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REVIEW

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NEW ROLES FOR SYNAPTIC INHIBITION IN SOUND LOCALIZATION

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Preface

The arrival times of a sound at the two ears are only microseconds apart, but both birds and mammals can use these interaural time differences to localize low-frequency sounds. Traditionally, it was thought that the underlying mechanism involved only coincidence detection of excitatory inputs from the two ears. However, recent findings have uncovered profound roles for synaptic inhibition in the processing of interaural time differences. In mammals, exquisitely timed hyperpolarizing inhibition adjusts the temporal sensitivity of coincidence detector neurons to the physiologically relevant range of interaural time differences. Inhibition onto bird coincidence detectors, by contrast, is depolarizing and devoid of temporal information, providing a mechanism for gain control.

Summary

- . Interaural time differences (ITDs) are the main cue for localizing lowfrequency sounds. As they are only in the range of microseconds, ITD detection requires the most elaborate mechanism for temporal processing in the mammalian or avian brain.
- The textbook view of how ITD processing is achieved has been dominated by the seminal model put forward by Jeffress in 1948. This model incorporates excitatory projections from both ears that faithfully time-lock to the temporal structure of sounds and converge onto binaural coincidence detector neurons. These fire maximally when the two inputs arrive simultaneously. The model also assumes that a systematic arrangement of the length of the input fibres (delay lines), can produce different conductance delays that tune different coincidence detector neurons to different favoured ITDs. Such a system could then create a map of best ITDs, and hence of azimuthal space.
- ITD-sensitive coincidence detector neurons have been found in the mammalian medial superior olive (MSO) and in its avian analogue, the nucleus laminaris. In the bird ITD-processing circuits, delay lines have been described structurally and functionally, and there is good evidence for a topographic representation of ITDs (and, hence, of

azimuthal space) at least in the barn owl auditory system. By contrast, the existence of delay lines in mammals has been controversial, and convincing evidence for topographic maps of ITDs is lacking. Recent evidence indicates that, in mammals, the representation of azimuthal space calculated from ITDs might be organized in a fundamentally different way than proposed by Jeffress.

- Our view of the representation of ITDs in mammals, and also of the mechanism of ITD processing itself, is undergoing marked changes. In birds and mammals, profound inhibitory inputs have to be added to our picture of ITD processing. These inhibitory inputs have entirely different functions in birds and mammals. Whereas in birds tonic depolarizing GABA (*Y*-aminobutyric acid)-mediated inhibition accounts for differential gain control and a general improvement of the coincidence detection mechanism, temporally precise inhibition onto ITD-sensitive neurons in the mammalian MSO actively contributes to the ITD tuning itself.
- The ITD-processing circuits in birds and mammals are an excellent example of how evolution of the vertebrate nervous system can produce very different functional solutions for the same computational problem.

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