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HST .722 – Brain Mechanisms of Hearing and Speech
Topic proposal

# Corticothalamic feedback connections

## Introduction

The thalamus is the main sensory input to the cerebral cortex, not only for auditory stimuli, but also for visual and somatosensory stimuli (Alitto and Usrey, 2003). On the other hand, approximately half of the neuron input to the dorsal thalamus come from the cortex. These corticothalamic feedback connections seem to be important for sensory processing in the visual, auditory and somatosensory systems. In this topic, we will specifically look at corticothalamic connections in the auditory system.

First of all, some background on the auditory thalamus and the corticothalamic feedback connections will be given. Then, we will discuss two papers related to the effects of cortical inactivation and stimulation on thalamic processing. Finally, possible functional roles played by these connections will be discussed, and in particular the idea that the thalamus is an adaptive filter controlled by the auditory cortex, and that the left corticothalamic feedback system may help in speech separation tasks.

## Background

### *The Auditory Thalamus*

Several nuclei of the thalamus are involved in the processing of acoustic information, such as the lateral part of the posterior nucleus, the reticular nucleus, and the medial geniculate body. The medial geniculate is an obligatory connection for the inferior colliculus and for the auditory cortex (cf. figure 1). It can be divided into several subnuclei, based on the shape and density of their neurons, as well as on their projections and inputs.

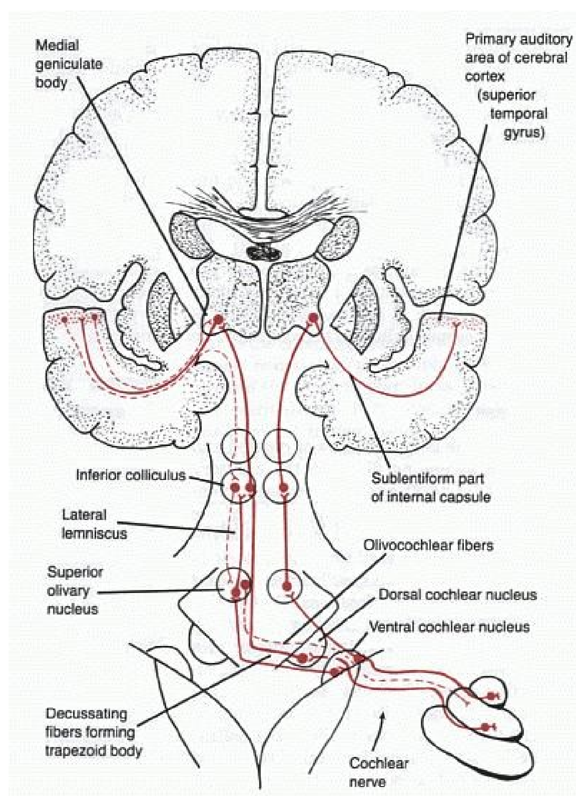

*Figure 1: The Thalamus in the Auditory System(dashed lines are descending pathways)*

Multiple parallel ascending pathways converge to the thalamus from the inferior colliculus (de Ribaupierre, 1997). Anatomical and physiological evidence suggests that these distinct channels are maintained up to the auditory cortex. The ascending pathways between the thalamus and the cortex can be divided into three main systems: a tonotopic system, a diffuse system, and a polysensory system, which connect different parts of the thalamus to different parts of the cortex, with some degree of superposition between the systems.

Conversely, information that is processed in the auditory cortex is sent to various subcortical and cortical targets. Among these targets is the auditory

thalamus, which suggests that feedback control from the auditory cortex to the thalamus is functionally important. We will focus on these corticothalamic connections.

***Anatomical Characteristics of the Corticothalamic Connections***

It is thought that the medial geniculate receives as many descending connections from the auditory cortex as ascending connections from the inferior colliculus (de Ribaupierre, 1997). It has been shown with retrograde labeling from the medial geniculate body (Rouiller and de Ribaupierre, 1985) that these descending connections originate from pyramidal neurons in layers V and VI of the auditory cortex. It is interesting to note that these connections respect the tonotopic organization and are reciprocal, i.e. they target the same location in the thalamus from which they receive their input (Winer and Lee, 2007).

## Effects of cortical inactivation and stimulation on thalamic processing

***Effects of cortical inactivation***

One approach to study corticothalamic connections is to record from thalamic neurons during a temporary inactivation of the auditory cortex, and compare their response to a baseline condition prior to inactivation. This is the approach adopted by Villa et al (1991). They circulated ice-cold water in an aluminum cylindric core in contact with the dura mater of anesthetized cats in order to inactivate the cortical synapses. They monitored cortical inactivation by observing the shape of evoked potentials, and they recorded from single units in various locations of the auditory thalamus.

They looked at the changes produced by cortical inactivation on various parameters of interest. First of all, the spontaneous activity in all locations tended to decrease, except for a minority of neurons for which it either decreased or did not change. They also recorded thalamic activity in response to pure tones, and observed a change in frequency response range (either an increase or a decrease) for many units under cortical inactivation condition. They also looked at the best frequency of these units before and after cortical cooling, and noted that for many units, there was a significant change. These results are shown in figure 2a. Finally, they used white noise burst stimuli and observed changes in the peri-stimulus time histograms. For most units, the initial shape was recovered after cortical inactivation was stopped. An example of recording in response to noise bursts is shown on figure 2b.

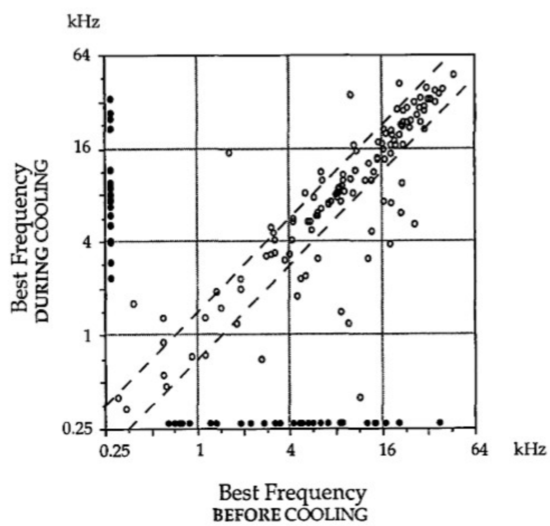


*Figure 2a: Best Frequency of Tuning before vs. after cooling*

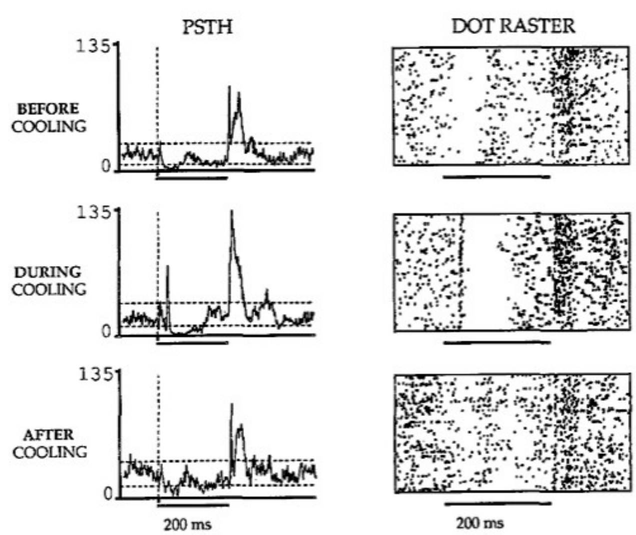


*Figure 2b: Single unit response to 200ms noise bursts*

Their experiments suggested that cortical inactivation had an influence on thalamic activity, in a way that was specific to the anatomical subdivision of the auditory thalamus. Tuning as well as temporal processing characteristics were affected in each subdivision. This paper will also be interesting for a discussion of their methodological approach, which could have contributed to alter the neuronal activity in the thalamus.

***Effects of cortical stimulation***

He et al (2002) propose an alternative way to look at the influence of cortex activity on thalamic output. Instead of cooling down the cortex temperature to inactivate it, which is not very selective, they implanted electrodes in the cortex of guinea pigs and stimulated it electrically. A sound stimulus was delivered to the contralateral ear after a delay, following the end of the cortical stimulation. Responses of thalamic neurons were recorded before and after the stimulation condition. They specifically focused on the ventral part of the medial geniculate body.

They found, first of all, that a low stimulation current had a facilitatory effect on thalamic activity; nonetheless, this effect was not monotonic with current intensity, until becoming inhibitory for very large currents. An effect of the interval between the electrical stimulation and the acoustic stimulus was observed. Tuning curves were also modified by corticofugal activation, in various ways. Finally, the firing patterns showed some changes in their temporal structures (cf. figure 3).

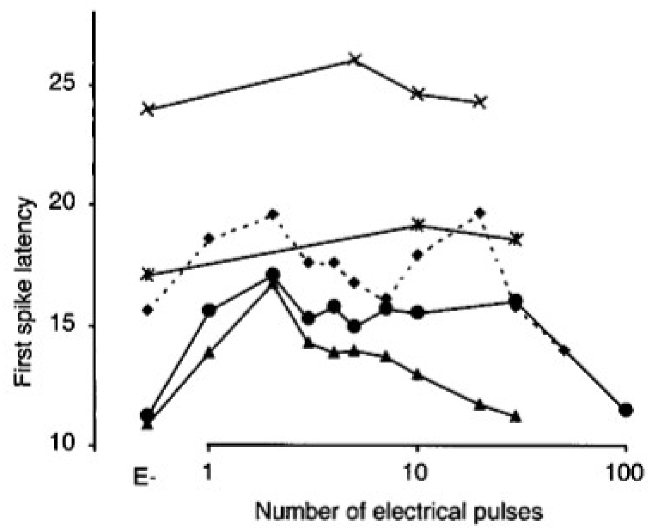


*Figure 3: Changes of the first spike latency caused by cortical stimulation*

## Functional roles of the corticothalamic connections

***Adaptive filtering***

As we discussed earlier, several studies suggest that the auditory cortex is able to precisely control thalamic activity. Therefore the auditory cortex changes its own input by changing the processing characteristics of the thalamus. In that sense, it can be considered as an adaptive filtering function, since the filter parameters are adjusted over time as a function of the filter output. Villa et al go even further in the analogy with an adaptive filter model. They argue that such a system could be used to segregate sources, since the corticothalamic feedback connections could enhance some channels over others, based on the correlation between a reference signal provided by the cortex and the thalamic output signal.

***Speech separation***

According to the model, this adaptive filtering mechanism could be used for any type of signal, as long as there is a reference signal to compare to. The particular case of a speech signal is of great interest. In an fMRI study, Alain et al (2005) tested listeners in a vowel separation and identification task. Two vowels were presented simultaneously, and the change in brain activity between the case when the two vowels were correctly identified, and the case when only one sound was correctly

identified, was measured. Among other results, it is striking to see that a significant increase in activation occurred in the left thalamus, primary auditory cortex, and planum temporale (cf. figure 4). This is consistent with the view that the interaction between cortex and thalamus may be involved in source segregation. The fact that most differences were seen in the left hemisphere is also consistent with the dominance of this hemisphere for language functions in most individuals.

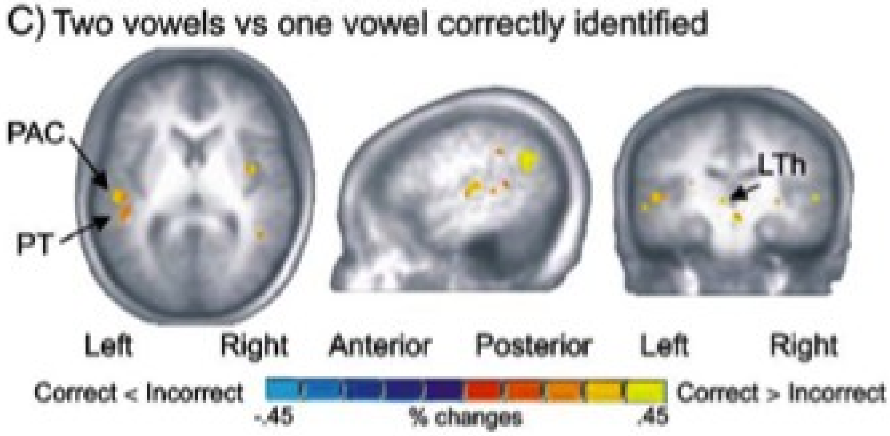


*Figure 4: Difference in activation when participants successfully identified both vowels relative to when only one vowel was correctly identified*

## Conclusion

This topic aims at emphasizing a particular descending pathway of the auditory system: the corticothalamic feedback connections. The papers I proposed for background reading and discussion suggest that these connections have significant and various effects on thalamic output. The function of these connections could be to adjust the processing parameters of the thalamus, which would act as an adaptive filter controlled by the auditory cortex. This could play a role in source segregation and speech separation in particular.

Many aspects of this theme need to be further investigated, and, in particular: what are the neural circuits accounting for these cortex-induced changes in activity? what functions do these corticothalamic interactions realize? do the other descending pathways from the auditory cortex (to the inferior colliculus, or even to the cochlear nucleus) have the same modulatory effects, and to what extent can they be compared?

Finally, I think this topic fits well in the set of topics covered in class, for several reasons. First, it involves the auditory thalamus, which is a center that we did not specifically target in the existing class topics; nonetheless, it would be interesting to compare the response types and possible functions with other centers, such as the dorsal cochlear nucleus, that we studied earlier in the semester. Moreover, the model proposed by Villa et al has some similarities with the model of DCN function that we studied, in the sense that in both cases a reference stimulus is used to suppress an expected response. Another connection with other topics is made by the fMRI paper selected here, which showed clear left-right differences in a language-related task. Finally, this topic naturally relates to the descending pathway topic, but with a focus on a particular cortical descending pathway, whereas the existing topic that we will discuss soon is more concerned with olivocochlear efferents.

## References

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* Papers for discussion
† Background reading