The Influence of Sound Source Position on Free-Field Measurements of the Precedence Effect in Cats

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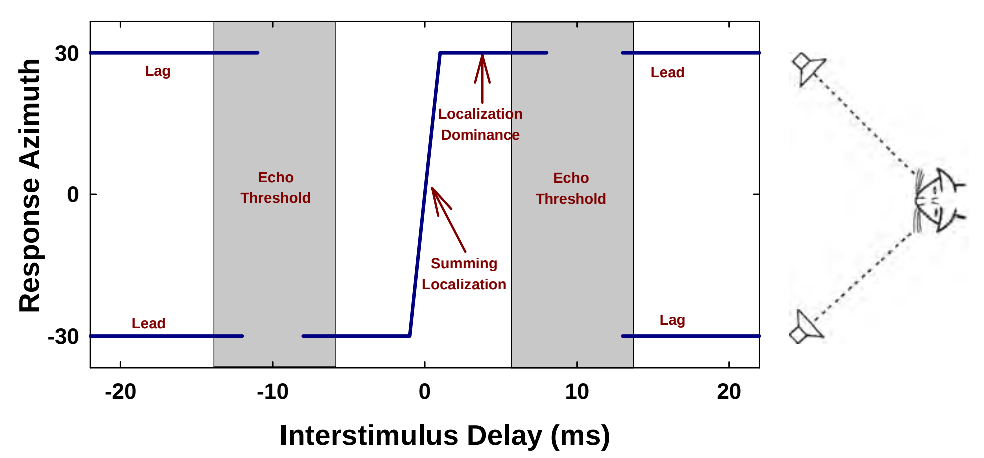
1 Introduction

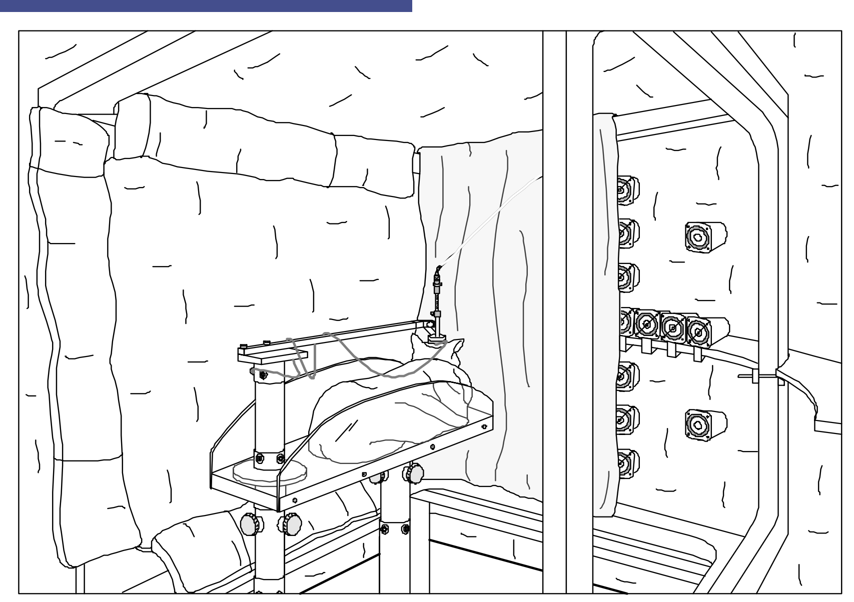
Behavioral studies of sound localization in cats have shown that these nocturnal predators can be trained to accurately saccade to broadband sounds in anechoic space (Populin and Yin, 1998). Less is known, however, about localization accuracy in more natural, echoic environments. Psychophysical experiments on the precedence effect (PE) in cats have shown that their localization of pairs of auditory stimuli presented from different locations in space is dependent upon the interstimulus delay (ISD) between the stimuli, in a manner similar to humans (Tollin and Yin, 2003). For pairs of transient stimuli with ISDs from about 0.4-10 ms, cats orient only to the lead stimulus location, a time frame known as **localization dominance** (below). At ISDs < 0.4 ms, the cats orient to a 'phantom' source between the lead and lag stimuli, a time frame known as **summing localization**. At ISDs > **echo threshold** (about 10 ms), the cats saccade to either the location of the lead or the lag.



The neural correlates to the PE are less well known, especially in unanesthetized animals. In single unit recordings from the inferior colliculus (IC) of awake cats, neurons respond to both lead and lag sounds at ISDs above behavioral echo thresholds, but, consistent with localization dominance, the response to the lag is reduced at shorter ISDs.

Here, the influence of lead and lag source locations on the PE were measured behaviorally in a psychophysical task where cats were required to saccade to the perceived location of targets for a food reward and physiologically with single unit recordings in the IC.

2 Methods

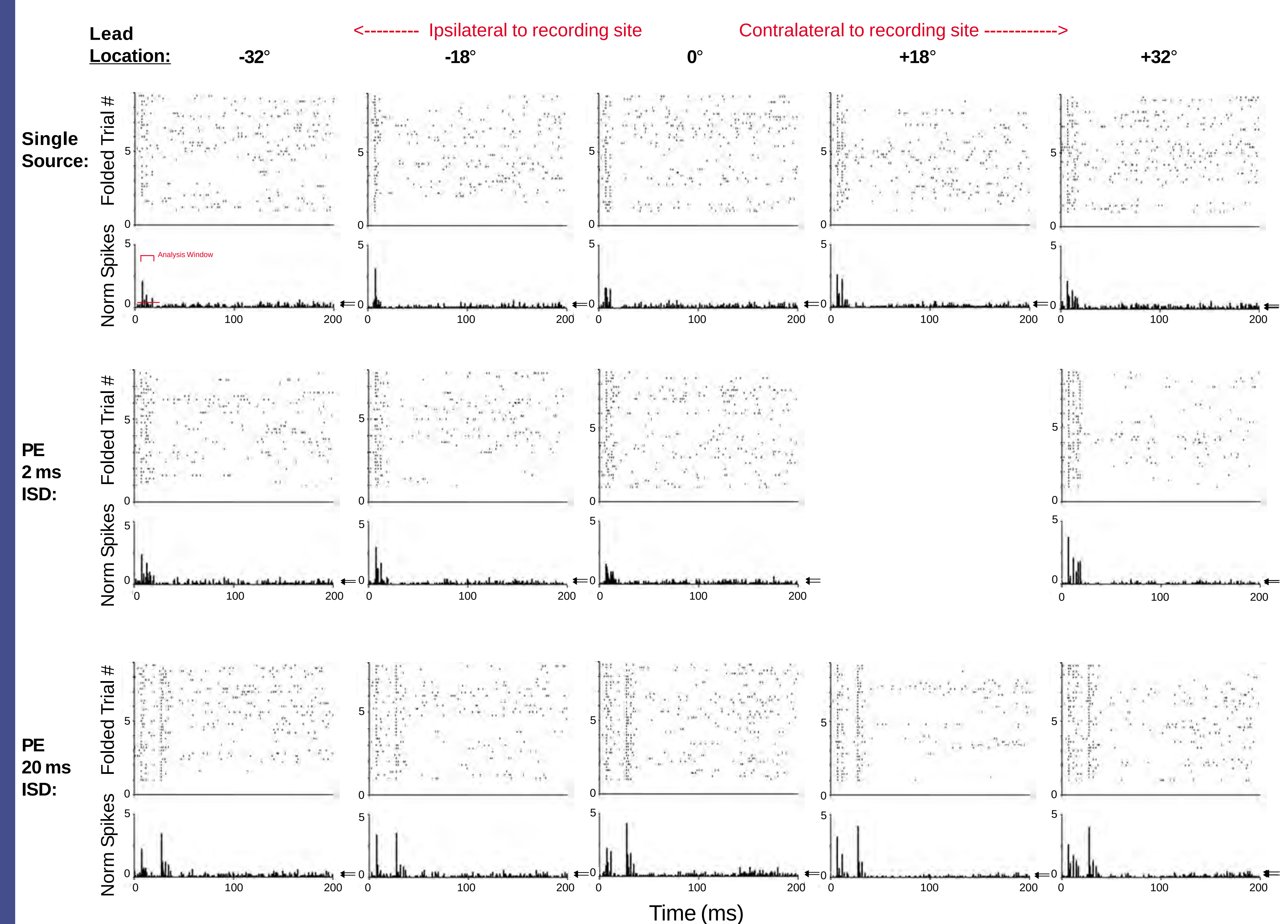


A head holder, eye coils, and a recording chamber were implanted in three adult cats to hold the head, monitor eye position using the magnetic search coil technique, and to record single unit responses. The cats were placed in a sound attenuating chamber lined with acoustic foam to minimize echoes (above, from Populin and Yin, 1998). Hidden in front of the cat was an array of up to 15 matched speakers, each with an LED positioned at the center of the cone.

Using operant conditioning, the cats were trained to fixate on an LED at the midline (0°, 0°) and then to make saccades to the position of sound sources following the onset of the acoustic target and simultaneous offset of the LED. Gaze responses were measured with the head free; these responses had to be maintained within a temporal and spatial window centered on the target for a food reward. The stimuli for the PE trials, which only comprised 10% of the trials and were always rewarded, were trains of transients (five 10 ms broadband noise bursts) presented at a rate of 5 Hz from two different locations and separated by a short ISD. PE functions were obtained for several stimulus separation distances ranging from 20° to 160°.

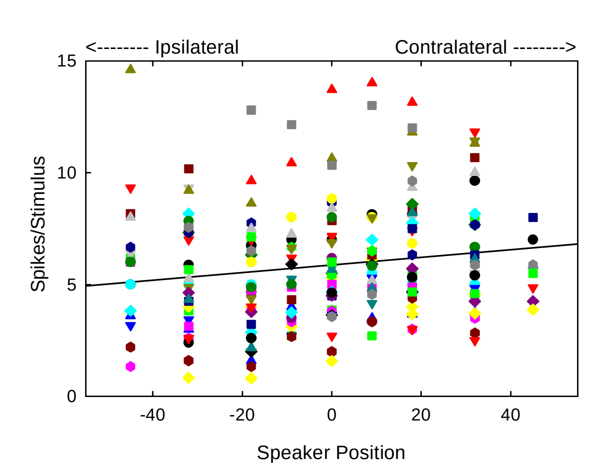
In the physiological experiments, extracellular responses in the IC to PE stimuli were recorded with tungsten microelectrodes when the cats were required to maintain fixation on the LED with their heads fixed while the acoustic stimuli were presented. Here, the position of the lag remained constant from trial to trial while the lead stimulus was moved closer to or further from the lag in space.

3 Physiological Data



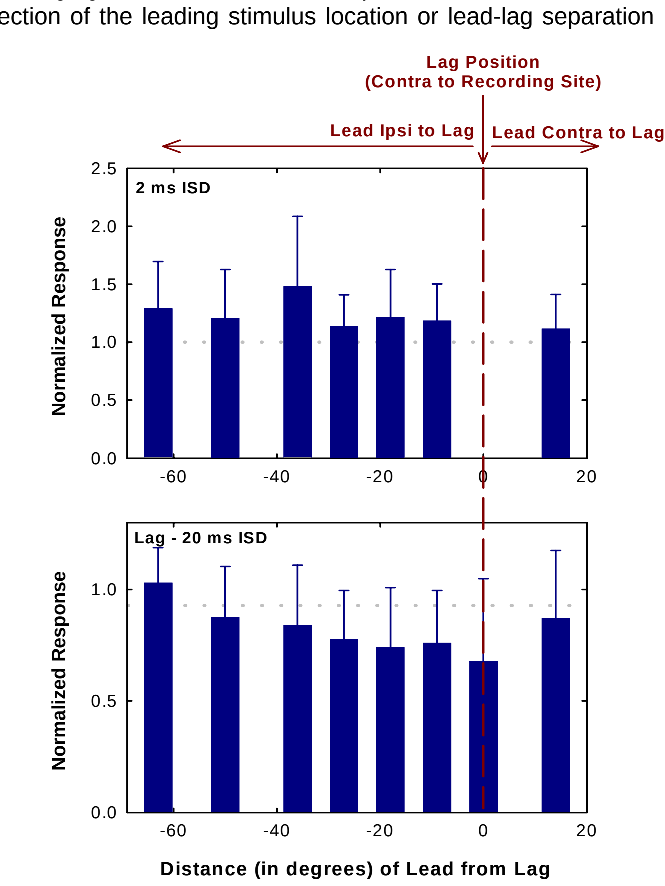
A. IC units respond to SS and PE stimuli at various locations:

Dot rasters and histograms of the responses of one IC unit (#44) to single source (top row) or paired source (bottom two rows) stimuli. The location of the SS or lead PE stimulus is noted at the top of the column, the lag was always at +18°. On each histogram, the small arrows at the right show the spontaneous rate (bottom) and 2 standard deviations above spontaneous (top). Spikes that exceed the top arrow and within the analysis window are counted as responses for the SS stimuli and for the paired stimuli, shifted in time by the ISD. This unit responds well to SS stimuli presented from all locations ranging from -32° to +32°. Responses to the PE stimuli at both the 2 and 20 ms ISDs are more vigorous than those to the SS at all locations, regardless of the direction of the leading stimulus location or lead-lag separation distance.



B. Most IC units respond better to stimuli in the contralateral hemifield:

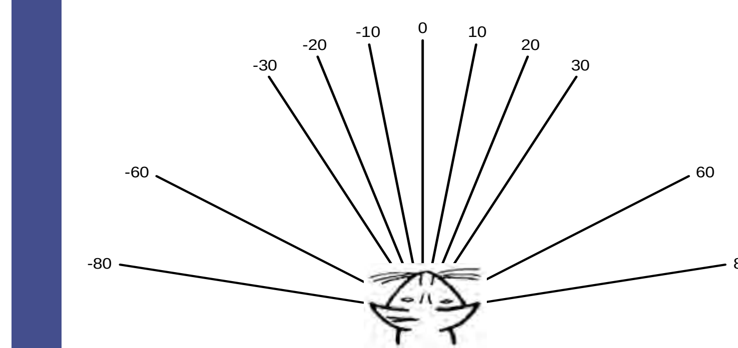
Spikes/stimulus for 34 individual neurons to SS stimuli as a function of speaker position (above). The regression line was fit to all points and has a slope of 0.02 (r = 0.14).



C. Speaker separation influences firing rate at long delays:

Average normalized responses to the PE stimuli are shown for 2 (total response), and 20 ms ISDs (lag response) as a function of lead-lag separation distance (29 units each). Error bars represent standard deviations. To evaluate the influence of the location of the leading on the lagging stimulus, we chose an analysis window that included only the lagging response for the 20 ms ISDs (bottom) but for the 2 ms ISD the total response is calculated (top). The responses are normalized to the SS stimuli at the same position to account for the directionality of the units. For the 2 ms ISD, there was no influence of lead-lag separation distance on the normalized response to the paired stimuli (p > .05). There was an increase in reponses to the lag at the 20 ms ISD as separation distance increased, however (p < .05).

4 Psychophysical Data

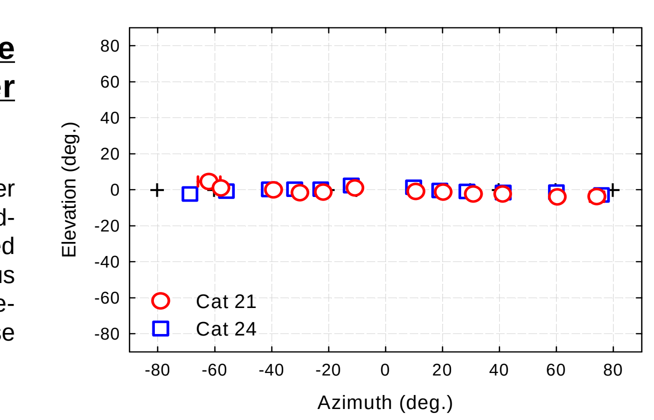


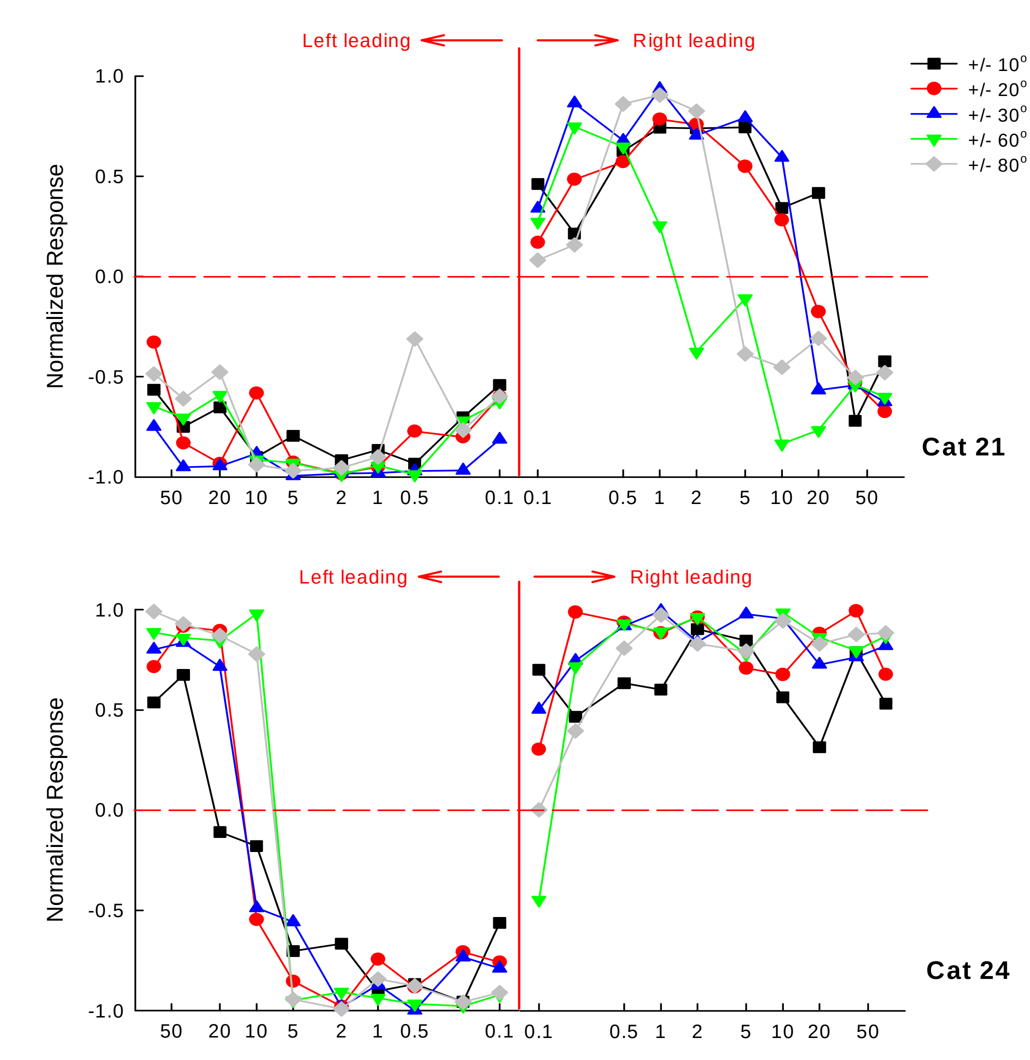
A. We varied the locations of the lead and lag stimuli:

Paired stimuli were delivered symmetrically around the midline in front of the cats, from +/- 10, 20, 30, 60, or 80°. Localization of PE stimuli was measured as a function of ISD for each separation distance, for ISDs ranging from 0.1 to 70 ms.

C. Localization of single source stimuli also varies with speaker separation distance:

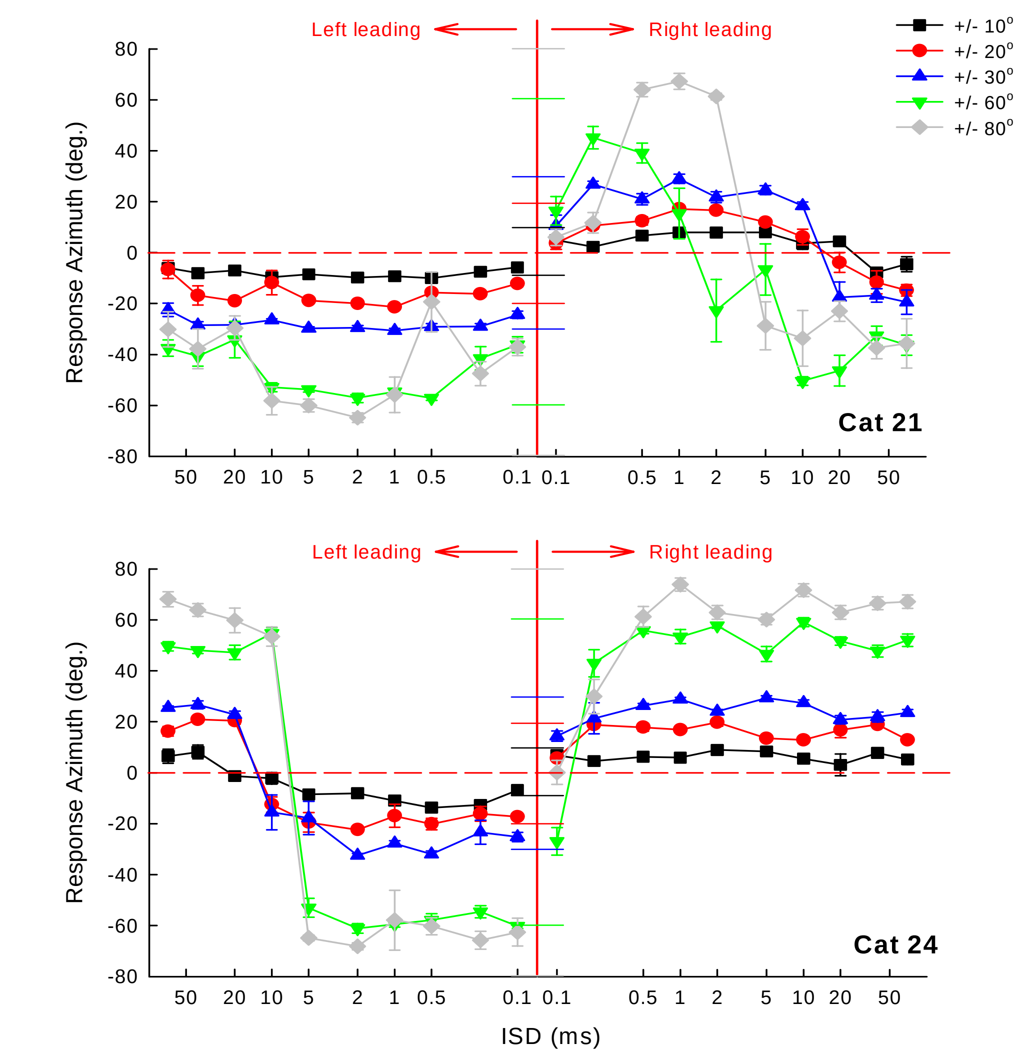
Single source localization as a function of speaker position for both cats shows less errors for midline stimuli but larger errors for stimuli presented more peripherally. To see the effects of stimulus separation distance on PE localization, the responses must be normalized to account for these differences in accuracy.





D. Localization dominance does not change with speaker separation:

The responses of the cats to the PE stimuli were normalized by the response to SS stimuli presented at the lead location in isolation, as shown in Figure C. Responses close to +1 represent responses entirely to the right location and responses towards -1 represent responses entirely to the left location. These normalized functions also show that summing localization and localization dominance are similar at all speaker separation distances, but that echo thresholds (0 crossing points) are earlier for the larger speaker separations.



B. Cats show all three components of the precedence effect at all speaker separation distances:

Localization functions are shown for two cats as a function of ISD for speaker separation distances ranging from 20° to 160°. Both cats exhibit summing localization, localization dominance, and echo thresholds for all speaker separation distances, although to varying degrees. At the largest speaker separation distances, localization dominance is less pronounced and echo thresholds are earlier. Note the asymmetries seen for both cats: when two stimuli are heard, at ISDs past the echo threshold, both cats preferentially respond always to one side regardless of whether that side is the lead or the lag.

5 Conclusions

Recordings from the IC of these cats show that neural responses to lead and lag stimuli were robust at longer ISDs, but the response to lag stimuli were greatly diminished at shorter ISDs, paralleling behavioral measurements.

- Neural responses to SS and PE stimuli were generally greater in the contralateral hemifield than the ipsilateral hemifield.
- Neural responses to PE stimuli, when normalized for the directional firing patterns of the units, did not differ across stimulus locations, except for the response to the lag at a 20 ms ISD.

Cats behaviorally exhibit summing localization, localization dominance, and echo thresholds when presented with PE stimuli, regardless of stimulus separation distance.

- Behaviorally, there are no effects of lead-lag separation distance on localization under conditions of summing localization or localization dominance.
- There are effects of lead-lag separation distance on echo thresholds: echo thresholds are earlier for PE stimuli with larger separation distances.

The physiological results at the 2 ms ISD parallel the psychophysical results: there are no influences of lead-lag separation distance on localization dominance.

The physiological results at the 20 ms ISD also parallel the psychophysical results: behavioral and physiological data suggest earlier echo thresholds with larger speaker separation distances.

6 References and Acknowledgements

Populin, L.C., and Yin, T.C.T. (1998). Behavioral studies of sound localization in the cat. J. Neurosci. 18, 2147-2160.

Tollin, D.J., and Yin, T.C.T. (2003). Psychophysical investigation of an auditory spatial illusion in cats: The precedence effect. J. Neurophysiol. 90, 2149-2162.

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