

The Jeffress Model is a neurocomputational model that explains how auditory systems can register and analyze small differences in the arrival time of sounds at the two ears in order to estimate the direction of sound sources in the azimuthal plane.

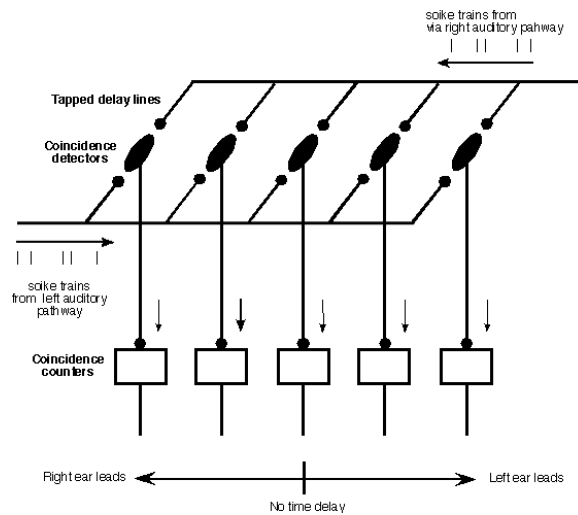
In 1948 Lloyd Jeffress sought to outline “a structural mechanism for representing a time difference spatially” (Jeffress, 1948). Jeffress explicitly had E.G. Boring’s general neural place-theory hypothesis in mind: that “all ‘knowledge’ [conscious distinction] is potentially spatial in the physiological sense” and that “we are looking for a ‘place theory’ of every dimension” ((Boring 1933) quoted in (Jeffress, 1948), brackets mine).

His proposed time-delay neural network model receives two sets of stimulus-locked spike train signals from the left and right auditory pathway and uses a set of delay lines and coincidence detectors to compute a temporal cross-correlation function. Due to the systematic spatial arrangement of the delay lines and coincidence detectors, the network converts an interaural temporal disparity into a maximum “place” of neural excitation. The network was perhaps the first explicit neural information-processing model to successfully account for major aspects of perceptual function.^[1] Although many of its details have been revised over the last half century, the Jeffress architecture, with its temporally coded input signals, delay lines, and coincidence detectors remains at the core of current models of how humans and animals perform binaural localization using interaural time difference cues.

Psychophysics. The model was formulated to account for binaural psychophysical observations. Humans are capable of using interaural time-of-arrival differences (ITDs) of as small as 10-20 microseconds to distinguish directional differences of sound sources in the horizontal plane as small as 1-2 degrees (azimuth). Typically ITDs range from 0 for sounds coming from directly in front to about 700 microseconds or sounds coming directly from either side (see (Colburn and Durlach 1978) for comprehensive reviews of binaural psychophysics)).

Time-delay neural network. The time-delay neural architecture (Fig. 1) consists of 1) temporally-coded input signals consisting of spikes that are time-locked to the waveform of the acoustic stimulus, 2) two sets of tapped conduction delay lines that convey spike trains encoding monaural signals are fed into 4) an array of binaural spike coincidence detectors, whose outputs are then in turn fed into 5) coincidence counters. The delay lines are arranged in antiparallel fashion to implement a range of possible relative delays between the two sets of monaural lines. These relative delays then are systematically mapped to particular spatial “places” within the coincidence array. The axonal conduction lines make excitatory synapses onto the coincidence detector elements. When incoming pulses arrive at roughly the same time at a given detector, within a given temporal coincidence window, the detector emits an output pulse. Trains of output pulses are then transmitted to coincidence counters, which sum spikes over a given temporal integration window to compute the running firing rates of their respective coincidence detectors. In the 1948 paper Jeffress did not explicitly include coincidence counters or discharge rate integrators, but instead talks in terms of more or less excitation (higher firing rate) in one or another part of the delay array. For example, a sound source directly

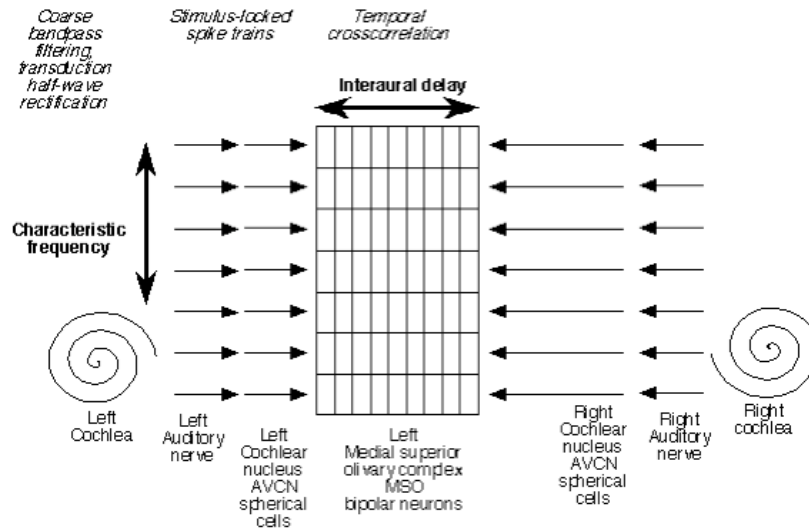
in front of the listener would maximally excite coincidence detectors in the middle of the array, whilst a highly lateralized source at the sides would excite detectors at one edge of the array.



[[Image:JeffressFig1.gif|thumb|400px|right|label|Figure 1. The tapped delay lines, coincidence detectors and coincidence counters (rate integrators) of the Jeffress model.]]

Jeffress envisaged that each cochlear “place” or frequency channel would map to a separate neural cross-correlation circuit, such that the whole architecture consists of an array of these circuits (Fig. 2).

The inputs to the binaural time-delay cross-correlator come from the left and right auditory neural pathways. In mammalian auditory systems, incoming acoustic signals are first mechanically filtered by the outer, middle, and inner ear (cochlea) and transduced by inner hair cells of the cochlea into synaptic currents that in turn produce action potentials in auditory nerve fibers. Each auditory fiber innervates one cochlear inner hair cell and projects in a cochleotopic manner to a small number of spherical bushy cells in the anteroventral cochlear nucleus. Their large, highly secure synapses, called endbulbs of Held, drive the target spherical cells to produce trains of action potentials that replicate the input spike trains almost on a spike-by-spike basis as well as preserving precise spike timing. The spherical cells, in turn, bifurcate and project to bipolar cells in both the left and right brainstem, medial superior olivary nuclei (MSO), again preserving the cochleotopic organization of the mappings. (see (Casseday and Covey 1987) for an overview of the neuroanatomy).

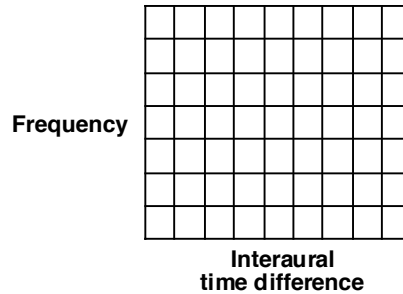


[[Image:JeffressFig2.gif|thumb|400px|right|label|Figure 2. Inputs to the left binaural cross correlator.]]

Although the rough outlines of major ascending auditory pathways and the existence of phase-locked responses in the auditory nerve were known in 1948, the circuitry in the auditory brainstem that might support binaural crosscorrelation had not been worked out. Jeffress considered both the lateral superior olivary complex and the lateral lemniscus as possible loci, but correctly rejected them on physiological grounds. Jeffress was then left with situating his coincidence detectors either in the auditory midbrain (inferior colliculus) or thalamus (medial geniculate body).^[2]

The architecture computes a binaural crosscorrelation function for each frequency region of the cochlea (Fig. 3), resulting in two (left and right) identical frequency-ITD rate-place maps. Thus a pattern of temporal disparities is mapped onto a spatial pattern of excitation (“place principle”).

The model has been implemented in silico using analog very large scale integrated (VLSI) circuits (Lazzaro et al 1991; Lazzaro and Mead 1989, 1990). Subsequent neuroanatomy and neurophysiology has largely confirmed the basic premises of the basic model (see (Joris and Yin 2007; Joris 2006; Joris et al 1998) albeit (arguably) with better correspondences in birds than in mammals and with some adjustments that include precisely timed inhibitory inputs and overrepresentation of characteristic frequencies below 1 kHz (McAlpine 2005; McAlpine and Grothe 2003). See (Colburn 1996) and (Albeck 1995) for additional discussions.



[[Image:JeffressFig3.gif|thumb|400px|right|label|Figure 3. The output representation of the Jeffress network. The output of the network is a spatial map of running coincidence rates, arranged by frequency channel (cochleotopic projection) and interaural delay.]]

The 1948 Jeffress model for binaural localization was closely followed in 1951 by J.C.R. Licklider's "duplex" temporal autocorrelation model for pitch (Licklider 1951) in which monaural signals were delayed relative to a copy of themselves. As with the Jeffress model, each cochlear place (frequency channel) mapped into its own autocorrelation circuit. Thus, Licklider's model was able to simultaneously produce both temporal and rate-place representations of pitch. In order to account for both monaural and binaural hearing, Licklider's triplex model (Licklider 1959) combined a Jeffress-like crosscorrelation stage (sans rate integration) followed by an autocorrelation stage to form a generalized central correlation analyzer. Colin Cherry also proposed an architecture for monaural and binaural scene analysis (Cherry 1961) that utilized monaural autocorrelation analyses followed by binaural crosscorrelation operations.

In addition to binaural localization, the Jeffress model is potentially applicable to any sensory system in which 1) timing of spikes is correlated with the time structure of an external stimulus ("stimulus-locked" or "phase-locked") and 2) there is a temporal disparity between the arrival times of a stimulus at different locations of receptor surfaces. In addition to auditory localization such systems include mechanoreception, electroreception, and vision (Carr 1993). In a series of striking experiments (many of them on himself), Georg von Békésy showed how small (< 1 ms) temporal disparities in the stimulation of skin using delayed mechanical and electrical pulse pairs produce systematic changes in the perceived locus of the stimulus on the body surface (Békésy von 1967). He carried out similar delayed pulse pair experiments using odorants puffed to the two nostrils (Békésy von 1964a) and tastants spritzed to the two sides of the tongue (Békésy von 1964b). Like auditory and mechanoreceptive afferents, visual neurons also phase-lock to the temporal modulations that are produced at each retinotopic location when an image moves relative to a retina. Reichardt detectors compute temporal crosscorrelations between spikes produced when a visual image is successively presented to two visual receptor elements (ommatidia) at two different times (i.e. a moving image) (Reichardt 1961). An array of Reichardt motion detectors arranged to detect many different temporal delays across nearby retinal elements is therefore analogous (albeit with more dimensions) to a Jeffress coincidence architecture that detects delays across the two ears.

The Jeffress architecture is a classical example of a time-delay neural network that converts temporal disparities in the arrival of input signals into a rate-place frequency-ITD pattern. Valentino Braitenberg proposed a Jeffress-like architecture for his general-purpose cerebellar timing model (Braitenberg 1961; Braitenberg 1967; Braitenberg 2000) and delay-coincidence models for the cerebral cortex and hippocampus are also conceivable. Although the dominant assumption has been that time patterns are converted to rate-place patterns or rate-based channel-activation, other Jeffress-like cross-correlation networks can readily be envisioned that produce other kinds of output representations. For example, a neural cross-correlator can have as its output a spatiotemporal pattern of relative response latencies (if the different coincidence units have different conduction velocities that systematically amplify delay durations). The response latencies produced by the cross-correlator can then be compared with those of an unprocessed signal. In the binaural case, hypothetically, the longer the detour through the binaural cross-correlator relative to the ipsilateral direct monaural path might indicate a greater degree of lateralization on the ipsilateral side. If the temporal structure of the coincidence output spike trains are analyzed (rather than simply reporting firing rate), a general purpose cross-correlator can be used for a variety of temporal pattern recognition operations, e.g. as a temporal pattern sieve for extracting embedded spike patterns and for separating (demultiplexing) temporal pattern mixtures into their respective components (Cariani 2001).

Notes

1. The spatial shifter circuits proposed by Pitts and McCulloch in 1947 ("How we know universals: the perception of auditory and visual forms" *Bull. Math. Biophys.* **9** 127-147) for musical transposition and visual magnification invariance have not passed the test of time. It is entirely puzzling why the Jeffress and Licklider models have been almost completely omitted from the neurocomputational canon.
2. It is possible that auditory scientists of the time could have considered the medial superior olivary nucleus as a possible (correct) candidate, since Lorente de No had carried out his pioneering neuroanatomical study of the auditory brainstem by the early 1930's. Unfortunately, Lorente's work was not published until nearly 50 years later (Lorente, 1981) because of Depression-era budgets and the expense of publishing the many Golgi photomicrographs that constituted the primary evidence.

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