A neural network model of the inferior colliculus with modifiable lateral inhibitory synapses for human echolocation

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Abstract. We propose a neural network model of the inferior colliculus (IC) for human echolocation. Neuronal mechanisms for human echolocation were investigated by simulating the model. The model consists of the neural networks of the central nucleus (ICc) and external nucleus (ICx) of the inferior colliculus. The neurons of the IC receive interaural sound stimuli via multiple contralateral delay lines and a single ipsilateral delay line. The neurons of the ICc send output signals to the neurons of the ICx in a convergent manner. We stimulated the ICc with pairs of a direct sound (a sonar sound) and an echo sound (the reflection from an object). Information about the distance between the model and the object is expressed by the delay time of the echo sound with respect to the direct sound. The results presented here show that neurons of the ICc responsive to interaural onset time differences contribute to the creation of an auditory distance map in the ICx. We trained the model with various pairs of direct-echo sounds and modified synaptic connection strengths of the networks according to the Hebbian rule. It is shown that self-organized long-term depression of lateral inhibitory synaptic connections plays an important role in enhancing echolocation skills.

1 Introduction

It is somewhat surprising that visually impaired individuals have the ability to echolocate as bats and dolphins do. Although visually impaired individuals cannot achieve echolocation with high efficiency, they can learn to use artificial sonar sounds such as foot scrapping sounds (Strelow and Brabyn 1982; Seki et al. 1994) and long-cane tapping sounds (Schenkman and Jansson 1986) for echolocation. They detect the time difference between a direct sound (a sonar sound) and an echo sound (the reflection from an object) and obtain information about distance to the object. Auditory distance perception is also found in sighted individuals; however, echolocation skills in visually impaired individuals are remarkable by comparison. Their echolocation skills seem to be acquired through great training efforts. It is quite interesting to ask how visually impaired individuals have succeeded in acquiring such enhanced echolocation ability.

Bats are known to have a remarkable ability of echolocation (Suga 1988, 1995; Yan and Suga 1996). Mustached bats emit acoustical sonar sounds and get information about distances to targeted objects by detecting returning echoes from the objects. Information about delay times of echoes with respect to the emitted sonar sounds (direct sounds) is represented as a “distance map” in the auditory cortex. In this map, delay times of echoes ranging from 0.4 ms to 18 ms are systematically expressed.

For humans and most non-echolocating mammals, such a sophisticated auditory distance map has not been observed in the auditory cortex. Humans, rather, have developed an auditory system that suppresses echoes in order to catch the leading (direct) sounds (Grantham 1995). When the delay time of an echo is less than the “echo threshold”, it cannot be perceived as a distinctive sound. For example, when an echo delay keeps under 5–10 ms (for a single click or a brief noise burst), humans can perceive only the direct sound, not the echo sound. That is, the echo sound is completely suppressed.

This means that it is difficult for humans to perceive echoes that are sent back from “close” objects. In fact, humans generally cannot echolocate objects closer than about 2–3 m (Schenkman and Jansson 1986). However, there has been evidence that visually impaired individuals are able to lower the echo threshold through training (Schenkman and Jansson 1986; Seki et al. 1994), whereby enhancing performance on echolocation of closer objects. The important questions are how humans echolocate, how visually impaired individuals manage to lower the echo threshold, and what their exact neuronal mechanisms are.

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With respect to brain areas that may subserve for human echolocation, we have had a special interest in the dynamic properties of the inferior colliculus (IC). Neurons in the cats IC have been found that specifically respond to onset time differences between interaural stimuli. The number of these neurons confirmed is, at present, not large (7%). However, it is noteworthy that they have shown a specific response only when the ipsilateral stimulus is delayed with respect to the contralateral one (Kuwada and Yin 1983). That is, these IC neurons are “delay-tuned”.

Experimental data in rats (Horikawa and Murata 1988) have indicated that a delay axis is organized along the dorsocaudal–ventrocranial IC, ranging between 3.5 ms and 34 ms. The dorsocaudal and ventrocranial regions tend to respond to auditory stimuli with a shorter latency (~3.5 ms) and a longer latency (~34 ms), respectively. Similar delay axes have also been found in other non-echolocating animals such as gerbils (Semple and Kitzes 1985) and cats (Schreiner and Langner 1988; Irvine and Gago 1990). In bats, a similar latency axis is found in the dorsal–ventral IC (Yan and Suga 1996). Delay-tuned neurons could be systematically organized along a delay axis made by multiple delay lines (Suga 1995). Our main idea is that delay-tuned IC neurons organized along the delay axis may serve to process human echolocation.

The objective of this study is to propose that the IC is a brain area for processing echolocation in humans, and to investigate neuronal mechanisms underling human echolocation by simulating the neural network model of the IC. We also investigate neuronal mechanisms by which visually impaired individuals acquire their remarkable echolocation skills through training.

The model consists of two neural networks of the central nucleus (ICc) and external nucleus (ICx) of the IC. Its basic neuronal architecture was proposed by Hoshino and Kuroiwa (2000a,b). The neurons of the ICc receive interaural sound stimuli via multiple contralateral delay lines and a single ipsilateral line with no delay. A delay axis is formed on the contralateral side. The ICc neurons send output signals to the ICx neurons in a convergent manner. To understand the basic properties of the model, we stimulate the contralateral and ipsilateral afferent lines with various onset time differences. We apply pairs of direct-echo sounds and analyze the dynamics of the network system. To investigate how training improves echolocation skills, we modify synaptic connection strengths according to the Hebbian rule during an echolocation task.

2 Neural network model

The whole structure of the present neural network model is shown in Fig. 1a. The inferior colliculus (IC) consists of the central nucleus (ICc) and external nucleus (ICx). The ICc consists of five frequency arrays (fn; n = 1, 2, 3, 4, 5) and each neuron belonging to array fn is tuned to a particular sound frequency corresponding to fn, where f1 = 250 Hz, f2 = 167 Hz, f3 = 125 Hz, f4 = 100 Hz, and f5 = 83 Hz. Thus, these neurons create a tonotopic map in the ICc. Within the same frequency arrays, each neuron laterally inhibits other neurons via inhibitory synaptic connections. There is no synaptic connection across the arrays. The ICx receives excitatory inputs from the ICc in a convergent manner, and each neuron of the ICx laterally inhibits other neurons.

Anatomical and electrophysiological experiments (Rose et al. 1963; Merzenich and Reid 1974; Aitkin