest reliability and concurrent validity of this app under controlled laboratory settings, finding both reliability (intraclass correlation coefficient r_{ICC}: 0.78) and validity (r_{ICC}: 0.76–0.82) to be high. Moreover, these authors explored the ecological validity of the iDichotic app by releasing the app to the iTunes App Store and collecting data from the general public. Comparable to the laboratory version of the Dichotic listening paradigm, they found a significant right ear advantage. Based on these findings, Bless et al. (2013) concluded that the iDichotic app presents a valid and reliable method for administering the dichotic listening paradigm.

In the present study, this app was used to test families (parents and offspring) in their homes in order to disentangle heritability and cognitive factors from performance on the dichotic listening task.

2. Materials and methods

2.1. Participants

Overall, we tested 103 families consisting of one offspring, one mother and one father. All parents were biological, not adoptive parents, as evidenced by self-report. Offspring were mostly university students. All participants were fluent German speakers and indicated that they were neurologically and psychiatrically healthy adults. Mean age of the offspring group was 25.97 years (SD: 8.10), mean age of the mothers was 53.86 years (SD: 7.52) and mean age of fathers was 56.59 years (SD: 7.30). Within the offspring group, 60 participants were female (58%) and 43 participants were male (42%). As a pretest, all prospective participants were instructed to take a simple hearing test administered within the iDichotic app (Bless et al., 2013, 2015). In this pretest, participants listen to a continuous pure tone of 1000 Hz and are asked to reduce the sound level by sliding a bar on the iPhone display to the left until they are unable to hear the sound. The sound level when the participants cannot longer hear the tone is stored. Only participants with normal hearing capabilities and no more than 20% hearing difference between the ears were included in the sample. All participants gave written informed consent prior to testing, and they were treated in accordance with the declaration of Helsinki. The study was approved by the local Ethics Committee of the Faculty of Psychology at Ruhr-University Bochum, Germany.

2.2. Behavioral testing

Participants were tested in the comfort of their own home. After the experimenter had explained the aim of the study and participants had signed the informed consent form, handedness was assessed using the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971). This ten-items questionnaire yields a laterality quotient, indicating the individual strength and direction of handedness from consistent left-handedness (−100) to consistent right-handedness (+100). Afterwards, dichotic listening performance was assessed using the iDichotic app for iOS (available free of charge on Apple's App Store). Participants were tested with an iPod touch (Apple Inc., Cupertino, CA) and over-the-ear headphones outfitted with disposable hygienic sleeves. The stimuli used within the app were based on the standard Bergen dichotic listening paradigm (Hugdahl, 2003) and consisted of six consonant-vowel syllables (/ba/, /da/, /ga/, /ta/, /ka/, /pa/). The stimuli were presented simultaneously in pairs, resulting in 30 dichotic and 6 homonym stimulus pairs, yielding a total of 36 pairs. As testing took place in Germany, the German language stimulus set within the app was used. Stimuli were spoken by a male speaker with constant intonation and intensity. The stimulus duration was between 400 and 500 ms and the inter-stimulus interval was 4000 ms. Onsets of the initial stop-consonants were temporally aligned to each other syllables within each pair.

All three family members were tested individually one after the other in a room without background noise. The total stimulus set was presented three times, each time with a different instruction. The non-forced condition (NF), implemented as "Listen" in the application, was always presented first, and included the instruction to report the syllable they heard best after each trial. In the forced-left condition (FL), implemented as "Concentrate Left" in the app application, participants were instructed to only concentrate on the left ear and report the syllable they heard on that ear. In the forced-right condition (FR), implemented as "Concentrate Right" in the app application, participants were instructed to only concentrate on the right ear and report the syllable they heard on that ear. Participants reported which stimulus they heard best by touching one out of six syllables on the touchscreen of the mobile device. The order in which the syllables appeared on the screen was randomized between the three instruction conditions.

2.3. Statistical analysis

Statistical analysis was performed using IBM SPSS Statistics 20. For the handedness data, an lateralization quotient (LQ) was calculated based on the formula $LQ = [(R - L)/(R + L)] * 100$, with

R indicating the number of preferred right-handed activities and L indicating the number of preferred left-handed activities in the EHI. For the dichotic listening data, percentage of correctly reported syllables for each ear and condition was used as dependent variables. The dichotic listening data were analyzed using 3×2 repeated-measures ANOVAs with the within-subjects factors Condition (NF, FR, FL) and Ear (left, right).

To relate parent and offspring data, parent-offspring regressions were calculated. To this end, dichotic listening LQs comparable to the EHI data were calculated for the three attention instruction conditions. In addition to the LQs, we also calculated three 'gain' variables that reflected the extent to which cognitive processes modulated the performance in the FL and FR condition (Reinvang, Bakke, Hugdahl, Karlsen, & Sundet, 1994; Westerhausen, Bless, Passow, Kompus, & Hugdahl, 2015). These variables were:

- Gain FR: LQ FR – LQ NF
- Gain FL: LQ FL – LQ NF
- Gain FRFL: LQ FR - LQ FL

In order to be able to estimate heritability, data from parents was averaged to have a single mid-parent value for parental influences. Heritability (h^2) in this model is equivalent to the regression coefficient b of the offspring-midparent regression (Visscher, Hill, & Wray, 2008).

3. Results

3.1. Handedness

The mothers had a mean LQ of 81.03 (SD: 45.14), with 8 participants (7.8%) being left-handed and 95 participants (92.2%) being right-handed. The fathers had a mean LQ of 82.51 (SD: 39.11), with 6 participants (5.8%) being left-handed and the remaining 97 participants (94.2%) being right-handed. Participants in the offspring-group had a mean EHI LQ of 75.66 (SD: 50.67), with 10 participants (9.7%) being left-handed (EHI LQ lower than 0) and 93 participants (90.3%) being right-handed. Thus, participants in both the parent- and offspring-groups roughly showed the 90/10% distribution of right-handedness and left-handedness typically observed in the general population, with slightly lower percentage of left-handedness in the parent-group. There was no significant difference in EHI LQ between male and female offspring ($t_{101} = 1.47$; $p = 0.14$).

3.2. Dichotic listening performance

For the offspring group, both main-factors (Condition: $F_{(2,204)} = 5.98$; $p < 0.01$; partial $\eta^2 = 0.06$; Ear: $F_{(1,102)} = 46.66$; $p < 0.001$; partial $\eta^2 = 0.31$) and the interaction Condition $\times$ Ear ($F_{(2,204)} = 25.83$; $p < 0.001$; partial $\eta^2 = 0.20$) reached statistical significance. To further analyze the significant interaction, Bonferroni-corrected post-hoc-tests were calculated. This analysis revealed an expected significant right-ear advantage (REA) in the NF condition (right ear: 42.71%; SE: 1.06; left ear 31.88%; SE: 0.87; $p < 0.001$), as well as in the FR condition (right ear 49.00%; SE: 1.28; left ear: 28.87%; SE: 1.17; $p < 0.001$). In contrast, no REA was observed in the FL condition (right ear: 38.93%; SE: 1.43; left ear: 37.59%; SE: 1.30; n.s.), also as expected.

For the mothers, both main-factors (Condition: $F_{(2,204)} = 25.94$; $p < 0.001$; partial $\eta^2 = 0.20$; Ear: $F_{(1,102)} = 27.19$; $p < 0.001$; partial $\eta^2 = 0.21$) and the interaction Condition $\times$ Ear ($F_{(2,204)} = 14.35$; $p < 0.001$; partial $\eta^2 = 0.12$) reached statistical significance. Bonferroni-corrected post-hoc-tests revealed a significant REA in the NF condition (right ear: 37.06%; SE: 1.26; left ear 29.04%; SE: 1.10; $p < 0.001$), and in the FR condition (right ear 45.42%; SE: 1.47; left ear: 29.34%; SE: 1.28; $p < 0.001$) but not in the FL condition (right ear: 37.73%; SE: 1.47; left ear: 34.71%; SE: 1.32; n.s.).

For the fathers, both main-factors (Condition: $F_{(2,204)} = 7.39$; $p < 0.01$; partial $\eta^2 = 0.70$; Ear: $F_{(1,102)} = 46.89$; $p < 0.001$; partial $\eta^2 = 0.32$) and the interaction Condition $\times$ Ear ($F_{(2,204)} = 3.57$; $p < 0.05$; partial $\eta^2 = 0.03$) reached statistical significance. Bonferroni-corrected post-hoc-tests again showed a significant REA in the NF condition (right ear: 39.50%; SE: 1.32; left ear 27.05%; SE: 1.17; $p < 0.001$). The REA was further increased in the FR condition (right ear 44.33%; SE: 1.63; left ear: 27.42%; SE: 1.42; $p < 0.001$). In contrast to the offspring and mothers groups, a significant REA was also observed in the FL condition, although the absolute difference was smaller than in the two other conditions (right ear: 40.36%; SE: 1.36; left ear: 29.69%; SE: 1.31; $p < 0.001$). This REA was not significantly smaller than in the NF condition ($p = 0.50$), but significantly smaller than in the FR condition ($p < 0.05$).

When the performance of the mothers and fathers was compared against each other, a significant difference was only observed for the left ear in the FL condition ($t_{(102)} = 3.13$; $p < 0.01$). All other comparisons failed to reach significance (all p's > 0.13). To test for sex-differences in the offspring group, we compared male and female offsprings with t-tests for the involved variables. There were no significant sex-differences in the offspring group for any variable (all p's > 0.36). Also, to test for potential age effects, we correlated all dependent variables with age. For offspring and mothers, all correlation coefficients failed to reach significance, indicating no age-effects. For fathers, two correlations reached significance (LQ FL: $r = 0.26$, LQ FR: $r = 0.20$, $p < 0.05$).

3.3. Parent-offspring regressions

Dichotic listening LQs for the three attention instruction conditions are shown in Fig. 1. The distribution of parent-offspring scores, split for dichotic listening instruction conditions and Gain-scores, are shown in Fig. 2 as scatter-plots. The results of the parent-offspring regressions are summarized in Table 1. Parent-offspring regressions did not reach significance for EHI LQ ($h^2 = 0.06$; $p = 0.71$) and LQ NF ($h^2 = 0.003$; $p = 0.98$). Heritability was low for these two variables. In contrast, significant positive relationships with moderate heritability was observed for LQ FR ($h^2 = 0.36$; $p < 0.01$) and LQ FL ($h^2 = 0.28$; $p < 0.05$). In general, the

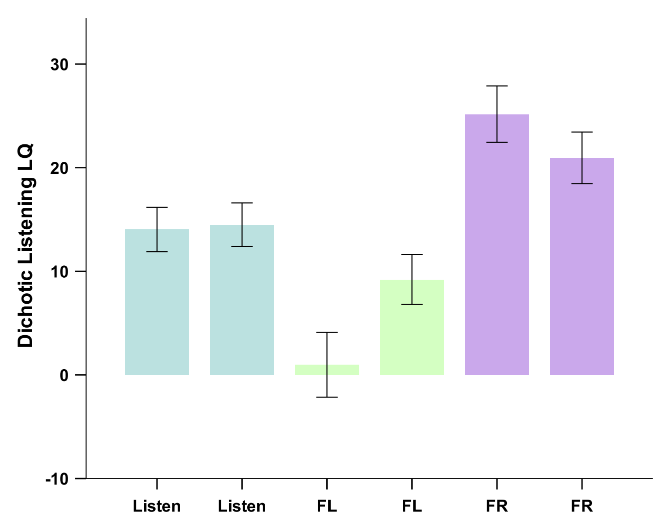

Fig. 1. Dichotic Listening LQs for parents (average of father and mother) and offspring for the different conditions of the iDichotic app.

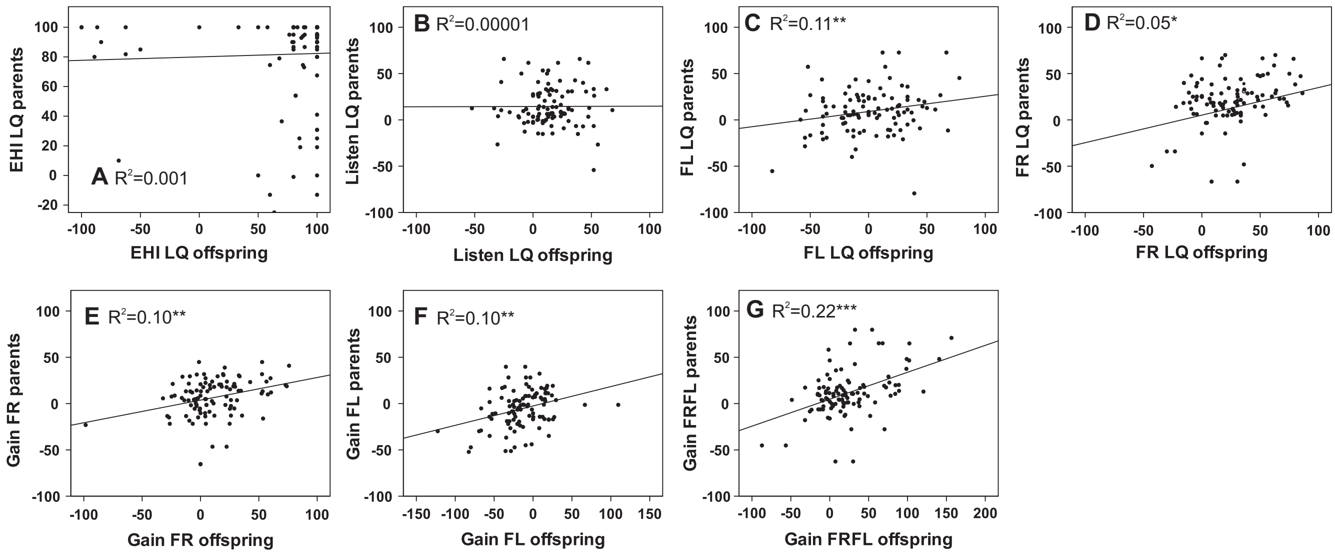

Fig. 2. Scatterplots showing the relation of parent and offspring data for the different parent-offspring regression analysis (A: EHI LQ; B: Listen LQ; C: FL LQ; D: FR LQ; E: Gain FR; F: Gain FL; G: Gain Forced Right-Left). R^2 indicates the coefficient of determination for the different regression models and asterisks indicate their significance (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

Table 1
Parent-offspring regression analyses for lateralization quotients (LQ) for the Edinburgh Handedness Inventory (EHI) and the three dichotic listening conditions Listen, Forced Right (FR) and Forced Left (FL), as well as for the three Gain variables. R^2 indicates the coefficient of determination and F the F-value with degrees of freedom and p-value for the model. h^2/b indicates the heritability coefficient and T its T-value.

Variable	R^2	F	h^2/b	T
EHI LQ	0.001	$F_{(1,\ 102)} = 0.14$; $p = 0.71$	0.06	$T = 0.38$; $p = 0.71$
LQ Listen	0.00001	$F_{(1,\ 102)} = 0.001$; $p = 0.98$	0.003	$T = 0.032$; $p = 0.98$
LQ FR	0.11	$F_{(1,\ 102)} = 11.96$; $p < 0.01$	0.36	$T = 3.46$; $p < 0.01$
LQ FL	0.05	$F_{(1,\ 102)} = 4.87$; $p < 0.05$	0.28	$T = 2.21$; $p < 0.05$
Gain FR	0.10	$F_{(1,\ 102)} = 10.77$; $p < 0.01$	0.39	$T = 3.28$; $p < 0.01$
Gain FL	0.10	$F_{(1,\ 102)} = 11.59$; $p < 0.01$	0.49	$T = 3.41$; $p < 0.01$
Gain FRFL	0.22	$F_{(1,\ 102)} = 27.62$; $p < 0.001$	0.74	$T = 5.26$; $p < 0.001$

'Gain' variables showed higher absolute values for heritability than the LQs. Here, Gain FR ($h^2 = 0.39$; $p < 0.01$) and Gain FL ($h^2 = 0.49$; $p < 0.01$) showed moderate heritability, while Gain FRFL ($h^2 = 0.74$; $p < 0.001$) showed high heritability, see Fig. 2 for further details.

4. Discussion

In the present study we used the iDichotic smartphone app (Bless et al., 2013, 2015) to test heritability of laterality and cognitive factors for dichotic speech sound perception. In line with the results by Bless et al. (2013) and Bless et al. (2015), the successful collection of data from 103 families with the help of an iPod Touch app shows that mobile-based data collection is an effective method to test large samples that might be difficult to access in traditional laboratory settings. As a first summary of the main findings, we could not identify any evidence for a shared genetic background of handedness and language lateralization, which is in line with previous studies considering both functions as relatively independent instances of hemispheric specialization (e.g. Bryden, 1975; Somers et al., 2015). A quote from Bryden's (1975) paper may be relevant in this context:

"In summary, the present study has failed to find any particularly compelling evidence for a genetic basis for speech lateralization. While the problems associated with the use of an indirect measure of only moderate reliability may have doomed this study from the start, it does suggest that one should at least consider seriously the hypothesis that speech lateralization is primarily determined by environmental factors."

[Bryden, 1975, page 209]

The findings for the NF condition (which closely resembles the free-report paradigm used by Bryden, 1975) are very much in line with this conclusion. The variable LQ NF showed a non-significant h^2 of 0.003, indicating heritability of less than 1%. While this result is in accordance with Bryden's (1975) finding, it is somewhat in contrast to the study by Somers et al. (2015) who estimated heritability of language lateralization measured with functional transcranial Doppler sonography during speech production to be 31%. This difference provides some hints for differential genetic influences onto speech production and perception (as indicated by dichotic listening), but it may as well reflect differences in the methods used in the studies. Doppler measures blood flow in the targeted brain region, while dichotic listening reflects performance, and there is no simple 1:1 relation between changes in blood flow and performance. These findings indicate that there seems to be a considerable phenotype-dependent variability regarding the heritability of language lateralization. The same also might be true for handedness. We found EHI LQ to show low and non-significant heritability ($h^2 = 0.06$; $p = 0.71$), which is somewhat in contrast with two recent twin studies indicating that additive genetic effects account for about 25% of the variance in handedness data (Medland, Duffy, Wright, Geffen, & Martin, 2006; Medland et al., 2009). However, these authors used handedness direction, i.e. left- or right-handers and not an interval-scaled variable like LQ as dependent variable. Thus, our findings indicate that LQ as a combined measure of handedness strength and direction might have a lower heritability than handedness direction alone.

While independent replication in larger samples and with different phenotypes is needed before any final conclusions can be drawn, our data tentatively suggest that non-genetic factors might play a considerable role for the ontogenesis of language lateralization. This idea is in line with the conclusion of a review article by Schaafsma, Riedstra, Pfannkuche, Bouma, and Groothuis (2009) who concluded that the explanatory power of the predominant models for human handedness and language lateralization is not sufficient to account for all empirical data, and that functional hemispheric asymmetries are likely to be modulated by non-genetic factors. They suggested that perinatal asymmetrical perception and social modulation might be potential influence factors as also indicated by animal models (e.g. Manns, 2005; Manns & Güntürkün, 2009; Manns & Ströckens, 2014). While the identification of such factors goes beyond the scope of the present study, our data suggest that further exploring these factors in relation to dichotic listening performance might be an interesting endeavor for future studies.

In contrast to the results of the NF condition, the results of the two forced conditions (which were not included in Bryden's (1975) original study) as well as the analysis of the three 'Gain' variables revealed that other aspects of dichotic listening performance might be more heritable. The LQs in both the FR and the FL condition as well as the 'Gain' variables showed significant positive parent-offspring regression and correlations, with moderate heritability. This shows that parents that were quite able to concentrate on the syllable coming from one ear also had offspring who were quite able to do so, even though the ability to utilize cognitive control processes, as seen in the FL condition, changes during life span development (Passow et al., 2013; Westerhausen et al., 2015). The range of the 'Gain' in the 'Concentrate' condition indicates to what extent top-down processes are able to modulate stimulus-driven bottom-up processing. The effects measured in the 'Concentrate' conditions are relatively late-developing cognitive processes, elicited by the instructions to focus attention towards one ear (Passow et al., 2014). Thus, our data suggest that the extent of cognitive modulation a participant can exhibit over their performance in the dichotic listening task is partly heritable. This finding is in line with a recent study assessing cognitive control processes in a large-scale web-based family study. Sabb et al. (2013) reported that both working memory and response inhibition had significant heritability, with several variables in their experiments reaching heritability values over 0.60. Interestingly, Gain FL ($h^2 = 0.49$) had a higher heritability than Gain FR ($h^2 = 0.39$). This is in line with the interpretation suggested by Hugdahl et al. (2009) that paying attention to and reporting the left ear stimulus requires stronger cognitive control processes than paying attention to the right ear stimulus, as it lacks the perceptual salience of the right ear stimulus during dichotic listening. This idea was supported by the fMRI activations observed by Kompus et al. (2012), who showed that the right inferior frontal gyrus and caudate were activated in both conditions, but only in the FL condition there were additional significant activations in the left inferior prefrontal gyrus and caudate nucleus, brain areas which considered to be involved in cognitive control (e.g. Roberts & Hall, 2008).

The present study has a few methodological limitations that future studies should address. First, despite testing more than 100 families, our sample size could be considered as small for a study investigating heritability. This is particularly the case as the distribution of the trait of interest is skewed, with much less participants showing a left ear advantage than a right ear advantage. Related to this problem is the fact that we only included a small number of left-handers. As handedness has been shown to correlate with language lateralization, future replication studies in larger cohorts should ensure a sufficient number of left-handed participants. A third problem that might occur when using a smartphone app instead of testing under controlled laboratory conditions is an elevated level of noise in the data. While Bless et al. (2013) could show that the iDichotic app yields comparable results to a laboratory version of the dichotic listening paradigm, this potential issue should be closely monitored in subsequent experiments. Moreover, future studies could reduce the potential impact of individual hearing differences on dichotic listening performance by integrating the results from the hearing test included in the iDichotic app as a covariate into their analyses. The present findings also have interesting theoretical implications for future studies. First, the higher heritability in the Doppler sonography study by Somers et al. (2015) compared to Bryden's (1975) and our work highlight the importance of the method used to assess the phenotype for the outcome of studies on the ontogenesis of language lateralization, especially whether it assesses language production or perception (Ocklenburg, Hugdahl, & Westerhausen, 2013). It would be interesting if future studies could compare different behavioral (e.g. dichotic listening and divided visual field paradigms) and neurophysiological measures (e.g. Doppler sonography, fMRI and EEG) of language lateralization to unravel developmental patterns of different aspects of a cognitive function. Furthermore, as patients with schizophrenia and especially those experiencing auditory hallucinations frequently show a reduced REA in the dichotic listening task (e.g. Green, Hugdahl, & Mitchell, 1994; Løberg, Hugdahl, & Green, 1999; Ocklenburg, Güntürkün, Hugdahl, & Hirnstein, 2015; Ocklenburg, Westerhausen, Hirnstein, & Hugdahl, 2013; Sommer, Ramsey, Kahn, Aleman, & Bouma, 2001), using the iDichotic app in these patients and their parents could yield interesting insights into the ontogenetic overlap between lateralization and psychiatric disorders. Moreover, as our findings implicate a substantial influence of non-genetic factors on the ontogenesis of language lateralization, it would be of central importance to identify such factors and the molecular mechanisms by which they alter brain structure. Animal models provide important insight into the mechanisms mediating the impact of lateralized sensory experience by activity-dependent processes (Manns & Güntürkün, 2009; Rogers, 2014). These studies indicate a differential role of ascending (bottom-up) (Manns & Güntürkün, 2009; Rogers, 2014), descending (top-down) (Manns & Ströckens, 2014) and commissural (interhemispheric) (Manns & Römling, 2012) systems for the generation of lateralized functions. Moreover, recent research demonstrates that conserved epigenetic mechanisms promote the generation of neuronal asymmetries (Nakano, Stillman, & Horvitz, 2011). As several authors found evidence for lateralization of conspecific vocalization in different animal species (reviewed in Ocklenburg, Ströckens, & Güntürkün, 2013), comparative approaches might be particularly helpful to approach this question.

5. Conclusion

This study reveals that the REA in the standard dichotic listening task shows weak and non-significant heritability, implicating a major contribution of non-genetic factors on this phenotype. In contrast, cognitive factors that modulate the REA showed significant heritability, both for non-executive attention and cognitive control, as was seen in the FR and FL instruction conditions.

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