

Investigations of the precedence effect in budgerigars: The perceived location of auditory images

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(Received 15 May 2002; revised 10 January 2003; accepted 24 January 2003)

The perceived location of auditory images has been recently studied in budgerigars [Dent and Dooling, *J. Acoust. Soc. Am.* **113**, 2146–2158 (2003)]. Those results suggested that budgerigars (*Melopsittacus undulatus*) perceive precedence effect stimuli in a manner similar to humans and other animals. Here we extend those experiments to include the effects of intensity on the perceived location of auditory images and the perceived location of paired stimuli from multiple locations in space. We measured the abilities of budgerigars to discriminate between paired stimuli separated in time, intensity, and/or location. Increasing the intensity of a lag stimulus disrupted localization dominance. Budgerigars also perceived simultaneously presented (away from the midline) stimuli as very similar to a single sound presented from the midline, much like the phantom image reported in humans. The perception of paired stimuli from one side of the head versus two sides of the head was also examined and showed that the spatial cues available in these stimuli are important and that echoes are not perceptually inaccessible during localization dominance conditions. The results from these experiments add further data showing the precedence effect in budgerigars is similar to that found in humans and other animals. © 2003 Acoustical Society of America.

[DOI: 10.1121/1.1560161]

PACS numbers: 43.80.Lb, 43.66.Gf, 43.66.Qp [WA]

I. INTRODUCTION

A variety of techniques have been used to measure aspects of the precedence effect in animals. For instance, behavioral studies tracking eye movements of cats previously trained to look at the position of a single sound source show that two sounds played simultaneously caused the cats to look directly ahead, at a “phantom” image location, much like summing localization in humans (Populin and Yin, 1998; Tollin *et al.*, 2000). At increasing delays, the cats shifted their eyes towards the location of the lead sound, suggesting that the cats perceive a single sound at the location of the lead during that timecourse, again in a manner similar to humans. At even longer delays, cats often looked towards the location of the lead and then the position of the lag, or vice versa. This suggests that at those timecourses, they perceive both the lead and lag at their respective locations, similar to what happens once past the echo threshold in humans (Tollin *et al.*, 2000).

In another study, Cranford (1982) trained cats to release either a right or left foot pedal, whichever corresponded to the side of the leading sound source location. At intermediate interstimulus delays, the position of leading source was identified on close to 100% of the trials. At shorter and longer delays, performance was at chance levels. Here, the cats were unable to reliably locate the position of the leading sound source. Taken together, the results from these independent laboratories using different methodologies suggest that cats do indeed perceive summing localization and localiza-

tion dominance stimuli in a manner similar to humans.

The precedence effect has also recently been found in budgerigars (*Melopsittacus undulatus*). Rather than the identification methods used above, discrimination experiments utilizing the buildup and breakdown of localization dominance were used as an assay of the precedence effect. The results obtained here are consistent with the three phases of the precedence effect (summing localization, localization dominance, and echo thresholds) and the timecourses were similar to those found in humans and other animals (Dent and Dooling, 2003). To review these data, budgerigars had difficulty discriminating the L-R (left-right) background pairs from R-L (right-left) target pairs with the same interstimulus interval at the timecourses where summing localization is operating in humans (below 1 ms). At these timecourses, the perceived location of the auditory image is in-between the actual locations of the sound sources. Budgerigars had little difficulty discriminating the L-R background from the R-L target at the timecourses where localization dominance operates in humans (1–5 ms). Here, the perceived location of the auditory image is at the location of the lead stimulus only. These results suggest that in budgerigars, as in humans, the spatial attributes of the lag are perceptually inaccessible. At longer timecourses, where the echo thresholds are found in humans (5–10 ms), budgerigars again had difficulty discriminating background stimuli from targets.

The present experiments test the validity of these earlier results by measuring whether an intensity increase in a lag stimulus can decrease performance and whether simultaneously presented sounds are perceived from a phantom location in space. In humans, it is known that intensity differences can elicit localization dominance and summing

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localization, and that there is a time-intensity trading effect when the intensity of the lead stimulus is decreased (Haas, 1951; Leakey and Cherry, 1957). Less is known about the effects of intensity on the precedence effect in animals, however. Hoeffding and Harrison (1979) and Kelly (1974) found thresholds of 3–5 dB for discriminating pairs of stimuli separated by intensity differences only, although the latter authors could not disrupt performance by decreasing the intensity of the lead when time differences were introduced, suggesting that the time-intensity trading ratio is not found in all animals. Here, we measure the intensity differences required for discrimination between simultaneously presented stimuli and test whether a time-intensity trading can disrupt performance in these birds.

In a second experiment, the nature of summing localization in budgerigars is investigated. Cats look towards the midline when presented with simultaneously presented sounds (Populin and Yin, 1998), behaving as if they perceive a phantom image in a similar manner as humans. It is not known, however, whether the quality of that phantom image perceived by cats is indistinguishable from a single sound presented from that central location. Using a discrimination paradigm, we measured the ability of birds to discriminate between a centrally located single stimulus and laterally located paired stimuli presented simultaneously.

In a third series of experiments, we measure the discriminability of “echoes.” During normal localization dominance conditions, animals behave appropriately towards a primary sound source while ignoring echoes that may be only a few decibels below and a few ms after the primary sound. It is important to note that although the echoes are ignored, they do affect perception—listeners can easily discriminate between sounds with and without echoes. Perrott *et al.* (1987, 1989) found that spatial resolution for stimuli under localization dominance conditions was only mildly affected. Litovsky and MacMillan (1994) found that minimum audible angles for lead stimuli were better than those for lag stimuli, but they were still measurable in the lag. The delay between presentation of the lead and lag sounds also has an effect on the extent that the lag affects the perceived location of the sound image. During summing localization, both the lead and lag contribute to the perceived location, while during localization dominance, the lag has little to no effect on the perceived location of the auditory image.

Some researchers have stressed the positive perceptual influences of having echoes present and only their directional cues rendered inaccessible. Echoes can have an effect on speech communication and can enhance the overall quality of complex sounds (Haas, 1972; Freyman *et al.*, 1998; Mershon *et al.*, 1989). In humans, perceived distance judgments of a sound source in a room became much more accurate as the number of reflections is increased up to a certain point (Bronkhorst and Houtgast, 1999). Recent field work suggests that birds may be able to use reverberations of calls as cues for auditory distance perception (Naguib, 1995; Nelson and Stoddard, 1998), and of course bats and some species of birds are able to use returning echolocation signals for maneuvering in their environment (Griffin, 1958; Griffin and Suthers, 1970; Konishi and Knudsen, 1979). So while the

precedence effect allows humans and other animals to disregard echoes as true separate sound sources, the preservation of the information in those echoes may also be providing listeners with important cues about their auditory environment. For this reason, a detailed examination of the potential uses and perceptual accessibility of these cues is important for understanding hearing mechanisms as well as acoustic communication strategies. In three experiments, we measure the discrimination of paired stimuli presented unilaterally or bilaterally to determine the nature of echo perception and discrimination in these small birds. As a whole, these experiments will lend further support to the hypothesis that the precedence effect, its component phenomena, and the general perception of echoes are similar across all animals.

II. GENERAL METHODS

A. Subjects

Four adult budgerigars (three males, one female) were used in these experiments. The number of subjects used within each individual experiment is noted within that experiment. The birds were either bred from commercial stock in a vivarium at the University of Maryland or purchased from a local breeder. The birds were housed in individual cages and kept on a normal day/night cycle correlated with the season at approximately 90% of their free-feeding weights. All animal experimentation was conducted under the auspices of an approved protocol from the Animal Care and Use Committee at the University of Maryland, College Park.

B. Testing apparatus and stimuli

The psychoacoustic experiments took place in a wire test cage ($25 \times 18 \times 14 \text{ cm}^3$) mounted 115 cm from the ground in a sound-attenuating chamber ($2.8 \times 2.5 \times 2.0 \text{ m}^3$). The test cage consisted of a perch, an automatic feeder on the floor of the cage (food hopper), and two vertical response keys extending from the floor in front of the bird. The response keys were two sensitive microswitches with 8-mm light emitting diodes (LEDs) located just above the food hopper. The bird pecking the LED tripped the microswitch. The left microswitch and LED served as the observation key, and the right microswitch and LED served as the report key. During a session, a small light at the top of the test cage illuminated the chamber. The behavior of the animals during test sessions was monitored at all times by an overhead video camera system.

The experiment was controlled by an IBM Pentium III microcomputer operating Tucker-Davis Technologies (TDT, Gainesville, FL) modules. The stimuli were 1-ms broadband clicks presented at 70 dB SPL (unless otherwise noted). Stimuli were generated in advance of testing, stored in digital form, and output at a sampling rate of 50 kHz via a timing generator (TDT, Model TG6) to a four-channel D/A converter (TDT, Model DA3-4). Each signal was then output from a separate channel of the D/A converter to a separate digital attenuator (TDT, Model PA4) and a separate amplifier (TDT, Model HB6) to separate speakers located in the testing chamber (Realistic 3" midrange tweeter). The speakers were

placed at the same height as the cage, 60 cm from the position of the bird's head during testing. Stimulus calibration was performed with a Larson-Davis sound level meter (Model 825, Provo, UT) with a 20-ft extension cable and $\frac{1}{2}$ -in. microphone and measured at the position normally occupied by the bird's head during testing.

C. Training and testing procedures

The training and testing procedures have been described in detail in Dent and Dooling, (2003). The birds were trained by a standard operant autoshaping program to peck at the microswitch keys for food reinforcement. First, they pecked repeatedly at the left key (observation key) during repeating presentations (rate of 2/s) of a stimulus emitted from single source (background; e.g., a left speaker only). After a random interval of 1–6 s, the same stimulus was played from a different source (target; e.g., from the right speaker). The bird was trained to peck the right key (report key) when it detected this change in order to obtain food. The birds were rewarded on 70% of the trials with a 2-s free access to seed if they detected the change. Percent correct hit values on trials involving a change from background to target were recorded for further analysis.

Incorrect report key pecks were punished with a timeout during which all of the room lights were extinguished. A miss was recorded if the bird failed to peck the report key within 2 s of the change in stimulus presentation. Sham trials, where there was no change of sound presentation type from background to target, consisted of 30% of all trials. Pecks to the report key during these trials were counted as false alarms, and the birds were again punished with a lights-out period. Sessions with a false alarm rate of 15% or higher were discarded. Approximately 6% of all sessions were discarded for this reason. An experimental session consisted of 100 trials. The birds were tested at least two sessions a day, and between 5 and 7 days a week. Each bird was run on at least 200 trials at each experimental condition, and the last 100 trials after discrimination performance stabilized were analyzed.

III. EXPERIMENT 1: TIME-INTENSITY TRADING RATIO

The first experiment tested whether intensity differences would elicit localization dominance in budgerigars, and if there was a time-intensity trading ratio for localization dominance, in other words, if intensity differences between stimuli could abolish the buildup of localization dominance that was due to time differences between stimuli. In humans, increasing the intensity of the echo sound relative to the primary sound can disrupt localization dominance on stimuli separated by a short delay (Leakey and Cherry, 1957; Wallach *et al.*, 1949). Snow (1954) investigated the time differences between two stimuli that could be compensated for by level differences between the stimuli. Placing a primary speaker at -45° azimuth and an echo speaker (delayed for a few ms) at $+45^\circ$ azimuth (where normally the perceived sound would be at -45°), Snow (1954) showed that decreasing the intensity of the primary speaker by 5–8 dB actually

centered the perceived auditory image at 0° . The birds were tested on their discrimination of stimuli with a similar manipulation.

A. Methods

Once the birds were trained to peck the observation key repeatedly during presentation of a single stimulus emitted from the left speaker (-90° , repeating background) and to report a change in the location of this repeating background ($+90^\circ$ target) by pecking the report key, paired stimuli were substituted for the single stimuli. Here the repeating background involved presenting the stimuli from two speakers [for a detailed explanation, see Dent and Dooling (2003)]. The birds were required to discriminate a L-R (left first, then right) paired background from a R-L paired target. The inter-stimulus interval (ISI) between the right and left stimuli was the same from background to target; the lead-lag click delay was merely reversed in location. The lead-lag clicks constituting the background were played at a rate of 2/s a random number of times (between 6 and 12) before the targets were presented. The lead-lag clicks constituting the targets were presented four times (also at a rate of 2/s) or until the birds responded.

Three budgerigars were tested on discrimination of pairs of 1-ms broadband clicks at three different ISIs (0, 1, and 5 ms). Here, the task was to discriminate a repeating click pair background with the left speaker leading the right by some ISI from a repeating click pair target with the right speaker leading the left by the same ISI. Baseline (time differences between lead and lag only) discrimination performance for all L-R stimulus discriminations at different ISIs had been determined earlier [Fig. 2 of Dent and Dooling (2003)]. The subjects were then retested with the "echo" (second click in the pair of clicks) at 3, 5, 7, and 10 dB more intense than the lead sound at each of the three ISIs.

In the intensity difference *only* condition, the sounds were presented simultaneously from the left and right speakers. One of the clicks was less intense during the repeating background, and the other one was less intense during the target. In the intensity *and* time difference condition, the leading sound was less intense than the lagging sound during the repeating background. When the targets were presented, the ISIs and intensities of the lead and lag were switched. For instance, if the less-intense lead was on the left and the more-intense lag was presented from the right in the repeating background, when the targets were presented the less-intense lead was switched to the right speaker and the more-intense lag was switched to the left speaker. The leads and lags retained their timing and intensity separation from background to target; they merely changed locations. Overall discrimination performance was determined for each intensity and time difference combination in each separate session for each bird.

B. Results

Discrimination performance as a function of stimulus intensity difference for the three subjects is shown in Fig. 1 for three different ISIs. The mean false alarm rate for all experiments was 4% (mean d' value=2.32). The interindi-

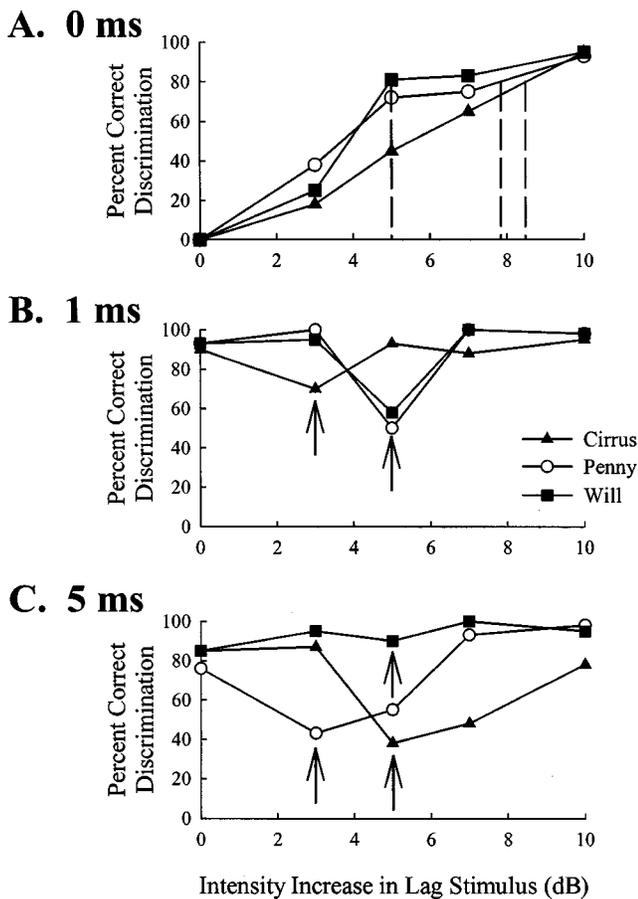


FIG. 1. Discrimination performance for three individuals (Cirrus=black triangles, Penny=white circles, Will=black squares) tested at three ISIs [(a)=0 ms, (b)=1 ms, (c)=5 ms], with the lag stimulus equal in intensity to (0 on the x axis) or more intense than the lead (>0 on the x axis).

vidual variation in the data shown in this experiment is fairly conservative compared to similar experiments in humans (see, for example, Litovsky and Shinn-Cunningham, 2001). With a 0-ms ISI [clicks presented simultaneously from the L and R speakers; Fig. 1(a)], it took between 5 and 8 dB to increase the discrimination performance to an arbitrary 80% criterion level (dotted lines). For the 1- [Fig. 1(b)] and 5-ms [Fig. 1(c)] ISIs, it took between 3 and 5 dB to decrease responding (arrows). Here, although the click on the left was presented first (either 1 or 5 ms earlier than the lag), the later click on the right was louder. This stimulus condition disrupted discrimination abilities for all three birds, although to varying degrees for each subject. At the 0-ms ISI, as intensity differences between the two stimuli increased, discrimination performance increased. At the 1-ms ISI, performance fell from close to 100% correct to under 60% correct for two birds (Penny and Will) and to 70% for one bird (Cirrus). At 5 ms, performance fell to almost 40% correct for two birds (Cirrus and Penny) but barely decreased for the third bird (Will). After this intensity increase in the lag caused a decrease in discrimination, performance returned to high levels for all three birds with further intensity increases in the lag. This experiment shows that intensity differences as well as time differences can have an effect on discrimination of paired sounds during the timecourse of localization dominance, although this effect is variable across subjects.

IV. EXPERIMENT 2: THE DISCRIMINATION OF MULTIPLE SOUND SOURCES

In humans, two simultaneously presented sounds from opposite sides of the listener result in an identification of that source at the midline (Wallach *et al.*, 1949). Cats, too, look towards the midline at simultaneously presented sounds (Populin and Yin, 1998). Although the budgerigars do not identify the location of the auditory image in our discrimination paradigm, we test the discrimination of two simultaneously presented sounds from the sides from one sound played from the midline. Difficulty in discriminating between the two stimulus conditions would suggest that budgerigars, like humans and cats, perceive a phantom midline image, and that the image has similar spectral qualities as well.

A. Methods

In this experiment, three budgerigars were tested on their discrimination of single or multiple source stimuli from different locations. The background 1-ms click stimuli were presented from one of four location conditions during each session: -60° , $+60^\circ$, 0° , or simultaneously from $+60^\circ$ and -60° . The targets in a session consisted of stimuli presented from the other three background conditions. All background-target combinations were tested. When the simultaneously presented $+60^\circ$ and -60° sounds were played, they were attenuated so that the signal received at the ears of the birds equaled that of a single sound source reaching the ears of the birds.

B. Results

When the task was a simple discrimination (e.g., left background versus right target), discrimination performance was close to 100% (Fig. 2). This was true when discriminations involved a large spatial separation (e.g., left versus right) or a smaller separation (e.g., left versus center). When the discriminations involved simultaneously presented backgrounds or targets from $+60^\circ$ and -60° , discrimination of a single sound source from the side was high (80%–90% correct), while discrimination of a single sound source from the center was very low (25%–40% correct). These birds could not easily discriminate a 0° background from a simultaneously presented -60° and $+60^\circ$ target, and vice versa, while a 0° background was easily discriminated from either the -60° or $+60^\circ$ targets when they were presented alone. Although these results were well above chance levels of performance, these discriminations were 65% lower than in the simpler discrimination tasks. These results suggest that budgerigars perceive simultaneously presented clicks at -60° and $+60^\circ$ as qualitatively similar to a single click presented alone at 0° .

V. EXPERIMENT 3: THE IMPORTANCE OF SPATIAL CUES

This experiment was a test of whether the spatial cues of the paired stimuli were salient to budgerigars, especially in light of the fact that they have generally poor sound localization abilities (Park and Dooling, 1991). In earlier prece-

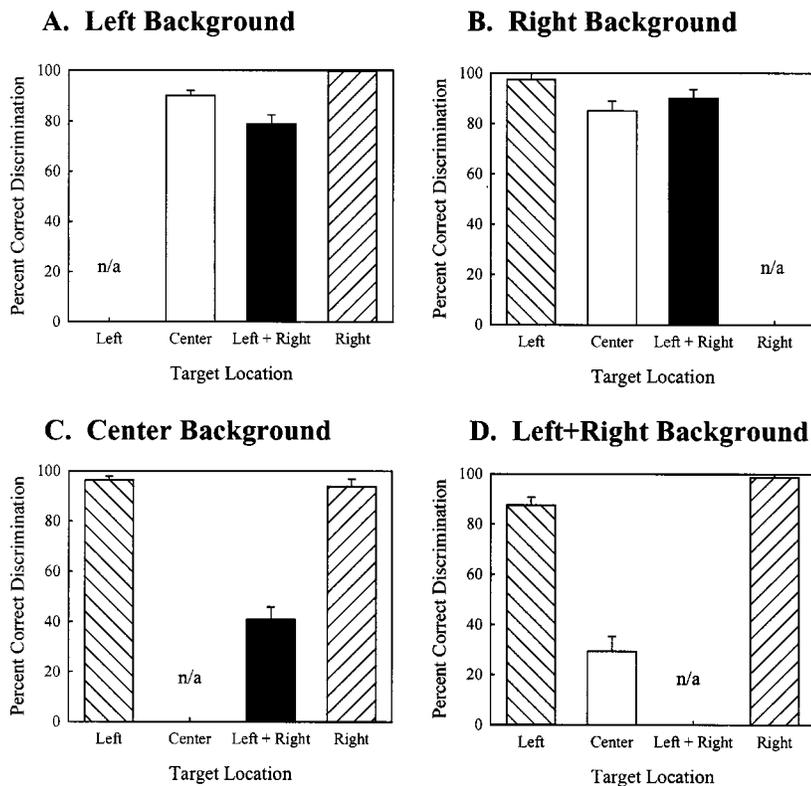


FIG. 2. Means from three individuals tested on discrimination of one of four background location conditions (A–D) and the corresponding three target location conditions.

dence effect experiments with budgerigars (Dent and Dooling, 2003), stimuli were presented at different times as well as from different locations. Here, a single click from one location was the background, and paired clicks from either one or two locations was the target. If the birds are able to use spatial cues in this task, discriminating between pairs of clicks from a single location should be more difficult than discriminating among pairs of clicks from multiple locations because of the added location cues.

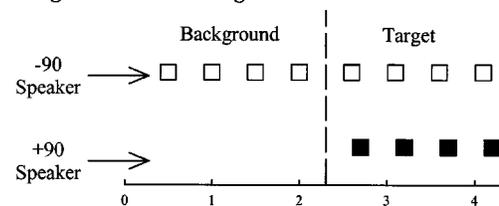
A. Methods

In this experiment, a single 1-ms click located at -90° was the background and the four subjects were required to discriminate targets where the lead was at -90° and the lag was at $+90^\circ$ [Fig. 3(a)] or where the targets had the same temporal properties of the previously mentioned lead-lag targets, but no spatial cues—because the targets were both at -90° and played from the same speaker [Fig. 3(b)]. The birds were tested on six lead-lag delays ranging from 0.1 to 20.0 ms. The single-side (-90°) targets ranged from clicks with a longer duration (0.1- to 1-ms ISI) to two clicks separated by a delay (5- to 20-ms ISI). This is not a precedence effect experiment because the repeating backgrounds were only single clicks presented from a single side. If the spatial cues are important, the task where the lag was on the opposite side of the lead [Fig. 3(b)] should be easier than the task where the lead and lag were on the same side [Fig. 3(a)] at each ISI. If *only* temporal factors play a role in discriminating these stimuli, performance should be equal for the two conditions and would increase with increasing ISI for both conditions.

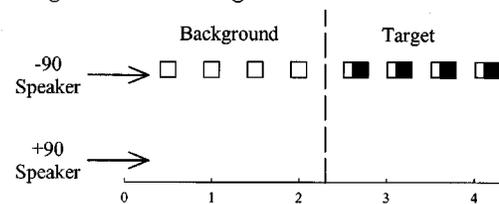
As a control to ensure that the target speaker's location was the only cue, and not the temporal onset of the stimuli

(because at the shorter ISIs, the single speaker was simply emitting one long click where the onset of the second click was smeared into the first click), the condition where the target leads and lags were presented from one speaker on one side was compared for two of the subjects to the condition where two speakers were placed on top of each other at -90° (putting two speakers on top of each other ensures that the onsets of both clicks were present). In this configuration, the centers of the speakers were 11 cm apart. A second control experiment was conducted to measure potential monaural intensity cues that may have been created when presenting the two sounds from two speakers. Here, the background

A. Background = -90° / Targets = $+90^\circ$ and -90°



B. Background = -90° / Targets = -90°



Time (s)

FIG. 3. Schematic of stimulus presentation. Background stimuli were presented from a -90° speaker. Targets were presented either from (a) -90° and $+90^\circ$ or from (b) -90° only.

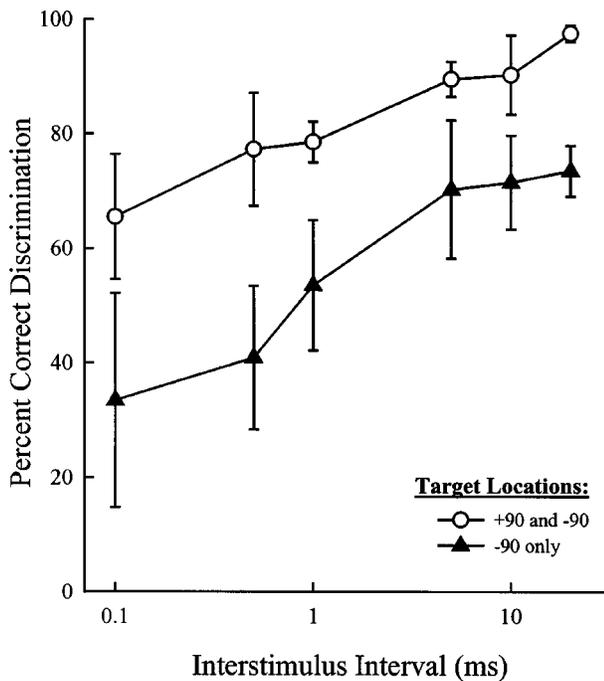


FIG. 4. Mean of four individuals tested on discrimination of a background from -90° versus targets from -90° and $+90^\circ$ (white circles) or from -90° only (black triangles). Error bars represent standard errors.

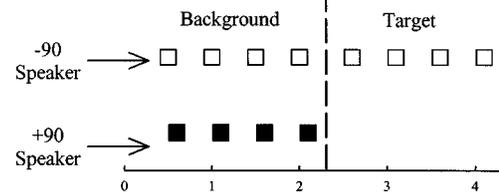
and target stimuli were roved by ± 4 dB from presentation to presentation and discrimination was compared for two subjects in the roved versus unroved conditions.

B. Results

For all four budgerigars, as ISI increased, discrimination performance increased for both target location conditions (Fig. 4). Additionally, the condition where the targets were emitted from two locations in space (white circles) yielded higher performance levels than the condition where the targets were only emitted from one location (black triangles). A two-way (ISI \times target speaker condition) repeated measures ANOVA showed that there was a significant effect of ISI [$F(5,33) = 5.91$, $p < 0.001$] and target speaker location condition [$F(1,33) = 29.36$, $p < 0.001$], but no significant interaction between the two variables [$F(5,33) = 0.36$, $p > 0.05$]. A *posthoc* Bonferroni *t*-test showed that the performance at 0.1-ms ISI was significantly lower than the 5–20-ms ISIs ($p < 0.05$). The increase in ISI and the addition of a second speaker location (black versus white symbols) both increased discrimination performance.

The control experiment where the lead and lag on one side came from one speaker was not significantly different from the condition where the lead and lag on one side came from two speakers for either subject tested in this condition, as shown by paired *t*-tests [CIRRUS: $t(5) = 0.85$, $p > 0.05$; WILL: $t(5) = 0.29$, $p > 0.05$]. There were also no differences in the control roved versus unroved conditions, again shown by paired *t*-tests for each subject [CIRRUS one-side target: $t(5) = 0.39$, $p > 0.05$; CIRRUS two-sides target: $t(5) = 1.57$, $p > 0.05$; WILL one-side target: $t(5) = 1.74$, $p > 0.05$; WILL two-sides target: $t(5) = 2.26$, $p > 0.05$]. The re-

A. Background = -90 and $+90$ / Targets = -90



B. Background = -90 / Targets = -90

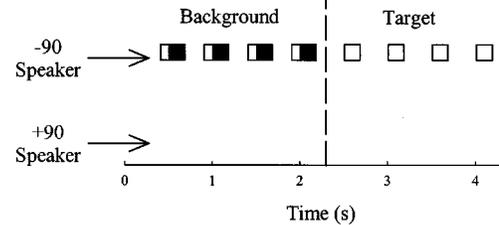


FIG. 5. Schematic of stimulus presentation. Target stimuli were always presented from -90° . Backgrounds were presented either from (a) -90° and $+90^\circ$ or from (b) -90° only.

sults from this experiment showed that the spatial properties of the stimuli in all of these experiments were salient cues for discrimination by the birds.

VI. EXPERIMENT 4: THE DISCRIMINATION OF ECHOES

In humans, under localization dominance conditions, the lag stimulus adds fullness to perceived images, even though its spatial properties are not perceived (e.g., Blauert, 1997). Humans can also distinguish between trials where a lag is presented and when a lag is not presented [see review in Litovsky *et al.* (1999)]. In this experiment, we tested whether the lag clicks are perceived, and whether the spatial properties of the lag clicks have an influence on discrimination performance. Paired stimuli from either one or two locations were the background conditions in this experiment, and birds were required to discriminate a single target located at the position of the background's lead click location. If the lag stimuli are perceptually inaccessible, discrimination should be very difficult. If only the spatial attributes of the stimuli are inaccessible, discrimination performance should not differ across lag location conditions. Further, performance should change across lead-lag interstimulus intervals in conjunction with the timecourses of summing localization, localization dominance, and echo thresholds.

A. Methods

In this experiment, the four budgerigars were required to discriminate between a repeating background pair of clicks from a single-click target located at -90° (opposite background-target conditions from experiment 3). The lead-lag background clicks were presented from opposite sides of the cage at $\pm 90^\circ$ [Fig. 5(a)] or on the same side (at -90° only) but with the same temporal properties as in the bilateral speaker condition [Fig. 5(b)]. The birds were tested on six lead-lag ISI backgrounds ranging from 0.1 to 20.0 ms.

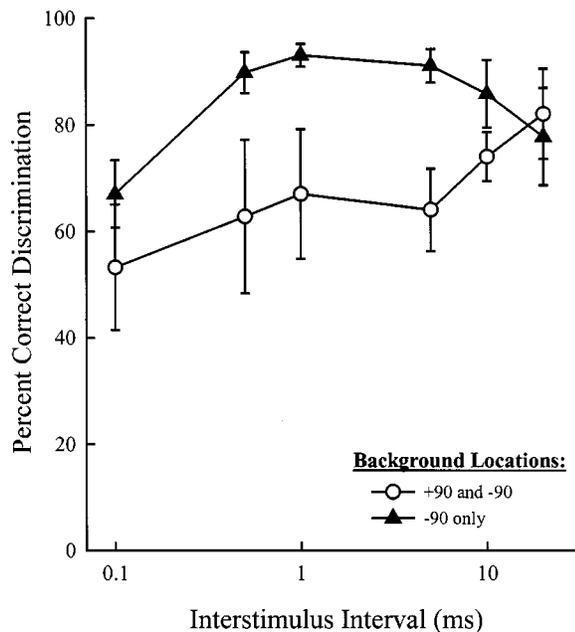


FIG. 6. Mean of four individuals tested on discrimination of a target from -90 versus backgrounds from -90 and $+90$ (white circles) or from -90 only (black triangles). Error bars represent standard errors.

As a control that the background speaker location was the only cue and not the temporal onset of the stimuli, two birds were tested on one additional speaker location condition. The condition in which the lead and lag were on the same side and presented from one speaker was compared to a second condition in which two speakers were placed on top of each other at -90° . As another control for potential intensity cues resulting from the addition of two sounds, two of the birds were retested with the stimuli roved by ± 4 dB from presentation to presentation.

B. Results

Unlike the results for experiment 3, in this experiment there was not a simple monotonic increase in discrimination performance with increasing ISI in either condition (Fig. 6). The condition where the background was emitted from two locations [shown in Fig. 5(a)] was more difficult than the condition where the background was emitted from only one location [shown in Fig. 5(b)], especially at the intermediate ISIs (0.5–10 ms). A two-way (ISI \times background speaker condition) repeated measures ANOVA showed that there were significant effects of ISI [$F(5,33)=2.79$, $p<0.05$] and target speaker condition [$F(1,33)=19.88$, $p<0.001$], but no interaction between the two variables [$F(5,33)=1.79$, $p>0.05$]. A posthoc Bonferroni t -test showed that within the 0.5-, 1-, and 5-ms ISIs, there were differences in discrimination between the two background speaker conditions ($p<0.05$), the same ISIs where localization dominance is operating in budgerigars (Dent and Dooling, 2003).

The control condition where the lead and lag from one side were emitted from one speaker was not significantly different from the condition where the lead and lag from one side were emitted from two speakers for either bird [Cirrus: $t(5)=1.52$, $p>0.05$; Spike: $t(5)=1.10$, $p>0.05$]. The

temporal onsets of these stimuli were not the important factor in discrimination between the backgrounds and targets. In the second control experiment, the condition where the intensities were roved was not significantly different from the condition where the intensities were held constant [Cirrus one-side background: $t(5)=0.97$, $p>0.05$; Cirrus two-sides background: $t(5)=2.08$, $p>0.05$; Spike one-side background: $t(5)=2.40$, $p>0.05$; Spike two-sides background: $t(5)=0.56$, $p>0.05$]. Making the intensity cues unpredictable did not change discrimination in this experiment either.

This experiment demonstrates that the discrimination of paired stimuli from two locations [shown in Fig. 5(a)] from a single target was more difficult than in a single source stimulus condition [paired one-location background shown in Fig. 5(b)]. Further, the differences between the two background conditions are largest during the timecourses of localization dominance and smaller during the timecourses of summing localization and echo thresholds [where the spatial attributes of the lag are known to have an influence on the perception of the auditory image(s)]. Overall, these results support previous findings in humans that the spatial properties of the lag stimulus are inaccessible during localization dominance conditions.

VII. EXPERIMENT 5: THE DISCRIMINATION OF PAIRED STIMULI

Experiment 4 demonstrated that during localization dominance timecourses, the spatial properties of the lag click are inaccessible as localization cues, not the lags themselves. Paired background stimuli (bilateral or unilateral) were always perceived as being different from a single target stimulus, however, because discrimination was greater than 0% at all ISIs. In this experiment, we attempted to decrease discrimination performance further by making the targets even more similar to the backgrounds. Here, the task was to discriminate pairs of background stimuli from pairs of target stimuli where only one of the pairs contained stimuli from two locations (e.g., we tested whether a pair of background clicks located at -90° and $+90^\circ$ were perceived as being the same as a pair of target clicks both located at -90° and vice versa).

A. Methods

A pair of clicks located at $+90^\circ$ and -90° separated by an ISI was the repeating background in the first task [Fig. 7(a)]. The four birds were required to discriminate targets with the same temporal properties of the previously mentioned lead-lag background but with both targets located at -90° . In another task, they were tested on the reversed background/target conditions [Fig. 7(b)]. In both tasks, the birds were tested on six lead-lag delays ranging from 0.1 to 20.0 ms.

Experiment 3 showed that under nonprecedence effect conditions (discriminating a single click from a pair of clicks), the spatial and temporal properties of the stimuli could both be used as discrimination cues. Experiment 4, however, showed that under precedence effect conditions and only during localization dominance timecourses, the spatial properties of the stimuli are inaccessible and the birds are not

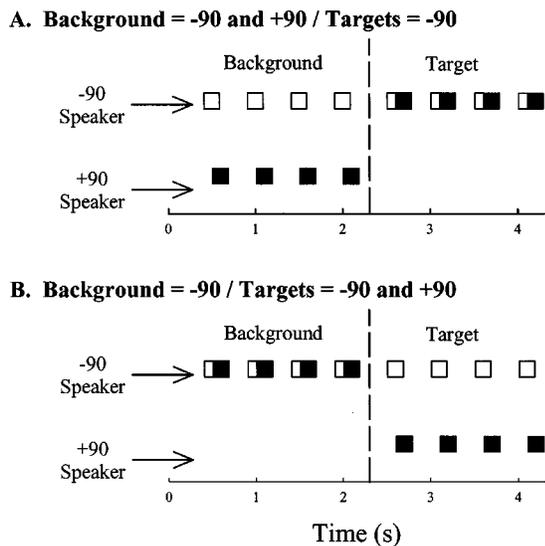


FIG. 7. Schematic of stimulus presentation. (a) Background stimuli were presented from -90 and $+90$. Targets were presented from -90 only. (b) Background stimuli were presented from -90 only. Targets were presented from $+90$ and -90 .

able to use them as cues for discrimination. If the spatial cues of the lag are completely inaccessible, then discrimination between a bilateral pair of background clicks and a unilateral pair of target clicks should be extremely difficult during the timecourses of localization dominance.

There should be differences in discrimination performance between the two tasks, however, because of the buildup and breakdown of localization dominance. In humans, the lag is reported as “fading out” after repeated presentations of lead-lag pairs (e.g., Clifton and Freyman, 1989). In budgerigars, discrimination of paired stimuli during localization dominance timecourses improves with repeated presentations of lead-lag pairs (Dent and Dooling, 2003). In this experiment, the task where the background stimuli are emitted from two locations [Fig. 7(a)] should be more difficult than the task where the background stimuli are emitted from only one location [Fig. 7(b)]. In the former condition, repeated presentations of the background are concurrent with decreased availability of spatial information from the lag. That would make the background and target very similar when the targets are finally presented.

In the condition where the background is unilateral and the bilateral targets are presented suddenly, it is possible that the spatial information from the lag will be immediately available (no fading out of the echo yet), and discrimination will be easier. If the buildup of localization dominance is important for the budgerigars, then there should be significant differences between the two conditions in this experiment.

B. Results

Like the results from experiment 4, there is not a monotonic increase of discrimination performance with increasing ISIs in either condition of this experiment (Fig. 8). The condition where the backgrounds were coming from two locations and the targets from one location (white circles) was

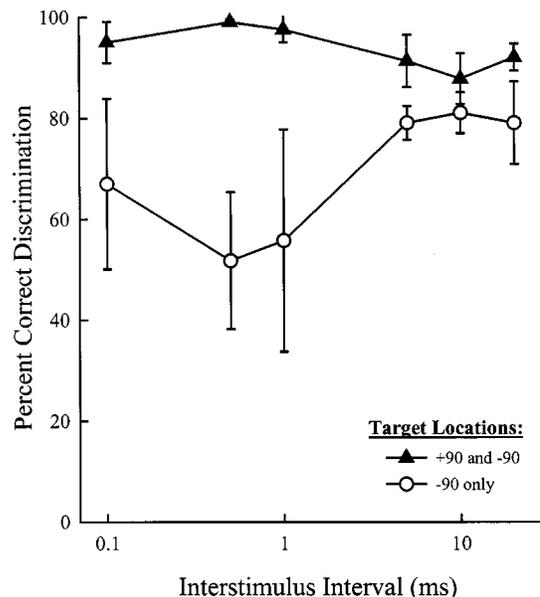


FIG. 8. Mean of four individuals tested on discrimination of a background from -90 versus targets from -90 and $+90$ (black triangles) or the reverse background/target condition (white circles). Error bars represent standard errors.

much more difficult than the reverse condition (black triangles), especially at the low and middle ISIs (0.1–5 ms), despite the only difference between the two data points at each ISI being a reversed background/target presentation condition. A two-way (ISI \times speaker conditions) repeated measures ANOVA showed that there was no significant effect of ISI [$F(5,33) = 0.51$, $p > 0.05$], there was an effect of speaker condition [$F(1,33) = 23.76$, $p < 0.001$], but there was not an interaction between the two variables [$F(5,33) = 1.83$, $p > 0.05$]. A posthoc Bonferroni t -test showed that within each ISI, there were differences in discrimination between the two background speaker conditions for the 0.1-, 0.5-, 1-, and 5-ms ISIs ($p < 0.05$), the same ISIs where localization dominance and summing localization were found to be operating in budgerigars (Dent and Dooling, 2003). There were no differences between the speaker conditions at the 10- and 20-ms ISIs ($p > 0.05$). This experiment showed that in the bilateral background stimulus condition only [Fig. 7(a)], the spatial properties of the lag sound were inaccessible and discrimination was difficult due to the buildup and breakdown of localization dominance.

VIII. DISCUSSION

A. Time-intensity trading

The present findings show how much of a change in intensity between the lead and lag stimuli was required to elicit localization dominance (0-ms ISI) or to abolish localization dominance (1- and 5-ms ISIs). In budgerigars, when simultaneous sounds were presented, the “echo” (not later in time, just less intense) needed to be 5–8 dB lower in intensity for high levels of discrimination. Hoeffding and Harrison (1979) found similar values in rats (~ 5 dB) although Kelly (1974) had somewhat lower values (~ 2.8 – 4.2 dB) for rats.

The echo (later sound source) being louder than the direct (first) sound source is not a natural occurrence in nature, but it is of interest that the results presented here are similar to those found for humans (e.g., Babkoff and Sutton, 1966; Blodgett *et al.*, 1956). Babkoff and Sutton (1966) found that in humans, echo thresholds changed from 3.8 to 2.4 ms when the lag was changed from 0 to 8 dB more intense than the lead stimulus. Increasing the intensity of the lag made the lag more detectable at shorter ISIs. Unfortunately, Kelly (1974) could not replicate this effect in rats, even when the lead click was attenuated by up to 20 dB. Leakey and Cherry (1957) found that, in humans, two clicks separated by a delay (so that the sound image was perceived to be coming from one side) could be perceptually recentered if the lag click was made louder than the lead click. With an ISI of 0.9 ms, that required intensity difference was found to be 8.6 dB, an ISI of 1.8 ms required an intensity difference of 10.6 dB, and an ISI of 2.2 ms required an intensity difference of 10.4 dB. At longer ISIs, more and more of an intensity increase in the lag was needed to recenter the image in humans. Mickey and Middlebrooks (2001) recently found that ISIs of 0.6 to 0.8 ms needed only a concurrent 5-dB increase in the lag to shift the perceived judgments back to the midline.

Although there are significant task differences between the experiments on humans and budgerigars, and the birds were only tested at two ISIs, it seems for both species that increasing the intensity of the lag does change the perceived location of the image. In humans, larger intensity differences are needed for larger time differences between lead and lag. It is difficult to tell from the experiments reported here whether the same holds true for budgerigars due to large between-subject variability and the testing of only two interstimulus intervals. In fact, it did not seem to hold for the 1- and 5-ms interstimulus intervals for the birds. Although in both cases the intensity differences could override the time differences, the intensity differences were similar for both time difference conditions. Generally, though, this experiment showed that in budgerigars, as in humans, intensity differences between lead and lag stimuli could elicit localization dominance—and they could even override localization dominance in certain conditions.

B. Discrimination of phantom sound images

The results here are among the first to show that animals perceive phantom sound images at a location that is different from the location of the presented sound sources. Although the task did not require budgerigars to identify the location of the auditory image, we tested the birds' ability to discriminate two simultaneously presented sounds from the sides from one sound presented from the midline. Failure to discriminate would indicate that budgerigars perceived a phantom midline image. The results here were intermediate, suggesting that, like humans, the birds are perceiving a difference in the fullness or richness quality of the auditory image when stimuli are emitted from two locations instead of one (e.g., Perrott *et al.*, 1989). However, discrimination performance was poor overall; the budgerigars could not easily distinguish between the two stimulus types. It was not a function of poor sound localization abilities, however, be-

cause discrimination of the midline stimulus from either of the side stimuli alone was good. The perception of a phantom image has also been described by Populin and Yin (1998) in cats and Keller and Takahashi (1996) in barn owls using different techniques. All of the studies so far suggest that animals perceive summing localization stimuli in a similar manner as humans.

C. Discrimination of paired stimuli

The present results show that the spatial cues of the stimuli are important in these experiments, along with the temporal cues. If the temporal onset of the stimuli were the critical cue, the results from experiment 3 with the bilateral target location would have been exactly the same as the results with the unilateral target location. This was not the case, however. The temporal onsets of these stimuli do not seem to be the only important factor in the discrimination between the backgrounds and targets. The control roved intensity condition showed that making potential intensity cues extremely unreliable also did not affect discrimination in this experiment. Taken together, the results show that both spatial and temporal cues are used by birds in these experiments, despite their poor sound localization abilities (Park and Dooling, 1991).

Experiment 4 used the reverse background/target conditions from experiment 3. Results here showed that increasing the temporal interval between paired clicks was enough to support discrimination of a pair of clicks from a single click. Also, under non-localization dominance conditions, both temporal and spatial cues could be used to improve discrimination. Interestingly, in humans, localization dominance has been reported to be stronger when the lead and lag are spatially coincident than when they are spatially distant (Litovsky and Shinn-Cunningham, 2001). This was not true for the budgerigars, however. Budgerigars were worse at distinguishing a pair of stimuli from different locations from a single target [experiment shown in Fig. 5(a)] than they were at distinguishing a pair of stimuli from the same location from a single target [experiment shown in Fig. 5(b)]. One interpretation is that there is less accessibility of the information from the echoes in the experiment shown in Fig. 5(a) than in the experiment shown in Fig. 5(b), counter to the results from humans. The differences between the budgerigars and humans may be related to the psychophysical tasks. Recall that humans were asked to identify the location of the lead, but budgerigars were asked only to discriminate between a paired background lead and single source lag. However, the results from Dent and Dooling (2003), where localization dominance was stronger and echo thresholds were later with larger speaker separation distances, further support the results from this experiment.

There were several potential outcomes of this experiment. First, if the echoes in this experiment were accessible, then performance for the experiment shown in Fig. 5(a) should have been better than performance for the experiment shown in Fig. 5(b). Second, if the echoes were inaccessible, then performance where the lag was located on the opposite side of the lead [shown in Fig. 5(a)] should have been very poor compared to the condition where the lag was at the

same location as the lead [shown in Fig. 5(b)] because the perception would have been of a single 1-ms click located at -90° in the second scenario and a very long or double click in the first scenario. Third, if only the spatial properties of the lag were inaccessible, then the performance between the two conditions should have been identical across ISIs. The temporal properties of the background would have been identical in the experiments shown in Figs. 5(a) and (b). The results from experiment 4 lie somewhere in-between the latter two possible outcomes. The addition of a second speaker location did hinder performance, suggesting that the echoes were at least partially inaccessible under localization dominance conditions. The echoes were not completely inaccessible, however, because discrimination performance was above chance level at all ISIs. The difference between these two conditions at certain ISIs strongly suggests that more than the spatial properties of the lag stimuli were inaccessible for budgerigars.

Of course there are other possible cues to discrimination that the birds could have been using in these experiments. The overlapping stimuli from multiple locations could have created signals with complex acoustic features such as rippled spectra. Budgerigars are very good at discriminating between sounds with flat- and rippled-spectra (Amagai *et al.*, 1999). As a hedge against the birds using other potential acoustic cues, the stimuli were roved in intensity from presentation to presentation by ± 4 dB. This makes other potential acoustic cues unreliable as a basis for discrimination. The overall duration of the stimuli are another cue to discrimination that the birds could have used. The duration discrimination abilities of birds are generally not well known, especially for very short stimuli. The evidence to date suggests that birds probably need about a 10%–20% change in the overall duration of a stimulus to discriminate a change (Dooling and Haskell, 1978). The non-monotonic discrimination functions (not increasing with increasing separation delays) in the third and fourth experiments suggest that the budgerigars are using neither of these cues.

Finally, the results from experiment 5 strongly support the hypothesis that localization dominance is operating in these birds. The task of discriminating background from target in the first speaker condition [Fig. 7(a)] was identical and opposite to the discrimination of target from background in the second speaker condition [Fig. 7(b)]. The two discrimination functions should have been identical across all ISIs. Yet, there were differences in response levels AND these differences were large at the low and intermediate ISIs where summing localization and localization dominance operate in humans. The more difficult discrimination, where the background lead was at $+90^\circ$ and the background lag was at -90° [shown in Fig. 7(a)] was difficult because only the spatial location of the lag was inaccessible, and the birds could not discriminate the target trials where the lead and lags had the same temporal properties but different spatial properties. In the reverse condition, and because of the requirement by these birds for a buildup of localization dominance [found in the companion paper, Dent and Dooling (2003)], the backgrounds coming from only one side being easy to discriminate from the targets in two locations [shown

in Fig. 7(b)] was not surprising. Here, localization dominance was not operating on the background (as shown also in experiment 4), and the targets had additional spatial cues (shown in experiment 3) to aid in discrimination. This made discrimination easier in this condition [Fig. 7(b)] than in the reverse condition [Fig. 7(a)]. The results showing that discrimination between the two conditions was not different at the long ISIs, past the echo thresholds, lends further support for this line of reasoning.

IX. CONCLUSIONS

Overall, the results from these experiments lend further support that the precedence effect exists in all animals as a mechanism to resolve potential confusions that may arise from multiple, competing sound sources. These experiments showed that intensity and location are two more potential sources of confusion a bird may overcome when localizing a sound source. Taken together, the results from these experiments, as well as those from Dent and Dooling (2003), extend the database of behavioral data describing the many facets of the precedence effect and their similarities and differences across species. The experiments here further suggest that the precedence effect acts in a similar manner across animals regardless of general hearing or sound localization abilities, habitats, or evolutionary histories.

ACKNOWLEDGMENTS

This work was supported by NIH Grant No. DC-00198 to RJD and NRSAs from NIH (DC-00046 and MH-12698) to MLD. We are very grateful to B. Brittan-Powell, F. Kubke, M. Leek, D. Yager, C. Carr, C. Moss, R. Litovsky, T. Takahashi, and D. Tollin for their comments on earlier versions of this manuscript.

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