

Parallel Emergence of Spatial Tuning and Echo Suppression in the Auditory Midbrain? Focus on “A Neuronal Correlate of the Precedence Effect Is Associated With Spatial Selectivity in the Barn Owl’s Auditory Midbrain”

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The localization of sound sources in reverberant environments is complicated by the presence of acoustic reflections (echoes) that can produce spatial masking and can alter directional cues. The fact that localization behavior is not seriously impaired in reverberant spaces suggests some form of perceptual constancy or compensation for the effects of echoes. One probable source of such compensation is demonstrated by the precedence effect (PE) (Wallach et al. 1949; see Litovsky et al. 1999 for a recent review). The PE reflects a dominance of early arriving sound (i.e., direct sound) over delayed sound (i.e., reflections) on spatial perception. It is demonstrated by presenting pairs of sounds—separated by a delay—from different locations in space. At short delays (~1–5 ms for clicks or other impulsive sounds), listeners experience a single “fused” event near the location of the earlier-presented (“leading”) stimulus and impaired discrimination of the delayed (“lagging”) stimulus. These results suggest that leading stimuli trigger the suppression of neural responses to lagging stimuli at some level of the auditory pathway. Although the neural basis of the PE is not completely understood, proposed mechanisms include delayed inhibition (Lindemann 1986; Zurek 1980) and interaction between stimulus representations in the auditory periphery (Tollin and Henning 1998).

In this issue (p. 2051–2070), Spitzer and colleagues examine neurophysiological correlates of the PE in the inferior colliculus (IC) of the anesthetized barn owl. Briefly, they presented pairs of broadband noise bursts (50–100 ms in duration) from locations in virtual acoustic space. Each pair consisted of a “target” stimulus, located within a neuron’s spatial receptive field, and a “masker,” located away from that position. Suppression of neuronal responses to target stimuli was measured as a function of the inter-stimulus delay, which ranged from +200 ms (target leads masker) to –200 ms (masker leads target). By isolating the effects of temporally asymmetric suppression (which depends on the temporal order of target and masker) and temporally symmetric suppression (which does not), they demonstrate a clear role of lead-triggered inhibition lasting tens of milliseconds in the IC. Moreover, the magnitude of temporally asymmetric suppression is correlated with the response latency and overall spatial sensitivity of IC neurons in their sample. Spitzer and colleagues thus argue that spatial tuning and the PE emerge in parallel through local inhibitory processing within the barn owl IC.

The use of long-duration overlapping stimuli in this study extends our view of the PE in naturalistic listening situations. Impulsive sounds (e.g., clicks or noise bursts) typically used to study the PE eliminate concerns about masking caused by

acoustic superposition of the stimuli, but naturally occurring sounds with longer durations—perhaps hundreds of milliseconds longer than the typical echo delay—overlap their echoes in time. Understanding the dynamics of the PE with such stimuli is important to developing useful models of auditory function “in the wild.” Psychophysical *echo thresholds* (the maximum delay at which fusion occurs) for impulsive stimuli—typically 5–10 ms (Litovsky et al. 1999)—are significantly shorter than values of 30–40 ms reported for long-duration stimuli such as continuous speech or music (Haas 1951; Wallach et al. 1949). The difference suggests that suppressive effects might be extended by overlap. This interpretation is clouded, however, by strong contextual cues in speech and music known to extend echo thresholds (see Clifton et al. 1994; Hafter et al. 1988). In contrast, at least one recent study using 500-ms complex tones measured echo thresholds of 7–8 ms, similar to clicks (Hafter et al. 2000). Consistent with that result, Spitzer and colleagues demonstrate a time course of suppression for overlapping sounds similar to that seen with impulsive stimuli.

The use of long-duration stimuli does more than simply enhance experimental realism. By exploiting the temporal overlap between stimuli, Spitzer and colleagues are able to isolate suppression explainable by simultaneous acoustic masking, alteration of spatial cues, lateral inhibition, or peripheral interaction from temporally asymmetric suppression indicative of long-lasting, onset-triggered inhibition. That the authors found such inhibition primarily among IC neurons with sharp spatial tuning (also thought to reflect inhibition) and long response latencies fits well with the idea that spatial sensitivity and the PE emerge in part through local inhibitory processing within the IC.

Spitzer and colleagues additionally employ signal-detection analysis to show that IC responses exhibit suprathreshold discrimination even during the suppressed period. This finding is significant because suppression of responses to lagging stimuli extends to delays much longer than psychophysical echo thresholds. The *half-maximal delay* (the delay at which responses to a lagging target recover to 50% of the response in the absence of a leading masker) of responses in the IC (~20 ms) (Yin 1994) and cortex (~100 ms) (B. J. Mickey and J. C. Middlebrooks, unpublished observations) of anesthetized cats significantly exceed behavioral values. Although the effects of anesthesia are not entirely known, it is anticipated that suppressive effects may be exaggerated. Indeed, reported half-maximal delays in the IC of awake rabbit (~6–12 ms) (Fitzpatrick et al. 1995) and cat (~10 ms) (Tollin et al. 2004) are shortened relative to the anesthetized case. Spitzer and colleagues, however, demonstrate that recovery from suppression

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is not necessary for detection of a lagging target, which was achieved at delays of 1~30 ms; the same units' half-maximal delays ranged 1~100 ms.

The results of this study help clarify the role of inhibition in simultaneously shaping spatial sensitivity and the PE. These results additionally support the view that spatial sensitivity emerges through local processing within the IC and greatly extend our understanding of the neural mechanisms underlying the PE.

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