



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 [16,23,35,36,63]. 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 [10,27,47]. 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 [9,41,75], some studies also suggested a role of earlier perceptual processes [34,50]. In particular, a recent fMRI study by [34] 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 [34] 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. [52]), 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. [75] presented words and non-words in horizontal and vertical presentation format to participants using the divided visual field technique (e.g. [2,5,44]). 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. [75] while recording event-related potentials (ERPs). In order to determine, whether analogous to Kell et al. [34] 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 [39,60]. It is centred over the occipital lobe [39] 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 [39]. The earliest visual ERP component reflecting leftward language dominance is the N1 [39]. It is associated with early visual attention towards verbal stimuli and discrimination between linguistic and non-linguistic stimuli [69] and peaks about 150–200 ms after stimulus presentation [37]. Anatomically, the N1 has been associated with the occipital lobe [24] and more specifically the extrastriate cortex [66]. Typically, the N1 shows left lateralisation after presentation of words, which is thought to reflect an efficacy advantage for the speech-dominant LH [19,1,38].

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 [75] 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 [54]. 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. [74]. 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 350 ms. 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 [61,50,49]). 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 5 kΩ 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

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