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Editorial

Neuroanatomy of Language: New Insights from Lesioned and Healthy Brains

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Language, spoken and written, the most complex of the higher cognitive brain functions, is unique for the humankind and the reason we can create science and civilization. The ability to map words on to meaning expanded our horizons. Irrespective of the coding system, creation of languages was driven by the same principle, the intrinsic need for communication and the brain's capability to support it. Across history and continents, among human races and ages many different languages have been created, ideographic or alphabetic, making possible our communication through meaningful symbols, expressions and comprehension of ideas and concepts. The need for communication is not only human of course, and language was not a recent and sudden development in human evolution. Unrevealing the neural networks that serve language is a central and difficult challenge in neurosciences. Across the years progress has been achieved by studying mainly brain lesioned aphasic patients, as it is not possible to develop non-human models of language processing (except in the case of extracting informative connectional data on neuroanatomical homologies from non-human models) as we do for many other brain functions [1].

From Broca's era, when language research was autopsy driven [2], until today, when new imaging and neuromodulation techniques are available [3], the investigation of the neural basis for human language was based mainly on the study of brain damaged aphasic patients, and patients undergoing electrical stimulation mapping during neurosurgical procedures. A new era began, when neuroscience conquered safe tools and techniques for clinical and experimental applications of neuroimaging and artificial manipulation, stimulation or depression, of brain activity. We can now provide a more detailed description of the functional neuroanatomy of language, modeling human brain responses during speech perception and production both in health and disease, linking language to other cognitive functions such as memory, attention, and executive functions, following diseased aphasic brains' functional reorganization underlying recovery, describing new entities such as primary progressive apraxia of speech [4], or introducing and discussing controversial terms such as "presbyphasia", which reflects the activation of ancillary networks in aging brains supplementing the core language networks.

The Wernicke-Lichtheim, or alternatively the Broca-Wernicke-Lichtheim-Geschwind classical model, based on the work of Broca, Wernicke, Lichtheim, Geschwind and others predominated for more than a century as the standard neurological model of language, in which Wernicke's area is connected to Broca's area by the arcuate fasciculus, guided research for long and is still useful for a first approach into the classical categorization of aphasic syndromes. It is now outdated, because it proved that "it could not account for the range of aphasic syndromes, and it is linguistically and anatomically underspecified" [5]. As recently stated by Trembley and Dick, the classical model is based on an outdated brain anatomy, it does not adequately represent the distributed connectivity relevant for language, it offers a modular perspective, and it focuses on cortical structures, leaving out subcortical regions and relevant connections [6]. One of the most serious gaps was the lack of circuit information regarding the neural connections of the brain areas involved.

New observations on auditory processing in non-human primates and speech perception in normal subjects have produced a fundamental shift away from the standard model to modern network-based models composed of parallel and interconnected streams involving both cortical and subcortical areas, emphasizing speech processing in "dorsal" and "ventral" pathways [7]. Hickok and Poeppel [8] outlined a dual-stream model of speech processing: a ventral stream processes speech signals for comprehension, and a dorsal stream maps acoustic speech signals to parietal and frontal-lobe articulatory networks. The ventral stream is largely bilaterally organized from the temporal pole to the basal occipitotemporal cortex, with anterior connections (with important computational differences between the left- and right-hemisphere systems) and the dorsal stream is strongly left-hemisphere dominant, from the poster superior temporal to the inferior frontal cortices [9]. The function of the dorsal route is mainly restricted to the sensory-motor mapping of sound to articulation, whereas linguistic processing of sound to meaning is transmitted via the ventral route [10]. Anatomical and functional interactions, 'bottom up' or 'top down' processes or recurrent feedback loops between dorsal and ventral processing networks, must further be investigated [11].

Although the model describes the anatomical foundations of normal, and not disordered, speech and language processing, Fridriksson., *et al*. in an elegant, recently published, follow-up study tried using lesion data from patients with stroke to explain aphasic symptoms in the context of this model, examining the effect of both cortical damage and disconnection on aphasic impairment [12]. They found that measures of motor speech impairment mostly involve damage to the dorsal stream, whereas measures of impaired speech comprehension are more strongly associated with ventral stream involvement. Additionally, and importantly they showed that language functions such as naming, speech repetition, or grammatical processing rely on a broader cortical network and on interactions between the two streams, and this finding explains why patients with dissimilar lesion locations often experience similar impairments on given subtests.

Support to the dual-stream model, but furthermore, a novel synthesis of traditional and contemporary views of the cognitive and neural architecture of language processing is provided by the work of Mirman., *et al* [13]. Their results revealed two major divisions within the language system-meaning versus form and recognition versus production. Phonological form deficits were associated with lesions in peri-Sylvian regions, whereas semantic production and recognition deficits with damage to the left anterior temporal lobe and white matter connectivity with frontal cortex, respectively. The peri-Sylvian regions involved in phonological processing were further subdivided into supra-Sylvian regions for speech production and infra- Sylvian regions for speech recognition. The extra-Sylvian regions involved in semantic processing were also divided between production and recognition processes. Impairment of semantic production, reflected in semantic errors, was strongly associated with left ATL lesions, whereas multimodal semantic recognition deficits were associated with impaired connectivity between the frontal lobe and other brain regions involved in semantic processing. Moreover, this work illuminated the importance of tracts beyond the arcuate fasciculus, i.e. the uncinate fasciculus, the inferior fronto-occipital fasciculus, and the anterior thalamic radiations.

Hurth and colleagues used a novel generative model with data collected while subjects listened to hours of narrative stories to create a detailed semantic atlas [14]. They showed that the semantic system is organized in our brains into intricate patterns that seem to be highly consistent across individuals. The distribution of semantically selective areas within the semantic system represent information about specific semantic domains, or groups of related concepts and is relatively symmetrical across the two cerebral hemispheres. This finding is inconsistent with human lesion studies that support the idea that semantic representation is lateralized to the left hemisphere, however, in alignment with the bilateral distribution of ventral stream of dual-stream model.

What about the cerebellum? The cerebellum does not appear either in the classical nor in the modern models of the neuroanatomy of language, although cerebellar lesions do cause aphasia [15] and the cerebellum's role in a wide range of nervous system's cognitive and affective functions, among them language, is being revealed [16]. The cerebellum's role opens new basic science and clinical questions as to the real extend of the brain networks serving speech and language, questions that challenge the existing models and must be addressed.

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