Psychophysical Investigation of an Auditory Spatial Illusion in Cats: The Precedence Effect

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Submitted 16 April 2003; accepted in final form 7 June 2003

Tollin, Daniel J. and Tom C.T. Yin. Psychophysical investigation of an auditory spatial illusion in cats: the precedence effect. J Neurophysiol 90: 2149–2162, 2003. First published June 11, 2003; 10.1152/jn.00381.2003. The precedence effect (PE) describes several spatial perceptual phenomena that occur when similar sounds are presented from two different locations and separated by a delay. The mechanisms that produce the effect are thought to be responsible for the ability to localize sounds in reverberant environments. Although the physiological bases for the PE have been studied, little is known about how these sounds are localized by species other than humans. Here we use the search coil technique to measure the eye positions of cats trained to saccade to the apparent locations of sounds. To study the PE, brief broadband stimuli were presented from two locations, with a delay between their onsets; the delayed sound meant to simulate a single reflection. Although the cats accurately localized single sources, the apparent locations of the paired sources depended on the delay. First, the cats exhibited summing localization, the perception of a “phantom” sound located between the sources, for delays ≤400 μs for sources positioned in azimuth along the horizontal plane, but not for sources positioned in elevation along the sagittal plane. Second, consistent with localization dominance, for delays from 400 μs to about 10 ms, the cats oriented toward the leading source location only, with little influence of the lagging sound source, both for horizontally and vertically placed sources. Finally, the echo threshold was reached for delays >10 ms, where the cats first began to orient to the lagging source on some trials. These data reveal that cats experience the PE phenomena similarly to humans.

INTRODUCTION

The spatial location of sources of sounds can be accurately determined over a wide range of listening conditions including variations in overall sound duration (Hoffman and Van Opstal 1998), level (Macpherson and Middlebrooks 2000), and variable spectral content (Wightman and Kistler 1989). Accurate localization is also retained in natural environments, where sounds arrive at the two ears not only directly from the actual source but also indirectly a short time later as reflections from surrounding objects. Because each reflection could be interpreted as a different source at a different location, reflections should interfere with sound localization. Yet in humans localization remains accurate despite reflections, and observers typically experience only a single “fused” sound image near the location of the source, with little influence from the spatial attributes of the reflections (Haas 1951; Hartmann 1983; Wallach et al. 1949). These perceptual phenomena, collectively referred to as the precedence effect (PE; Wallach et al. 1949), represent a spatial illusion because sound location is preserved in the face of conflicting reflections many of which, if presented individually to an observer, would be expected to be heard and located. Moreover, the perception of a single source is not consistent with the physical reality that many “sources” (i.e., reflections) are actually present. The PE is largely a spatial phenomenon given that psychophysical studies in humans (Divenyi 1992; Freyman et al. 1998; Gaskell and Henning 1998; Zurek 1980) and owls (Spitzer et al. 2003) have consistently shown that the PE does not result from a peripheral masking of the lagging stimulus by the leading stimulus, given that many nonspatial attributes of the lag can be discriminated.

Naturally, it has been hypothesized that the neural mechanisms that produce the PE allow for accurate localization in the presence of acoustic reflections, whether actual or simulated in the laboratory, by somehow restricting the computation of location to that based on the spatial cues of the sound that arrives at the ears first from the true source (Wallach et al. 1949; Zurek 1987). This “localization” aspect of the PE has been called localization dominance (Litovsky et al. 1999). We shall refer to the previous hypothesis as the localization dominance hypothesis because little is actually known about localization dominance in that few studies have measured the apparent spatial locations in 2 dimensions of the stimuli actually experienced by observers during the PE. The localization dominance hypothesis predicts that 2-dimensional sound localization judgments will be dominated by the leading sound. Although the physiological basis for the PE has been studied at virtually all levels, from auditory nerve to cortex, using stimuli expected to evoke the PE, and specifically localization dominance (see Fitzpatrick et al. 1999 and Litovsky et al. 1999), only particular psychophysical aspects of the PE have been demonstrated in experimental animals [crickets (Wyttenbach and Hoy 1994); birds (Dent and Dooling 2003; Keller and Takahashi 1996]; rats (Kelly 1974]; cats (Cranford 1982); humans (Wallach et al. 1949)], but mostly using psychophysical discrimination procedures.

Here we measure behavioral localization capabilities of cats under stimulus conditions similar to those that have been used in prior psychophysical studies in humans and that have also been used for physiological studies in experimental animals.

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The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
We have already shown that cats experience some important phenomena related to the PE, in particular summing localization (Populin and Yin 1998; Tollin and Yin 2003). We show here that cats exhibit localization dominance and we also determined their echo thresholds, the shortest delay at which a reflection is localized near its source. This study is the first strong test of the localization dominance hypothesis in any species as it pertains to the actual 2-dimensional localization of sound sources in a simulated reflective environment. These data also establish temporal constraints on the various PE phenomena and as such have important implications for the study of the neural mechanisms that mediate the PE and sound localization in general.

**METHODS**

**General**

Five adult female cats chosen for their friendliness and clean middle ears were used in these experiments. All procedures used were approved by the University of Wisconsin Animal Care and Use Committee and complied with the National Institutes of Health guidelines for animal use. Cats were outfitted with stainless steel headposts and fine wire coils (AS631 or AS632, Cooner Wire, Chatsworth, CA) under the conjunctiva of each eye (see Populin and Yin 1998 for more detailed descriptions). Surgeries were carried out using standard aseptic techniques. Briefly, anesthesia was induced by intramuscular injection of ketamine (20 mg/kg) and acepromazine (0.2 mg/kg) and maintained with isoflurane (1–2% in 1 l/min of O₂) administered by inhalation through a tracheal cannula. Postoperative analgesia and antibiotics were provided once a day for up to 3 and 7 days, respectively. Wound edges were treated as needed with triple-antibiotic ointment. Animals were allowed about 2 wk to recover from surgery and were then gradually acclimated to the head-restraint device before training.

Experiments were conducted in a dimly illuminated (or dark) sound-attenuating chamber (2.2 × 2.5 × 2.5 m). All walls and major pieces of equipment were covered with sound-absorbing acoustic foam (10.2 cm, Sonex; Ilbruck, Minneapolis, MN) to minimize acoustic reflections. Auditory and visual stimuli could be presented from one of 15 different spatial locations situated within the oculo-motor range of the cats (about ±25°) by loudspeakers or light-emitting diodes (LEDs), respectively.

When statistical analyses of the data were necessary, we used 2-tailed Student’s t-test with the level of significance α = 0.05. When multiple independent comparisons were made, the level of significance was appropriately adjusted downward using the Bonferroni correction to ensure that the overall level of significance across all comparisons remained at 0.05 (Hays 1988).

**Psychophysical procedure, training, and reward contingencies**

Using operant conditioning, the cats were trained to make orienting saccades to the locations of the visual and acoustic targets provided by LEDs and loudspeakers, respectively. The cats were food deprived for 5–6 days/wk and fed without restriction on nontesting days. During the psychophysical task, the cats earned food rewards, consisting of a puree of canned cat food, finely ground cat chow, and water, delivered after each “successful” trial to a point 1–2 cm in front of the cat’s mouth by a peristaltic pump. Weight was monitored daily and the cats fed as necessary to maintain their weight within about 15% of pre-experiment weight.

Under computer control, the cats were rewarded if their eye position was maintained within a rectangular electronic acceptance window (±8–16°) centered on the target for a predetermined period of time, usually 600–900 ms. During training, the acceptance windows for the trials with visual targets were gradually decreased to ±4–5° to encourage accurate and precise responses. The windows for the auditory trials remained large (±8–16°) to encourage the cats to look to the apparent locations of the sound sources themselves without training them to look to particular locations in space. Target fixation times were initially short (about 600 ms) but gradually increased as the cats acquired the different task types.

Although the cats performed a number of different types of trials on any given day of testing (outlined below), all data reported here were collected only from the saccade task (Populin and Yin 1998), a general schematic of which is shown on Fig. 1A, top. An LED was illuminated at one of the 15 possible target locations. To initiate the trial, the cats fixated the LED and maintained fixation within the acceptance window for a variable period of time (500–1,000 ms). We varied the fixation time from trial to trial so that the cats could not anticipate when the target stimuli would be presented. If these conditions were met, the fixation LED was extinguished and an acoustic or visual target was simultaneously presented from one of the target locations. The cats were then required to make a saccadic eye movement to and maintain fixation at the apparent location of the target. If eye position was within the acceptance window, a food reward was given followed by a variable intertrial interval of about 10–15 s, which was sufficient for the cat to consume the reward before the next trial.

Cats were trained to perform types of tasks other than the saccade task outlined above, including fixation, delayed saccade, and sensory probe tasks (see Populin and Yin 1998), although data from those tasks are not detailed here. During training and experimental sessions, the cats were presented with each of these task types at random from trial to trial so that they could not anticipate what task they would be performing. This training regime was essential for our subsequent physiological experiments in these animals.

**Eye coil calibration**

The scleral search coil (CNC Engineering, Seattle, WA) technique (Fuchs and Robinson 1966), which has a resolution of 0.1°, was used to measure the 2-dimensional position of the eyes. Eye-position data were saved to hard disk by sampling the analog output of the coil system at 500 Hz. Eye coils were calibrated using a behavioral procedure where the cats were required to look at each of the LEDs, located along the cardinal planes, horizontal and vertical, in turn. No training was required for this task because the cats instinctively looked at the LEDs when illuminated. Eye position was continuously monitored using an oscilloscope. During fixation of each of the LEDs, we sampled the output voltage of the coil system and computed the linear regression between voltage and target position. Coefficients of determination of the fit (r²) were typically 0.97 or greater. The coefficients of the fit were then used by the data collection software to convert the voltage output of the coil system to actual degrees of visual angle.

**Analysis of final eye position**

The dependent variable in these experiments was the final 2-dimensional eye position after the saccadic eye movement to the apparent location of the target. The method outlined in Populin and Yin (1998) was used to compute separately the final horizontal and vertical eye positions. Briefly, we used a velocity criterion to determine when the eye movements began and ended by determining the time at which the magnitude of the velocity exceeded 2 SD of zero velocity computed during the fixation of the initial LED from 100 ms before to 30 ms after the onset of the target stimulus when the eyes are stationary. The return to fixation was computed as the time at which the magnitude of the velocity trace returned to within 2 SD of zero velocity. Again, at this point, the eyes were expected to be stationary and fixating the
Apparent location of the target. On some trials, corrective eye movements, defined as those that were initiated within about 200 ms of the end of the initial saccadic eye movement, were made. When a corrective saccade was made, the final eye position for that trial was determined from the return to fixation of the corrective saccade. We did not consider any eye movements made after the reward. On any given testing day, the final eye positions on all trials were included in the data even if the cat was not rewarded so that the localization performance reported here was not confounded by the size of the acceptance windows.

Stimuli: general

The cats were presented with a variety of stimuli using the various types of psychophysical tasks outlined above. Targets consisted of either visual or acoustic stimuli from one of 15 different locations at a fixed distance of 62 cm (measured from the center of the head) arranged in azimuth along the horizontal plane, in elevation along the median plane, and diagonally. Acoustic stimuli were delivered from one of 15 Radio Shack super tweeters (model 40-1310B), modified to transduce low frequencies, resulting in a frequency range of about 1.5–40 kHz. The 15 loudspeakers with the best matching frequency responses, chosen from a large number of loudspeakers, were used. The voltage waveforms for the acoustic stimuli were generated digitally by the custom-built digital stimulus system (Rhode 1976) with built-in attenuators and played out at a rate of 100 kHz to a 15-channel multiplexer. To minimize the chances of acoustic artifacts attributed to speaker selection, each of the 15 possible speakers was connected to its own independent audio amplifier rather than the output of a single amplifier to the 15 speakers. This configuration eliminated a faint transient when the background noise to any speaker was switched on. In addition, before each trial all 15 outputs were first simultaneously selected and then all outputs were simultaneously deselected except for the one or two speakers that served as targets on that trial (see Populin and Yin 1998 for details).

Acoustic stimuli for the precedence effect

Although the cats were exposed to a variety of different acoustic stimuli on a daily basis, the primary stimulus used here consisted of a train of broadband (limited by the frequency response of the loudspeakers) noise bursts of 10 ms duration repeated at a rate of 5 Hz for 1 to 2 s (see Fig. 1A, top). Each individual noise burst in the train was gated with a rectangular window. This stimulus was chosen for its broadband and transient nature, factors known to be important in eliciting the PE (Haas 1951; Wallach et al. 1949), and because it was well localized in preliminary tests. The same 10-ms token of noise was used within a given trial and also from trial to trial. The 5-Hz repetition rate was chosen to facilitate our physiological studies of the PE phenomena (e.g., Tollin et al. 2000), the results of which are detailed in a forthcoming paper. This stimulus was presented either from single spatial locations (“single source”) or from two different spatial locations (“paired source”) but with an interstimulus delay (ISD) between the initial stimulus onsets; the delayed stimulus was meant to simulate a single reflection. Aside from the ISD, the stimuli

**FIG. 1.** Saccadic eye movements to sounds presented from single sources for one cat. A: horizontal components of eye position (left ordinate) from primary position (0°,0°) as function of time to 2 different locations along horizontal plane (−18°,0°) and (18°,0°), during several different trials in saccade task for cat 21. Each trace represents separate trial and all trials were collected during 1 day of testing. Targets are indicated by arrows (right) and brackets indicate acceptance window for reward on this day. Temporal sequence of saccadic task showing illumination condition of fixation LED (ON or OFF), located at midline (0°,0°) for these trials, as well as onset and duration of acoustic stimuli. Time of offset of visual fixation LED and simultaneous onset of acoustic stimulus was defined as 0 ms. B: vertical components of eye position during same day of testing for targets located along median sagittal plane at (0°,18°) and (0°,−14°). C: final 2-dimensional eye position (open symbols) for acoustic stimuli presented from 8 target locations (corresponding filled symbols) collected over 16 days (n = 634 trials). D: mean final 2-dimensional eye position (±1 SD) for same 8 locations as in C. In C and D, midline fixation LED is shown as open circle.
in the paired source condition were delivered to the 2 chosen loud-speakers at the same overall level and in phase.

**Reward contingencies for the precedence effect trials**

Some special considerations were required with the paired-source conditions. Because we expected these stimuli to elicit the spatial illusions associated with the PE, it was not clear what the “correct” behavioral response should have been for a reward. For the paired-source conditions, we wanted the cats to respond simply according to the apparent location of the stimulus, whatever that might be, so we rewarded the cats on every single presentation of the paired-source condition. The reward was given about 1 s after the onset of the stimuli, allowing the cats sufficient time to orient to the apparent location; 1 s was approximately the time at which the reward would be delivered for a correct response in the single-source condition. To keep the cat honest, we presented the paired-source stimuli at a low probability (<5–10%) of the total number of trials and often ran experimental sessions that did not contain any paired-source stimuli.

**RESULTS**

These experiments were designed to determine whether cats experience the different perceptual phenomena associated with the precedence effect, including summing localization, localization dominance, and the echo threshold. The results and statistical analysis are based on data collected from 3 adult cats (cats 18, 21, and 22) and all of the observations were confirmed in 2 other cats (cats 19 and 20) that were tested less extensively.

The results are presented in 3 sections. First we discuss the accuracy and precision by which the cats localized the single-source stimuli. Then we show that cats localized the same stimuli presented from paired sources with small ISDs in a manner suggesting that they experienced both summing localization and localization dominance. Finally, we show that the echo threshold is reached with larger ISDs in that the cats made saccades to the lagging source near its actual position on some trials. Because all of the cats performed similarly with these stimuli, we shall often use data from single cats to highlight particular common aspects of their behavior.

**Apparent location of single-source stimuli**

A fundamental assumption to all of the conclusions in this study is that the cats are looking to the perceived location of the acoustic stimuli. Therefore it is useful to explore this assumption in some detail by examining the responses of the cats to single-source sounds before we consider their responses to paired sounds. Figure 1A shows the horizontal components of typical saccadic eye movements for several trials of one cat to single-source auditory stimuli presented from two different locations on the horizontal plane (18°, 0°) and (−18°, 0°), during a single day of testing. On each trial, the cat made stereotypic short latency eye movements toward the target positions. Similar saccades were made to targets located in elevation along the median sagittal plane: Fig. 1B shows the eye movements for different trials with targets located in elevation at (0°, 18°) and (0°, −18°).

Figure 1C shows the final eye position for individual trials, from multiple experimental sessions, by cat 21 for single-source stimuli at each of the 8 sources tested most extensively. Although there is some scatter in the responses from trial to trial at each location, the data points form clusters in the vicinity of the target. Figure 1D summarizes the data in Fig. 1C by plotting the mean final eye position ±1 SD at each of the target locations. The left panels of Fig. 3, A and B show the mean apparent locations for the single-source stimuli presented from the same 8 sources for the other 2 cats tested most extensively. With these stimuli, all cats tended to under- or “undershoot,” the actual positions of the sources. With these cats, the degree of undershooting was less for broadband stimuli of longer duration and was virtually nonexistent for visual stimuli. Because the remaining 2 cats that were tested less extensively also behaved similarly, we summarize in Fig. 3C (left panel) the performance across the 5 cats by computing the average of the mean apparent locations for the 8 sources.

Consideration of the saccadic eye movements (e.g., Fig. 1, A and B) along with the mean apparent locations (Fig. 1D and Fig. 3, A–C, left hand panels) indicated by the cats suggest that the saccades were goal directed in that the eye movements were always short latency and intentionally made to the vicinity of the actual spatial location of the sound sources. The average response latencies (computed, separately for each cat, across all trials for each individual target location) ranged from a minimum of 66 ms to a maximum of 357 ms. These data suggest that the cats were actively indicating the apparent position of the acoustic targets by their eye movements within 3 or fewer presentations of the 10-ms noise bursts constituting the stimuli (see Fig. 1A, top).

**Apparent location of paired sources varying in azimuth**

The localization dominance hypothesis predicts that, in the presence of reflections, the perceived location of a sound source, in both azimuth and elevation, will be consistent with the actual source location of the leading sound. Figure 2A shows saccades of cat 21 to paired sources positioned along the horizontal plane when the ISD was +2 ms (source “A” leading) and −2 ms (source “B” leading) during the same day of testing as in Fig. 1A. Like saccades to single sources, the saccades to paired sources were generally stereotypic, had short latencies, and were goal directed in that the cat was orienting to a “source” in the vicinity of the leading source location. (Response latencies to single and paired sources are discussed in a later section.) Figure 2B shows for the same cat the final 2-dimensional eye positions for many individual trials and several days of testing for an ISD of 2 ms. The apparent locations of the paired stimuli on individual trials (Fig. 2B, open symbols) were similar, in both azimuth and elevation, to that obtained when the same stimulus was presented at the “leading” source position in isolation (Fig. 2B, filled symbols with error bars). The similar response elevations in the 2 conditions were not necessarily a foregone conclusion for at least 2 reasons: 1) previous studies of localization dominance have not reported quantitatively the 2-dimensional apparent locations of paired sources, so there was no a priori reason for expecting similar responses; and 2) we showed in a previous report (Tollin and Yin 2003) that for small ISDs, the apparent elevations were not consistent with the actual elevations of the 2 sources as illustrated in Fig. 2C (bottom panel).

In the paired-source condition, the orienting behavior of the cats depended on the ISD. The top and bottom panels consti-
tuting Fig. 2C show the mean final horizontal and vertical eye positions, respectively, over many trials for cat 21 for paired sources as a function of ISD between +10 and −10 ms. Positive ISDs indicate that the rightmost source was leading. For example, the data points for ISDs of +2 ms and −2 ms were derived from the data shown in Fig. 2B. Responses are plotted only for ISDs ≤10 ms because, as we discuss later, the behavioral responses for ISDs beyond 10 ms are dramatically different. Figure 3, A and B (right panels) shows similar data for cats 18 and 22. Because all 5 cats performed similarly as a function of ISD, Fig. 3C (right) shows a summary of the data averaged across the 5 cats. Not all cats were tested with all ISDs shown.

SUMMING LOCALIZATION. For ISDs between about ±400 μs, the apparent location depended on ISD. Consistent with summing localization, stimuli with the smallest ISDs (50 μs) were localized near the midline and as ISD increased, response azimuths increased systematically toward the leading source until about 400 μs, whereupon further increases in ISD had little effect on response azimuth. As we reported earlier (Tollin and Yin 2003), all cats localized these paired sources at the short ISDs near 0 ms with a consistent upward bias of about 9° (e.g., Fig. 2C and Fig. 3, bottom), which appears to be in accord with the spectral cues created by the paired-sound sources.

LOCALIZATION DOMINANCE. For ISDs >400 μs, further increases in ISD had little effect on either the response azimuth or elevation, provided the ISD was ≤10 ms (Figs. 2C and 3). The later-arriving stimulus, although easily locatable by all cats when presented in the single-source condition (e.g., Fig. 1D and Fig. 3, left panels), had little influence on the ability of the cats to indicate the location of the leading stimulus. The data show that cats experience the PE and support the localization dominance hypothesis.

With the paired sources, all cats looked toward the leading source but tended to undershoot the azimuth reported with single-source stimuli at the leading source position, which in turn undershot the target position. This additional undershoot, which can be seen in the individual data (Fig. 2C, Fig. 3, A and B) was observed for all cats and for most ISDs between 1 and 10 ms. At no ISD was the mean response azimuth larger in magnitude than the response azimuth to the single source (e.g., Fig. 1D and Fig. 3, left panels), and elevations (bottom panel) ≥1 SD for stimuli presented in single-source condition (n = 212 trials for single sources and 451 trials for paired sources). For ISDs of +2 ms and −2 ms, data in C were derived from data in B.

FIG. 2. Final eye positions to horizontally placed paired sources for one cat. A: examples of horizontal component of eye position to paired sources during 1 day of testing with ISD of 2 ms. Black traces: saccades for positive ISDs [i.e., leading source A at (18°,0°), lagging source B at (−18°,0°)]. Positions of 2 sources along horizontal plane are indicated by arrows (right). Gray traces: saccades to paired sources with negative ISDs. B: final eye positions to paired-source stimuli with ISD of 2 ms and with leading source on left (top) or right (bottom) side (n = 85 trials). In each panel are shown 2 source locations (filled symbols without error bars), mean final eye positions ±1 SD for “leading” single-source location (filled symbols with error bars), and final eye positions for many trials in paired-source condition (open squares). C: mean final eye positions ±1 SD for paired sources as function of ISD. Note change in scale of abscissa between −1 and +1 ms. Filled symbols and error bars show mean response azimuth (top) and corresponding mean response elevation (bottom). For reference, solid and dashed horizontal lines indicate mean response azimuths (top panel) and elevations (bottom panel) ±1 SD for stimuli presented in single-source condition (n = 212 trials for single sources and 451 trials for paired sources).
responses with a 10-ms ISD were also consistent with localization dominance, we did not include them in the analysis because 10 ms was near the echo threshold. Across the 3 cats and 4 leading-source positions there were 12 total tests. Here we discuss the results of the 6 tests for the two horizontally placed paired sources; the results of the remaining 6 tests for the 2 vertically placed sources are discussed in the next section. In 5 of the 6 tests, the cats significantly \( P > 0.05 \) undershot the apparent azimuth they reported for the “leading” single source. Although significant, the mean undershoot was small, averaging \( 2.1 \pm 0.6^\circ \) across these 3 cats and ISDs. The significant undershooting indicates that there was a real, albeit small, residual effect of the lagging stimulus that “pulled” the apparent location of the paired stimuli toward the spatial location of the lagging source. Hence, localization dominance, although still very strong, was not complete.

**Apparent location of paired sources varying in elevation**

In natural environments sources of sounds and their reflections can arrive from any direction. Therefore we expected localization dominance also to be retained for paired-source locations in elevation confined to the median sagittal plane. Similar in style to Fig. 2A, Fig. 4A shows for cat 21 with vertically placed paired sources, positioned at \((0^\circ,18^\circ)\) and \((0^\circ, -14^\circ)\), the final 2-dimensional eye positions for many individual trials and several days of testing when the ISD was \(-2\) ms (lower source leading, left panel) and +2 ms (right panel). Also shown is the mean apparent location of the 2 single sources (filled symbols with error bars). As was the case for horizontally placed paired sources with a 2-ms ISD, the cat also orients to the vicinity of the leading source, both in azimuth and in elevation. Figure 4B shows the mean response elevations for cat 21 as a function of ISD, and Fig. 5 shows data for two other cats. Two of the 3 cats performed similarly at each ISD (cat 21 in Fig. 4B and cat 18 in Fig. 5A); they experienced localization dominance in that the apparent elevation and azimuth (not shown) of the paired-source stimuli for delays between 1 and 10 ms was dominated by the spatial location of the leading source. The remaining cat (cat 22, Fig. 5B) exhibited localization dominance when the leading source...
was above the horizontal plane for all trials, but only on some trials and for some ISDs (e.g., 1 ms) when the leading source was below. The orienting responses of cat 22 when the lower source was leading were bimodal, with some responses toward the lagging, upper source and some toward the lower, leading source. The weakened localization dominance for the low-elevation source is reflected in the mean response elevations near 0° and large variability.

As we showed previously (Tollin and Yin 2003), cats do not experience summing localization with paired sources in elevation as they do in azimuth in that there was not an orderly change in the apparent elevation of the paired-source stimuli as the ISD was changed from −400 to +400 μs. For the small ISDs associated with summing localization, all cats tended to orient toward the upper source even when the lower source was actually leading, and there was no dependency on the ISD. Not until the lower source was leading by 1–2 ms did the cats begin to orient toward that source.

Using the same testing strategy outlined in the previous section, 3/6 tests of whether the cats undershot with paired sources in the median sagittal plane reached significance (α = 0.05). All 3 significant tests occurred for the condition when...
the leading stimulus was lower in elevation at \((0^\circ,-14^\circ)\), suggesting that for these conditions the lagging stimulus still had some residual effect on sound localization. Unlike the case for horizontally placed sources, where there was left–right symmetry in the undershooting to paired sources, for the vertically placed sources used here there is an apparent asymmetry where undershooting occurred only when the leading source was lower in elevation.

**Saccade response latencies to paired sources are similar to single sources**

When human observers are presented with paired-source stimuli with ISDs that result in summing localization and localization dominance, they report hearing only a single fused “phantom” image even though 2 stimuli were actually presented. This has been called fusion, and it is considered another important aspect of the PE phenomena (Litovsky et al. 1999). Unfortunately we had no way of assessing directly whether the cats perceived a single fused sound or 2 separate sounds because the cats were trained to respond to the apparent locations of the targets, not the number of targets. As one test of whether the cats oriented to these illusory sources in a manner consistent with the hypothesis that they experienced only a single “fused” and spatially compact auditory image, we compared the saccade kinematics for the single- and paired-source conditions. We used the end of fixation as a measure of response latency and assumed that this is correlated with the cats’ uncertainty of the source location, with longer latencies expected for those source locations that are more ambiguous (Luce 1986). Consistent with those illustrated in Fig. 1, A and B for single sources, the saccade-onset latencies to the paired-source stimuli were also short and similar to the latencies to single-source stimuli at the corresponding “leading” location. Figure 6, A and B shows mean response latencies for horizontally and vertically placed paired sources, respectively, for cat 21 for the 4 different leading locations to both single sources (solid horizontal lines) and paired sources (filled symbols) as a function of ISD. Latencies to the paired sources were either similar or, more often than not, slightly longer than the latencies to single sources at the leading location. The other 2 cats produced similar patterns of data, although the latencies were shorter on average for cat 18 and longer for cat 22. Examination of data like those in Fig. 6, A and B suggest that, in terms of latency, the cats responded to these illusory stimuli just as they did to an actual single-source stimulus presented from the leading location.

To examine this hypothesis more closely, for 3 cats we computed the mean saccade onset latencies in the paired-source conditions averaged across the ISDs for which they experienced localization dominance, 1, 2, and 5 ms. As for the single-source conditions, the mean latencies varied from cat to cat and also depended on the leading source location. The mean paired-source latencies ranged from a minimum of 75 ms to a maximum of 351 ms and, as reported above, the single-source latency ranged from 66 to 357 ms. We tested the hypothesis that the response latencies for the paired sources were not significantly different from those for the corresponding single sources at the “leading” source position during localization dominance by performing, for each of the 3 cats, 4 independent \(t\)-tests—one test for each of the 4 possible “leading” locations (\(\pm 18^\circ\) on the horizontal plane and the two positions, \(18^\circ\) and \(-14^\circ\), on the vertical plane). The level of significance was adjusted for the number of comparisons as described in METHODS. Only 2/12 tests reached significance of \(P > 0.05\), and both from the same cat (cat 21 for the lead locations of \((-18^\circ,0^\circ)\) (“B” in Fig. 6A) and \((0^\circ,-14^\circ)\) (“B” in Fig. 6B) and in both cases the response latencies were longer for the paired-source condition).

In general, there was little evidence that the cats responded in a dramatically different way to the paired-source stimuli that evoked the PE illusion than they did to the single-source stimuli. This finding supports the hypothesis that the cats perceived an acoustic image in the paired-source conditions that was as salient in terms of its apparent spatial location as an equivalently located single source. However, we cannot be sure whether they perceived a single “fused” stimulus similar to that experienced by humans for ISDs of this size or 2 independent images. Finally, the response latencies for both single- and paired-source conditions show that the cats were orienting to the sources within no more than 2–3 presentations of the 10-ms noise bursts within the train of stimuli.

**Echo threshold at longer ISDs**

Here we address the cats’ behavior for ISDs \(\geq 10\) ms. Figure 7 shows for one cat (cat 18) the horizontal component of the saccadic eye movements to paired-source stimuli over a number of trials for ISDs from 10 to 30 ms. In Fig. 7, responses for each ISD were taken from single days of testing, but from different days of testing across ISDs. The data in black show the paired-source condition where the leading source was located at \((18^\circ,0^\circ)\), whereas the data in gray show the condition where the lead was at \((-18^\circ,0^\circ)\). When the ISD was 10 ms (Fig. 7, top row), all cats made stereotypic short-latency saccades toward only the leading
FIG. 7. Horizontal eye position for paired-source stimuli with ISDs from 10 to 30 ms for cat 18. Black traces: saccades to paired-source stimuli for positive ISDs (i.e., leading source A to right). Positions of 2 sources along horizontal plane indicated by arrows at right of each panel. Gray traces: saccades to paired sources with negative ISDs. ISD is denoted on right. At ISDs >10 ms, cats make saccades toward lagging source on some trials consistent with echo threshold. Data for each ISD were from different single days of testing.

source location consistent with localization dominance. The responses were similar to those shown in Fig. 1A for cat 21 for single sources and in Fig. 2A for paired sources. However, for ISDs >10 ms, there were several different variations in the types of saccadic responses that were generally not seen for smaller ISDs. We attempted to use these response differences to measure the echo threshold. First, response latencies tended to be somewhat more variable with the presence of relatively long latencies on some trials (e.g., Fig. 7, ISDs of 15 and 20 ms). However, this qualitative observation did not always translate into consistent quantitative changes with ISD for all cats, as can be seen in the data for cat 21 in Fig. 6. Second, for some cats and at some ISDs there was an increase in the number of trials for which they did not even initiate a saccade, as defined by our criterion, relative to that for single sources (e.g., Fig. 7, ISDs of 15 and 20 ms). As was the case for latency, this metric did not change consistently with ISD for all cats. Third, on some trials, the cats made initial saccades toward the lagging source location (e.g., Fig. 7, 20-ms ISD). Finally, on some trials, the cats made initial saccades toward the leading- or lagging-source location, but then made corrective saccades back toward the lagging or leading source (e.g., Fig. 7, ISDs of 20 and 30 ms). These latter 2 observations were graded with the magnitude of the ISD and were consistent across cats. In general, however, these trends together suggest that the cats experienced the paired-source stimuli with ISDs >10 ms differently than they did for ISDs <10 ms.

However, do the cats experience the 2 different sound sources at these larger ISDs at 2 different spatial locations? At what ISD can they actually locate the lagging source? With similar transient stimuli, when ISDs exceed about 5 to 10 ms, human observers often report hearing 2 sounds, one associated with the lead and one with the lag (Clifton 1987; Litovsky et al. 1999). Some experimenters have called the shortest ISD at which 2 sounds are heard, as opposed to a single “fused” sound, the echo threshold (Blauert 1997; Litovsky et al. 1999). However, we did not train the cats to indicate how many independent sounds they perceived, but rather to indicate the location of the target. So it was possible that 2 sounds were actually heard at ISDs <10 ms where the cats experienced localization dominance (Figs. 2–5), although we had no way of assessing that.

In spite of this limitation, we felt that it was important to try to estimate quantitatively the echo threshold for these stimuli. To do so, we took advantage of previous reports showing that, although 2 sounds can be heard near their locations, it can be difficult to accurately determine which one was actually the lead and which was the lag (Stellmack et al. 1999). Here we assigned the echo threshold as the ISD at which the lagging stimulus location could be determined by the cats (e.g., Blauert 1997). We used the initial saccadic response azimuths and elevations to determine the ISD at which the cats reported in any way the lagging source at or near its actual location. For example, in Fig. 7, when the ISD was 20 and 30 ms, the cat made saccades to the lagging source for the condition where A led B, but localized the lead when B led A. The saccades were generally goal directed in that they were not saccades to random locations but rather to one of the 2 sources actually emitting sound on that particular trial. Recall that the cats were presented from trial to trial with a variety of different acoustic stimuli from many different locations, and that the paired-source stimuli were presented at very low probabilities. Similar observations were made for the paired-source conditions with sources in the vertical plane (not shown).

We used the goal-directed saccadic responses of the cats for ISDs >10 ms to estimate the echo thresholds. Here we show the analysis of data for paired sources positioned along the horizontal plane. The same analysis was applied to the data for paired sources positioned along the median sagittal plane. For each cat separately we first computed the mean horizontal eye movements toward the location of the leading source regardless of whether the source was on the right or on the left (or up and down for the paired sources in the vertical plane) so that responses toward that leading location had positive values and responses away had negative values. Next we normalized the orienting responses to the single and paired sources by the mean response azimuth to the single sources at the 2 leading positions. As a result, the normalized mean response azimuth to the “leading” location presented in isolation in the single-source condition took a value of 1.0. Figure 8 shows for 3 cats the mean normalized final eye positions toward the leading
source in the paired-source condition as a function of ISD from 2 to 20 or 30 ms.

As demonstrated in the previous sections, for ISDs between 2 and 10 ms, the cats oriented to the leading source only, consistent with localization dominance. For ISDs about 15 ms and greater, the cats often made saccades to the lagging source on some trials and toward the leading source on other trials. This type of overt behavioral response is consistent with the hypothesis that at these ISDs, the cats perceived 2 source locations but could not consistently identify which was actually the leading source. The bimodal distributions of responses effectively increased the variability of the mean normalized responses as well as pulled the mean response azimuths toward the midline. For these 3 cats, these changes in their orienting responses began to occur for ISDs of 15 ms. Similar data (not shown) were obtained for paired sources in the median sagittal plane, although for one cat, these types of responses were occurring by 5 ms (see cat 22, Fig. 5B). These data together suggest that, for these cats with these stimuli, the localization dominance illusion breaks down and information about the spatial location of the lag first emerges for ISDs of between 10 and 15 ms. At these ISDs the spatial information about the lag is sufficient to support saccadic eye movements toward the source emitting the lagging stimulus on some trials.

**Discussion**

We investigated whether cats experience the 3 perceptual phenomena most often associated with the PE: summing localization, localization dominance, and the echo threshold. The data support the hypothesis that cats, like humans, not only experience all 3 of the phenomena, but, with the exception of summing localization, do so over similar ranges of ISDs. Unlike previous behavioral investigations in different species that have employed discrimination procedures to infer that those species were experiencing correlates of the PE, here we measured directly the apparent locations of the stimuli by the cats. As such, these data represent the first measurements in any nonhuman species of the 2-dimensional apparent locations of stimuli expected to evoke the precedence effect.

**Cats underestimate the apparent location of single-source stimuli**

Sound localization capabilities of cats have been examined in previous studies using different psychophysical techniques (Beitel and Kaas 1993; Casseday and Neff 1973; Heffner and Heffner 1988; Martin and Webster 1987; May and Huang 1996; Populin and Yin 1998; Thompson and Masterton 1978). Some of these studies that have measured in cats the apparent locations of sounds in 2-dimensional space (May and Huang 1996; Populin and Yin 1998) also reported undershooting in azimuth and elevation, as reported here. Human observers exhibit similar underestimation (Feddersen et al. 1957; Hoffman and Van Opstal 1998; Macpherson and Middlebrooks 2000), particularly for brief, high-frequency stimuli like those employed here, although the magnitude of the undershoot is generally smaller than that seen here. Undershooting is not just an auditory phenomenon, given that it has also been shown to occur in cats with transient visual stimuli (Populin and Yin 1998; Tollin and Yin, unpublished observations). The degree of undershooting was less for broadband sounds of longer duration and virtually nonexistent for long-duration visual stimuli (Populin and Yin 1998). The underestimation of sound location may be attributed jointly to the brief duration and absence of low-frequency energy (see METHODS) in the stimuli we used here. In addition, preliminary data from our lab indicate that the degree of undershooting can be reduced by freeing the head of the cats (Populin et al. 2000).

**Cats experience summing localization**

For small values of ISD, the apparent positions of paired sources depended critically on the ISD, as has been reported for human observers (Blauert 1997; Litovsky et al. 1999; Mickey and Middlebrooks 2001; Wallach et al. 1949; Zurek 1987). Based on data from discrimination experiments with horizontally placed sources, it had been inferred that cats experience summing localization (Cranford 1982; Kalmykova 1993). We have confirmed that hypothesis here and in our previous reports (Populin and Yin 1998; Tollin and Yin 2003). Interestingly, the ISD range for summing localization in cats...
was smaller (about ±400 μs) than for humans (about ±800 μs) (Blauert 1997), and 400 and 800 μs are approximately the size of the maximum interaural time disparity that adult cats (Roth et al. 1980) and humans (Fedderson et al. 1957), respectively, would be expected to experience given the different head diameters. It has been hypothesized that the ISD at which summing localization transitions into localization dominance is proportional to the maximum interaural delay (Lindemann 1986; Mickey and Middelbrooks 2001; Zurek 1980, 1987). Although our data are consistent with this hypothesis, data from experiments in mammals (Hoenfelding and Harrison 1979; Kelly 1974) and birds (Dent and Dooling 2003) with very small head diameters, and thus very small ranges of maximum interaural delay, are not.

The spatial illusion that occurs during summing localization has been shown to be attributed to the binaural localization cues present at the 2 ears that result from the linear summation of the 2 sounds from 2 different locations and are not considered further here (Blauert 1997; Mickey and Middelbrooks 2001; Tollin and Henning 1999; Tollin and Yin 2003). We have shown further that the apparent elevations of the horizontally placed paired sources (bottom panels of Figs. 2C and 3) are explicable based on the broadband spectral patterns that result at the ears when presented with sounds from the 2 different spatial locations used here (Tollin and Yin 2003). These data support the hypothesis that spatial location—dependent broadband spectral patterns at the ears are used for determining the elevation of sound sources (Blauert 1997).

Summing localization does not operate in the vertical plane as it does for horizontally placed sources in that the cats did not perceive a “phantom” sound at a position between the physical sources whose location was systematically dependent on ISD (Tollin and Yin 2003). Few human studies have reported on summing localization in the vertical plane. Blauert (1971) found summing localization—like effects for ISDs between +880 and −880 μs. In another free-field study (Harima et al. 1997), observers were presented with paired sources in the midsagittal plane with a 0-ms ISD. Although the average apparent locations reported were generally consistent with an image midway between the sources, there was a bias toward the upper source, consistent with that found here, and the variability in the responses was very large. One possibility for the lack of summing localization in cats could be that the localization cues for the lower source were simply less salient than those for the higher sources so when presented together with a small ISD, the more salient cues dominate even when the lower source leads. However, there was little indication that the ability of the cats to localize single-source stimuli at these two locations was substantially different (see Figs. 1 and 3).

We have shown that the broadband spectral cues that are used for sound elevation that result in the paired-source conditions actually specify a “source” at a higher elevation rather than a position between the two sources (Tollin and Yin 2003). As is the case for the horizontally placed sources where apparent azimuth is determined by the resultant interaural cues, the apparent elevation for vertically placed sources is also determined by the resultant broadband spectral cues. So if it is assumed that the phenomenon of summing localization is based on the localization cues that result in the paired-source conditions, then there is indeed a summing localization effect for vertically placed sources.

**Cats experience localization dominance**

When the ISD was increased beyond approximately 400 μs, provided that the ISD was 10 ms or less, the cats generally oriented only toward the vicinity of the leading source location consistent with localization dominance. However, the mean apparent locations for ISDs encompassing localization dominance undershot the positions for single sources at the “leading” locations. We previously reported this undershooting (Populin and Yin 1998; Tollin et al. 1999). Similar undershooting has been documented in human studies (Chiang and Freeman 1998; Mickey and Middelbrooks 2001).

Localization dominance in cats has been inferred from previous discrimination studies. Those studies showed that cats could indicate the side from which single-source stimuli were delivered on nearly 100% of trials (Cranford 1982; Cranford and Oberholzer 1976; Kalmykova 1993). With paired sources, performance was also high for ISDs between 1 and about 10 ms, consistent with localization dominance, although performance was always lower than that for single sources, parallelizing the undershooting of paired sources by our cats. For increases in ISDs beyond about 10 ms in those studies, performance declined substantially and approached chance at larger ISDs. The chance level of performance for identifying the leading source location by those cats is wholly consistent with the endpoint of localization dominance, that is, echo threshold, as we measured here (Fig. 8).

In a recent study in humans, Mickey and Middelbrooks (2001) found that with ISDs between 0.8 and 1.4 ms, the apparent azimuths reported by their observers were in the direction of the leading source, but undershot considerably the horizontal apparent location that each observer reported for single-source stimuli delivered from the “leading” source. Stecker and Hafter (2002) also found strong localization dominance for ISDs of 1–8 ms, but the observers’ responses were slightly biased toward the lagging location. Neither study reported the response elevations for these horizontally placed sources. Several other studies have also demonstrated that the spatial attributes of the lag can still affect the apparent location of the lead stimulus (Chiang and Freyman 1998; Litovsky and Macmillan 1994; Litovsky et al. 1997; Rakerd and Hartmann 1985; Shinn-Cunningham et al. 1993; Tollin and Henning 1998; Wallach et al. 1949). Hence, localization dominance is not complete under these “optimal” experimental conditions, for both cats and humans, suggesting common mechanisms for its production in both species.

Few studies have examined localization dominance for sources positioned along the vertical plane (Litovsky et al. 1999). Litovsky et al. (1997) showed indirectly localization dominance for sources along the median sagittal plane and 2 of their findings were consistent with ours here: 1) localization dominance was strongest for ISDs between 1 and 5 ms and began to break down by 10 ms, and 2) localization dominance was not as strong for vertically placed sources as it was for horizontally placed sources. Blauert (1971) also demonstrated localization dominance for sources along the median—sagittal plane provided the ISD was greater than about 550 μs. Dent and Dooling (2003) made similar observations in birds. The localization dominance aspect of the PE appears to be a general spatial localization phenomenon that permits the quick and
reasonably accurate localization of sounds irrespective of where the source and the later arriving reflections originate.

Although we interpret the undershooting in both the paired-source conditions as a pulling of the apparent location of the leading source toward the lagging, an alternative explanation might be that the paired-source stimuli simply produce a more ambiguous acoustic image and when faced with this uncertainty, the cats opt not to make large-amplitude eye movements away from the central fixation point. Although it is difficult to completely rule out the latter explanation, at least 2 aspects of the cats’ behavior argue against it: First, visual inspection of the SDs of the mean response azimuths and elevations (Figs. 2–5), for horizontally and vertically placed paired sources, respectively, show that they are similar to those obtained for single sources at the leading location. Second, analysis of the response latencies (Fig. 6) indicates that the cats initiate their responses to single and paired sources similarly. Any uncertainty as to source location for paired sources might be reflected in more variable response azimuths and elevations leading to larger SDs as well as increased response times relative to that obtained for single sources.

The echo threshold for paired sources

When the ISD was increased beyond 10 ms, on many trials the cats oriented toward the leading and/or lagging source locations. That the cats made responses toward lagging locations at all suggests that there was sufficient information about the spatial location of the lag to permit an overt goal-directed orienting response to its position. For paired sources located in azimuth along the horizontal plane, echo thresholds were between 10 and 15 ms. Echo thresholds were slightly smaller for paired sources in elevation along the median plane. Using discrimination techniques, Kalmykova (1993) was the first to estimate echo thresholds in cats with horizontally placed sources. For the stimulus conditions most similar to those here (i.e., clicks presented at 4 Hz for 1–2 s), the mean echo threshold computed across his 4 cats was about 16 ms, ranging from 12 to 19 ms. Similar estimates from cats can be computed from Cranford (1982). Thresholds of about 10 ms have also been obtained in owls (Keller and Takahashi 1996) and parrots (Dent and Dooling 2003).

In humans, echo thresholds tend to be smallest for transients and larger for longer-duration stimuli, such as speech and music (Blauert 1997; Litovsky et al. 1999). For brief broadband stimuli presented in the free field, echo thresholds based on techniques where observers were required to indicate in some way the actual location of the lagging source range from 8 to 16 ms (Freyman et al. 1991; Stecker and Hafer 2002; Thurlow and Parks 1961; Wallach et al. 1949; Yang and Grantham 1997). Litovsky and Shinn-Cunningham (2000) reported large individual differences in echo thresholds. Our estimates of echo threshold in the cats based on their orienting responses are similar to those measured in human and several nonhuman species with similar stimuli. However, our method likely overestimates echo threshold because the cats may have been reluctant to saccade toward the lagging source location if 2 sounds were actually perceived, but that the leading source location was simply more salient.

Finally, a potentially important difference between this study and similar studies with human observers is that the noise-burst stimuli were repeated several times, whereas stimuli used in many human experiments were often presented only once. It has been shown that the precedence effect “builds up” with repeated stimulus presentations in human observers (e.g., Freymann et al. 1991) in that the effect of the lagging source on the localization of the leading source can be reduced through multiple presentations of the stimuli. If such a buildup phenomenon occurs in cats, then the localization performance reported here might be better than that expected for single presentations.

In conclusion, the mechanisms that produce the precedence effect, specifically localization dominance, are important because they work to preserve the spatial location of sound regardless of reflections, noise, and so forth. It is instructive to point out that if sound location did not remain constant in the face of changes in the environment, then source location would surely have lost its value as an important auditory property. This would be particularly true for those species that rely heavily on sound localization for survival, such as nocturnal predators such as the cat, as well as more “specialized” species like owls and bats. Although behavioral studies have shown that the sound localization capabilities of bats and owls are similar to, and under some conditions exceed, that of humans, detailed psychophysical studies of localization dominance have not been initiated in bats. Only recently have owls been shown to exhibit behavioral correlates of localization dominance using discrimination procedures (Spitzer et al. 2003), confirming earlier observations (Keller and Takahashi 1996).

The physiological mechanisms that produce the various perceptual phenomena associated with the PE have been studied at virtually all levels of the auditory system, from the auditory nerve (Parham et al. 1996), the brain stem (Fitzpatrick et al. 1995; Parham et al. 1998; Wicksberg 1996), and inferior colliculus (Fitzpatrick et al. 1995; Litovsky and Yin 1998a,b; Tollin et al. 2000; Yin 1994), to the auditory cortex (Fitzpatrick et al. 1999; Mickey and Middlebrooks 2001; Reale and Brugge 2000; Whittfield 1974). Many of these studies have used cats as the model system and have used paired-source stimuli with ISDs that, based on human psychophysical studies, might have been expected to evoke the PE illusion in the experimental animals. The data reported here demonstrate that cats actually do experience the 3 major perceptual phenomena of the PE and we detail the ranges of ISDs over which these phenomena are experienced. These ISD ranges can be used to help interpret the past physiological studies of the PE as well as assist in designing and testing further hypotheses regarding the neural mechanisms that produce the PE.

We acknowledge the assistance of J. Sekulska and R. Kochhar for help with computer programming, J. Hudson, J. Ruhland, and J. Moore for help with animal training and data analysis. Special thanks to Dr. Luis Populin for guidance during animal training and surgery. We thank Dr. Michael Dent and three anonymous reviewers for commenting on earlier versions of the manuscript.

DISCLOSURES

This work was supported by National Institutes of Deafness and Other Communicative Disorders Grants DC-00116 and DC-02840 to T.C.T. Yin and an Individual National Research Service Award DC-00376 to D. J. Tollin.
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J Neurophysiol • VOL 90 • OCTOBER 2003 • www.jn.org


