Azimuthal position of low-frequency (< 1500 Hz) sounds is determined by humans using differences of some tens of microseconds in the timing of the signals at the two ears. The accepted model to account for this remarkable binaural sensitivity is the Jeffress delay line model. An array of coincidence detectors receives inputs from the two ears such that a given neurone fires maximally when the difference in arrival time at the two ears resulting from the location of a sound source offsets the difference in neural transmission time. Azimuthal location is encoded by the position of the peak in the array. The questions we address here are (1) whether such a simple coincidence model is sufficient to account for midbrain sensitivities to interaural time differences (ITDs) and (2) whether the position of maximal discharge is important in encoding the value of the ITD.

To answer these questions the responses of low-frequency, delay-sensitive neurones in the inferior colliculus (IC) of the anaesthetized guinea pig were studied. First, we assessed the best interaural phase (BP) of each neurone in response to a range of stimulating frequencies. Phase plots (stimulating frequency- vs-BP) were produced, from which measures of the characteristic delay (slope; CD) and characteristic phase (intercept; CP) of each neurone were obtained. The CD provides an estimate of the difference in travel time from each ear to brainstem neurones that act as coincidence detectors. The CP indicates the mechanism underpinning the coincidence detector responses. A linear phase plot indicates a single, constant delay between the coincidence detector inputs from the two ears. In over half (54/90) of the neurones, the phase plot was not linear (as shown in Figure 1A). We hypothesized that neurones with non-linear phase plots received convergent input from brainstem coincidence detectors with different CDs. Presentation of a second tone with a fixed, unfavourable delay suppressed the response of one input, linearizing the phase plot and revealing other inputs to be single CD coincidence detectors (Figure 1B). For neurones with linear phase plots, a second tone presented at worst delay either completely abolished their responses, or reduced their discharge rate with no change
in BP. By selectively suppressing inputs with a second tone, we are able to reveal the nature of underlying binaural inputs to IC neurones, confirming the hypothesis that the complex phase plots of many IC neurones are a result of convergence from simple brainstem coincidence detectors.

![Figure 1](image.png)

**Figure 1** A. Phase plot of a single IC neurone measured with binaural beats. B. Re-measurement of phase plot in the presence of a suppressor tone indicated by the arrow. The unfilled circles represent re-measurement of the original points shown by the unfilled squares.

To address the second question we used both interaurally delayed noise and tones and found a systematic relationship between neuronal best frequency (BF) and peak sensitivity to ITDs; neurones with relatively low best-frequencies responded best to long ITDs, whilst neurones with relatively high BFs responded best to short ITDs (Figure 2A). The shortest ITDs were not signalled at all by peak firing in low-frequency neurones. Additionally, most response-versus-ITD functions were asymmetric with the most rapid change in response, with change in ITD, generally occurring on the side nearest the midline (zero ITD). The consequence of these observations is that the steepest region of the response versus ITD function fell close to midline for all neurones irrespective of their BF (red bars Figure 2B).

The peak firing of ITD sensitive neurones is often taken to indicate the ITD value even though it often occurs outside the physiologically plausible range (open bars Figure 2B). However, our data suggest that the activity level across a population of ITD sensitive neurones could signal the ITD value. Changes in ITD within the physiological range of even small animals would significantly change this population response. Our data, consistent with suggestions made by previous authors, indicate
that for mammalian localisation the position of the peaks of ITD functions may be unimportant compared with the position of greatest sensitivity to the change in ITD.

**Figure 2 A.** Noise delay functions averaged across the functions of individual neurones with BFs falling in bands around 250 Hz (black), 335 Hz (red), 425 Hz (blue), 500 Hz (green), 700 Hz (brown), 1.0 kHz (grey) and 1.4 kHz (dark green). **B.** Distribution of the maximum firing (open bars) and maximum slope (red bars) with ITD of noise delay functions

If the slope through midline is important in signalling ITD changes a valid question is whether it can account for the human resolution of about 10-20 \( \mu s \). It has been assumed that discrimination thresholds this low could only be achieved by combining responses from many cells. Here we use actual neuronal responses from 61 neurones to estimate directly the minimal detectable change in ITD. The ability of a neurone to signal small ITD changes is determined both by the steepness of response-versus-ITD function and by the variability of the response. We determined the detectability of small changes in ITD by using Receiver Operating Characteristic (ROC) analyses. Individual IC neurones are capable of discrimination performance of 30-50\( \mu s \). This is not quite low enough to explain best human performance, but factors such as signal duration, recording location and species may account for the short-fall.

To summarise: Low-frequency neurones in the IC are not generally simple coincidence detectors. Low-frequency IC neurones show BF dependent delay tuning: peak ITDs are relatively long for lowest BFs and decrease as BF increases. ITD functions show the greatest slopes close to zero ITD. These physiological data support a model in which the value of the ITD can be determined by the total activity in two broadly tuned channels, one on each side of the brain.