SPECIAL ISSUE: INTRODUCTION

INTEGRATIVE MODELS OF BROCA'S AREA AND THE VENTRAL PREMOTOR CORTEX

Ricarda I. Schubotz[1] **and Christian J. Fiebach**[1,2]

([1]Max Planck Institute for Human Cognitive and Brain Sciences, Department of Cognitive Neurology, Leipzig, Germany; [2]Neurocognition and Cognitive Neurology Group, Psychological Institute and Department of Neurology, Ruprecht-Karl-Universität of Heidelberg, Germany)

The present special issue of *Cortex* originated in a workshop that was held at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig in September 2003, that brought together cognitive neuroscientists working in two different sub-fields, language processing and actions processing. This workshop aimed to examine the degree of compatibility between functional models of Broca's area and the premotor cortex from the perspective of these two fields. Furthermore, the possibilities of integrating such models into a more general account of this region's function were discussed.

It is the aim of modern cognitive neuroscience to explore the neuroanatomical underpinnings of perception, cognition, and goal-directed action. As a result of traditional specializations within experimental psychology, as well as pragmatic necessities, most researchers focus their efforts on component processes such as, for example, visual perception, memory, language, or executive functions. While this strategy is common in cognitive neuroscience, there is a potential danger of producing neurocognitive models for certain cognitive processes that are incompatible with models for other processes, while at the same time targeting identical brain regions.

In our work, we experienced that the two fields, language (or, most specifically, syntactic processing) and action perception, both consider Broca's area and the adjacent ventral premotor cortex (vPMC) as crucial components of the brain circuitry involved in sentence comprehension and in the perception of others' actions, respectively. This may reflect that indeed the same neural mechanisms are involved in both sentence processing and action perception/execution. Alternatively, such common activation patterns may also be the result of an involvement of distinct neural populations that are very closely located, i.e., within the same macro-anatomical region. Most neurocognitive models proposed in either field take a domain specific approach to accounting for Broca/vPMC involvement in the respective process, and do not explicitly consider how the involvement in the respective other process may be explained. Few exceptions try to bridge the gap between language and action, for example on the basis of a hypothesis concerning a common evolutionary precursor of both brain regions in question here (Rizzolatti and Arbib, 1998).

It is our strong belief that neurocognitive models that attribute certain functions to specific brain regions also have to take into account empirical results on how these brain regions are involved in other cognitive processes. The present Special Issue, as well as the workshop held in Leipzig, are intended as a platform for presenting models of the functionality of Broca's area and ventrolateral premotor cortex that originate from the domains of language or action perception, and – most importantly – for identifying commonalities and areas of discrepancy, as well as possible interfaces between the different approaches. Our focus on one circumscribed cortical region should not be taken to indicate that the contributors to this Special Issue do believe this is the only critical region for the processing of language and actions. In fact, we believe that distributed networks of cortical and subcortical brain regions are involved in both processes of interest. Nevertheless, the present effort focuses on one shared component of these distributed networks. It is an attempt at determining whether or not it is necessary, plausible, and feasible to conceptualize the functions of Broca's area and the vPMC on a level that is meaningful for both research domains (and possibly also others such as, for example, working memory or music perception). To this end, several outstanding researchers from both fields came together to present and discuss their models and positions.

In this special issue of *Cortex*, the workshop participants and other invited representatives of the two research fields provide a set of short position papers where they present their models and discuss their theoretical positions regarding a general cognitive mechanism for Broca's area and the vPMC. These position papers reflect a broad range of perspectives, ranging from proponents of the view that language-specific mechanisms are represented in Broca's area (Grodzinsky, 2006, this issue; Caplan, 2006, this issue), to accounts assuming relative specialization for language but

allowing also for an involvement in non-language domains (Friederici, 2006, this issue; Dominey and Hoen, 2006, this issue; Ullman, 2006, this issue), to accounts that explicitly assume that there is a common functionality of Broca's area and vPMC that contributes to different processing domains (Fadiga and Craighero, 2006, this issue; Tettamanti and Weniger, 2006, this issue; van Schie et al., 2006, this issue; Fiebach and Schubotz, 2006, this issue), to models that assume shared cortical networks for different higher cognitive functions (Iacoboni and Wilson, 2006, this issue), to more general theoretical accounts that integrate language and action (Arbib, 2006, this issue). The behavioral benefits of an action perception/execution matching system that has been proposed to reside in Broca's area and vPMC are also discussed (Prinz, 2006, this issue).

These position papers are supplemented by some broader perspectives onto the present topic, including an overview of Broca's area and vPMC involvement in music processing (Koelsch, 2006, this issue) and an alternative theoretical position concerning the development of possible communication systems in vPMC that may be evolutionary pre-cursors of language (Wise, 2006, this issue). A position paper by Amunts and von Cramon (2006, this issue) discusses how functionally defined brain regions can serve as a starting point for employing modern neuroanatomical methods to delineate previously un-identified brain regions. This point is illustrated with a brain region that directly borders Broca's area and premotor cortex, and that may house cognitive mechanisms critical for a wide range of processes. Finally, a review article by Corina and Knapp (2006, this issue) discusses the brain systems of sign language in the context of current knowledge concerning the mirror neuron hypothesis.

In addition to this theoretical section, the present special issue also provides room for nine original research papers that focus on various aspects of Broca's area and language processing. Two contributions focus on the role of Broca's area for morphological processing, one using functional imaging methods (Sahin et al., 2006, this issue) and the other using a neuropsychological and computational modeling approach (Penke and Westermann, 2006, this issue). These two articles challenge earlier models of morphological processing by opposing the notion of separate systems for regular *versus* irregular inflection. Sahin et al. (2006, this issue) conclude that Broca's area supports grammatical processes that cannot be explained in terms of more general cognitive mechanisms. Importantly, activations in Broca's area as well as other areas involved in inflectional processing did not distinguish between regular and irregular inflection in this study. Penke and Westermann (2006, this issue) conclude from the results of a computational modeling study that selective deficits for one type of inflection, as reported by these authors for irregular inflection in German and Dutch Broca's aphasics, cannot be taken as evidence for separate cognitive or neural mechanisms for regular and irregular inflection.

Three contributions investigate the role of Broca's area during sentence processing using functional magnetic resonance imaging. Love et al. (2006, this issue) explore how sentence complexity effects, generally attributed to Broca's area, may be dependent on the specific demands of the cognitive task. They demonstrate that Broca's area activation reflects task demands, and argue that Broca's area underlies mnemonic and integrative functions that are important for language and other cognitive processes. A second paper, by Chen et al. (2006, this issue), also relates syntactic complexity effects observed in Broca's area to specific task demands. Most specifically, Chen et al. (2006, this issue), report that complexity effects in Broca's area in the context of a plausibility judgment task are a result of the ease of thematic role assignment. In a third contribution, Hoen et al. (2006, this issue) compare activation in Broca's area elicited by the processing of sentences and abstract, non-linguistic sequences. Their finding of shared neural substrates for sentence and sequence processing in the left posterior inferior frontal gyrus speaks directly to the main question of the present special issue, i.e. whether or not neural mechanisms of Broca's area are unique to language or shared with other domains.

Two further research articles target functions of Broca's area for phonological processing during reading (Fiez et al., 2006, this issue) and speech perception (Burton and Small, 2006, this issue). Fiez et al. take a very detailed lesion-based approach to explore the necessity for word and nonword reading of a left fronto-opercular region that was repeatedly reported in functional imaging studies. Based on a comparison of brain activation elicited during speech and tone segmentation, Small and Burton (2006, this issue) propose a domain general account of Broca's area's involvement in phonological processing. According to this view, the role of Broca's area during phonological tasks is not speech specific, but related to the demand of segmenting and comparing acoustic stimuli.

Finally, Uylings et al. (2006, this issue) provide a detailed anatomical study of Brodmann's areas 44 and 45, which are, in the left hemisphere, the constituent regions of Broca's area. By comparing cortical volume and neuron counts between these regions in the left and right hemispheres, these authors provide additional evidence for linking functional asymmetries of Broca's area to an anatomical basis.

Together, these position papers and original research papers provide a broad view into current research conducted in the investigation of the

neural bases of language perception. The theoretical perspectives onto language research that are provided by researchers in the field of action perception and imitation, music perception, and abstract sequence processing in their position papers, outline some of the challenges for future research for all fields of research that have been involved in the present special issue. We hope that this unique collection of theoretical and empirical research papers is as stimulating for the readers as it has been for us in the past months while working on editing the present issue of *Cortex*.

We want to express our gratitude to the directors of the Max Planck Institute of Human Cognitive and Brain Sciences, Angela Friederici and Yves von Cramon (2006, this issue), for generously supporting the workshop that inspired the present special issue. We further want to express our appreciation for all the colleagues who served as reviewers for the manuscripts that appear in this Special Issue. We finally also want to thank Dorothea Weniger and Sergio Della Sala for making this special issue possible.

References

Amunts K and von Cramon DY. The anatomical segregation of the frontal cortex: What does it mean for function? *Cortex, 42:* 525-528, 2006.

Arbib MA. A sentence is to speech as what is to action? *Cortex, 42:* 507-514, 2006.

Burton MW and Small SL. Functional neuroanatomy of segmenting speech and nonspeech. *Cortex, 42:* 644-651, 2006.

Caplan D. Why is Broca's area involved in syntax? *Cortex, 42:* 469-471, 2006.

Chen E, West WC, Waters G and Caplan D. Determinants of BOLD signal correlates of processing object-extracted relative clauses. *Cortex, 42:* 591-604, 2006.

Corina DP and Knapp H. Sign language processing and the mirror neuron system. *Cortex, 42:* 529-539, 2006.

Dominey PF and Hoen M. Structure mapping and semantic integration in a construction-based neurolinguistic model of sentence processing. *Cortex, 42:* 476-479, 2006.

Fadiga L and Craighero L. Hand actions and speech representation in Broca's area. *Cortex, 42:* 486-490, 2006.

Fiebach CJ and Schubotz RI. Dynamic anticipatory processing of hierarchical sequential events: A common role for Broca's area and ventral premotor cortex across domains? *Cortex, 42:* 499-502, 2006.

Firz JA, Tranel D, Seager-Frerichs D and Damasio H. Specific reading and phonological processing deficits are associated with damage to the left frontal operculum. *Cortex, 42:* 624-627, 2006.

Friederici Angela D. Broca's area and the ventral premotor cortex in language: Functional differentiation and specificity. *Cortex, 42:* 472-475, 2006.

Grodzinsky Y. The language faculty, Broca's region, and the mirror system. *Cortex, 42:* 464-468, 2006.

Hoen M, Pachot-Clouard M, Segebarth C and Dominey PF. When Broca experiences the Janus syndrome: An ER-fMRI study comparing sentence comprehension and cognitive sequence processing. *Cortex, 42*: 605-623, 2006.

Iacobini M and Wilson SM. Beyond a single area: Motor control and language within a neural architecture encompassing Broca's area. *Cortex, 42:* 503-506, 2006.

Koelsch S. Significance of Broca's area and ventral premotor cortex for music-syntactic processing. *Cortex, 42:* 518-520, 2006.

Love T, Haist F, Nicol J and Swinney D. A functional neuroimaging investigation of the roles of structural complexity and task-demand during auditory sentence processing. *Cortex, 42:* 577-590, 2006.

Penke M and Westermann G. Broca's area and inflectional morphology: Evidence from Broca's aphasia and computer modelling. *Cortex, 42:* 563-576, 2006.

Prinz W. What re-enactment earns us. *Cortex, 42:* 515-517, 2006.

Rizzolati G and Arbib MA. Language within our grasp. *Trends in Neuroscience, 21:* 188-194, 1998.

Sahin NT, Pinker S and Halgren E. Abstract grammatical processing of nouns and verbs in Broca's area: Evidence from fMRI. *Cortex, 42:* 540-562, 2006.

Tettamanti M and Weniger D. Broca's area: A supramodal hierarchical processor? *Cortex, 42:* 491-494, 2006.

Ullman MT. Is Broca's area part of a basal ganglia thalamocortical circuit? *Cortex, 42:* 480-485, 2006.

Uylings HBM, Jacobsen AM, Zilles K and Amunts K. Left-right asymmetry in volume and number of neurons in adult Broca's area. *Cortex, 42:* 652-658, 2006.

Van Schie HT, Toni I and Bekkering H. Comparable mechanisms for action and language: Neural systems behind intentions, goals, and means. *Cortex, 42:* 495-498, 2006.

Wise SP. The ventral premotor cortex, corticospinal region C, and the origin of primates. *Cortex, 42:* 521-524, 2006.

Ricarda I. Schubotz, Max Planck, Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1A, 04103 Lepzig, Germany. e-mail: Schubotz@abs.mpg.de

Christian J. Fiebach, Neurocognition and Cognitive Neurology Group, Psychological Institute and Department of Neurology, Ruprecht-Karl-Universität Heidelberg, Germany. e-mail: christian@fiebach.org