TNS Journal Club: Sound localization and delay lines do mammals fit the model? McAlpine and Grothe, Tends in Neuroscience, 2003

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Introduction

• In this paper we look at:

• Lateral position location of a source using interaural time differences (ITDs)

• Back of the envelope calculation: head width/velocity of sound = $0.2m/300ms^{-1}=700\mu\text{seconds}$: upper ITD limit

• Observations:
  1. corresponds to a frequency of 1500Hz - but phase locking is hard at high frequencies
  2. neuron membrane time constant 10-100ms
Current thinking: “The Delay Line Hypothesis” Jeffrees

- There are coincident detector neurons which have inputs from both ears.
- One input is delayed with respect to the other (by a 'path' difference).
- Therefore, the neuron is tuned to fire at a specific interaural time difference.
- The lateral position of a sound source is determined by the position of maximal activation within an array of such neurons, over which ITDs are topographically mapped.
Current thinking continued...

- This must be repeated at all frequency bands
- Supported by experimental results in the barn owl
- Recent evidence from mammals casts doubt as to the universality of the model
- This paper reviews the new evidence and proposes:
  A new mechanism for tuning individual neurons to delays
  A new way of organising these neurons as populations
Gerbils and Barn Owls - a new ITD tuning mechanism

- In both barn owls and mammals, action potentials phase-locked to the stimulus waveform converge from each ear onto single neurons in the brainstem to generate interaural-delay sensitivity.

- But this may not be the only or most important mechanism.

- The Gerbil appears to use temporally precise inhibition to localise low frequency (less than 1500Hz) sounds.

- This was demonstrated as follows:
Gerbils - a new ITD tuning mechanism

- Medial superior olivary nucleus (MSO) neurons receive bilateral excitatory innervation and inhibitory (glycinergic) inputs from the brainstem medial and lateral nuclei of the trapezoid body.

- Idea: Block the inhibition (iontophoresis) and record the response from MSO cells to interaurally delayed pure tones.

- Find: (1) discharge rates increased compared with control conditions, in an ITD-specific manner,

- (2) the TD that evoked the peak response shifted from outside to inside the physiological range of the gerbil, to peak at, or very close to, zero ITD.
What this means for the Jeffree’s model

• Phase locked inhibition by glycine determines the tuning of an MSO neuron for ITD because without this inhibition the axonal conduction delay is effectively zero. (Backed up by computational work)

• So, is it just the case that the inhibition implements the delay lines in a slightly different way than we thought?

• NO - MSO neurons were found to be tuned to ITDs outside the natural range - usually corresponding to a pi/4 phase shift at each frequency

• There is no ‘Jeffress Matrix’ for these cells.
What’s the difference between a Owl and a Gerbil?

- For a fixed width, broad ITD tuning curve, putting the peaks of the response functions outside the normal range puts the region of highest slope inside the natural range aiding detection of changes in ITDs (usual Fisher information argument - maximise IF(stimulus))

- Owls can utilize ITDs for localizing high-frequency carriers, of up to 9 kHz, far above the range at which the temporal information required for binaural hearing is lost in mammals.

- This means their specialised ITD detecting neurons have much narrower tuning curves - they can therefore have more conventional tuning curves.
Conclusions

- The Jeffree’s model may apply to Owls but in Mammals...

- Phase locked inhibition provides a mechanism for ITD tuning (may be easier to tune than ‘pruning’/‘lengthening’ of delay lines)

- The broad tuning curve of ITD sensitive neurons in mammals necessitates a different population code from the labelled line of the Jeffrees model.

- The lateral position of a sound source may be determined by the relative activity within two populations of neurons that are broadly tuned for ITD.