

Psychophysical and Physiological Evidence for a Precedence Effect in the Median Sagittal Plane

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Litovsky, Ruth Y., Brad Rakerd, Tom C. T. Yin, and William M. Hartmann. Psychophysical and physiological evidence for a precedence effect in the median sagittal plane. *J. Neurophysiol.* 77: 2223–2226, 1997. A listener in a room is exposed to multiple versions of any acoustical event, coming from many different directions in space. The precedence effect is thought to discount the reflected sounds in the computation of location, so that a listener perceives the source near its true location. According to most auditory theories, the precedence effect is mediated by binaural differences. This report presents evidence that the precedence effect operates in the median sagittal plane, where binaural differences are virtually absent and where spectral cues provide information regarding the location of sounds. Parallel studies were conducted in psychophysics by measuring human listeners' performance, and in neurophysiology by measuring responses of single neurons in the inferior colliculus of cats. In both experiments the precedence effect was found to operate similarly in the azimuthal and sagittal planes. It is concluded that precedence is mediated by binaurally based and spectrally based localization cues in the azimuthal and sagittal planes, respectively. Thus, models that attribute the precedence effect entirely to processes that involve binaural differences are no longer viable.

INTRODUCTION

A room plays havoc with sound. The waves emitted by a source are reflected and rereflected many times by the room surfaces. Therefore a listener in a room is exposed to multiple versions of any acoustical event, coming from many different directions in space. The auditory system can cope with this sonic clutter because of the precedence effect, a remarkable neural process that fuses the direct sound and its reflections into a single image (Haas 1951; Wallach et al. 1949). The precedence effect also discounts the reflected sound in the computation of location so that a listener perceives the source near its true location. The standard theoretical model for this effect is an extension of the binaural model for localization, a neural coincidence detector that operates on the difference in arrival time of signals at left and right ears (Jeffress 1948). The extension postulates an inhibitory response generated by the leading sound (Franssen 1963; Lindemann 1986). Physiological evidence for the coincidence detector has been found in the medial superior olive (Goldberg and Brown 1969), and psychophysical evidence for the extension to precedence has been found in headphone experiments (Zurek 1980).

The binaural difference model successfully describes many aspects of localization, but it does not account for the localization of sources in the median sagittal plane, which

is symmetrical with respect to the two ears. Although microphone measurements normally find some binaural differences for sources in the sagittal plane (Searle et al. 1975; Wightman and Kistler 1989), the preponderance of evidence shows that these differences are not reliable enough to serve as localization cues (Asano et al. 1990; Hebrank and Wright 1974; Middlebrooks and Green 1991). Instead, sources in the median sagittal plane are localized on the basis of spectral shape cues, peaks and valleys introduced by direction-dependent filtering performed by the external ears, head, and torso (Blauert 1983; Gardner and Gardner 1973; Roffler and Butler 1968).

The present study is a search for a precedence effect in the median sagittal plane, a precedence effect that is mediated by spectral shape cues. Early evidence that such an effect likely exists was found in a front-back competition experiment by Blauert (1971). The present search was conducted on two levels: one psychophysical in humans, the other physiological in cats.

METHODS

Psychophysics

The psychophysical experiments were performed in a 32-m³ anechoic room with the use of loudspeakers to simulate direct sounds and reflections. There were five matched speakers: directly in front at 0°, behind, 90° to the left, 90° to the right, and overhead. On each experimental trial there were eight pairs of leading and lagging clicks (each 0.025 ms in duration) repeated every 110 ms. Such a click train allows the precedence effect to build to a maximum (Freyman et al. 1991). Trials were presented in blocks consisting of trials in the azimuthal plane (left, front, and right sources) or the sagittal plane (front, overhead, and behind sources). All permutations of leading source location, lagging source location, and eight values of interclick delay (ICD) ranging from 0 to 10 ms were tested. The experiments measured localization in a competition experiment, so that after the stimulus was presented the subject had to decide which of the three loudspeakers in the plane was closest to the location of the sound image. Eight subjects each completed a total of 10 blocks for each plane, with blocks for the different planes randomly interspersed.

Physiology

Physiological experiments paralleled the psychophysical ones by using click sources in a free-field, anechoic chamber and comparing azimuthal and sagittal plane responses. Extracellular recordings were made in 38 neurons (characteristic frequencies ranging from 500 to 24,000 Hz) in the central nucleus of the inferior colliculus (ICC) of barbiturate-anesthetized cats. The animal's head was in

the center of semicircular arrays (radius of 1.2 m) of loudspeakers positioned along the azimuthal and sagittal planes at 15° intervals. Positive angles refer to sounds in the contralateral hemifield in azimuth and above the interaural line in elevation. The precedence effect was probed by delivering clicks from two different speakers with varying ICDs, with 50 trials for every condition. We measured precedence by the degree of suppression of the response to the lagging click as a function of the presence of a leading click at different ICDs.

RESULTS

Psychophysics

Figure 1 shows the percentage of responses that matched the leading click location at each ICD. If the precedence effect is operating, this percentage will be high. Open symbols show the results in the azimuthal plane, where binaural difference cues are present. These results are in good agreement with previous studies of precedence (Yost and Soderquist 1984; Zurek 1980). When ICDs were <1 ms, the precedence effect was incomplete; leading and lagging clicks both affected the perceived location to some degree, an effect that has been called summing localization (Warncke 1941). At ICDs of 1.0 and 2.0 ms, precedence with binaural differences was maximal, although still not entirely complete; subjects chose the leading click location on as many as 95% of all trials. As the ICD increased to 5.0 ms, the lagging click began to be audible, and it was chosen as the location of the sound source on some trials, indicating that the precedence effect became weaker. The filled symbols in Fig. 1 show the results for the sagittal plane experiment. They show that a spectrally mediated precedence effect exists, and that its dependence on ICD is comparable with that of the binaural difference precedence effect. The only appreciable difference is that the spectrally mediated effect was somewhat weaker at its maximum.

Physiology

In the physiological experiments for each neuron, we first measured the receptive field properties with the use of single clicks (0.1 ms in duration) at a level ~ 10 –15 dB above threshold (Fig. 2A). To compare the degree of suppression for stimuli on the azimuthal and sagittal planes, we always chose the speaker directly in front, which lies at the intersection of the two planes, to be the lagging source; and to control for possible influences of response rate, we chose the locations of the two leading sources such that the responses to a single click were approximately equal. In Fig. 2 the leading sources were placed at $+90^\circ$ azimuth and $+75^\circ$ elevation. The dot rasters in Fig. 2B show that, for leading clicks in the azimuthal plane, at long ICDs (>40 ms), there is a response at a latency of ~ 16 ms to the leading click and a later response at about the same latency following the lagging click. The response to the lagging click gradually diminishes as the ICD is shortened and disappears for ICDs <31 ms. Figure 2C shows nearly identical behavior when the leading click was in the sagittal plane. Figure 2D shows little difference in the suppression of the response to the lagging click in the two different planes when plotted as normalized recovery curves.

To quantify the extent of suppression, from the recovery curves we measured the ICD at which the lagging response was suppressed by 50%. The similarity in the values of half-maximal suppression shown in Fig. 2D is typical of that observed in most cells in the population, although the overall shapes of the recovery curves in Fig. 2D are more similar than usually seen. Figure 3 shows a scatter plot of the ICDs for half-maximal suppression along the azimuthal and sagittal planes for 38 cells. There are two striking features of the data shown in Fig. 3. First, there is considerable variability in the degree of suppression between different cells in the ICC, ranging from ~ 0 to >100 ms. Such variability has

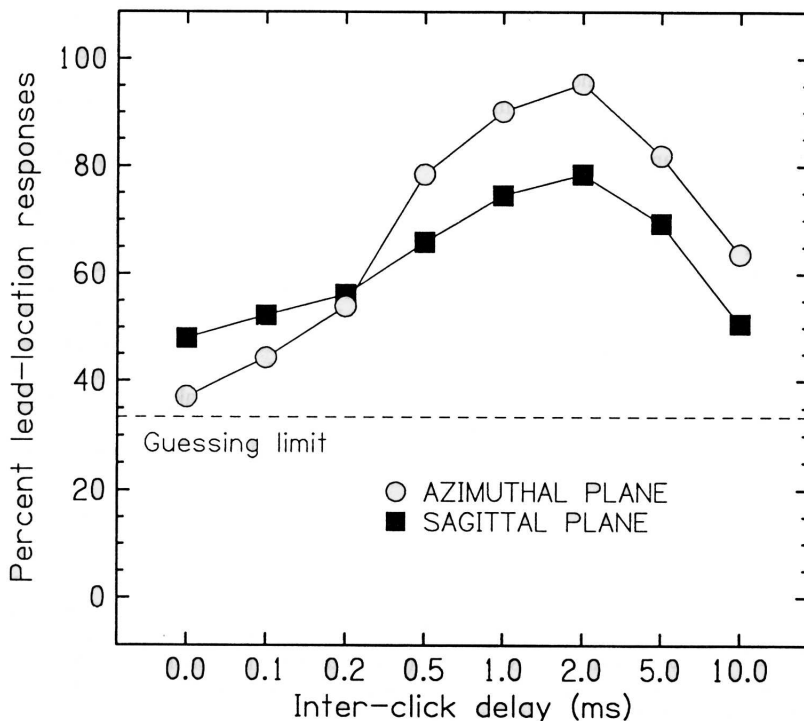


FIG. 1. Mean responses for 8 subjects. For both source planes, the plot shows the percentage of trials in which the sound image appeared at the position of the leading source. High percentages indicate a strong precedence effect. Similar functions of the interclick delay (ICD) occur for both planes, although the precedence effect is stronger when binaural differences are present (open symbols).

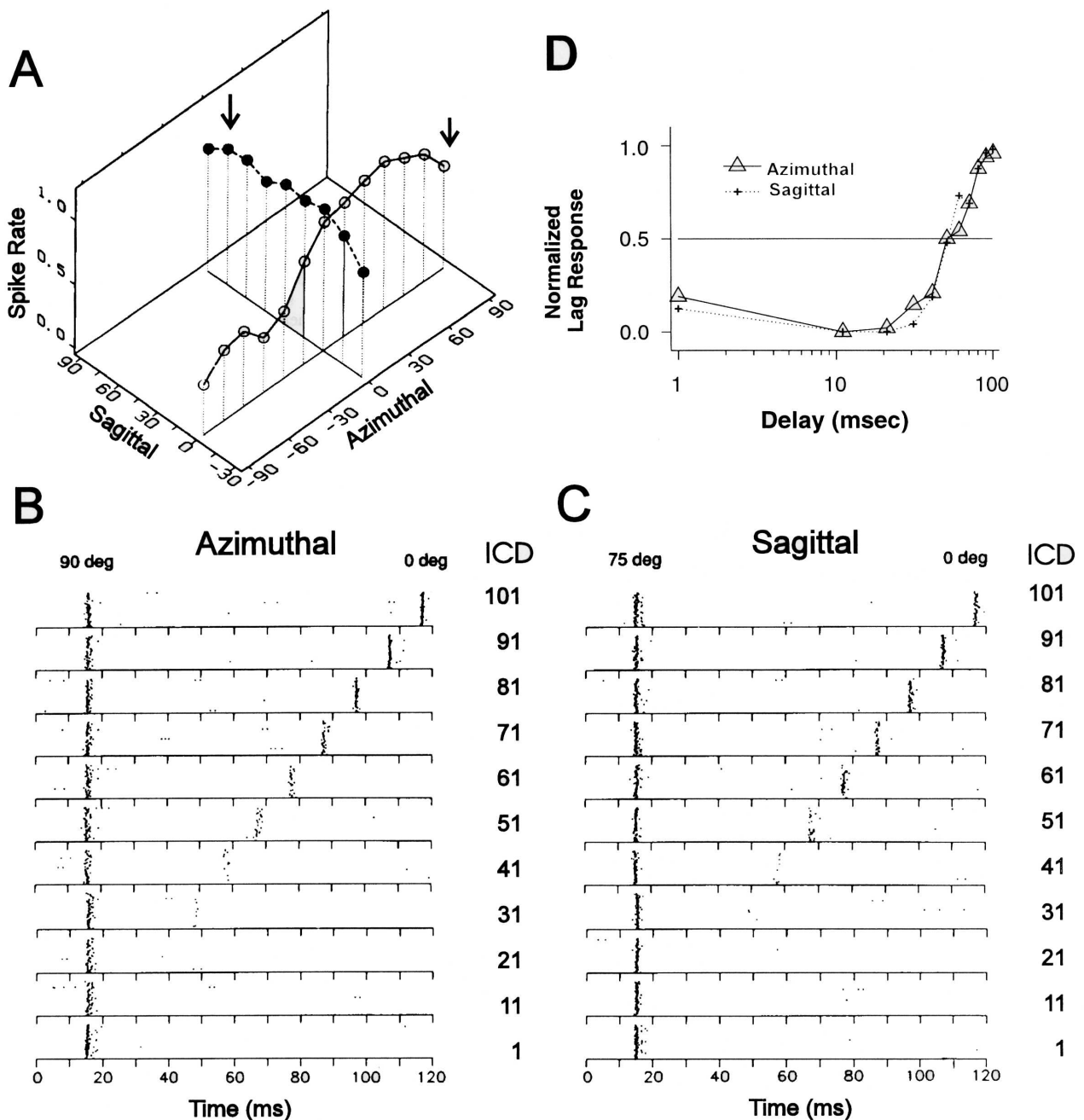


FIG. 2. Physiological evidence for precedence in the azimuthal and sagittal planes for 1 neuron. *A*: azimuthal and sagittal rate functions. At each location, 50 repetitions of clicks were presented with a period of 300 ms. The number of spikes per stimulus is plotted against azimuthal and sagittal locations. Arrows: leading source location for *B* and *C*. *B* and *C*: dot rasters showing the responses of the same neuron at ICDs ranging from 1 ms (*bottom*) to 101 ms (*top*) along the azimuthal (*left*) and sagittal (*right*) planes. *D*: recovery functions for the lagging responses shown in *B* and *C*, normalized by the response to the same stimulus in absence of the leading stimulus.

previously been seen in the ICC under other conditions (Carney and Yin 1989; Yin 1994). Second, for each cell there is a strong correlation ($r = 0.8$) between its suppressive effect in the two planes. Thus for any given cell in the ICC the degrees of suppression of the lagging click to a leading click in the sagittal and azimuthal planes are comparable.

DISCUSSION

The variability in suppression delays mirrors the range of delays at which the precedence effect is observed behavior-

ally. Although the dominance of the leading source in localization is maximal ~ 2 ms, suppression of the lag as an independent auditory event can extend to 50 ms, as in echo suppression in concert halls (Kuttruff 1979). Localization dominance of the lead was the only behavioral measure probed by the psychophysical experiments above.

In summary, the experiments reported here show that the precedence effect operates similarly in the azimuthal and sagittal planes. Because the degree of suppression varies with changes in relative location of the leading and lagging sources in both planes (Litovsky and Yin 1994), precedence

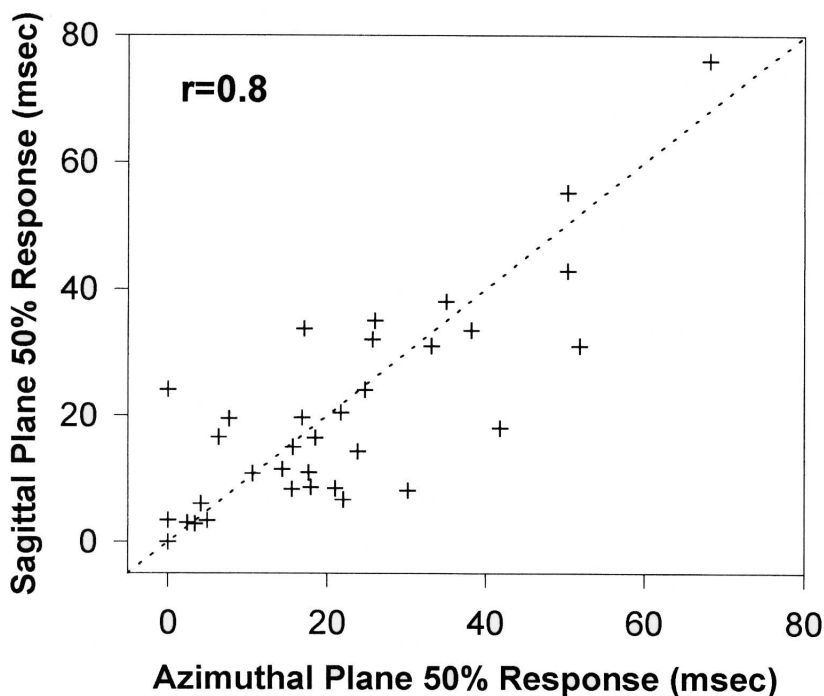


FIG. 3. Correlation of 50% maximal response along the azimuthal vs. sagittal planes. Each asterisk represents the values for 1 neuron.

is mediated by binaurally based and spectrally based localization cues, in the azimuthal and sagittal planes, respectively. Therefore models that attribute the precedence effect entirely to processes that involve binaural differences are no longer viable. However, precedence is not identical in all planes; the psychophysical localization experiments show that it is stronger in the azimuthal plane. This difference might be related to the fact that neurons in the ICC show stronger firing rate variation with source position in the azimuthal plane compared with the sagittal plane. Despite the quantitative differences, precedence appears to operate similarly whether the localization cues are binaural or spectral.

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