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Asymmetric intra- and interhemispheric interactions during covert and overt sentence reading

Christian Keller, Christian A. Kell*

Brain Imaging Center and Department of Neurology, Goethe University, Frankfurt, Germany

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ABSTRACT

Covert and overt sentence reading evoke lateralized activations in overall bihemispheric networks. We assumed that the study of functional connectivity may reveal underlying principles of functional lateralization. Left-lateralized activations could relate to stronger reading-related modulation of intrahemispheric functional connectivity in the left than the right hemisphere. Alternatively, left-lateralization could result from suppression of contralateral processing and thus reflect asymmetric interhemispheric interactions. To address this issue, this functional MRI study investigated the regional lateralization of covert and overt German sentence reading in 39 healthy participants. Further, it revealed the modulation of the lateralized brain regions' functional connectivity and their contralateral homotopes by covert and overt reading (psychophysiological interactions).

Left-lateralization during covert reading was associated with stronger intrahemispheric coupling particularly in the left dorsal stream rather than with suppression of contralateral processing. Lateralization during overt sentence reading instead went along with additional recruitment of right perisylvian cortices involved in articulation by asymmetric positive heterotopic interhemispheric interactions. Given the paucity of interhemispheric anti-correlations with homotopic regions, functional lateralization is likely a consequence of a task-dependent interplay between asymmetric positive intra- and interhemispheric coupling.

1. Introduction

A major acquisition of cultural evolution is communicating and conserving linguistic information by means of writing and decoding this information by reading. This functional MRI study investigates the contributions of both hemispheres to covert and overt reading of German sentences and identifies regional lateralization of the underlying activations. More importantly, it investigates the reading-related modulation of functional connectivity of the lateralized seed regions and compares it with reading-related changes in functional connectivity of the contralateral homotopes. Based on ample evidence that functional specialization of a given region is associated with its functional connectivity, we presupposed that functional lateralization in terms of activation could be related to integration of the lateralized region into a specialized intrahemispheric network (Simonyan and Fuertinger, 2015; Stephan et al., 2007) that could be detected by comparing the intrahemispheric reading-related modulation of functional connectivity of the seed region (i.e. psychophysiological interactions, PPI) with the one of its contralateral homotope (asymmetric intrahemispheric functional connectivity, Fig. 1, left column). Alternatively, lateralization of a given brain region could arise from suppression of contralateral processing that could potentially be assessed on the blood-oxygen-level-dependent (BOLD) level by studying negative PPI (reading-related interhemispheric anti-correlations) between a given seed region and its homotope.

In addition, regional lateralization could also be associated with stronger interhemispheric interactions with contralateral brain regions compared to the interhemispheric functional connectivity profile of the homotope (asymmetric interhemispheric interactions, Fig. 1, right column). Such positive interhemispheric coupling between a seed region and the contralateral hemisphere can be interpreted as information transfer and/or recruitment of the contralateral hemisphere for processing (Stephan et al., 2007). Altogether, studying the asymmetry in functional connectivity of lateralized brain regions and their homotopes may reveal underlying principles of functional lateralization (Simonyan and Fuertinger, 2015; Stephan et al., 2007).

So far, no study investigated the asymmetry of task-modulated functional connectivity of the lateralized brain regions involved in covert or overt sentence reading. Given that the majority of

* Corresponding author.
E-mail address: c.kell@em.uni-frankfurt.de (C.A. Kell).

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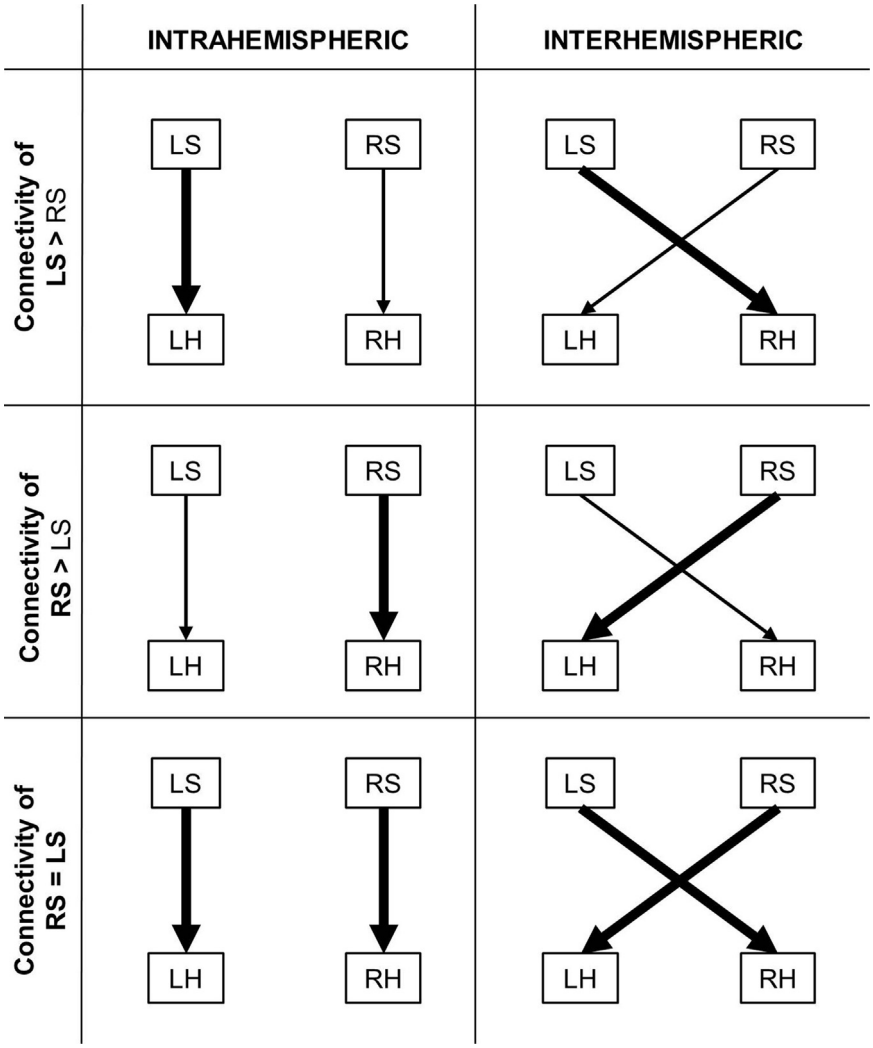

Fig. 1. *Possible hemisphere effects in speech processing-related psychophysiological interactions.* Left column (Intrahemispheric): a given region in the left (LH) or right hemisphere (RH) could have stronger intrahemispheric functional connectivity with its ipsilateral seed (left seed, LS) or right homotopic seed (RS) than its homotope with its respective seed (left > right upper row, right > left middle row) implying asymmetric intrahemispheric PPI. Alternatively, modulation of intrahemispheric functional connectivity could be not significantly different in the left and right hemisphere (lower row). Right column (Interhemispheric): a given region in the left or right hemisphere could interact more strongly with its contralateral seed than its homotope with its respective contralateral seed indicating asymmetric positive interhemispheric interactions. Note that arrows in this illustration do not indicate directed interactions but label seeds (start point of the arrows) and putative target regions (arrowhead) and that arrow thickness illustrates the interaction strength.

reading studies investigated covert single word reading, we will briefly present findings and models related to word level processing before summarizing previous literature regarding sentence processing followed by a synthesis of studies on overt reading. The emphasis is placed on the lateralization of task-related activity and the so far under-investigated asymmetries of reading-related functional connectivity changes.

1.1. Covert reading

Reading relies on the transformation of orthographic information into meaning. Two cognitive models of single word reading propose transformations of orthography to semantics either directly or via phonology. One model is connectionist (Harm and Seidenberg, 2004; Plaut et al., 1996) and the other one constitutes a dual-route model (Coltheart et al., 2001). Covert single word reading has been studied intensively using functional imaging. Meta-analyses of these reports provide a picture of left-lateralized inferior and middle temporal activations that have been related to direct transformations from orthography to semantics (components of the direct reading route) and left-lateralized superior posterior temporal and frontoparietal activations have been associated with indirect transformations via phonological representations (components of the indirect reading route, Binder et al., 2009; Jobard et al., 2003; Price, 2012; Taylor et al., 2013). These activations form intrahemispheric functional ventral and dorsal occipito-temporo-frontal streams and can be detected through effective connectivity analyses. They originate in the left inferior occipital and left fusiform gyrus, relay in the posterior temporal cortices, project ventrally via the anterior temporal lobe to the triangular part of Broca's region (direct reading route) and dorsally via the temporo-parietal junction and the dorsal premotor cortex (dPMC) to the opercular part of Broca's region (indirect reading route, Heim et al., 2009; Jobard et al., 2003; Mechelli et al., 2005; Yvert et al., 2012). Please note a comparable ventral/dorsal gradient for semantic/phonological processing has also been observed within occipito-temporal streams (Richardson et al., 2011; Yvert et al., 2012) but within this manuscript, we refer to the temporo-parieto-prefrontal network as the dorsal stream. These functional streams appear stronger in the left compared to the right hemisphere (asymmetric intrahemispheric functional connectivity, Bokde et al., 2001).