



Left dominance for language perception starts in the extrastriate cortex: An ERP and sLORETA study

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HIGHLIGHTS

- Language lateralization is evident in early perceptual processing.
- Stimulus presentation format modulates N1 asymmetries.
- The extrastriate cortex drives N1 asymmetries.

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ABSTRACT

While it is well known that the left hemisphere is more efficient than the right in most tasks involving perception of speech stimuli, the neurophysiological pathways leading to these lateralised performance differences are as yet rather unclear. In particular, the question whether language lateralisation depends on semantic processing or is already evident in early perceptual stimulus processing has not been answered unequivocally. In the present study, we therefore recorded event-related potentials (ERPs) during tachistosopic presentation of horizontally or vertically presented verbal stimuli in the left (LVF) and the right visual field (RVF). Participants were asked to indicate, whether the presented stimulus was a word or a non-word. On the behavioural level, participants showed stronger hemispheric asymmetries for horizontal, than for vertical stimulus presentation. In addition, ERP asymmetries were also modulated by stimulus presentation format, as the electrode by visual field interactions for P1 and N1 were stronger after vertical, than after horizontal stimulus presentation. Moreover, sLORETA revealed that ERP left-right asymmetries were mainly driven by the extrastriate cortex and reading-associated areas in the parietal cortex. Taken together, the present study shows electrophysiological support for the assumption that language lateralisation during speech perception arises from a left dominance for the processing of early perceptual stimulus aspects.

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1. Introduction

Language is the most important aspect of human communication and investigation of the neural basis of speech one of the major topics within neuroscientific research [16,23,36,37,64]. A striking feature of the neuroanatomy of the human language system is an asymmetrical distribution of involved cerebral areas, which has been known since the early findings of Broca [7]. This struc-

tural asymmetry is paralleled by a functional cerebral asymmetry (FCA), i.e., a relative efficacy advantage for processing verbal stimuli within the left compared to the right hemisphere in most individuals [10,28,48]. This does however, not imply that the right hemisphere is not involved in language processing. For example, it has shown that the right temporal cortex plays a fundamental role in perceiving paralinguistic and prosodic contents of speech [3]. While the neuroanatomical structures involved in language production and perception are well known [15], the neurophysiological pathways leading to lateralised performance differences are still largely unclear. One of the most important questions in this regard is to determine on which level of stimulus processing lateralised processing becomes evident first. While it was initially assumed that language lateralisation originates in later semantic

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stimulus processing [9,42,78], some studies also suggested a role of earlier perceptual processes [35,51]. In particular, a recent fMRI study by [35] demonstrated that for speech production, sensory areas in the temporal cortices already showed lateralisation when speaking was intended. In contrast, speech executive areas in the frontal lobe only showed lateralised activity during speech execution. This pattern of results lead [35] to the assumption, that functional lateralisation of sensory areas in the temporal cortex could drive functional language lateralisation during speech production. From a systems neurophysiology perspective, however, it is unclear whether this is a principle that affects language lateralisation in general or only applies to language production. Since speech perception has been shown to activate partly different brain areas than speech production (e.g. [53]), it is important for our understanding of functional lateralisation as an important organisational principle in the language system to clarify this question.

One way to experimentally assess the impact of early perceptual processes on language lateralisation is to change perceptual features of words presented to participants without changing their semantic content. For example, Windmann et al. [78] presented words and non-words in horizontal and vertical presentation format to participants using the divided visual field technique (e.g. [2,5,45]). Interestingly, participants showed stronger leftward asymmetries for horizontal than for vertical stimulus presentation, suggesting that perceptual stimulus features indeed affect FCA's during language perception. However, based on these behavioural findings one cannot make inferences on the systems neurophysiological level. We therefore used a paradigm similar to that of Windmann et al. [78] while recording event-related potentials (ERPs). In order to determine, whether analogous to Kell et al. [35] findings, sensory brain areas play a role in this process, we used sLORETA to reconstruct the spatial sources of left-right asymmetries in the ERP data.

We focused on two ERP responses to visual sensory input: the P1 and the N1. The P1 is an early positive ERP component, which sets of around 60 ms, but peaks around 80–120 ms after stimulus presentation [40,61]. It is centred over the occipital lobe [40] is generated in the dorsal extrastriate cortex, while the late phase is generated in the ventral extrastriate cortex [13]. The P1 is modulated by variations in stimulus parameters [40]. The earliest visual ERP component reflecting leftward language dominance is the N1 [40]. It is associated with early visual attention towards verbal stimuli and discrimination between linguistic and non-linguistic stimuli [72] and peaks about 150–200 ms after stimulus presentation [38]. Anatomically, the N1 has been associated with the occipital lobe [24] and more specifically the extrastriate cortex [68]. Typically, the N1 shows left lateralisation after presentation of words, which is thought to reflect an efficacy advantage for the speech-dominant LH [19,1,39].

The aim of the present study was to get a deeper understanding of the neuronal processes underlying the emergence of FCA's during language perception. Based on the findings by [78] we assume that early perceptual processing is relevant for FCA's during language perception. Thus, stimulus presentation format should affect behavioural asymmetries as well as ERP asymmetries, particularly in the N1. Moreover, if indeed early perceptual processes were relevant for FCA's, ERP differences between left and right visual field stimulation should be driven by brain areas involved in visual perceptual processing, such as the extrastriate cortex [55]. In contrast, if only semantic stimulus content would be relevant for language lateralisation, stimulus presentation format should not show any effect on ERP asymmetries at early stages in the processing stream. Taken together, this study allows for a major insight in the emergence of perceptual FCA's by clarifying their neurophysiology and neuronal sources.

2. Material and methods

2.1. Participants

Overall, 40 subjects (20 males and 20 females) with no history of neurological or psychiatric disease and a mean age of 24.4 years were tested. All participants reported having normal or corrected-to-normal vision and were right-handed with laterality quotients between 50 and 100 (mean 91.4), according to the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). All participants gave written informed consent, were treated in accordance with the declaration of Helsinki and received a compensation of 30€. The experiment was conducted with approval from the institutional ethics committee, Faculty of Psychology, Ruhr-University Bochum.

2.2. Task

The experimental paradigm used in the present study (see Fig. 1) was based on an earlier behavioural study by Windmann et al. [78]. Stimuli consisted of 80 German nouns as well as 80 pronounceable non-words. As words, 80 German substantives (e.g., Signal) were used. By exchanging two or more letters (preferably vowels, but never the initial letter) within the noun, 80 corresponding non-words were created. These 160 items were tachistoscopically (160 ms) presented either horizontally or vertically on a 17 inch CRT computer monitor in black against white background. Half of them were shown in the left visual field (LVF) and the other half in the right visual field (RVF).

The experiment consisted of two blocks, each beginning with 10 test trials (which were excluded from later analysis), followed by 160 valid trials, resulting in an overall number of 320 experimental trials. Stimuli were presented in randomised order. At all times, a central fixation cross with a size of 1° by 1° visual angle was presented and participants were to fixate the fixation cross during the entire session. Stimuli were presented laterally at a distance of 2° visual angle from the fixation cross. At the start of the experiment, participants were instructed to lay their chins on a chinrest in 57 cm distance to the computer screen and to focus on the fixation cross. In order to avoid confounding handedness effects, participants were asked to only use their dominant right hand to press either the arrow up key or arrow down key on a standard PC keyboard to determine if the presented item was a word or a non-word. Participants had 2000 ms time to react. Thus, the overall trial duration was 2160 ms. The intertrial interval (ITI) had a randomised length between 150 and 350ms. This randomisation was performed to avoid possible expectancy effects [10] on the ERP data.

2.3. EEG recording and analysis

EEG data were recorded using a 65 Ag–AgCl electrode system (actiCAP ControlBox and QuickAmp 72, Brain Products GmbH, Gilching, Germany), positioned at standard scalp locations (see [62,51,50]). Data was recorded with a sampling rate of 1000 Hz, later down-sampled to 500 Hz. FCz was used as reference electrode during recording. A band-pass filter ranging from 0.5 to 20 Hz (48 dB/oct) was applied and the impedances of all electrodes were kept below 5kΩ to ensure a low level of noise within the data. After recording, Brain Vision Analyser software (Brain Products GmbH) was used to further process raw data. Beginning with a visual inspection, all EEG-sections containing technical artefacts were rejected. Subsequently, an independent component analysis (ICA) applying the Infomax algorithm was used on the un-epoched data, in order to eliminate reoccurring artefacts, such as blinks, horizontal eye movements and pulse artefacts. Thereafter, FCz and all previously rejected channels (if there were any) were calculated using topographic interpolation with spherical splines. The

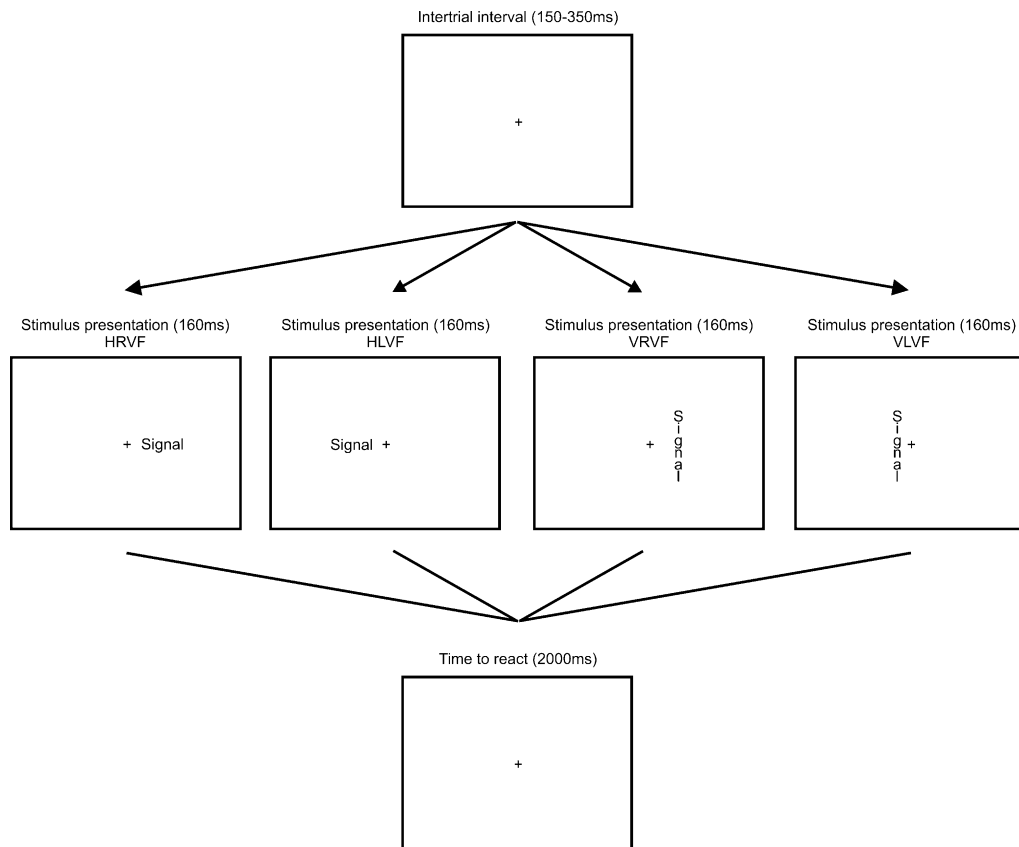


Fig. 1. Schematic overview of paradigm. Stimuli were presented either horizontally (H) or vertically (V) in the right (RVF) or left visual field (LVF). Please note that proportions have been altered to increase visibility in the figure, for the exact dimensions of stimuli and distances, please refer to the Section 2.

data was then epoched into 1200 ms segments, extending from 200 ms prior to stimulus presentation to 1000 ms post-stimulus presentation. Then, automatic artefact rejection procedures were applied. This was done to exclude any non-physiological artefacts in the ERP data set. A maximum allowed voltage step of $50 \mu\text{V}/\text{ms}$, a maximum value difference of $200 \mu\text{V}$ within a 200 ms interval or activity below $0.1 \mu\text{V}$ served as artefact rejection parameters. Overall the number of rejected trials was well below 5% of all trials in each condition and for all EEG channels. Subsequently, a CSD-transformation [60] was applied in order to eliminate the reference potential from the data. After the CSD-transformation, the epoch from 0 to 1000 ms after stimulus presentation was corrected relative to a predefined baseline (200 ms before stimulus presentation until stimulus onset) and P1 and N1 amplitudes and latencies were averaged for all conditions for each participant separately. For all further analyses, amplitude and latency only for those trials in which the participants reacted correctly were used. Based on previous findings and scalp topography (see results section), P1 (60–120 ms after stimulus presentation) and N1 (130–200 ms after stimulus presentation) amplitudes and latencies were quantified at electrodes O1 and O2.

2.4. sLORETA

For both horizontal and vertical stimulus presentation, sLORETA (Standardised low resolution brain electromagnetic tomography) was used to determine the cortical distribution of source locations of the P1 and N1 after LVF compared to RVF stimulus presentation. sLORETA [57] is a method providing a single linear solution to the inverse problem of brain function source localisation based on extracranial data [41]. sLORETA serves as an improved version to the previously developed LORETA [59], determining source locations without localisation bias [67,17,56], under the assumption

of similar electrical activation of neighbouring neuronal sources followed by a standardisation of the current density [58], thus creating an image of electric neuronal activity. Several studies have validated the localisation accuracy by combining sLORETA with tomographic techniques such as fMRI/EEG [54] or PET [12]. In a realistic head model [17] using the MNI152 template [43] with the three-dimensional solution space restricted to cortical grey matter, sLORETA calculates the standardised current density at each of the 6239 voxels at 5 mm spatial resolution in which the intracerebral volume is partitioned in.

In a first step, data transformation from Brain Vision Analyser to sLORETA software was performed, using a protocol by Mückschel et al. [46]. Using the sLORETA software, we then performed voxel-wise randomisation tests with 5000 permutations, based on statistical non-parametric mapping (SnPM). These were carried out to compare the voxel-based sLORETA images with regard to stimulus presentation within the LVF or RVF [48]. Voxels with significant differences (for corrected $p < 0.01$) were located in specific brain regions with BA (Brodmann) and MNI (Montreal Neurological Institute) coordinates being provided by the software.

3. Results

3.1. Behavioural data

3.1.1. Correct responses

The behavioural data (percentage of correct responses and reaction times) were analysed using repeated-measures ANOVAs with the within-subject factors Condition (horizontal presentation, vertical presentation) and Visual Field (LVF, RVF). For correct responses (see Fig. 2), the main effect Condition ($F_{(1,39)} = 88.49$; $p < 0.001$; partial $\eta^2 = 0.73$) reached significance, indicating that

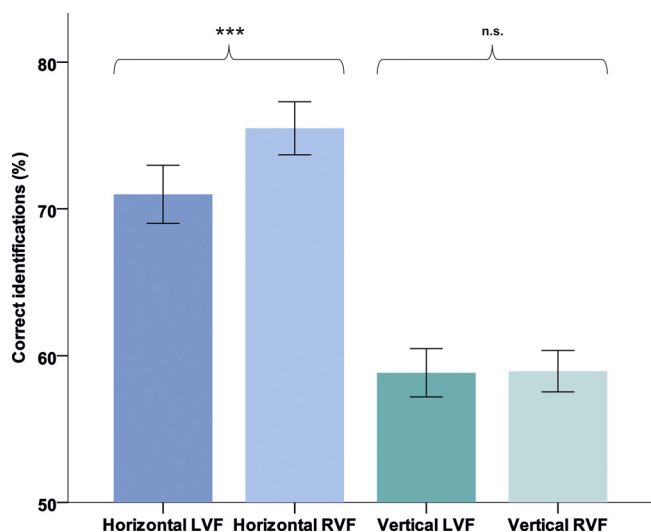


Fig. 2. Behavioural data: distribution of correct responses (in percent), arranged by presentation format (horizontal, vertical) and visual field (LVF, RVF). Error bars show standard error. Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s.: not significant.

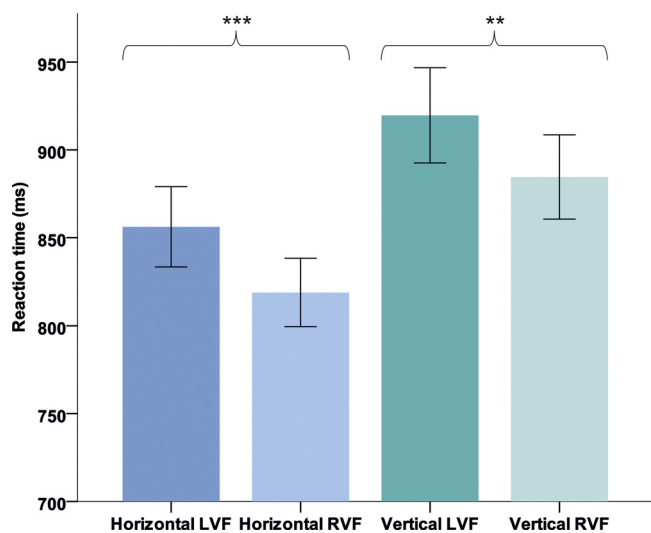


Fig. 3. Behavioural data: distribution of reaction times (in milliseconds), arranged by presentation format (horizontal, vertical) and visual field (LVF, RVF). Error bars show standard error. Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s.: not significant.

participants identified more stimuli correctly if stimuli were presented horizontally (mean: $73.24\% \pm 1.79$) than when presented vertically ($58.89\% \pm 1.33$). Moreover, the main effect of Visual Field reached significance ($F_{(1,39)} = 4.51$; $p < 0.05$; partial $\eta^2 = 0.12$), indicating that participants were able to correctly identify more of the stimuli presented in the RVF ($67.22\% \pm 1.41$) than in the LVF ($64.91\% \pm 1.55$). Interestingly, the main effect of Visual Field was modulated by Condition, as indicated by a significant interaction between the two factors ($F_{(1,39)} = 6.23$; $p < 0.05$; partial $\eta^2 = 0.16$). While there was a significant asymmetry in accuracy in the horizontal condition (LVF: $70.99\% \pm 1.98$; RVF: $75.49\% \pm 1.81$; Bonferroni-corrected post-hoc test: $p < 0.001$), no accuracy difference between the two visual fields was observed in the vertical condition (LVF: $58.84\% \pm 1.65$; RVF: $58.95\% \pm 1.41$; Bonferroni-corrected post-hoc test: $p = 0.94$).

3.1.2. Reaction times

For reaction times (see Fig. 3), the ANOVA revealed a significant main effect of condition ($F_{(1,39)} = 15.79$; $p < 0.001$; partial $\eta^2 = 0.32$),

indicating that participants reacted faster if stimuli were presented horizontally ($837.54\text{ms} \pm 20.81$) than when they were presented vertically ($901.12\text{ms} \pm 24.96$). Moreover, a significant main effect of Visual Field ($F_{(1,39)} = 24.10$; $p < 0.001$; partial $\eta^2 = 0.42$) indicated faster reaction times if stimuli were presented within the RVF ($851.74\text{ms} \pm 20.28$) than when they were presented in the LVF ($887.93\text{ms} \pm 23.23$). When the two conditions were analysed separately, the Visual Field effect reached significance for both horizontal ($p < 0.001$) and vertical ($p < 0.01$) condition. The interaction Condition \times Visual Field failed to reach significance ($p = 0.87$) for reaction times.

3.2. EEG data

3.2.1. P1

3.2.1.1. Amplitude. The P1 data (see Fig. 4) were analysed using repeated-measures ANOVAs with the within-subject factors Electrode (O1, O2), Condition (horizontal presentation, vertical presentation) and Visual Field (LVF, RVF). The analysed electrode positions were chosen based on topography (see Fig. 4). For the amplitudes, the analysis revealed a main effect of Condition ($F_{(1,39)} = 5.26$; $p < 0.05$; partial $\eta^2 = 0.13$), indicating a higher P1 amplitude after vertical (18.28 ± 1.54) than after horizontal stimulus presentation (16.05 ± 1.50). While the main effect of Visual Field barely missed significance ($F_{(1,39)} = 4.06$; $p = 0.051$), there was a clear interaction Visual Field \times Electrode ($F_{(1,39)} = 92.53$; $p < 0.001$; partial $\eta^2 = 0.71$). At the left-hemispheric electrode O1, the P1 was higher after stimulus presentation in the LVF (23.77 ± 2.39), compared to the RVF (10.08 ± 1.47 ; Bonferroni-corrected post-hoc test: $p < 0.001$). In contrast, at the right-hemispheric electrode O2, the P1 amplitude was higher after stimulus presentation in the RVF (26.80 ± 2.22) compared to the LVF (8.03 ± 1.36 ; Bonferroni-corrected post-hoc test: $p < 0.001$). All other main effects and interactions failed to reach significance (all p 's > 0.08).

For the horizontal condition, the difference in P1 amplitudes between presenting stimuli in the LVF and RVF was due to differences in activation (see Fig. 5) in the left extrastriate cortex (BA18) and left angular gyrus (BA39). For vertical stimulus presentation, no significant clusters were observed.

3.2.1.2. Latency. For P1 latencies, the main effect Condition ($F_{(1,39)} = 17.82$; $p < 0.001$; partial $\eta^2 = 0.33$) reached significance, indicating a faster P1 in the vertical ($106.94\text{ms} \pm 1.30$) than in the horizontal ($117.05\text{ms} \pm 2.23$) condition. Moreover, the main effect of Electrode reached significance ($F_{(1,39)} = 6.09$; $p < 0.05$; partial $\eta^2 = 0.14$), indicating a slightly faster P1 at the left-hemispheric electrode O1 (110.48 ± 1.38) than at the right-hemispheric electrode O2 (113.53 ± 1.63).

In addition to the main effects, the interactions Visual Field \times Electrode ($F_{(1,39)} = 559.68$; $p < 0.001$; partial $\eta^2 = 0.94$) and Visual Field \times Electrode \times Condition ($F_{(1,39)} = 8.31$; $p < 0.01$; partial $\eta^2 = 0.18$) reached significance. To further investigate this key interaction, we calculated two separate ANOVAs with the within subject factors Electrode (O1, O2) and Visual Field (LVF, RVF) for the two stimulus presentation conditions. For the horizontal condition, the interaction Visual Field \times Electrode reached significance ($F_{(1,39)} = 312.08$; $p < 0.001$; partial $\eta^2 = 0.89$). This interaction indicated that at the left-hemispheric electrode O1, the P1 had an earlier onset after stimulus presentation in the contralateral RVF ($88.81\text{ms} \pm 2.74$) than in the ipsilateral LVF ($142.30\text{ms} \pm 2.47$; difference: 53.49). In contrast, at electrode O2 this pattern was reversed (LVF: 92.33 ± 4.16 ; RVF: 145.54 ± 2.40 ; difference: 53.21). For the vertical condition, the interaction Visual Field \times Electrode also reached significance ($F_{(1,39)} = 628.48$; $p < 0.001$), but had a higher effect size (partial

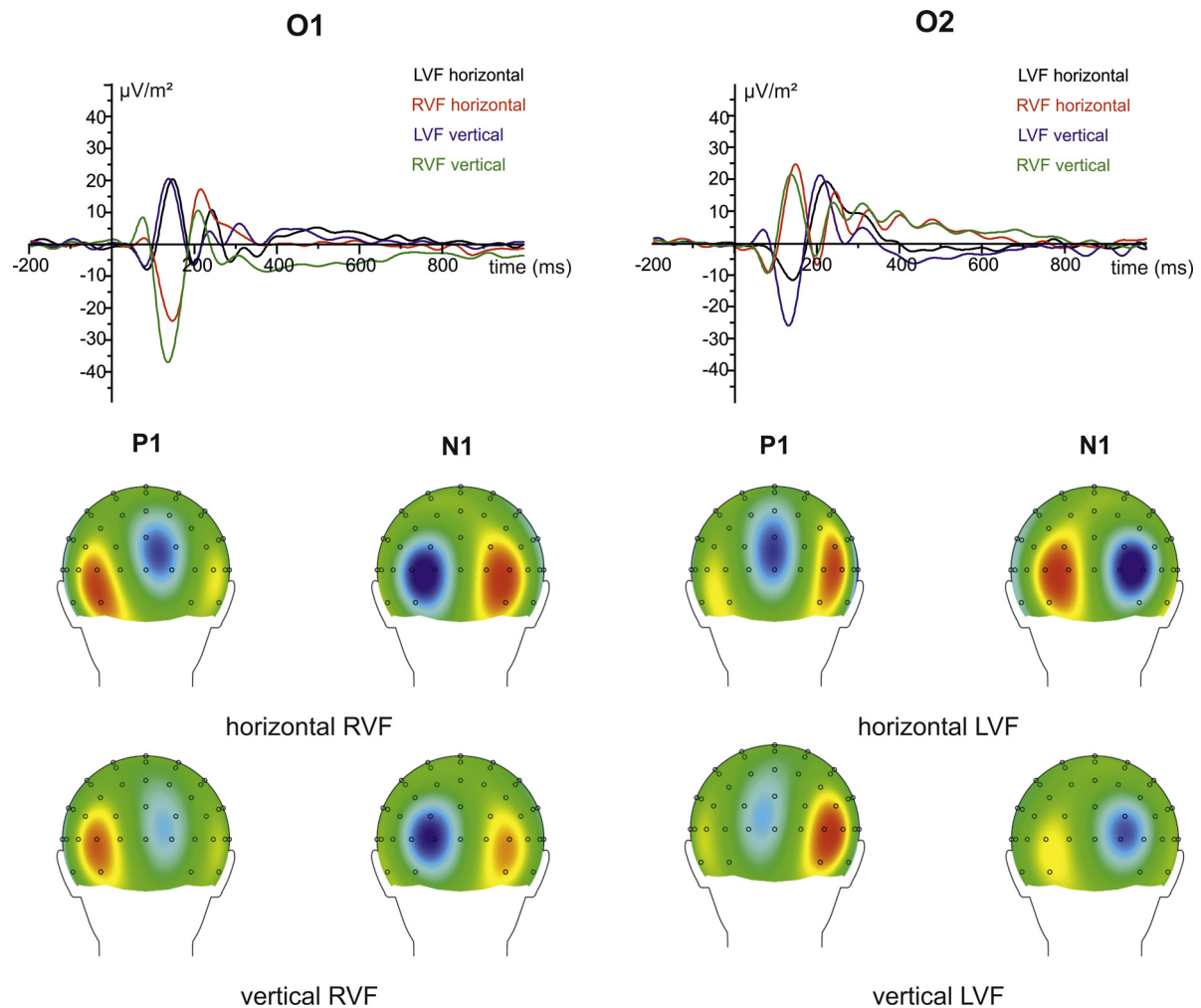


Fig. 4. Time course of ERP components at electrodes O1 and O2 elicited by vertical or horizontal stimulus presentation in the LVF or RVF. Stimulus presentation was at 0 ms. The lower panel shows the topographical maps for the P1 and the N1 after vertical and horizontal stimulus presentation in the LVF or RVF.

$\eta^2 = 0.94$) than in the horizontal condition. Again, this interaction indicated that at the left-hemispheric electrode O1, the P1 had an earlier onset after stimulus presentation in the contralateral RVF (75.21 ms \pm 1.63) than in the ipsilateral LVF (136.37 ms \pm 1.93; difference: 61.16), while at electrode O2 this pattern was reversed (LVF: 77.80 \pm 3.01; RVF: 139.67 \pm 2.23; difference: 61.87). Thus, the absolute latency differences between LVF and RVF stimulus presentation were higher for both electrodes in the vertical compared to the horizontal condition. All other main effects and interactions failed to reach significance (all p 's $>$ 0.71).

3.2.2. N1

3.2.2.1. Amplitude. The N1 data (see Fig. 3) were analysed using repeated-measures ANOVAs with the within-subject factors Electrode (O1, O2), Condition (horizontal presentation, vertical presentation) and Visual Field (LVF, RVF). For N1 amplitudes, all three main effects reached significance. The main effect of Condition ($F_{(1,39)} = 18.22$; $p < 0.001$; partial $\eta^2 = 0.33$) indicated that that N1 amplitude was more negative after vertical (-24.80 ± 2.43) than after horizontal stimulus presentation (-18.68 ± 32.14). Additionally, the main effect of Electrode ($F_{(1,39)} = 6.04$; $p < 0.05$; partial $\eta^2 = 0.14$) showed that N1 amplitude was more negative at the left-hemispheric electrode O1 (-24.55 ± 2.49) than at the right-hemispheric electrode O2 (-18.92 ± 2.43). The main effect of Visual Field ($F_{(1,39)} = 5.95$; $p < 0.05$; partial $\eta^2 = 0.14$) indicated that the N1 amplitude was more negative after stimulus presenta-

tion in the RVF (-23.81 ± 2.63) than the LVF (-19.67 ± 2.00). Moreover, the interactions Visual Field \times Electrode ($F_{(1,39)} = 55.46$; $p < 0.001$; partial $\eta^2 = 0.60$) and Visual Field \times Electrode \times Condition reached significance ($F_{(1,39)} = 19.33$; $p < 0.001$; partial $\eta^2 = 0.34$) reached significance. To further investigate this key interaction, we calculated two separate ANOVAs with the within subject factors Electrode (O1, O2) and Visual Field (LVF, RVF) for the two stimulus presentation conditions. For the horizontal condition, the interaction Visual Field \times Electrode reached significance ($F_{(1,39)} = 23.29$; $p < 0.001$; partial $\eta^2 = 0.38$). This interaction indicated that at the left-hemispheric electrode O1, the N1 had higher amplitude after stimulus presentation in the contralateral RVF (-30.19 ± 3.82) than in the ipsilateral LVF (-11.23 ± 1.98 ; difference: 18.96). In contrast, at electrode O2 this pattern was reversed (RVF: -11.41 ± 2.97 ; LVF: -21.16 ; difference: 9.75). For the vertical condition, the interaction Visual Field \times Electrode also reached significance ($F_{(1,39)} = 65.83$; $p < 0.001$), but had a higher effect size (partial $\eta^2 = 0.63$) than in the horizontal condition. Again, this interaction indicated that at the left-hemispheric electrode O1, the N1 had a higher amplitude after stimulus presentation in the contralateral RVF (-43.33 ± 4.47) than in the ipsilateral LVF (-12.34 ± 2.04 ; difference: 30.99), while at electrode O2 this pattern was reversed (LVF: -32.43 ± 3.66 ; RVF: -10.53 ± 2.47 ; difference: 21.90). Thus, the absolute amplitude differences between LVF and RVF stimulus presentation were higher for both electrodes in the vertical compared to the hori-

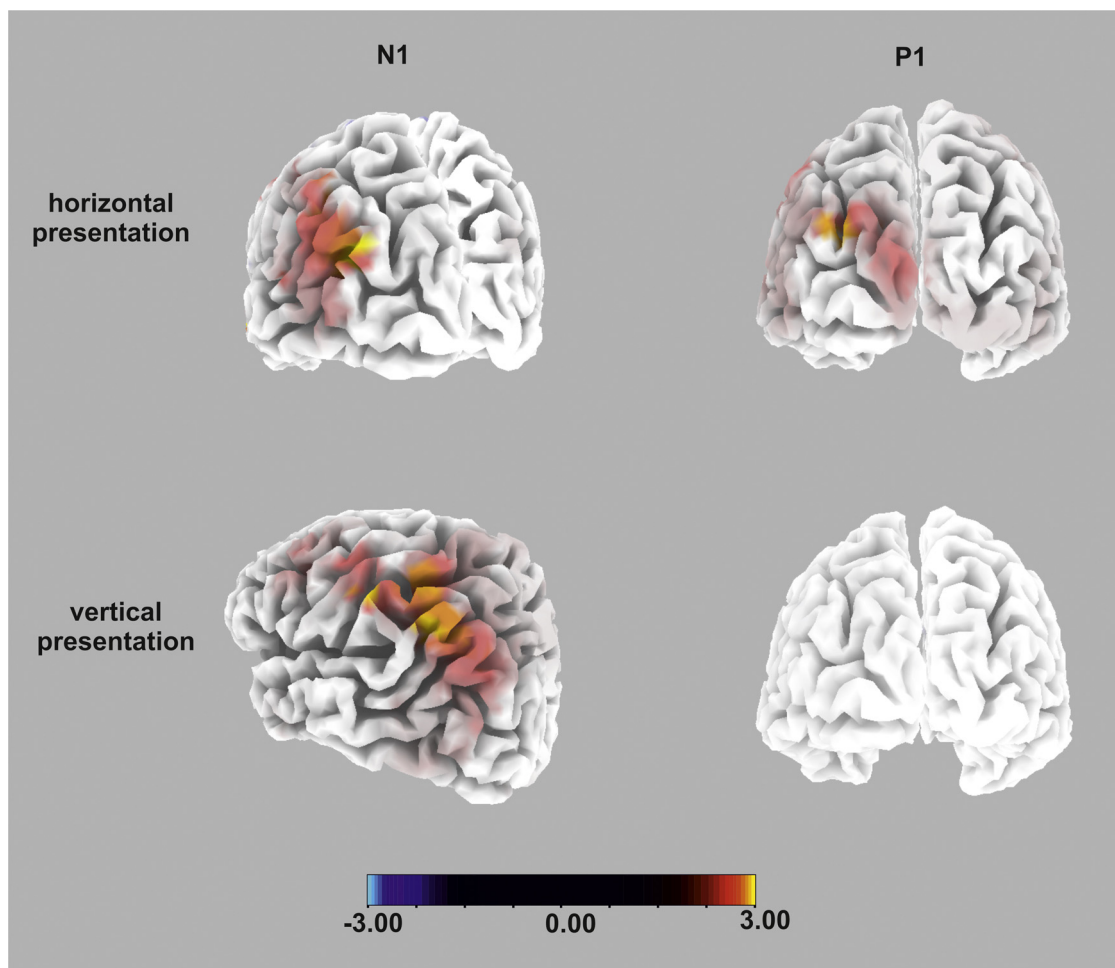


Fig. 5. Cortical distribution of activation differences causing the difference in P1 and N1 amplitudes between presenting stimuli in the LVF and RVF for vertical and horizontal stimulus presentation as revealed by sLORETA.

zonal condition. All other main effects and interactions failed to reach significance (all p 's > 0.17).

For the horizontal condition, the difference in N1 amplitudes between presenting stimuli in the LVF and RVF was due to differences in activation (see Fig. 4) in the left extrastriate cortex (BA19), the left angular gyrus (BA39) and the left supramarginal gyrus (BA40). Moreover, a small cluster in the temporal lobe centred around BA 21 was observed. For vertical stimulus presentation, the difference in N1 amplitudes between presenting stimuli in the LVF and RVF was due to differences in activation (see Fig. 4) in the left angular gyrus (BA39) and the left supramarginal gyrus (BA40), but no cluster in the extrastriate cortex was observed.

3.2.2.2. Latency. For N1 latency, the interactions Visual Field \times Electrode ($F_{(1,39)} = 467.55$; $p < 0.001$; partial $\eta^2 = 0.93$) and Visual Field \times Electrode \times Condition ($F_{(1,39)} = 21.00$; $p < 0.001$; partial $\eta^2 = 0.36$) reached significance. All other main effects and interactions failed to reach significance (all p 's > 0.08).

To further investigate the key interaction, we calculated two separate ANOVAS with the within subject factors Electrode (O1, O2) and Visual Field (LVF, RVF) for the two stimulus presentation conditions. For the horizontal condition, the interaction Visual Field \times Electrode reached significance ($F_{(1,39)} = 357.79$; $p < 0.001$; partial $\eta^2 = 0.90$). This interaction indicated that at the left-hemispheric electrode O1, the N1 had an earlier onset after stimulus presentation in the contralateral RVF (144.90 ms \pm 2.37) than in the ipsilateral LVF (192.00 ms \pm 2.90; difference: 47.1).

In contrast, at electrode O2 this pattern was reversed (LVF: 144.68 \pm 4.11; RVF: 194.76 \pm 3.04; difference: 50.08). For the vertical condition, the interaction Visual Field \times Electrode also reached significance ($F_{(1,39)} = 442.29$; $p < 0.001$), but had a higher effect size (partial $\eta^2 = 0.92$) than in the horizontal condition. Again, this interaction indicated that at the left-hemispheric electrode O1, the N1 had an earlier onset after stimulus presentation in the contralateral RVF (135.06 ms \pm 2.07) than in the ipsilateral LVF (193.51 ms \pm 3.12; difference: 58.45), while at electrode O2 this pattern was reversed (LVF: 135.51 \pm 2.98; RVF: 195.39 \pm 3.28; difference: 59.88). Thus, the absolute latency differences between LVF and RVF stimulus presentation were higher for both electrodes in the vertical compared to the horizontal condition.

4. Discussion

While countless studies have shown a dominance of the left hemisphere for most aspects of speech perception [11,49], the question, during which stage in the processing of verbal stimuli FCAs emerge first, has not yet been answered unequivocally. Several previous studies have proposed that FCAs in the language system depend on speech executive functions [8,42,78]. However, studies on animal vocalisations have shown that lateralisation can emerge even for rather basic forms of communication in non-human species (e.g. [6,70]). Additionally, a recent fMRI study investigating speech production [35] has shown an early emergence of FCA's in the sensory auditory areas before activation in

frontal areas. Thus, it could be assumed that the origins of human language lateralisation are more likely to lie in the perceptual processing of basic stimulus-features stimuli rather than in the speech executive functions [52]. In light of these conflicting theories, the aim of the present study was to determine the role of early perceptual processes for the emergence of FCAs in the language system, as well as the underlying neurophysiological processes. For this purpose we used a verbal decision task. The conceptual basis of this paradigm was the assumption that if early perceptual processing, as opposed to late semantic processing, is the decisive factor for the emergence of language lateralisation, then results on the behavioural and electrophysiological level should be modulated by stimulus presentation format.

On the behavioural level, the analysis revealed that participants were faster and more accurate when stimuli were presented horizontally rather than vertically, as demonstrated by [78]. This effect may be caused by the fact that vertical word presentation is visuospatially more demanding and suppresses reading-related learning effects [47,63]. Furthermore, an efficacy advantage of the LH for verbal stimuli (e.g., [11,29,74]) was reflected by faster and more accurate performance for stimuli presented in the RVF than in the LVF. Interestingly, we also observed an interaction between presentation format and visual field for correct responses. This interaction showed that the efficacy advantage of the left hemisphere vanishes when stimuli were presented vertically, as no significant asymmetry was observed when this condition was analysed separately. Thus, our behavioural findings clearly show that stimulus presentation format modulates verbal FCA's.

Interestingly, stimulus presentation format also modulated ERP asymmetries at early processing level. For the P1, we found higher amplitudes after vertical compared to horizontal stimulus presentation. This is in line with findings that the P1 shows a higher amplitude for inverted compared to non-inverted faces [20], indicating an effect of unexpected stimulus orientation on this ERP component. This finding is also in line with works that show the P1 has a higher amplitude when participants attend to a stimulus [21], as a more complex or unusual stimulus demands higher attention to be processed correctly. Moreover the Visual Field \times Electrode \times Condition interaction reached significance for P1 latency. While for both conditions, a shorter P1 latency was observed after contralateral compared to ipsilateral stimulus presentation at both electrodes, the extent of this asymmetry was larger after vertical compared to horizontal stimulus presentation. Thus, hemispheric asymmetries in the P1 data are enlarged by the unusual vertical stimulus presentation format, a finding that was also confirmed by the Visual Field \times Electrode \times Condition interaction for the latency data.

The sLORETA analysis revealed that the difference in P1 amplitudes between presenting horizontal stimuli in the LVF compared to the RVF was due to differences in activation in two different clusters. On the one hand, ERP asymmetries were driven by the left extrastriate cortex (BA18), an area involved in early visual perceptual processing [56]. For example, the extrastriate cortex (BA18 & BA19) has been shown to be involved in visual stereo-depth perception [14], visuospatial information processing [77], visual word perception [75] and feature-based attention [34]. On the other hand, ERP asymmetries were also driven the left angular gyrus (BA39). In fMRI studies, BA39 has been linked to reading-associated activation and it has been shown that words activate this area more strongly than pseudowords [30]. Interestingly, a functional connectivity study by [22] demonstrated a significant correlation between reading ability and the strength of the individual functional connection between left BA39 and Broca's area when subjects were reading. [33] suggested that this area is the neuronal substrate of the orthographic lexicon, and that it is relevant for the processing of highly lexicalised visual word representations.

The N1 is the earliest negative component that reflects verbal recognition [72], indicating early visual word discrimination [28]. After presentation of verbal stimuli, the N1 shows left lateralisation that is thought to reflect an efficacy advantage for the speech-dominant LH [18,1,39]. In contrast to classic N1 studies in which the stimuli are presented centrally, we used a divided visual field paradigm. Thus, left lateralisation of the N1 was represented on two levels. On the one hand, we observed greater negativity of the N1 at the left-hemispheric electrode O1 than at O2 in the right hemisphere, as reflected by the main effect for visual field. Moreover, the N1 was also more negative after stimulus presentation in the RVF and thus initial processing in the left hemisphere, than after stimulus presentation in the LVF. Thus, we could fully confirm earlier findings of a left-lateralisation of this ERP component. Additionally, N1 amplitude revealed a stronger negativity for vertical stimulus presentation format, which can be explained by spatial attention being drawn to stimulus with higher processing demands (e.g. [27]) or an initiation of discriminative processes [28]. Furthermore, N1 negativity was greater at both electrodes after stimulus presentation into the contralateral visual field [32,26], as the interaction electrode \times visual field demonstrated. The more pronounced left hemispheric N1, as opposed to the right hemispheric N1, also indicates a left hemispheric specialisation in verbal processing. In accordance to N1 amplitude findings, latency on both electrodes was shorter after stimulus presentation within the contralateral visual field, which has also been shown by Itzchak et al. [31]. These shorter latencies also highlight a faster verbal processing within the left hemisphere. Comparable to the P1 latency data, the Visual Field \times Electrode \times Condition interaction reached significance for N1 amplitude and latency. For both conditions an earlier N1 onset and higher amplitudes was observed after contralateral compared to ipsilateral stimulus presentation at both electrodes. However, the extent of these asymmetries was larger after vertical compared to horizontal stimulus presentation. These amplitude results were further confirmed by the latency results.

The sLORETA revealed that the difference in N1 amplitudes between presenting horizontal stimuli in the LVF compared to the RVF was due to differences in activation in two different clusters that were similar to that revealed for the P1. Again, the left extrastriate cortex (BA19 in this case) and the left angular gyrus (BA39) drove ERP asymmetries. Additionally, a cluster in the left supramarginal gyrus (BA40) emerged. The supramarginal gyrus is a parietal area that has been shown to be involved in phonological word processing [23], but also visual word recognition [71]. Stoeckel et al. [73] used TMS to investigate the functional specificity of the supramarginal gyrus during reading. They could show that stimulation of this area facilitated reaction times for both a phonological and a semantic task, concluding that the supramarginal gyrus is involved in visual word recognition independent of specific task demands. Interestingly, for vertical stimulus presentation, only the left angular gyrus (BA39) and the left supramarginal gyrus (BA40) drove N1 asymmetries, but no cluster in the extrastriate cortex was observed. This indicates that the later parietal areas in the visual word processing stream seem to be of the same relevance for ERP asymmetries in this condition as in the horizontal condition. However, the highly automated visual word-form processing driven by the extrastriate cortex [76] is not, indicating that these processes might not be triggered by the unusual stimulus presentation format in the vertical condition. The idea that other, perhaps more conscious processing strategies might be relevant in this condition is also supported by the fact that reaction times in the vertical condition were significantly longer than in the horizontal condition. Due to that fact that we used a divided visual field paradigm and analysed opposing electrodes in the two hemispheres, a direct comparison of ERP and behavioural data is difficult, since in the ERP analyses the additional factor electrode was present. While for the

behavioural data the Visual Field by Condition interaction reached significance, this interaction failed to reach significance for amplitude and latency for both ERP components. This, however, was not unexpected since obviously the effect of Visual Field on the ERP components is extremely dependent on the factor Electrode. However, the Visual Field \times Electrode \times Condition interaction reached significance for N1 amplitude and latency and P1 latency, clearly showing, that ERP asymmetries were also modulated by stimulus presentation format. Interestingly, ERP asymmetries were enlarged, and not diminished by vertical presentation format, indicating that P1 and N1 might not be the ERP components most behaviourally relevant to the response process in our task. Possibly, there might be top-down processes that affect functioning of the extrastriate cortex, as shown by Mechelli et al. [44] and Woodhead et al. [79] Thus, it might be of interest for future studies to investigate the interplay of visual word processing and response adaptation processes driven by fronto-striatal circuits [4].

Taken together, the present study shows clear electrophysiological support for the assumption that language lateralisation arises primarily from a left dominance for the processing of perceptual stimulus aspects and is secondarily influenced by early semantic top-down processing. The sLORETA findings show that these effects are mainly driven by the extrastriate cortex and reading-associated areas in the parietal cortex, but not by the left inferior frontal areas typically associated with semantic word processing [65]. This finding is consistent with a recent fMRI study in humans [35], as well as with translational research on lateralisation of vocalisation in non-human animals (e.g. [6,70]). Our electrophysiological results support the idea, that FCA's in speech executive functions might be caused by bottom-up processes triggered by the early perceptual functions.

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