Neural coding of speech and language : fMRI and EEG studies

CHAPTER 6

Summary and future directions

Perceiving and using spoken language is a fast and effortless capacity that is essential for verbal communication in everyday life. The function of speech perception transcends our ability to listen and understand someone else's speech. It is part of the cognitive machinery that enables us to speak in a connected manner, to think using a linguistic 'currency', to access (verbal) memories and to enjoy the benefits of a conscious mind. Efforts to understand the neural mechanisms of speech perception are essential to face the challenges underlying language disorders, to develop brain computer interfaces or to understand human cognition. Speech perception involves both the processing of lower-level perceptual features of speech as well as their link to higher-order speech and language networks. This thesis investigates two levels of neural representation during online speech perception, those at the interface with the semantic memory network (Chapters 2 and 3) and the sensorimotor systems (Chapter 4).

Speech comprehension demands the access to lexical-semantic networks that activate semantic-conceptual representations distributed throughout the cortex. The neural mechanisms supporting these semantic-conceptual representations remain largely unresolved (Damasio, 1989; Patterson et al., 2007). Sensorimotor integration links the auditory and the motor systems of speech enabling the exchange of relevant speech information during acquisition and development of speech and language, and speech production in everyday life (Guenther and Vladusich, 2011). The need for sensorimotor integration during speech perception is highly debated (Hickok et al., 2011; Pulvermuller and Fadiga, 2010; Galantucci, 2006). In particular, methodological constraints related to experimental design and analysis methods have so far prevented the disentanglement of neural responses to acoustic versus articulatory features of speech.

This thesis uses fMRI (functional magnetic resonance imaging) and EEG (electroencephalography) to image brain responses to particular properties of speech utterances, namely the semantic identity of words and concepts, and articulatory representations of spoken syllables. Multivariate pattern analysis

(MVPA) was employed to exploit the interaction between multiple brain imaging responses in combination with its capacity to predict information from complex response patterns (Formisano et al., 2008a; Pereira et al., 2009). Most crucially, we have employed generalization strategies that show the capacity to classify speech utterances across variation of other acoustic dimensions (Formisano et al., 2008b), such as concepts across different word forms from English and Dutch (Chapters 2 and 3), and articulatory features of syllables across other articulatory dimensions (Chapter 4). Furthermore, we have investigated a new approach to find connectivity between distributed brain regions encompassing the representation of brain-states as uncovered by fMRI-based MVPA (Chapter 5). This approach enables to study neural communication in brain networks based on the transfer of information representation instead of covariance of fMRI activity strength.

In chapter 2 and chapter 3 we investigate the neural representation of semantic concepts evoked by equivalent but acoustically distinct spoken Dutch and English words in bilingual subjects. We analyzed brain responses to several presentations of four monosyllabic animal words in each language. Using MVPA, we trained classifiers to predict the individual words participants were listening to within each language and thereafter tested whether this learning was generalizable to the other language. In chapter 2, we used fMRI and showed the feasibility of both within-language discrimination and across-language generalization using a focal multivariate approach – the *searchlight* method (Kriegeskorte et al., 2006). Our findings indicate that in bilingual listeners, language-independent semantic-conceptual knowledge is organized in abstract form in focal regions of the cortex. In particular, we observed language-independent representations of spoken words in the left anterior temporal lobe (ATL), which converges with previous findings showing fMR adaptation effects in this region for cross-language semantic priming of visual words in bilinguals (Visser et al., 2012). Furthermore, it corroborates the neuropsychological findings in semantic dementia (Damasio et al., 1996) and indicates a role of the left ATL as a central-hub in abstract semantic processing (Patterson et al., 2007).

In chapter 3 the same experimental design was adapted to EEG to investigate the temporal and temporal-oscillatory dynamics of spoken word comprehension using MVPA. We identified specific time windows and frequency bands enabling discrimination and generalization of individual spoken words. We demonstrated within-language word decoding in a broad time-window from ~50 to 620 ms after word onset with a strong contribution of slow oscillations (below 12 Hz). Most importantly, we were able to isolate specific time windows, including the 550-600 ms window, in which EEG features enabled the generalization of the meaning of the words across their Dutch and English word forms. The results of chapter 3 demonstrate the feasibility of using MVPA to identify individual word representations based on speech evoked EEG signals. Furthermore, they indicate the advantage of feature selection approaches in assessing temporal (Hausfeld et al., 2012; Chan et al., 2011) and temporal-oscillatory EEG response features in classification.

In chapter 4, we used fMRI in combination with similar cross-class generalization strategies to investigate the representation of articulatory features of spoken syllables during speech perception. In this study we explored whether during the perception of speech, the brain extracts motoric information of speech signals, such as related to their articulatory gestures instead of acoustic information alone. Using a *searchlight* approach we highlighted several cortical areas that are sensitive to articulatory features, such as place of articulation, manner of articulation and voicing. Crucially, using a generalization strategy we were able to decode articulatory features of spoken syllables, across acoustic variation of other articulatory dimensions. This strategy is important since most articulatory gestures of speech sounds also vary in acoustic properties, thus restricting the possibility to disentangle both types of representations. Our cortical generalization maps suggest invariant neural representations of manner and place of articulation within a distributed network of auditory, somatosensory and motoric neural populations and of voicing in a more restricted region in the right anterior temporal cortex. Furthermore, they support the notion that the representation of spoken syllables during on-line speech perception includes the transformation of acoustic input to abstract articulatory codes.

In chapter 5, inspired by the sensitivity of *searchlight* to find focal activity patterns informative of stimulus related brain-states, we developed and validated a novel approach for functional connectivity that relies on the availability of information instead of activation across brain regions. In this *information-based connectivity* (IBC) approach information representation obtained by MVPA in focal regions-of-interest is used to find region-pairs that encode the same information in a consistent manner across single-trials. The advantage of information- over activation-based connectivity relates to its potential to identify neural representation transfer across brain regions that originate from information fluctuations beyond co-variation in activation strength. Furthermore, current limitations of functional connectivity analysis based on fMRI time-series (activation strength) include the low temporal resolution of fMRI recordings and the inherent slow hemodynamic changes of neuronal activity (Eichler, 2005). IBC uses single-trial estimates to investigate functional connectivity at the informational level, which minimizes the risk for spurious interpretations of temporal correlations of BOLD responses across brain regions (Rissman et al., 2004; Waldorp et al., 2011).

Overall, the findings in this thesis follow on the success of the *searchlight* method as an approach to map information representation in the cortex (Kriegeskorte et al., 2007). Specifically, we have exploited the potential of *searchlight* and its characteristic of using patterns of small number of voxels (features), to generalize information across different stimulus dimensions. We propose that reduced feature spaces may maximize the ratio of generalizable features, and that this factor is crucial in designs that we refer here as *cross-class generalization*. Beyond discrimination, this strategy allows findings commonalities between information patterns. In chapters 4 and 5, the *searchlight* method was employed on the cortical surface (Chen et al., 2011) instead of in the volume, allowing a selection of focal features based on their geodesic rather than volumetric proximity. This methodological change posits an advantage to avoid cross-gyral overlap, and was particularly relevant to reduce the possible contamination of activity between auditory and motor regions. The *searchlight* method also served as an inspiration for the functional connectivity approach described in chapter 5. We are interested to further pursue the IBC method as a potential method to combine, at the informational level, recordings from different imaging modalities acquired simultaneously, such as fMRI and EEG. There, similar principles as in IBC may allow finding spatial and temporal associations between patterns from fMRI and EEG using their information-based single-trial predictions rather than relying on the disparate physiological nature of these signals.

Researching speech using multivariate classification was fundamental in this thesis. The findings with regard to conceptual and sensory-motor representations can help to formulate new and finer grained hypothesis for speech processing models. They will also bring a better understanding of functional (activation and information based) neural networks, representation, and computation. From a methodological point of view, to further our understanding on neural mechanisms of speech, we believe it is crucial to 1) increase the statistical sensitivity and specificity of data analysis methods, and 2) to pursue the within-category investigation of neural representations of individual speech items (e.g. syllables, words, etc), instead of their average activity across categories (e.g., words versus non-words). In fact, the capacity to discriminate between two items from the same category is crucial to understand and comprehend speech in everyday communication. MVPA provides the means to ask such questions with the adequate statistical sensitivity. Its capacity to unravel information discrimination together with information commonalities using generalization strategies employed in this thesis, also promises to study the interlinked representations between speech perception and speech production faculties. When combined with well-designed stimuli and experiments, this approach shows potential to answer a number of unresolved questions in speech research, such as 1) the link of speech perception and speech production with a network for conceptual knowledge, and 2) the similarity of articulatory representations during perception and production.

Our results also indicate potential to assess the contribution of temporal-oscillatory EEG response features in the representation of speech. Beyond spatial and temporal signatures of speech perception, temporal-oscillatory features relate to the neural mechanisms underlying spoken word and concept representation (Peelle and Davis, 2012; Giraud and Poeppel 2007; Lakatos et al., 2005). In the future, methods able to assess the multivariate contribution of more sophisticated aspects of temporal-oscillatory dynamics, such as phase-phase-coupling and phase-amplitude-coupling (Voytek et al., 2013) may allow identifying crucial aspects of speech perception and production that may relate to an entrainment of neural oscillations to temporal features of speech signals and synchrony mechanisms across different frequency bands over time.

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