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Sound localization: Jeffress and beyond

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Many animals use the interaural time differences (ITDs) to locate the source of low frequency sounds. The place coding theory proposed by Jeffress has long been a dominant model to account for the neural mechanisms of ITD detection. Recent research, however, suggests a wider range of strategies for ITD coding in the binaural auditory brainstem. We discuss how ITD is coded in avian, mammalian, and reptilian nervous systems, and review underlying synaptic and cellular properties that enable precise temporal computation. The latest advances in recording and analysis techniques provide powerful tools for both overcoming and utilizing the large field potentials in these nuclei.

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The Jeffress model, its variants and alternatives

How can an animal tell the direction a sound is coming from? In 1948, American psychologist Lloyd Jeffress published a germinal paper [1], in which he proposed that the time difference of low frequency sounds arriving at the two ears (interaural time difference, ITD) can be represented as a 'place' in an array of nerve cells. The place theory (hereafter also referred to as the Jeffress model) depends on three fundamental assumptions: (1) orderly arrangement in conduction times of ascending nerve fibers, which serve as 'delay lines', (2) conversion of input synchrony into output spike rates by 'coincidence detectors', and (3) systematic variation in spiking rates within the cell array to form a neuronal 'place map'. It was only after his death that the first reports appeared, demonstrating anatomically and physiologically the presence of the neuronal ITD maps in the barn owl [2,3]. In contrast to the success in the owl, however, two decades of research in mammals and reptiles have concluded that 'Jeffress is not the only answer' for sound localization. In this short review, we look first at various ITD coding schemes, then discuss their underlying synaptic and cellular properties, and briefly review recent advances in recording and analysis techniques.

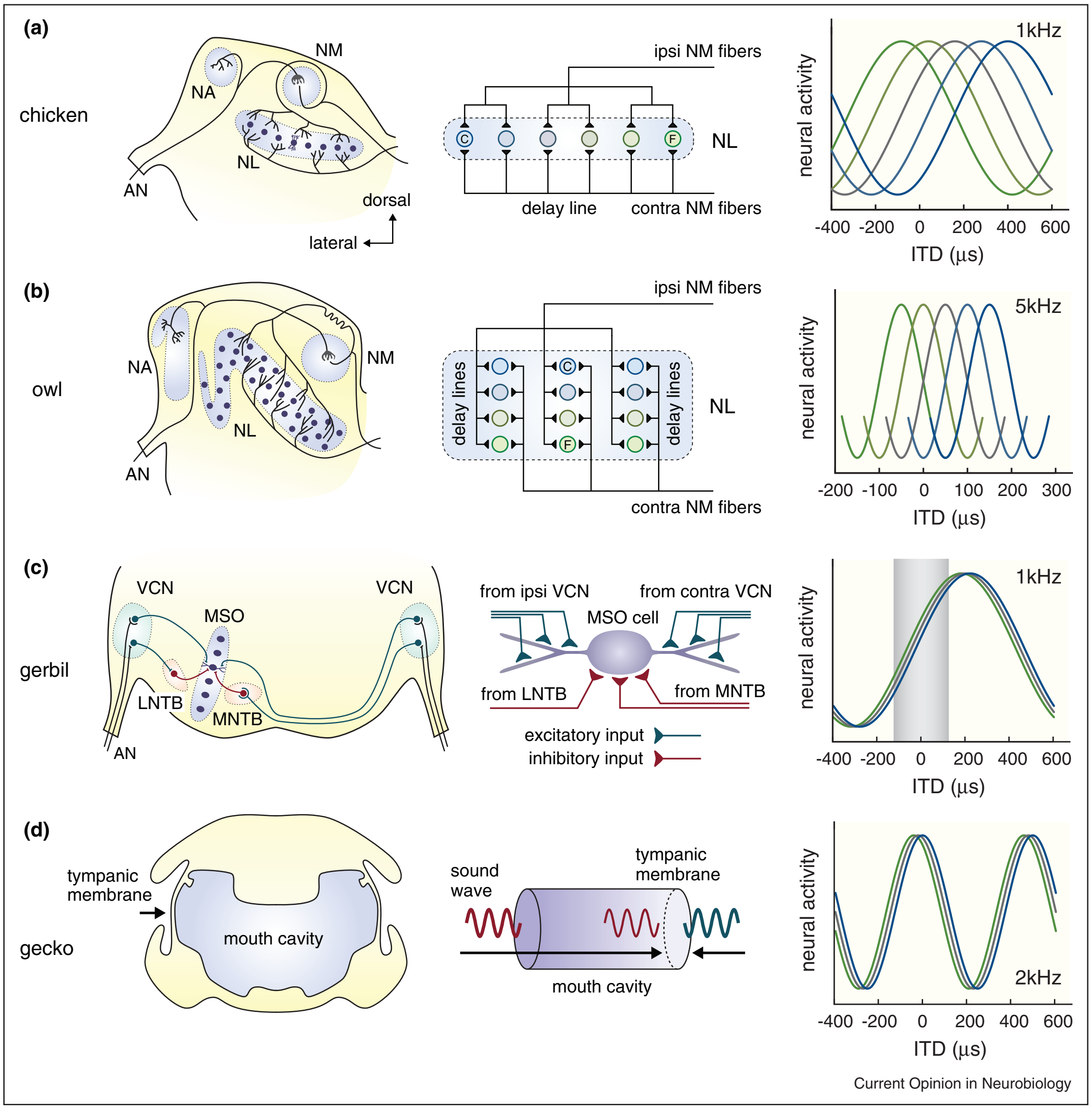
Birds

Chickens and owls are the most common birds used for the study of neuronal ITD coding. In these species, axons from the nucleus magnocellularis (NM) provide the delay lines, while the neurons in the nucleus laminaris (NL) serve as coincidence detectors and change their spike rates periodically with ITD (Figure 1a and b). In chickens, NL is a monolayer structure with cells tonotopically arranged mostly along the rostrocaudal axis. Within each single frequency band, the best ITD of the cell (i.e., the ITD to which the spike rate of the cell is maximal) gradually changes along the mediolateral positions [4], therefore forming a single ITD map (Figure 1a). A three-dimensional reconstruction of the chick NM fibers revealed that both axonal diameters and internodal distances, as well as the axonal length, play an fundamental role in creating the proper neural delays [5••]. In contrast to chickens, owls' NL neurons are sparsely distributed in the nucleus without forming a layered structure, resulting in multiple ITD maps in the dorsoventral dimension ([3] and Figure 1b). Anatomical and *in vitro* physiological evidence suggests that the emu also has a mono-layered place map in NL [6]. It is still unknown, however, whether the chicken-like single ITD map is prevalent among the bird species.

Mammals

In contrast to birds, the existence of ITD maps in mammals has been controversial [7–10]. Neurons in the medial superior olivary (MSO) nucleus change their spike rates in an ITD-dependent manner, but the peaks of the ITD-rate curves often lie outside the physiologically relevant time range (Figure 1c; see [9] for more detailed discussion). Moreover, most MSO cells in each hemisphere show similar ITD tuning. This suggests that the average spike rate of many MSO cells codes ITDs, using the 'slope' rather than the 'peak' of the tuning curves [11]. In the slope-coding framework, unlike the place codes found in birds (Figure 1a and b), sounds coming from the contralateral and ipsilateral sides, respectively, result in higher and lower average spiking rates of MSO neurons (Figure 1c). Note that this slope-coding theory is mostly based on the anatomical and physiological results in gerbils. Since recording from the MSO is highly challenging (we will discuss it later), only a limited amount of direct data in other species are available. Findings in guinea pigs seem to be in line with the slope-coding scheme [9]. Recent re-examination of

Figure 1



Various ITD coding strategies. (**a**) Chicken's ITD coding circuit. (*Left*) Schematic drawing of the chicken's brainstem. Axons from the ipsilateral NM enter NL dorsally, while those from contralateral NM enter ventrally. NL neurons are aligned in a thin flat layer. (*Center*) Jeffress-type organization of the chicken's NM-NL circuit. Axonal conduction times lead to a place map in NL. Neurons near the lateral border of NL (marked as 'C') response maximally to sounds coming from the far contralateral side, and cells located close to the medial edges of NL (marked as 'F') fires maximally to sounds originating from in front of the animal's head. (*Right*) Example ITD–response curves of NL cells tuned at 1 kHz. As stated above, the peak position of the tuning curve depends on the location of the neuron in the place map. Positive ITD values mean contralateral ear leading (i.e., sound arrives earlier at the contralateral ear than at the ipsilateral ear). (**b**) Owl's ITD coding circuit. (*Left*) Schematic drawing of the owl's brainstem. Similar to the chicken brainstem, axons from the ipsilateral NM enter NL dorsally, while those from contralateral NM enter ventrally. Owl NL neurons, however, are not aligned in a layered structure, but are distributed sparsely throughout the nucleus. (*Center*) Multiple Jeffress-type place maps of the owl's NM-NL circuit. Gradual changes in axonal conduction times along the dorsoventral dimension result in multiple place maps of NL cells. Neurons near the dorsal border of NL (marked as 'C') response maximally to sounds coming from the far contralateral side, and cells located close to the ventral edges of NL (marked as 'F') fires maximally to sounds originating from in front of the animal's head. (*Right*) Example ITD–response curves of NL cells tuned at 5 kHz. As in chickens' place map, the peak position of the tuning curve depends on the location of the neuron in the place map. (**c**) Gerbil's ITD coding circuit. (*Left*) Schematic drawing of the gerbil's brainstem. Spherical bushy cells in the VCN provide excitatory inputs to the MSO, while LNTB and MNTB neurons, which receive outputs of the globular bushy cells in the ipsilateral and contralateral VCN, respectively, send glycinergic inhibitory inputs to MSO. (*Center*) Schematic picture of a gerbil MSO neuron. The principal neuron of the MSO has bipolar dendrites segregating ipsilateral and contralateral excitatory inputs from the VCN. Inhibitory inputs from LNTB and MNTB are confined to the cell body region. (*Right*) Example ITD–response curves of MSO cells tuned at 1 kHz. In contrast to chicken's NL cells, the tuning curves of MSO neurons are very similar. Peak positions of the tuning curves can lie out of the physiological ITD range (i.e., ITDs encountered naturally) shown by the shaded area. (**d**) Gecko's ITD coding. (*Left*) Schematic drawing of the gecko's head. The inner ears of the gecko are interconnected through the mouth cavity. (*Center*) Gecko's ear as a pressure