Investigations of the precedence effect in budgerigars: Effects of stimulus type, intensity, duration, and location

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Auditory experiments on the localization of sounds in the presence of reflections, or echoes, that arrive later and from different directions are important to understanding hearing in natural environments. The perceived location of the auditory image can change with the time delay between the presentations of a leading and lagging sound. These changes in perceived location, encompassing the precedence effect, have been examined behaviorally or physiologically in humans and a number of animals. Here, these results are extended to include budgerigars. Behavioral methods were used to measure the discrimination performance between a stimulus presented at + and −90° azimuth with a delay (left-right), from the same two stimuli presented with the opposite delay (right-left). At short delays, where humans experience summing localization, budgerigars have difficulty discriminating between the two presentation types. With increasing delays, where humans experience localization dominance, budgerigars show improved discrimination performance. At even longer delays, where echo thresholds are found in humans, discrimination performance worsens again. The shapes of the discrimination functions are affected by the intensity, locations, and durations of the stimuli, and are subject to a buildup effect. These results show that budgerigars exhibit the phases of the precedence effect similar to humans and other animals. *© 2003 Acoustical Society of America.* [DOI: 10.1121/1.1558391]

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I. INTRODUCTION

The precedence effect is an important aspect of binaural hearing and has a long history in both psychoacoustic and neurophysiological experiments (e.g., Blauert, 1997; Litovsky *et al.*, 1999; Wallach *et al.*, 1949). Previous work has shown that the precedence effect has three critical time periods, based on judgments of the perceived location of the stimulus as a function of the interstimulus delay between two sounds and these are called summing localization, localization dominance, and echo threshold [see review in Litovsky *et al.* (1999)]. The echo threshold is defined as the ISI (interstimulus interval between a lead and a lag) past which an observer hears both the lead and lag stimuli at separate locations (Blauert, 1997; Freyman *et al.*, 1991). The echo threshold is the longest temporal interval relevant to the precedence effect, and, above this delay, the precedence effect is no longer evident. Within certain limits below the echo threshold, stimuli emanating from two different speakers produce the perception of a single stimulus coming solely from the position occupied by the leading speaker. The range of ISIs over which this perception occurs defines localization dominance. Finally, summing localization occurs when the ISI is even shorter than in localization dominance. Work with humans shows that during this time period, a phantom source is perceived as being somewhere between the two sound sources. The exact values of the time ranges described in the above three pieces of the precedence effect depend on the types of stimuli used (e.g., Schubert and Wernick, 1969), the instructions given to the listener (Blauert, 1997; Zurek, 1987), the location of the lead and lag stimuli (Litovsky and Shinn-Cunningham, 2001), and the immediately preceding history of the auditory information presented to the listener (Clifton, 1987). Taken together, these results suggest that the precedence effect is not a simple auditory echo suppression mechanism, but a more general auditory mechanism that improves hearing in natural situations.

Comparative studies of the precedence effect are much more difficult to conduct than those in humans because animals cannot be directly queried about the location of real or phantom targets in space. Behavioral and physiological studies, however, have both experienced some degree of success by using a wide variety of creative techniques to answer the question of underlying mechanisms of the auditory system. Litovsky, Yin, and colleagues (e.g., Litovsky and Yin, 1998a, b; Yin, 1994), for example, have conducted an extensive set of experiments on aspects of the precedence effect in cats. They have demonstrated some interesting underlying neural correlates to localization dominance, summing localization, and echo thresholds in the inferior colliculus of kittens and adult cats (*Felis catus*) and have compared these results with some of the behavioral findings in humans.

The behavior and underlying neural correlates of the precedence effect have also been demonstrated in several experiments with albino rats (*Rattus norvegicus*). Kelly (1974), for example, showed through behavioral procedures that discrimination between background click pairs from the right then left (R-L) and target click pairs from the left then right (L-R) with the same-but-opposite ISI occurred when one click in the pair was delayed or reduced in intensity over

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a certain range. Discrimination was worse at very short and very long delays, as in the cats. Generally, results from independent laboratories using different methodologies suggest that mammals do indeed perceive summing localization and localization dominance stimuli in a manner similar to humans [see review in Litovsky *et al.* (1999)].

Correlates of the precedence effect have been found in one bird species to date, the barn owl (*Tyto alba*). Keller and Takahashi (1996; see also Takahashi and Keller, 1994) measured responses to simulated echoes by neurons in the external nucleus of the inferior colliculus of the barn owl and correlated those responses to behavioral data. Keller and Takahashi (1996) found these birds perceived sounds presented simultaneously from two lateral speakers as coming from a central location in space in behavioral experiments. In these experiments, the barn owl's echo thresholds were found to be about 5 ms (Keller and Takahashi, 1996; Takahashi and Keller, 1994), similar to those found by Tollin *et al.* (2000) in the cat, and those found in humans (e.g., Blauert, 1997). While cats and barn owls have similar head sizes (and therefore similar interaural sound localization cues), they have extremely different evolutionary histories, life styles, and auditory neuroanatomy (Carr, 1992). Thus, it is interesting that their echo thresholds are so similar.

Measuring the precedence effect in barn owls is also interesting because, like cats, they are nocturnal predators with highly specialized auditory systems designed for tracking and capturing prey. It was not known whether other smaller birds without obvious external ear or central nervous system adaptations for sound localization would exhibit the precedence effect or whether the timecourses of summing localization, localization dominance, and echo thresholds would be similar across different bird species. This is a problem of some intrigue because small birds have small heads with closely spaced ears. These anatomical characteristics result in small interaural time and intensity differences, which would seem to work against a robust precedence effect.

The present study sought to investigate the precedence effect in the budgerigar (*Melopsittacus undulatus*), a small parrot and popular cagebird. It was unclear whether these birds would exhibit a robust precedence effect or how it would differ from that demonstrated in humans, other animals, and specialized birds such as barn owls. Budgerigars were chosen, in part, because they are well studied in the psychoacoustics field. More is known about hearing and auditory discriminations in this species, in both quiet and noisy backgrounds, than in any other bird (see, for example, Dooling *et al.*, 2000).

The capabilities of the budgerigar's binaural auditory system have also been investigated and show some intriguing results. For instance, absolute localization thresholds for these birds are not remarkable [about 20° for the budgerigar compared to 2° for the barn owl; review in Klump (2000)]. This is slightly, but not dramatically, better than what one would expect from their small heads and closely spaced ears. However, budgerigars do exhibit the phenomenon of binaural release from masking [the improvement in threshold when separating the signal from the background noise in space (Dent *et al.*, 1997)]. Masked thresholds for a tone embedded in noise emitted from one speaker on one side (e.g., right side tone, right side noise) of the birds were much worse than thresholds for a tone embedded in noise emitted from two speakers on two sides (e.g., right side tone, right and left side noise) of the birds. Moreover, the amount of binaural release from masking was similar to the amount seen in humans with much larger heads (Dent *et al.*, 1997).

One possible mechanism for this enhancement in free-field binaural masking release is the existence of the interaural canal in these and other birds [review in Klump (2000)]. Using laser vibrometry, it has been shown that the phase response of one tympanum is affected by sound traveling through the interaural pathway from the opposite ear, providing a potential mechanism for improving directional hearing, especially at low frequencies (Larsen *et al.*, 1997). The pressure-difference receiver can only aid in sound localization if the sound pressure level of the sound to the inner tympanum is not attenuated too much relative to the sound pressure level of the sound to the external surface of the tympanum [see review in Klump (2000)]. In budgerigars, especially at low frequencies, the attenuation of sounds through the interaural canal range from 2 dB at 0.5 kHz to 17 dB at 2 kHz (Larsen *et al.*, 1997). The experiments here attempted to determine whether budgerigars could enhance interaural timing information of primary sounds versus echoes using the interaural canal (or another) mechanism.

The results in humans suggesting that binaural time or intensity difference cues are not necessary for localization dominance or summing localization (Litovsky *et al.*, 1997; Rakerd and Hartmann, 1994; Rakerd *et al.*, 2000) are interesting with respect to budgerigars as well. It is known that (in humans at least) each position in space is associated with characteristic peaks and troughs in the spectrum of sounds and that human listeners can use this information for sound localization (Hebrank and Wright, 1974; Searle *et al.*, 1976). The head, pinnae, and body interacting with the sound at each position in space create these spectral peaks and troughs. It was not known how many cues these small birds with no pinnae might generate or if they would be able to exhibit the precedence effect with minimal binaural interaural time and intensity cues, so the precedence effect was also determined along the median sagittal plane. The results from these experiments should provide interesting insights as to the importance of the above-mentioned binaural cues for locating an object in space. The following experiments define the timecourses for echo thresholds, localization dominance, and summing localization in budgerigars and compares these values to those found in humans and other animals.

II. GENERAL METHODS

A. Subjects

Four adult budgerigars (three males, one female) were used in these experiments. 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

The psychoacoustic experiments took place in a wire test cage $(25\times 18\times 14\ \mathrm{cm}^3)$ mounted 115 cm from the ground in a sound-attenuated chamber $(2.8\times 2.5\times 2.0\ \mathrm{m}^3)$. 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. 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). Two 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) and 20-ft extension cable. For all measurements, a $\frac{1}{2}$-in. microphone was placed in the position normally occupied by the bird's head during testing. Additional measurements of the spectral and temporal characteristics of the stimuli were made by passing the output of the sound level meter to a Stanford Research Systems FFT spectrum analyzer (Model SR760, Sunnyvale, CA) and a Tektronix digital oscilloscope (Model TDS3014B, Portland, OR).

C. Training and testing procedures

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. 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 time-out 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 percent correct values stabilized were analyzed. To minimize any response biases, two of the birds were trained to repeating background sounds from the left speaker, and two were trained to repeating background sounds from the right speaker.

III. EXPERIMENT 1: THE EFFECTS OF STIMULUS TYPE

The exact values of the time ranges of summing localization, localization dominance, and echo thresholds depend on the types of stimuli used (e.g., Schubert and Wernick, 1969). In humans, different stimuli give very different echo thresholds [see reviews in Blauert (1997) and Litovsky *et al.* (1999)]. The onset durations, overall durations, and carrier frequencies of the stimuli can all have an influence on the timecourses of the precedence effect (Houtgast and Aoki, 1994; Rakerd and Hartmann, 1986; Yang and Grantham, 1997). In this first experiment, we tested the birds' discrimination of pairs of broadband noises (0.1, 1, and 50 ms in duration), as well as recorded natural contact calls of the budgerigar, at different ISIs.

The birds were also tested on discrimination of stimulus pairs with different lead locations. In humans, echo thresholds are higher (later in time) when the lead originates from the right and the lag from the left than the reverse condition. One of the arguments for this asymmetry is that overall hearing abilities are asymmetrical in humans (e.g., Ward, 1957; Emmerich *et al.*, 1988), so the suppression of echoes is more efficient when the direct source is presented to the better ear (Grantham, 1996). Asymmetrical hearing abilities have never been found in birds, which made them interesting subjects for a study of asymmetries in localization dominance and echo thresholds.

The budgerigar experiments here are modeled after earlier discrimination experiments on rats. Kelly (1974) tested rats on their ability to discriminate between paired-background sounds presented from a left then a right speaker (L-R) from paired-target presentations of sounds from a right then left speaker (R-L) with the same ISI between sound presentations. The rats had difficulty distinguishing between the two presentation types at extremely short delays (background versus target; 31–62 μs), where summing localization is operating. Presumably, the rats perceived only one

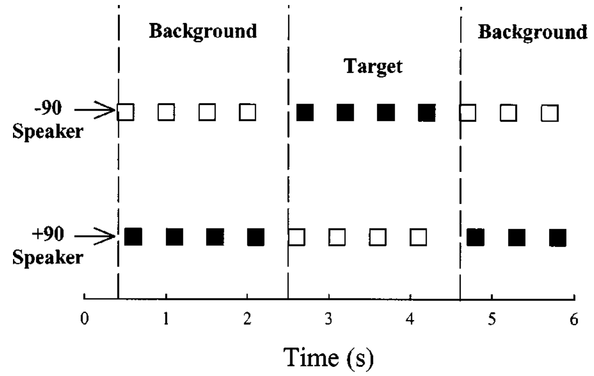

FIG. 1. Schematic of trial events. Stimuli are presented at a rate of 2/s. Stimuli are presented from the −90° speaker first, followed, after a short delay, from the +90° speaker. Background stimuli are presented a random number of times (6–12) before targets are presented. Targets have the same delay between lead and lag speakers, they are merely reversed in position. Birds have four presentations of the target to respond before the repeating background continues again for the next trial.

sound as coming from somewhere in the middle for both background and target presentation types (the phantom sound image) so they could not distinguish between the background and targets. The rats could easily discriminate the L-R pair from the R-L pair at presentation delays from 0.25 to 16.0 ms, where localization dominance is operating. The rats could distinguish the left-first from the right-first stimuli because they only perceived the sounds as coming from one speaker location in the background (the leading speaker position). Therefore, the perceived left-only background sound was easy to discriminate from the target. The rats became unable to distinguish between the two presentation types again with much longer delays (20–32 ms). This is above the echo threshold for the rats; they heard both sounds from separate locations during both the background and the target presentations. The sounds were too close together for rats to be able to tell which sound came first, however, so they could not discriminate between the background and target presentations. The first experiment was designed to measure whether budgerigars would exhibit the precedence effect using similar methods, what the timecourses of the components of the precedence effect were, and the effect of using different stimuli.

A. Methods

1. Procedures

Once the birds were trained to peck 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° target), paired stimuli were introduced into the experiments. Here, the repeating background involved presenting the stimuli from two speakers as in Kelly's (1974) experiment with rats (see Fig. 1). In other words, the background was a repeating stimulus involving the left then the right speakers, with very short delays between the two sound presentations. In each session, the target stimulus pairs had the same (but opposite) ISI between presentations as the repeating background stimulus pairs. The repeating background (L-R) was presented a random number of times (between 6 and 12) at a rate of 2/s before the targets (R-L) were presented. Target pairs were presented four times total (2 s), or until the birds responded. No sounds were played during the reinforcement period. Only one ISI was tested in each experimental session. Testing of the different ISIs was varied randomly between experimental sessions. These ISIs ranged from 0.1 to 40 ms (although some different ISIs were used in the different stimulus conditions), and a total of at least 13 ISI values were tested for each stimulus type.

All four subjects were tested on L-R versus R-L discriminations at different ISIs with 1-ms broadband noise pulses (clicks) to determine the nature of the precedence effect in budgerigars. To examine the effect of stimulus duration, two subjects (Penny and Will) were also tested on 0.1-ms clicks and 50-ms noise bursts. To assess the precedence effect using the natural vocalizations of these birds, three of the subjects (Penny, Will, and Spike) were also tested on three recorded contact calls from three different budgerigars.

Finally, two subjects (Cirrus and Will) were tested across all ISIs on both the left-first and the right-first click conditions, in a random order. They were also tested on the left-first clicks where the testing cage was rotated 180° within the chamber. This experimental condition measured the effect of the location of the lead stimulus on the precedence effect. In humans there is an asymmetry in the buildup of localization dominance depending on which side the leading sound is emitted (Clifton and Freyman, 1989; Grantham, 1996), and we could test for a similar phenomenon in birds. Results should also reveal whether any spectral artifacts or cues used for the precedence effect were due to the experimental setup.

2. Stimuli

All of the stimuli were presented at peak sound pressure level of 60 dB(A) SPL measured at the bird's head. The clicks had a 0-ms rise-decay time and the 50-ms noise bursts had a 5-ms rise-decay duration. The longer stimuli also generally contained more energy at higher frequencies than the shorter stimuli. This is unlikely to be a significant factor since the hearing abilities of these decreases dramatically above about 5 kHz. The contact calls were typical of budgerigar calls (see Farabaugh and Dooling, 1996): frequency modulated patterns with most of their energy between 2 and 4 kHz, durations of between 120 and 160 ms, and with onset times of approximately 5–10 ms.

As a control for potential monaural intensity fluctuations in the stimuli that the budgerigars may have used as cues for discrimination between background and target click pairs, the 1-ms click pairs were also tested with the intensity roved ±4 dB (around 60 dB) from presentation to presentation. Two of the budgerigars (Penny and Spike) were tested at all ISIs in this control experiment, and results were compared to their results from the 1-ms click pair discrimination experiment where the intensities were not roved.

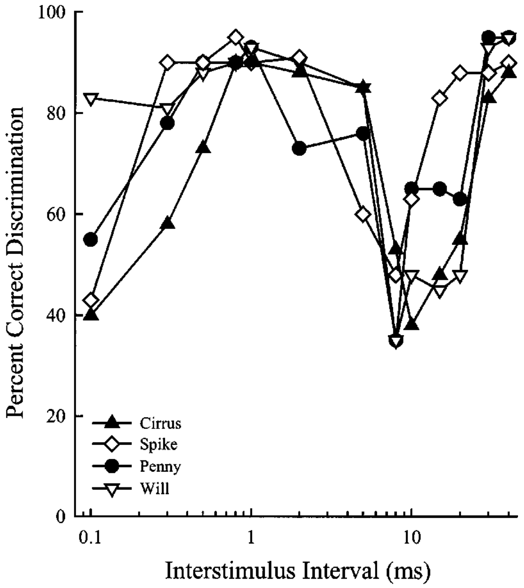

FIG. 2. Results from four individuals tested on the discrimination of 1-ms click pairs. Percent correct discrimination values are shown as a function of ISI.

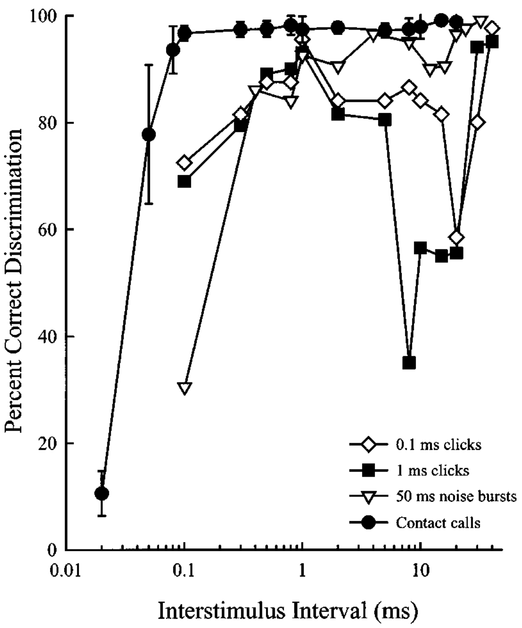

FIG. 3. Results from two individuals tested on the discrimination of three types of broadband stimulus pairs, and from three individuals tested on discrimination of budgerigar contact calls. Percent correct discrimination values are shown as a function of ISI.

B. Results

Discrimination for the single clicks used in training (left only background versus right only targets) was close to 100% for all four birds. Percent correct values for paired stimuli tested at different ISIs are shown in Fig. 2 for the four individual budgerigars tested on 1-ms clicks. Here, the task was to discriminate a L-R repeating background from a R-L target, at different ISIs ranging from 0.1 to 40 ms. Two of the birds were tested in the above-mentioned condition, with the L-R background and R-L targets (Cirrus and Spike), and two of the birds were tested in the opposite condition, with the R-L background and L-R targets (Will and Penny). For all four subjects, percent correct discrimination increased, decreased, and then increased again as ISIs increased. The four birds deviated by 3% to as much as 43% from each other in their discrimination values at the different ISIs, but shapes of the curves were similar across birds. As one check on whether the variation across birds was due to subject differences in perceptual processes or to subject differences in the adaptation to the testing procedures, a d' analysis was used. The average d' value across the four birds at all ISIs for this experiment was 2.32 and the range of d' values across birds was 2.05 to 2.53. The interindividual variation in the data shown in this experiment is fairly small compared to similar experiments in humans [see, for example, Litovsky and Shinn-Cunningham (2001)].

A one-way repeated measures analysis of variance (ANOVA) showed that there were significant differences across ISIs for all subjects [$F(12,36)=9.15$, $p<0.001$]. At intermediate delays (0.5 to 5 ms), all birds performed well—they easily discriminated the R-L target from the L-R background. *Posthoc* Bonferroni *t*-tests showed that the intermediate delays of 0.8, 1.0, and 2.0 ms were all significantly different from the shorter delay of 0.1 ms and the longer delays of 8, 10, and 15 ms ($p<0.05$). The percent correct values at these intermediate ISIs were significantly higher than those at the longer and shorter delays.

At shorter delays, percent correct values in the budgerigars for the 0.1 ms ISI were significantly lower than those from the 0.5-, 0.8-, 1.0-, 2.0-, 30.0-, and 40.0-ms intervals ($p<0.05$), and the 0.3- and 0.5-ms ISIs were significantly different from the 8.0-ms ISI ($p<0.05$). At the longer delays, the lowest percent correct values (at 8 ms) were significantly different from those at shorter ISIs (0.3, 0.5, 0.8, 1.0, 2.0, and 5.0 ms), and both the 8- and 10 ms-ISIs were significantly different from some longer ISIs (30 and 40 ms; $p<0.05$). These results, as a whole, establish that budgerigars do exhibit the phenomena of the precedence effect, including summing localization, localization dominance, and echo thresholds.

Two subjects were tested with the intensities of the stimuli roved by ±4 dB from presentation to presentation. The discrimination functions were not significantly different across ISI between the roved and unroved conditions for either bird as shown by a paired *t*-test [Penny: $t(12)=0.46$, $p>0.05$; Spike: $t(12)=0.65$, $p>0.05$]. The birds could not reliably use intensity difference cues to discriminate background from target in the roved condition, suggesting other mechanisms were shaping the discrimination functions.

To test the effects of stimulus duration on discrimination abilities, two budgerigars were additionally tested on stimulus pairs where the stimuli were 0.1 and 50 ms in duration (Fig. 3). The results for all three broadband stimuli are similar. Discrimination was low at the shortest ISIs, high at intermediate ISIs, and (somewhat) lower again at longer ISIs. At the shortest ISIs, the 0.1-ms click pairs were the easiest to discriminate, followed by the 1-ms clicks, and then the 50-ms noise bursts. The peak of responding (i.e., where localization dominance might be at a maximum) was at a similar I SI across stimulus types: at 1 ms for the 0.1-ms clicks, at 1 ms for the 1-ms clicks, and at 4 ms for the 50-ms noise bursts. Echo thresholds, or the lowest point of responding (lowest percent correct discrimination values), were at 20 ms for the 0.1-ms stimuli, at 8 ms for the 1-ms stimuli, and at 12-ms for the 50 ms stimuli.

The ISIs used for the three click conditions were not all exactly the same, so statistics were completed on the six ISIs that were tested with all three stimulus types (representative of short through long ISIs): 0.1, 0.8, 1.0, 2.0, 8.0, and 20.0 ms. A two-way repeated measures ANOVA (stimulus type × ISI) showed that there were significant differences across stimulus type ($F(2,17)=3.86, p<0.05$), across ISIs ($F(5,17)=9.54, p<0.001$), and a significant interaction between stimulus type and ISI ($F(10,17)=6.79, p<0.001$). *Posthoc* Bonferroni *t*-tests showed that at the shortest ISIs of 0.1 ms, the 50-ms stimulus was significantly different from the other two shorter stimuli ($p<0.05$), but the two shorter stimuli were not significantly different from each other.

Average results for three individuals tested on three different contact calls (calls from three different budgerigars) across ISIs are also shown in Fig. 3. Discrimination between these call pairs was high from 0.1 to 100 ms, so ISIs down to 0.02 ms were tested. The three birds were very similar in their discrimination abilities across ISIs and across contact calls. The contact calls varied in peak frequency, amounts of amplitude modulation, and duration, yet performance was similar for all three calls. These results show that contact calls can also elicit at least some of the components of the precedence effect.

The average percent correct discrimination functions across ISIs were compared for the left-first condition, the right-first condition, and with the cage rotated 180° within the testing chamber. Discrimination was almost identical regardless of which side the leading stimulus was located. A two-way (speaker location × ISI) repeated measures ANOVA showed that there was a significant effect of ISI [$F(10,32)=6.09, p<0.001$], but there were no significant differences between the speaker locations [$F(2,32)=0.86, p>0.05$] or an interaction effect between the two variables [$F(20,32)=0.19, p>0.05$]. Two important conclusions can be made from this experimental condition. First, the testing chamber is acoustically symmetrical, as seen when comparing the almost-identical right first and cage rotated 180° discrimination curves. Second, the location of the leading stimulus does not affect the timecourses of the precedence effect in budgerigars.

Average data from the four budgerigars using 1-ms clicks are plotted along with data from cats, rats, and humans in Fig. 4. The methodology across studies varies widely, but the overall shapes of the percent correct functions across ISIs can be compared in a very general sense. The rats were required to discriminate R-L from L-R clicks (Kelly, 1974), similar to the budgerigar task. The other rat data were from Hoeffding and Harrison (1979), where rats were required to identify the location of a leading source. Percent correct data for the cat gives the proportion of trials the cats correctly identified the location of the leading source in a pair of clicks (Cranford, 1982). Percent correct values for the humans give the proportion of trials that a sound image was identified at the position of the leading source (Litovsky *et al.*, 1997). For all experiments, a high percent correct value indicates that localization dominance was operating; in other words, the location of the lead was easily discriminated or identified. For all species, localization dominance was at a maximum at delays of 0.5–5.0 ms and at a minimum at longer and shorter ISIs.

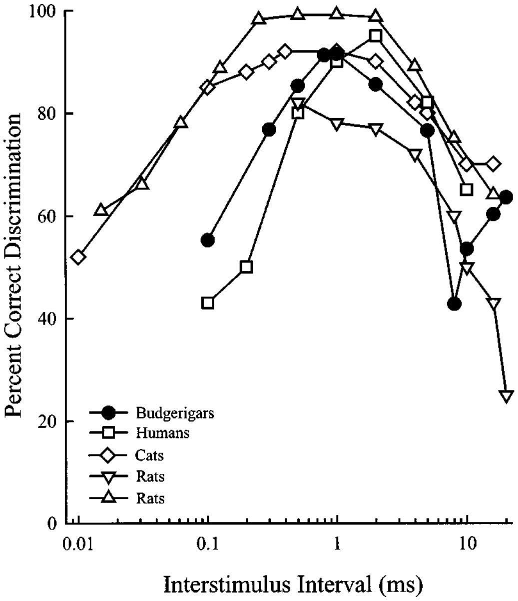

FIG. 4. Discrimination functions for budgerigars (1-ms clicks, this study), humans [0.025 ms clicks (Litovsky *et al.*, 1997)], cats [0.05-ms clicks (Cranford, 1982)], rats [triangles, 0.05-ms clicks (Kelly, 1974)], and rats [upside-down triangles, 0.05-ms clicks (Hoeffding and Harrison, 1979)].

IV. EXPERIMENT 2: THE EFFECTS OF FRONT VERSUS REAR STIMULUS LOCATION

This experiment tested whether the precedence effect occurred on the midline. In humans, the precedence effect occurs on the median sagittal plane at similar timecourses as are found in the azimuthal plane (Litovsky *et al.*, 1997; Rakerd and Hartmann, 1994; Rakerd *et al.*, 2000). To determine if the binaural properties of the sound were important or necessary for the precedence effect in budgerigars, similar procedures as described above were utilized in the median plane.

A. Methods

This experiment used same apparatus, 1-ms click stimuli, and procedures as in Experiment 1. Three of the budgerigars from experiment 1 (Penny, Spike, and Will) were used in this experiment. In this experiment, the lead and lag speakers were placed at 0° and 180° (directly in front of and directly behind the budgerigars at eye/ear level). The sounds were played from each speaker in quick succession during the repeating background (front then back with a short delay between presentations), and the order of presentation was reversed during the target trials (to back then front). Click delays ranging from 0.1 to 40 ms were tested in a random order, and results were compared to the results from these subjects tested in the left-right speaker condition in experiment 1. Although the budgerigars were free to move their heads during the course of these experiments, the requirement that the observation key be pressed down to initiate the presentation of the target stimulus pairs inhibited head rotation dramatically (±1 cm to the right or left).

B. Results

The variance between the three subjects in this experiment was much larger for the front back discrimination than for the left right discrimination at most ISIs, especially at the longest ones (above 2 ms). A two-way (speaker position $\times$ISI) repeated measures ANOVA showed that there were significant effects of speaker position $[F(12{,}52)=3.06$, $p<0.01]$ and ISI $[F(1{,}52)=8.29$, $p<0.005]$, but no significant interaction between the two variables $[F(12{,}52)=0.63$, $p>0.05]$. Overall, percent correct values were significantly higher for the left-right speaker condition than for the front-back speaker condition. For both conditions, there was a significant effect of ISI (as in previous experiments). A lack of a significant interaction between the two variables suggested that the shapes of the two functions were not significantly different. Discrimination of front-back stimuli was equivalent to that of left-right discrimination.

V. EXPERIMENT 3: THE EFFECTS OF STIMULUS SEPARATION DISTANCE

In humans, there are no differences in echo thresholds with changes in spatial separation of a lead and lag source (Litovsky and Shinn-Cunningham, 2001). However, localization dominance is stronger in stimuli that have smaller interaural time differences (closer together in space) than those with larger interaural time differences [further apart in space (Shinn-Cunningham *et al.*, 1993; Litovsky and Shinn-Cunningham, 2001)]. This experiment tested whether the timecourses of the components of the precedence effect changed with decreased speaker separation distance in budgerigars.

A. Methods

This experiment used same apparatus, 1-ms click stimuli, and procedures as in experiment 1. Three of the budgerigars from experiment 1 (Cirrus, Will, and Penny) were used in this experiment. In this experiment, the lead and lag speakers were at +30° and −30° or at +60° and −60°. Click delays ranging from 0.1 to 20 ms were tested in a random order under both speaker separation conditions, and results were compared to the results from these subjects tested in the ±90° speaker condition in experiment 1.

B. Results

The results for the three budgerigars tested on three stimulus separations are shown in Fig. 5. Discrimination performance was generally highest in the condition with the largest separation of lead-lag stimulus pairs. A two-way (stimulus separation$\times$ISI) repeated measures ANOVA showed that there was a significant effect of ISI $[F(10{,}53)=7.14$, $p<0.0001]$, stimulus separation $[F(3{,}53)=17.57$, $p<0.0001]$, and a significant interaction between the two variables $[F(30{,}53)=2.02$, $p<0.05]$. *Posthoc* Bonferroni *t*-tests found some differences in percent correct discrimination values across stimulus separations. The 30° and 90° speaker locations were significantly different at the intermediate ISIs of 0.8, 1, 2, and 5 ms ($p<0.05$). The 30° and 60° speaker locations were significantly different at the 2-ms ISI only ($p<0.05$). The 60° and 90° speaker locations were significantly different at the 5-ms ISI only ($p<0.05$). The echo thresholds across the three speaker conditions ranged from 5 ms in the 60° and 120° separation conditions to 8 ms in the 180° separation condition. Generally, at the timecourses where localization dominance was operating, discrimination performance was higher when the speakers were further apart than when they were closer together.

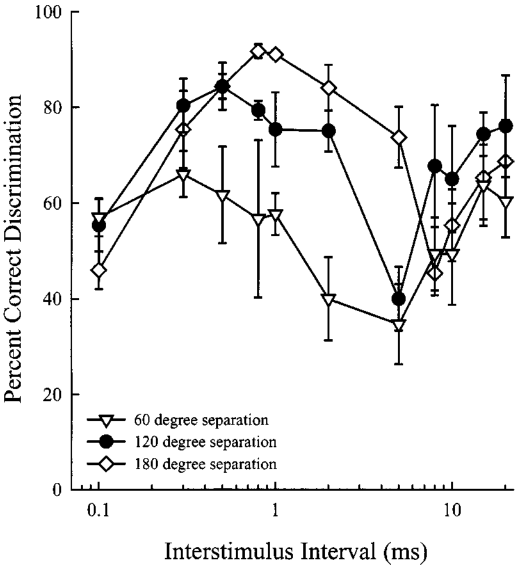

FIG. 5. Average discrimination functions for three budgerigars tested on discrimination of 1-ms click pairs as a function of ISI with the stimuli presented from ±30°, 60°, and 90°. Error bars represent between-subject standard errors.

VI. EXPERIMENT 4: THE EFFECTS OF STIMULUS INTENSITY

In humans, the precedence effect decreases at very low sensation levels (45 to 10 SL; Goverts *et al.*, 2000). However, Shinn-Cunningham *et al.* (1993) found only a small effect on localization dominance when increasing the stimulus levels from 80 to 110 dB. In two early studies with headphones in humans, an increase in click sensation level resulted in a decrease in echo thresholds (Babkoff and Sutton, 1966; Schubert and Wernick, 1969). The effect of stimulus level on the timecourses of localization dominance and echo thresholds have not been well examined in behavioral studies with animals. However, in cats, suppression decreased in most neurons in the inferior colliculus with increasing stimulus level (Litovsky and Yin, 1998a, b). Here, the birds were tested on 1-ms click stimuli at three different intensities to see if there was an effect of the intensity of the stimuli on the precedence effect.

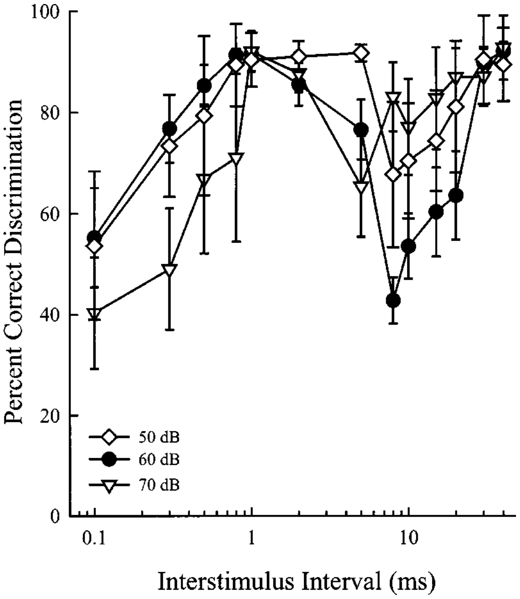

FIG. 6. Average discrimination functions for three budgerigars tested on discrimination of 1-ms click pairs as a function of ISI with the stimuli presented at three stimulus intensities. Error bars represent between-subject standard errors.

A. Methods

This experiment used the same apparatus, 1-ms click stimuli, and procedures as in experiment 1. Three of the budgerigars from experiment 1 (Cirrus, Penny, and Will) were also used in this experiment. Click-pair discriminations across ISIs were measured with the stimuli presented a level of 50 and 70 dB(A) SPL and compared to the results with 1-ms clicks measured at 60 dB(A) SPL in experiment 1.

B. Results

The average discrimination functions across ISIs for three different stimulus intensities are shown in Fig. 6 for three subjects. A two-way (stimulus intensity×ISI) repeated measures ANOVA showed that there was a significant effect of ISI $[F(12,76)=6.84, p<0.001]$, stimulus intensity $[F(2,76)=4.67, p<0.05]$, and a significant interaction between the two variables $[F(24,76)=2.05, p<0.01]$. *Posthoc* Bonferroni *t*-tests found some differences in percent correct discrimination values across stimulus intensities at both the long and short ISIs. At 0.1 ms, the 70 dB percent correct values were significantly different from those at 60 dB ($p<0.05$). At 0.3 ms, both the 50 and 60 dB percent correct values were significantly different from those at 70 dB ($p<0.05$). At these short ISIs, where summing localization is operating in humans, the stimuli presented at 70 dB SPL were more difficult to discriminate than those at the lower intensities.

Differences arose at the longer ISIs as well. At the 5 ms ISI, the 50-dB response levels were significantly higher than those at 70 dB ($p<0.05$). At the 8–10-ms ISIs, the discrimination between the 60- and 70-dB stimuli were also significantly different ($p<0.05$). Performance for the 70-dB stimuli dropped to its lowest point at 5 ms while performance did not drop to its lowest point for the 50- and 60-dB condition until 8 ms. These results show that echo thresholds occur later for less intense stimuli.

VII. EXPERIMENT 5: BUILDUP OF THE PRECEDENCE EFFECT

In humans, several repetitions of the pairs of lead-lag stimuli cause a ‘‘fading out’’ of the perceived location of the echo (Clifton and Freyman, 1989). This buildup of suppression in humans also occurs over a longer time period for longer ISIs, increasing the echo threshold with each presentation (Clifton and Freyman, 1989). The buildup and breakdown of the suppression of echoes has only been behaviorally found in one animal, the cat (Kalmykova, 1993). Kalmykova found that echo thresholds in cats increased from 12 to 17 ms with repeated lead-lag presentations. This is an interesting problem, but the neural substrates for this buildup effect have not yet been found (Litovsky and Yin, 1998a). This experiment tested whether localization dominance builds up for budgerigars in a manner similar to the way it builds up in humans.

A. Methods

This experiment used the same apparatus, 1-ms click stimuli, and procedures as in experiment 1. Three subjects from experiment 1 (Cirrus, Penny, and Will) were also used in this experiment. The birds' percent correct discrimination values following different numbers of background stimulus-pair presentations (ranging from 1 to 12 presentations at the 2/s rate) and at different ISIs (1, 2, and 5 ms) were measured. Because the number of background presentations had to be kept random from trial to trial to ensure validity in the psychophysical data from the birds, at least 600 total trials were collected from each bird at each ISI. Then, hits and misses for each number of background presentations at each ISI were counted. This resulted in approximately 60 trials (±10 trials) for each data point for each bird. As a control, the birds were tested on their discrimination of a single click from the left as the background and a single click on the right as the target after different numbers of background presentations (i.e., a simple localization task). This test determined whether the birds had a general tendency to respond correctly after an increased number of background presentations or whether the effect was unique to the precedence effect.

B. Results

Average percent correct values for three budgerigars across different numbers of background presentations are shown in Fig. 7. Each bird was tested on three ISIs of paired stimuli, with between 1 and 12 backgrounds presented before the targets were presented, and the control condition. In the control condition, percent correct discriminations were high across all number of background presentations. This was not the case for the paired click stimuli presented at different ISIs, however. For all three birds at all three ISIs, discrimination increased with increasing number of background pre-

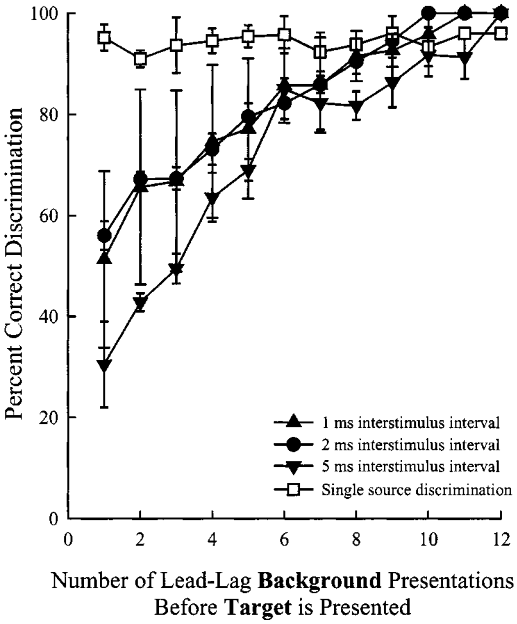

FIG. 7. Average of three individuals tested on discrimination of R-L background clicks from L-R target clicks as a function of the number of background presentations before the target is presented, at three ISIs. Open squares represent the control condition, where the background was a single click from the left and the targets were single clicks from the right. Error bars represent between-subject standard errors.

sentations. A two-way (number of backgrounds×ISI) repeated measures ANOVA showed that there was a significant effect of number of background repetitions [$F(11,94) = 16.06$, $p < 0.001$], ISI [$F(3,94) = 22.12$, $p < 0.001$], and a significant interaction between the two variables [$F(33,94) = 2.00$, $p < 0.001$].

Posthoc Bonferroni *t*-tests showed that within the 1-ms ISI condition, the 1–3 background presentations were significantly different from the 8–12 background presentations, and the 1 background presentation was also significantly different from the 5–7 number of backgrounds ($p < 0.05$). Within the 2-ms ISI condition, the 1–4 background presentations were significantly different from the 9–12 background presentations, and the 1 background presentation was also significantly different from the 6–8 background presentations ($p < 0.05$). Within the 5-ms ISI condition, the 1–4 background presentations were significantly different from the 8–12 background presentations, and the 1 background presentation was also significantly different from the 4–7 background presentations ($p < 0.05$). Within the control condition, however, there were no differences between any of the background presentation numbers ($p > 0.05$). Generally, within the paired click conditions, the higher the ISI, the more background presentations were necessary to increase the percent correct discriminations to the high rate of responding seen in the control condition.

Posthoc Bonferroni *t*-tests were also used to analyze whether the ISIs were significantly different from the control at each of the background presentation numbers. Within the 1–4 background presentations, the 5-ms ISI was significantly different from the control condition ($p < 0.05$). Within the 1–2 background presentations, the 2-ms ISI was significantly different from the control condition ($p < 0.05$). Within only the 1 background presentation, the 1-ms ISI was significantly different from the control condition ($p < 0.05$). Overall, as ISI decreased, the functions were increasingly more similar to the control function. The buildup of localization dominance was unique to the paired click stimuli and was not seen in the simple control discrimination task.

VIII. DISCUSSION

A. Summing localization, localization dominance, and echo thresholds

Using a discrimination paradigm, these experiments show that budgerigars exhibit summing localization, localization dominance, and echo thresholds in a manner similar to humans and other animals tested. The delays resulting in excellent discrimination by the birds in all experiments correspond to the delays where localization dominance is operating in humans. During the repeating lead-lag background, the lag's spatial location was suppressed. When the lead-lag stimulus locations changed during the targets, the suppression of the lag's position was released (the breakdown of localization dominance), and the birds easily heard the change from the background condition to the target condition, and discrimination values were high.

At shorter ISIs, discrimination performance was worse for the budgerigars. In humans, localization dominance is not yet complete at these short ISIs. The results from budgerigars lend support to a similar perceptual illusion as the phantom image location that humans report. If the birds perceived a "phantom" image somewhere in-between the positions of the lead and lag location due to summing localization, discrimination between the phantom image background and the phantom image target would have been very difficult due to the poor sound localization abilities of these birds. Park and Dooling (1991) found that single-source broadband noises needed to be separated by almost 30° for discrimination in budgerigars. Discrimination suppression experiments measuring minimum audible angles in humans have found that localization of paired sound sources is higher for leads and lags than for single sound sources [see review in Litovsky *et al.* (1999)]. If this is also true for budgerigars, it is not surprising that discrimination between the paired sound sources at short ISIs was poor.

At longer delays, where echo thresholds are found in humans, discrimination was also more difficult for the budgerigars. In humans, both sounds are heard at separate locations, but they often cannot distinguish which came first. If fusion also breaks down in budgerigars past 8 ms, this may be the reason that discrimination of these stimulus pairs became so difficult. If the repeating backgrounds were heard as two separate stimuli presented from two separate locations, and the targets were heard as two separate stimuli presented from two separate locations, the temporal resolution (pattern perception) of these birds is not good enough to resolve which came first in the pair during the background to notice that the sequence had changed during the targets. This could account for the drop in discrimination rates.

B. Effects of stimulus duration

The duration of the stimulus has an effect on discrimination in budgerigars during the ISIs where summing localization is operating in humans (i.e., discrimination was worse for the shorter stimulus types). In most studies of summing localization where the stimuli overlap significantly (i.e., the 50-ms stimuli), the perceived image is more than the ‘‘phantom’’ average of the positions of the lead and lag stimuli (Litovsky *et al.*, 1999; Tollin and Henning, 1998, 1999). Here, the combined amplitudes and phases of the sounds interact to create the perceived location of the sound source. This may explain why the discrimination of the shorter stimuli at the short ISIs was worse than for the longer stimuli. However, since the shorter stimuli had a slightly narrower bandwidths than the longer stimuli, spectral differences might also contribute to the differential discrimination of shorter and longer stimuli. Although the birds were not identifying the actual perceived location of the stimuli in these experiments, human listeners presented with pairs of broadband noises actually perceive images towards the location of the lag at very short ISIs (Tollin and Henning, 1998, 1999). This is due to the interaural spectral cues that result from delaying and adding identical stimuli to the two ears. This effect was not seen at longer ISIs. It was also not seen with shorter stimuli (such as the 1-ms clicks). Again, this may be due to the fact that shorter stimuli contained less energy at higher frequencies than did the longer stimuli. The results from these experiments suggest that summing localization inhibited discrimination between stimulus pairs at the shortest ISIs in these birds as it did in humans.

The peak of responding, or where localization dominance might be at a maximum, occurred at similar ISIs across all stimulus types: at 1 ms for the 0.1- and 1-ms clicks and at 4 ms for the 50-ms noise bursts. Generally, performance was above 80% from 0.5 to 5 ms for all three stimulus types. Stimulus duration does not seem to have a large effect on localization dominance in budgerigars.

Echo thresholds, or the lowest percent correct discriminations, did not increase from the 0.1- to 1-ms stimuli, but did increase with increasing stimulus durations from 1 to 50 ms. Echo thresholds were at 20 ms for the 0.1-ms stimuli, at 8 ms for the 1-ms stimuli, and at 12 ms for the 50-ms stimuli. In studies with humans, barn owls, and cats [see review in Litovsky *et al.* (1999); also Keller and Takahashi (1996) and Litovsky and Yin (1998a, b)], later echo thresholds are generally seen with longer stimuli. The average function for budgerigars did not follow this trend when increasing stimulus length from 0.1 to 1 ms. However, differences were found when examining individual results. In the discrimination functions for the 0.1-ms stimuli, one of the birds had an echo threshold at 2 ms while the other bird’s echo threshold was at 20 ms. Discrepancies between the birds are similar to those found in humans, however, where differences in echo thresholds can range from 1 to 50 ms across subjects (Litovsky and Shinn-Cunningham, 2001).

The echo thresholds for the 50-ms stimuli are also not as pronounced as in the shorter stimulus conditions. The birds slightly decreased their responses at the very long ISIs (~10 ms), the delay of the presumed echo threshold. It is possible that the echo thresholds coincided with the time interval where the birds were able to determine which came first in the pair of noise bursts (a pattern perception task) and were thus able to discriminate the background from the target. This could account for the decrease in discrimination compared to the other two stimulus conditions.

The echo thresholds in the contact call discrimination functions were not apparent at all. In humans, echo thresholds are later in short stimuli with abrupt onsets (e.g., Rakerd and Hartmann, 1986). These contact calls were more speech-like in their appearance than the broadband stimuli, lasting between 120 and 160 ms and with more gradual onsets than the broadband stimuli. This, along with the increased pattern perception abilities described above, may have masked the echo thresholds for these conditions.

Overall, the findings of increasing echo thresholds with increasing stimulus duration agree with the results from humans. Unfortunately, only one systematic study of the effect of stimulus duration (where the same procedures and setup were used) has been psychophysically conducted on humans. Schubert and Wernick (1969) found that the point where the lead and lag became ‘‘equally loud’’ increased significantly as stimulus duration increased from 20 to 100 ms. Physiological studies of the effect of stimulus duration in cats also showed increased timecourses of neural echo suppression in the central nucleus of the inferior colliculus with increased stimulus duration (Litovsky and Yin, 1998a, b). A review of the literature by Litovsky *et al.* (1999) shows that, across studies, echo thresholds are generally higher for speech than they are for noise bursts and higher for noise bursts than for clicks. Those findings are generally supported here in budgerigars as well.

C. Effects of stimulus location and intensity

No differences were found between the discrimination functions for budgerigars where the leading stimulus was located on the left and those where the leading stimulus were located on the right. In humans, there is an asymmetry in the buildup of localization dominance depending on which side the leading sound is emitted from (Clifton and Freyman, 1989; Grantham, 1996). One of the arguments for the left-right asymmetry of the precedence effect in humans is that overall hearing abilities are asymmetrical in humans (e.g., Ward, 1957; Emmerich *et al.*, 1988) and that suppression of echoes is better (due to different amounts of buildup) when the lead is presented to the better ear and the lag to the worse ear (Grantham, 1996). As far as we know, there is no ear advantage in hearing abilities in budgerigars, or any other bird, and the existence of such things as the interaural pathway would seem to work against such a phenomenon. Further research is needed to examine these interesting differences between budgerigars and humans, such as testing other animals with hearing asymmetries on the precedence effect to see if the correlation holds true for more than these two species.

Discrimination functions of budgerigars were also similar to each other when the lead and lag stimuli were presented from the front and back as opposed to the left and right. Their results are in accord with results from humans.

Several studies have found similar amounts of localization dominance on the front-rear and left-right planes in humans (Blauert, 1971; Litovsky *et al.*, 1997; Rakerd and Hartmann, 1994; Rakerd *et al.*, 2000). In those studies, localization dominance was found in humans with only monaural spectral cues and no binaural cues. While the birds' heads were not held in a fixed position in this experiment, the binaural difference cues the birds would have received were below the threshold for azimuthal cues found in earlier experiments (Park and Dooling, 1991). Yet, although overall discrimination performance was slightly lower, the precedence effect was still found because the shapes of the functions remained similar.

Head-related transfer functions have not yet been measured in budgerigars, and they have no external pinnae, but it is still possible that spectral changes in the stimuli caused by transformations of the sounds as they traveled through the external ear canal were sufficient to allow for discrimination between these stimulus pairs. In fact, in a study of azimuthal sound localization in budgerigars, when one ear was plugged (dramatically reducing most binaural cues) localization accuracy for broadband noise bursts only increased from 27° to 30° (Park and Dooling, 1991). Monaurally deafened birds, however, were unable to localize sounds separated in the azimuthal plane by as much as 180°. This suggests that even small binaural cues, possibly enhanced by tympanic coupling via the interaural canal, might have been sufficient for localization dominance on the median sagittal plane. Without holding the bird's head fixed, it is still unknown as to whether budgerigars can use spectral cues alone for the precedence effect, as in humans.

In humans, the suppression of the lag is greater when the lead and lag come from similar locations in space (Litovsky and Shinn-Cunningham, 2001). The data reported here for budgerigars do not support that idea; discrimination performance was actually highest in the condition with the largest separation of lead-lag stimulus pairs. At the timecourses where localization dominance was operating, discrimination performance was higher when the speakers were further apart than when they were closer together. These results are different from those in humans (Litovsky and Shinn-Cunningham, 2001). Here, the poor sound localization abilities of budgerigars may have affected discrimination performance for the stimuli that were closer together in space. Taken together, these experiments demonstrate that two speakers separated by a large spatial distance are adequate to produce the precedence effect whether they are located at the spatial position corresponding to the maximal ITDs and ILDs or not, but that interaural difference cues may, in fact, be related to some aspects of the precedence effect in budgerigars.

The results from the intensity experiment showed that more intense stimuli were more difficult to discriminate than the less intense stimuli at low and intermediate ISIs, and that echo thresholds were earlier for more intense stimuli. These results, as a whole, agree with those from humans that echo thresholds are later for less intense stimuli (Babkoff and Sutton, 1966; Schubert and Wernick, 1969). The effects of stimulus level on the timecourses of localization dominance and echo thresholds have not been well examined in behavioral studies with animals, but the results here support the findings in humans.

D. Buildup of the precedence effect

Experiment 5 showed that budgerigars exhibit the buildup and breakdown of localization dominance like humans. The precedence effect stimuli, but not the single source stimuli, required repeated background presentations to increase discrimination performance. Moreover, that discrimination performance increased at a slower rate for the 1- and 2-ms ISIs than for the 5-ms ISI. These results were consistent with the human results—more background repetitions were necessary for the precedence effect to build up at longer ISIs (Clifton and Freyman, 1989).

There were some interesting differences between the three subjects in this experiment. Penny and Will both showed higher responses as ISI decreased from 5 to 2 ms and from 2 to 1 ms. Cirrus, on the other hand, had an increase in responses from the 5-to the 2-ms conditions, but his lowest rate of responding was for the 1 ms ISI condition. In humans, one of the requirements for this buildup of echo suppression is that it only works at ISIs where localization dominance is strong. Figure 2 shows that Cirrus (in the original precedence effect experiment) had lower discrimination rates than the other two birds until the ISI reached 1 ms, suggesting that his localization dominance did not build up until later ISIs compared to the other birds. Localization dominance for the other two birds was seen at shorter ISIs, but not for Cirrus. It could be that localization dominance was not yet complete for Cirrus at the 1-ms ISI (he was still in summing localization), so his buildup and breakdown were not as strong as in the other two birds or in the other two ISIs.

Clifton *et al.* (1994) postulated that ongoing echoes provide the listener with some information about the room's acoustics and that making unlikely changes in the lead and/or the echo result in a release from suppression. The suggestion that the buildup process comes from expectations that human listeners have about room acoustics was strengthened in an experiment where the intensity and frequency spectra of the stimuli were changed from presentation to presentation, and the buildup still occurred (Clifton *et al.*, 1994). Changes in frequency and intensity are not ''unlikely'' events that would naturally occur in a room, so the buildup of echo suppression continued. The underlying neural correlates for buildup have yet to be discovered in any animal (Litovsky and Yin, 1998a), and buildup has previously been found behaviorally only once in nonhuman mammals (Kalmykova, 1993). The results here are the first that show that the buildup of echo suppression occurs in a bird species.

E. Conclusions

The present results extend what is known about hearing in budgerigars to a phenomenon known as the precedence effect. Results from these experiments move beyond studies of basic hearing and the limits of complex auditory temporal processing in budgerigars to a more complicated phenomenon—the precedence effect (Dent *et al.*, 1997;

Dooling *et al.*, 2000; Park and Dooling, 1991). Previous experiments examining simple sound localization abilities in simple acoustic environments are important for determining the basic capabilities of animals, but they tell us nothing about how an animal perceives the auditory world outside of the experimental situation. The present detailed examination of an auditory illusory phenomenon in an animal species provides further information about the complex auditory world of these small birds. It also suggests that studies that treat animals as simple auditory receivers may be missing some important complicated variables.

The purpose of these experiments was to define the timecourse of summing localization, localization dominance, and echo thresholds in budgerigars and to compare the results with those found in humans and other animals. Despite differences in experimental procedures and setups, as well as differences between species in their anatomical pathways for audition, ecological pressures of predation, and physical cues available for directional hearing, the comparative results are remarkably similar across all animals tested to date. These results support the notion that the precedence effect operates in budgerigars and thus provide evidence that the precedence effect is a general auditory mechanism that improves hearing in complex environmental conditions. As a whole, these results provide robust baseline data establishing this phenomenon in birds and also provide a foundation for future investigations of the anatomical and physiological substrates that can support this behavior.

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Babkoff, H., and Sutton, S. (**1966**). ‘‘End point of lateralization for dichotic clicks,’’ J. Acoust. Soc. Am. **39**, 87–102.

Blauert, J. (**1971**). ‘‘Localization and the law of the first wavefront in the median plane,’’ J. Acoust. Soc. Am. **50**, 466–470.

Blauert, J. (**1997**). *Spatial Hearing* (MIT, Cambridge, MA).

Carr, C. E. (**1992**). ‘‘Evolution of the central auditory system in reptiles and birds,’’ in *The Evolutionary Biology of Hearing*, edited by D. B. Webster, R. R. Fay, and A. N. Popper (Springer-Verlag, New York), pp. 511–543.

Clifton, R. K. (**1987**). ‘‘Breakdown of echo suppression in the precedence effect,’’ J. Acoust. Soc. Am. **82**, 1834–1835.

Clifton, R. K., and Freyman, R. L. (**1989**). ‘‘Effect of click rate and delay on breakdown of the precedence effect,’’ Percept. Psychophys. **46**, 139–145.

Clifton, R. K., Freyman, R. L., Litovsky, R. Y., and McCall, D. (**1994**). ‘‘Listners’ expectations about echoes can raise or lower echo thresholds,’’ J. Acoust. Soc. Am. **95**, 1525–1533.

Cranford, J. L. (**1982**). ‘‘Localization of paired sound sources in cats: Effects of variable arrival times,’’ J. Acoust. Soc. Am. **72**, 1834–1835.

Dent, M. L., Larsen, O. N., and Dooling, R. J. (**1997**). ‘‘Free-field binaural unmasking in budgerigars (*Melopsittacus undulatus*),’’ Behav. Neurosci. **111**, 590–598.

Dooling, R. J., Lohr, B., and Dent, M. L. (**2000**). ‘‘Hearing in birds and reptiles,’’ in *Comparative Hearing: Birds and Reptiles*, edited by R. J. Dooling, A. N. Popper, and R. R. Fay (Springer-Verlag, New York), pp. 308–359.

Emmerich, D. S., Harris, J., Brown, W. S., and Springer, S. P. (**1988**). ‘‘The relationship between auditory sensitivity and ear asymmetry on a dichotic listening task,’’ Neuropsychologia **26**, 133–143.

Farabaugh, S. M., and Dooling, R. J. (**1996**). ‘‘Ecology and evolution of acoustic communication in parrots: Laboratory and field studies in parrots,’’ in *Ecology and Evolution of Acoustic Communication in Birds*, edited by D. E. Kroodsma and E. H. Miller (Cornell U.P., Ithaca), pp. 97–117.

Freyman, R. L., Clifton, R. K., and Litovsky, R. Y. (**1991**). ‘‘Dynamic processes in the precedence effect,’’ J. Acoust. Soc. Am. **90**, 874–884.

Goverts, S. T., Houtgast, T., and van Beek, H. H. (**2000**). ‘‘The precedence effect for lateralization at low sensation level,’’ Hear. Res. **148**, 88–94.

Grantham, D. W. (**1996**). ‘‘Left-right asymmetry in the buildup of echo suppression in normal-hearing adults,’’ J. Acoust. Soc. Am. **99**, 1118–1123.

Hebrank, J., and Wright, D. (**1974**). ‘‘Spectral cues in the localization of sound sources on the median plane,’’ J. Acoust. Soc. Am. **56**, 1829–1834.

Hoeffding, V., and Harrison, J. M. (**1979**). ‘‘Auditory discrimination: Role of time and intensity in the precedence effect,’’ J. Exp. Anal. Behav. **32**, 157–166.

Houtgast, T., and Aoki, S. (**1994**). ‘‘Stimulus-onset dominance in the perception of binaural information,’’ Hear. Res. **72**, 29–36.

Kalmykova, I. V. (**1993**). ‘‘Investigation of the precedence effect in the cat auditory system,’’ Sens. Syst. **7**, 208–211.

Keller, C. H., and Takahashi, T. T. (**1996**). ‘‘Responses to simulated echoes by neurons in the barn owl’s auditory space map,’’ J. Comp. Physiol., A **178**, 499–512.

Kelly, J. B. (**1974**). ‘‘Localization of paired sound sources in the rat: Small time differences,’’ J. Acoust. Soc. Am. **55**, 1277–1284.

Klump, G. M. (**2000**). ‘‘Sound localization in birds,’’ in *Comparative Hearing: Birds and Reptiles*, edited by R. J. Dooling, R. R. Fay, and A. N. Popper (Springer, Berlin), pp. 249–307.

Larsen, O. N., Dooling, R. J., and Ryals, B. M. (**1997**). ‘‘Roles of intracranial air pressure on hearing in birds,’’ in *Diversity in Auditory Mechanics* (Bechtel Engineering Center, University of California, Berkeley), pp. 253–259.

Litovsky, R. Y., and Shinn-Cunningham, B. G. (**2001**). ‘‘Investigation of the relationship among three common measures of precedence: Fusion, localization dominance, and discrimination suppression,’’ J. Acoust. Soc. Am. **109**, 346–358.

Litovsky, R. Y., and Yin, T. C. T. (**1998a**). ‘‘Physiological studies of the precedence effect in the inferior colliculus of the cat. I. Correlates of psychophysics,’’ J. Neurophysiol. **80**, 1285–1301.

Litovsky, R. Y., and Yin, T. C. T. (**1998b**). ‘‘Physiological studies of the precedence effect in the inferior colliculus of the cat. II. Neural mechanisms,’’ J. Neurophysiol. **80**, 1302–1316.

Litovsky, R. Y., Colburn, H. S., Yost, W. A., and Guzman, S. J. (**1999**). ‘‘The precedence effect,’’ J. Acoust. Soc. Am. **106**, 1633–1654.

Litovsky, R. Y., Rakerd, B., Yin, T. C. T., and Hartmann, W. M. (**1997**). ‘‘Psychophysical and physiological evidence for a precedence effect in the median sagittal plane,’’ J. Neurophysiol. **77**, 2223–2226.

Park, T. J., and Dooling, R. J. (**1991**). ‘‘Sound localization in small birds: Absolute localization in azimuth,’’ J. Comp. Physiol. **105**, 125–133.

Rakerd, B., and Hartmann, W. M. (**1986**). ‘‘Localization of sound in rooms, III: Onset and duration effects,’’ J. Acoust. Soc. Am. **80**, 1695–1706.

Rakerd, B., and Hartmann, W. M. (**1994**). ‘‘More on the precedence effect in three planes,’’ J. Acoust. Soc. Am. **95**, 2917.

Rakerd, B., Hartmann, W. M., and Hsu, J. (**2000**). ‘‘Echo suppression in the horizontal and median sagittal planes,’’ J. Acoust. Soc. Am. **107**, 1061–1064.

Schubert, E. D., and Wernick, J. (**1969**). ‘‘Envelope versus microstructure in the fusion of dichotic signals,’’ J. Acoust. Soc. Am. **45**, 1525–1531.

Searle, C. L., Braida, L. D., Davis, M. F., and Colburn, H. S. (**1976**). ‘‘Model for auditory localization,’’ J. Acoust. Soc. Am. **60**, 1164–1175.

Shinn-Cunningham, B. G., Zurek, P. M., and Durlach, N. I. (**1993**). ‘‘Adjustment and discrimination measurements of the precedence effect,’’ J. Acoust. Soc. Am. **93**, 2923–2932.

Takahashi, T. T., and Keller, C. H. (**1994**). ‘‘Representation of multiple sound sources in the owl’s auditory space map,’’ J. Neurosci. **14**, 4780–4793.

Tollin, D. J., and Henning, G. B. (**1998**). ‘‘Some aspects of the lateralization of echoed sound in man. I. The classical interaural-delay based precedence effect,’’ J. Acoust. Soc. Am. **104**, 3030–3038.

Tollin, D. J., and Henning, G. B. (**1999**). ‘‘Some aspects of the lateralization of echoed sound in man. II. The role of the stimulus spectrum,’’ J. Acoust. Soc. Am. **105**, 838–849.

Tollin, D. J., Populin, L. C., and Yin, T. C. T. (**2000**). ‘‘Neural correlates of the precedence effect and echo threshold in the inferior colliculus of the behaving cat,'' paper presented at the 30th Annual Meeting of the Society for Neuroscience, New Orleans, LA.

Wallach, H., Newman, E. B., and Rosenzweig, M. R. (**1949**). ''The precedence effect in sound localization,'' Am. J. Psychol. **62**, 315–336.

Ward, W. D. (**1957**). ''Hearing of naval aircraft maintenance personnel,'' J. Acoust. Soc. Am. **29**, 1289–1301.

Yang, X., and Grantham, D. W. (**1997**). ''Cross-spectral and temporal factors in the precedence effect: Discrimination suppression of the lag sound in free-field,'' J. Acoust. Soc. Am. **102**, 2973–2983.

Yin, T. C. T. (**1994**). ''Physiological correlates of the precedence effect and summing localization in the inferior colliculus of the cat,'' J. Neurosci. **14**, 5170–5186.

Zurek, P. M. (**1987**). ''The precedence effect,'' in *Directional Hearing*, edited by W. A. Yost and G. Gourevitch (Springer-Verlag, New York), pp. 85–105.