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Editorial

Voices below the surface: Is there a role for the thalamus in language?

The idea that the thalamus plays a role in language (or any other cognitive process) has been debated for decades. In many ways, the debate about the thalamus in language is a surrogate discussion about the role of the thalamus in general. The thalamus projects to, and receives input from, all areas of the cerebral cortex and is an obligatory processing station for all sensory information en route to the cortex. Early case reports that demonstrated loss of language function after thalamic lesions (Fisher, 1959) suggested that the thalamus may be a key player in the core network of structures important for language. Other early models suggested that the thalamus may play a more supportive role, either as a central integrating center (Penfield & Roberts, 1959) or as a source of generalized activation of the cortex (Hunter & Jasper, 1949). This debate heated up in the 1970s and 1980s with the advent of CT scanning and the use of deep brain stimulation in the thalamus to treat movement disorders. This work led to seminal reviews on the subject by Crosson and colleagues (Crosson, 1985, 1999, 1992; Nadeau & Crosson, 1997). The last major review on the subject was over 10 years ago by Johnson and Ojemann (2000).

Since then, a series of new findings surrounding the role of the thalamus in information processing has led to a resurgence of interest in the role of the thalamus in cognitive functions, including language. Specifically, recent anatomical, physiological and imaging work has suggested that the thalamus, rather than being a simple gate for sensory information en route to cortex, may serve as a tunable filter to enhance or suppress subsets of information either from the sensory periphery, or between cortical areas, and that these functions may depend on the firing mode of the thalamus (Alitto & Usrey, 2005; Crabtree & Isaac, 2002; Lesica et al., 2006; Theyel, Llano, & Sherman, 2010; Wang et al., 2007; Zikopoulos & Barbas, 2006, 2012). Therefore, this Special Issue attempts to integrate new findings about thalamocortical organization into a framework that provides a functional basis for the role of the thalamus in language.

Herein, we present seven articles that reopen this debate. The Special Issue commences with a review by Charles Lee of the organization of the forebrain structures potentially important for speech processing. Special attention is paid to the 'non-primary' parts of the thalamus, that is, parts of the thalamus that have complex response properties and do not project to the middle cortical layers of the primary sensory cortices. Within this article, Dr. Lee explores different potential models of thalamocortical organization, and how the thalamus may interact with the cerebral cortex. He contrasts models that suggest that the nonprimary parts of the thalamus function to provide sustained activation to particular regions of cortex vs. other models that suggest that the thalamus may route information from one cortical area to another.

In "The organization of the auditory thalamus and its relationship to language," Ed Bartlett describes the organization of the projections between the posterior temporal cortex and thalamus. Importantly, he reviews the physiology of the auditory thalamus and cortex, with particular interest in the processing of temporally-modulated signals similar to those found in speech. Dr. Bartlett also describes the relationships between clinical disorders involving language or other cognitive dysfunction and thalamic dysfunction. For example, he details the distribution of the FOXP2 gene, implicated in language, in the thalamus and cortex and discusses the impact of various disease states, including dyslexia, schizophrenia and Alzheimer Disease, on auditory thalamocortical function.

Helen Barbas and colleagues discuss the relationship between areas of the frontal cortex involved with language and the thalamus. Using examples from the clinical literature and primate anatomical and physiological studies, they describe an expanded number of subcortical structures involved with language, including the basal ganglia, cerebellum and thalamic reticular nucleus. They integrate recent findings about the detailed laminar organization of both thalamocortical and corticothalamic projection systems, along with the organization of basal ganglia projections and modulatory dopaminergic projections, to develop a theory of how such a network can support the complex sequence of cognitive and motor events needed to produce language.

In "Functional imaging of the thalamus in language," I present a meta-analysis of 50 imaging studies (PET and fMRI studies) that reported thalamic activation in language tasks. I find that the language tasks most likely to elicit activation of the thalamus are tasks that involve the selection of a lexical item from semantic cues, and that the most common pattern of activation is left thalamic activation coupled to activation of 'traditional' language areas near the Sylvian fissure. In addition, I claim that developing more precise models of the role of the thalamus in language based on imaging is limited by both methodological and study design factors and propose approaches to address these.

In "Thalamic mechanisms in language: A reconsideration based on recent findings and concepts", Bruce Crosson characterizes the clinical and neuropsychological features of language deficits seen after thalamic damage. He then incorporates some of the recent findings in thalamocortical organization to propose several specific and testable theories about the role of thalamus, the thalamic reticular nucleus, basal ganglia and the cortex in language tasks. Specifically, Dr. Crosson describes the potential for cortical-thalamic interactions to mediate selective engagement of particular cortical loci important for language, the potential for the thalamus to pass information from one cortical area to another, for corticothalamic projections to sharpen sensory representations and how a network comprising frontal cortex, caudate/putamen, globus pallidus and thalamus may facilitate word selection.

In "Semantic Memory Retrieval Circuit: Role for BA6 and Thalamus," John Hart, Mike Kraut, and colleagues review a body

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of literature that examines interactions between the thalamus, caudate, and Brodmann's area 6 for retrieval of semantic information. They describe the performance, imaging and electrophysiological correlates of normal subjects, thalamic lesion patients and patients with other deficits in semantic retrieval on several semantic memory tasks, including a semantic object retrieval task. With respect to the thalamus, they propose a model whereby the pulvinar may play a role to synchronize neural activity across multiple brain regions to facilitate retrieval of a coherent, integrated semantic memory.

Lastly, we are honored to have the historical perspective from one of the 20th century pioneers in the neurobiology of language, George Ojemann, who has collaborated with Adam Hebb on "The Thalamus and Language Revisited." They take a historical view of the field and review a long line of deep brain stimulation studies. Many of these studies were originally done by Dr. Ojemann, who pioneered deep brain stimulation approaches to examine the impact of selective silencing or stimulation of the thalamus on performance of language tasks. They use the data from these findings, in conjunction with newer findings about thalamic organization, to support a "Specific Alerting Response" theory of thalamic function. The theory suggests different roles for specific groups of nuclei (ventral tier + intralaminar, posterior nuclei and intermediate nuclei), which may ultimately lead to testable hypotheses about the role of the thalamus in language.

These contributions remind us about an important literature documenting a role for the thalamus in language and help integrate that history with new findings about thalamocortical organization. It is hoped that these reviews will spark renewed interest in this topic and will generate new hypotheses to be tested. It is important to recognize that such work will not only provide insights into the secrets underlying the role of the thalamus, but will also help us to understand the broad networks underlying language function. The idea that understanding the thalamus will pay broad scientific dividends is not new – A. Earl Walker, in his groundbreaking monograph about the thalamus in 1938 (Walker, 1938), made this very point to us many years ago:

> *"The thalamus holds the secret of much that goes on within the cerebral cortex."*

I am sure that I speak for all the contributors in seconding this century-old view of the thalamus, and in hoping that our readers will gain an understanding of this perspective.

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Daniel A. Llano
University of Illinois at Urbana-Champaign,
Department of Molecular and Integrative Physiology,
2355 Beckman Institute, 405 N. Mathews Ave.,
Urbana IL 61801, United States
E-mail address: d-llano@illinois.edu