Spatial Unmasking of Birdsong in Zebra Finches (*Taeniopygia guttata*) and Budgerigars (*Melopsittacus undulatus*)

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Budgerigars and zebra finches were tested, using operant conditioning techniques, on their ability to identify a zebra finch song in the presence of a background masker emitted from either the same or a different location as the signal. Identification thresholds were obtained for three masker types differing in their spectrotemporal characteristics (noise, modulated noise, and a song chorus). Both bird species exhibited similar amounts of spatial unmasking across the three masker types. The amount of unmasking was greater when the masker was played continuously compared to when the target and masker were presented simultaneously. These results suggest that spatial factors are important for birds in the identification of natural signals in noisy environments.

Keywords: cocktail party effect, cocktail party problem, spatial unmasking, birds, binaural hearing

Animals sending acoustic signals often use a variety of strategies to augment communication effectiveness, including adding frequency and amplitude modulation to their signals, increasing the duty cycle of their signals, changing their singing position or posture, or calling at different times of the day (e.g., Bradbury & Vehrencamp, 1998). Signals differ in their effectiveness while being transmitted through the environment and the environment can impose a number of other constraints on acoustic signaling, including changing the temporal and spectral properties of the signal as it travels from the sender to the receiver (reviewed in Wiley & Richards, 1982). Noise is a particularly interesting feature of communication to study because it is clear that animals attend to the levels and spectral features of the noise in their environment, whether it is noise from conspecifics, the rain and wind, or whether it is anthropogenic noise. Animals increase the intensity of their vocal signals with increasing levels of noise on a real-time basis, a phenomenon known as the Lombard Effect (Cynx, Lewis, Tabel, & Tse, 1998; Manabe, Sadr, & Dooling, 1998). This suggests that animals adjust to the noise levels in their environment and that they fine-tune the signals they generate to optimize communication with one another. Several recent field studies have shown that animals have adjusted their communication signals to compensate for man-made noise sources. Examples include differences in the frequencies used by European great tits (*Parus major*) singing in cities or in the country (Slabekoorn & Peet, 2003), changes in the duration of killer whale (*Orcinus orca*) vocalizations correlated with increases in consumer boat traffic (Foote, Osborne, & Hoezel, 2004), and increased volume of city-dwelling nightingales (*Luscinia megarhynchos*), which sing louder on heavily trafficked weekdays than they do on the weekends (Brumm, 2004). From these studies and others, we can see the clear influence that noise is having on the lives of many animals. It is of great importance, therefore, to know as much as we can about how noise affects the ability of animals to communicate.

There have been several avian studies on the "cocktail party problem" (CPP; Cherry, 1953), which refers to the difficulties that humans (*Homo sapiens*) and other animals encounter when trying to communicate in noisy environments (recently reviewed in Bee & Micheyl, 2008). Communication becomes especially difficult when the spectro-temporal and spatial characteristics of the signal and masker are similar. Zebra finches (*Taeniopygia guttata*) experience the CPP when attempting to identify birdsongs embedded in various maskers; moreover, song identification degrades as the target-to-masker energy ratio (TMR) decreases (Narayan, Best, Ozmeral, McClaine, Dent, Shinn-Cunningham, & Sen, 2007). This also occurs in canaries (*Serinus canaria*) discriminating canary songs embedded in a chorus of other canary songs or in broadband noise (Appeltants, Gentner, Hulse, Balthazart, & Ball, 2005). Discrimination ability decreased for these birds as the number of maskers increased and as the signal-to-noise ratio decreased. Field studies on king penguins (*Aptenodytes patagonicus*) suggest that chicks are adept at detecting the calls of their parents at very low signal-to-noise ratios when those calls are mixed with the calls of several other adults (Aubin & Jouventin, 1998). Finally, Dent, Larsen, and Dooling (1997) showed that budgerigars (*Melopsittacus undulatus*) exhibited a large improvement in detectability of a pure tone signal as it was moved away from a broadband noise

masker (spatial unmasking). The amount of unmasking was comparable to that previously seen in humans (Saberi, Dostal, Sadralodabai, Bull, & Perrott, 1991) and ferrets (*Mustela putorius*; Hine, Martin, & Moore, 1994), despite large differences in these species' abilities to localize pure tones.

Unfortunately, none of the above-mentioned masking experiments that used natural acoustic signals examined spatial factors, and the only study on spatial unmasking in birds to date was conducted using pure tones and broadband noise (Dent et al., 1997). Here, we examined spatial unmasking in birds using ecologically relevant stimuli. We adopted the stimuli and basic paradigm of Best, Ozmeral, Gallun, Sen, and Shinn-Cunningham (2005), who studied spatial unmasking of zebra finch songs in human listeners. They found differences in masking and unmasking with different masker types, depending on their similarity to the target songs. The greatest amount of masking (and spatial unmasking) occurred with a chorus masker consisting of three songs that differed from the target but were similar in spectrotemporal character. Smaller amounts of masking (and less spatial unmasking) were observed for broadband noise maskers with flat or modulated temporal envelopes. These results were interpreted in terms of two very different categories of masking: "energetic" (masking explained entirely by acoustic overlap of target and masker energy) and "informational" (masking caused by spectrotemporal similarity of target and masker signals, associated with confusion and uncertainty; for a recent review see Kidd, Mason, Richards, Gallun, & Durlach, 2007). It has been shown in many human studies that spatial unmasking is greater for complex maskers such as speech than it is for simple maskers such as noise (Freyman, Helfer, McCall, & Clifton, 1999; Kidd, Mason, Brughera, & Hartmann, 2005).

We wished to extend the findings of Best et al. (2005) using bird models. Zebra finches and budgerigars were chosen as the models for several reasons. First, the Best et al. (2005) study used zebra finch songs as stimuli. This makes the stimuli ecologically relevant and meaningful for the zebra finches. Budgerigars and zebra finches can often be seen flocking together in the wild, and although it is unknown whether or not budgerigars extract any meaning from the zebra finch vocalizations, it is likely that zebra finch songs could act as maskers to budgerigar vocalizations. It is likely that our domesticated birds have a similar experience in our mixed species aviary. So although the ecological relevance of the zebra finch stimuli used in these experiments is lower for the budgerigars than for the zebra finches, it is surely higher than the broadband noise maskers and pure tones used by Dent et al. (1997). Second, the zebra finch song stimuli are complex in both spectral and temporal structure. As mentioned earlier, the only other controlled laboratory study on spatial unmasking in birds was conducted on budgerigars using simple stimuli. We wished to determine whether birds, like humans, show different amounts of spatial unmasking for simple and complex stimuli. Third, budgerigars and zebra finches have long been used as animal models for studies on acoustic communication, including both hearing and vocalizations (reviewed in Dooling, Lohr, & Dent, 2000; Farabaugh & Dooling, 1996). Audiograms, maximum and minimum temporal integration functions, pitch discrimination, discrimination and detection of calls and tones in various types of noise, the discrimination of temporal fine structure, and speech perception have all been measured in these two species of birds and on

many measures the two species show remarkable similarities (Dooling, Best, & Brown, 1995; Dooling et al., 2000; Lohr, Dooling, & Bartone, 2006; Lohr, Wright, & Dooling, 2003; Okanoya & Dooling, 1987, 1990; Weisman, Njegovan, Williams, Cohen, & Sturdy, 2004). One important difference in the perceptual abilities of these birds is their ability to localize pure tones. Budgerigars are much more accurate than zebra finches on this type of task (Park & Dooling, 1991), suggesting that these birds might possess a superior ability to extract three-dimensional spatial information from acoustic inputs. A study on the precedence effect in these two species shows that the timing of the suppression of acoustic echoes in these animals' environments is similar, but that the amount of suppression is much greater in budgerigars than zebra finches (Dent & Dooling, 2004). Zebra finches are also more prone than budgerigars to experiencing the Franssen Effect, an illusion thought to manifest itself in difficult localization environments (Dent, McClaine, & Welch, 2007). In the Franssen Effect, if a sound's onset is obscured by another sound from another location, listeners do not hear the second sound and instead continue to hear an auditory image at the first sound's location (even when the first sound has ended). If budgerigars do possess superior spatial auditory perception, the current task using identical procedures for both species should reveal it. If, however, the increased ecological relevance for zebra finches is important, it might be expected that zebra finches would show more unmasking than the budgerigars in these experiments.

Matching the paradigm used by Best et al. (2005) as closely as possible, we trained zebra finches and budgerigars to identify zebra finch songs in quiet and then measured identification thresholds in colocated and spatially separated (90°) masker conditions. Since the simple sound localization thresholds for zebra finches are more than three times worse than those of the budgerigars, we also tested the zebra finches on another condition separating the stimuli by 180°, rather than the 90° used in all of the other conditions.

During the course of our experiments, the task of identifying a target embedded in a simultaneously presented masker proved to be very difficult for the birds. This prompted Experiment 2, where we changed the paradigm to more closely match the Dent et al. (1997) study. Here, the masker ran continuously throughout the session making the target onset more prominent. However, the task for the birds remained the same: identify the zebra finch song embedded in a spatially coincident or spatially disparate masker.

Method

Subjects

Four adult zebra finches (one female, three males) and four adult budgerigars (two females, two males) were used as subjects in these experiments. One of the female budgerigars died before completing Experiment 2. All of the birds were individually housed in a vivarium at the University at Buffalo, the State University of New York (SUNY), and were kept on a day/night cycle corresponding to the season. The birds were either purchased from a local pet store or bred in the vivarium. They were kept at approximately 90% of their free-feeding weight during the course of the experiment. All procedures were approved by the University at Buffalo, SUNY's Institutional Animal Care and Use Committee

and complied with the National Institutes of Health (NIH) guidelines for animal use.

Testing Apparatus and Stimuli

The experiments took place in one of four identical psychoacoustic testing setups. The setups consisted of a wire test cage (61 × 33 × 36 cm³) mounted in a sound-attenuated chamber (Small Animal Chamber, Industrial Acoustics Company, New York) lined with sound-absorbent foam (10.2 cm Sonex, Ilbruck Co.). The cage consisted of a perch, an automatic food hopper (Med Associates Standard Pigeon Grain Hopper), and two vertical response keys extending downward from the inside of the hopper in front of the bird. The response keys were two sensitive microswitches with 1 cm-square green (left key) or red (right key) buttons glued to the ends. The birds pecked the colored keys, which tripped the microswitches. A small 7-W light at the top of the test cage illuminated the chamber and served as the experimental house light. An additional 30-W bulb remained on in the chamber for the entire session. The behavior of the animals during test sessions was monitored at all times by an overhead web-camera (Logitech QuickCam Pro, Model 4000). One speaker (Morel Acoustics, Model MDT-29) was hung directly behind the subject and one speaker was hung to the right of the subject. In one experiment, another speaker was also hung to the left of the subject. All speakers were at the level of the bird's head and 30.5 cm away from the bird during testing. The experiments were controlled by a Dell microcomputer operating Tucker-Davis Technologies (TDT, Alachua, FL) modules and SykofizX software.

Stimuli and Calibration

All of the birdsong target and chorus masker stimuli were recorded from zebra finches in a colony at Boston University and were thus unfamiliar songs to the birds at the University at Buffalo, SUNY. Songs were recorded in a single-walled sound-treated booth (Industrial Acoustics Company) using a single microphone (Audio-Technica AT3031) placed 17 cm above the caged bird (see Best et al., 2005, for further details about the stimuli and their recording procedures). The target stimuli were songs recorded from six zebra finches, with five similar song motifs selected from each bird's repertoire. Each motif was highly stereotypical for a particular bird but quite distinct from those of the other birds. The songs ranged in duration between 800 and 1000 ms, were low-passed filtered at 8 kHz, and were output at an overall RMS level of 65 dB SPL at a sampling rate of 50 kHz. A spectrogram representation of a sample target motif is shown in Figure 1A.

Three maskers were constructed for these experiments (after Best et al., 2005): noise, modulated noise, and chorus. All of the maskers had the same long-term, but not short-term, spectral characteristics. The chorus masker (Figure 1B) was generated by adding three motifs from nontarget birds together. The "song-shaped" noise masker (Figure 1D) was created by generating broadband noise with a spectral profile matching that of the average set of chorus maskers. The modulated noise masker (Figure 1C) was generated by modulating a song-shaped noise with the broadband envelope from a random chorus masker. All maskers were 1 s in duration to ensure that the target motifs could be fully masked in the time domain. In Experiment 1, the maskers started
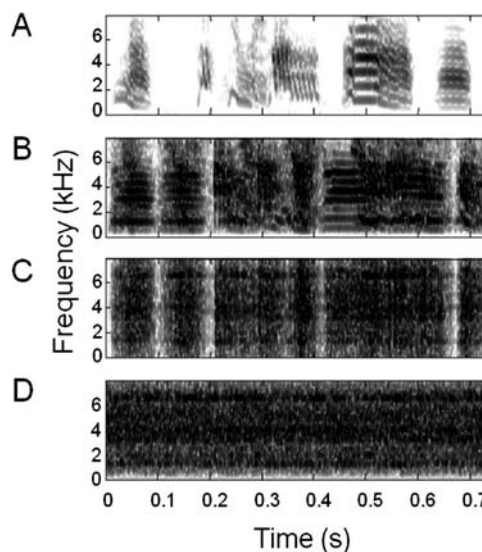

Figure 1. Sonograms of (A) one of the target zebra finch songs, (B) a chorus masker, (C) a modulated noise masker, and (D) a song-shaped noise masker.

at the same time as the targets. In Experiment 2, the maskers were played in a continuous loop throughout the experimental session.

During training, animals were required to identify all 30 target motifs (five motifs each from six birds). During the masking experiments, three motifs from each bird were randomly chosen as targets (18 motifs total). Each of the target motifs was presented at eight target-to-masker-ratios (TMRs). TMR was calculated using the broadband RMS level of the two signals. The target or masker level was varied to produce TMRs in 12 dB steps ranging between −48 and +60 dB. Stimulus calibration was performed with a Larson-Davis sound level meter (Model 825) and 20-ft extension cable. For all measurements, a .5-in microphone was placed in the position normally occupied by the bird's head during testing.

Experiment 1 was conducted using three renditions of each of the three masker types, and thresholds were found to be similar across those renditions (see Results). Thus, in the second experiment we used only one rendition of each masker. Each animal was tested at eight TMRs per condition, but as there were differences in sensitivity and motivation levels both across subjects and experimental conditions, the range of TMRs for each subject/condition could differ. The range was chosen to keep performance at optimal levels, avoiding both floor and ceiling of the psychometric function for the particular subject and condition.

Training and Testing Procedures

The birds were trained using operant conditioning procedures to peck the microswitches for food reinforcement. First, they pecked the left key to initiate a trial. After a variable interval of 2–7 s, a target was presented. The birds were trained to peck the left key again for one class of targets and to peck the right key for the other class of targets. If they correctly identified the class of sounds and pecked the appropriate key within 1.5 s following its presentation, they were rewarded with 1.5-s access to hulled millet from the illuminated food hopper for 70% of the correct trials. If they

responded incorrectly (indicating the wrong class), the house light was extinguished for 5 s.

The six target songs were arbitrarily placed into two classes, and a different combination of classes was used for each bird (e.g., Truman had to peck left for songs 2, 4, and 6 and right for songs 1, 3, and 5, while Cosmo had to peck left for songs 1, 2, and 3, and right for songs 4, 5, and 6). The birds were initially trained on two songs at a time (five motifs per song, 10 motifs total to classify).

Performance started at approximately 50% correct (chance performance levels), and progressively improved as training continued. Once the birds were responding at a criterion rate of at least 85% correct for three successive sessions, two more songs were added (10 more motifs, 20 motifs total). Once the birds reached criterion on the four songs, the final two songs were added (10 more motifs, 30 motifs total). After approximately 10 sessions with performance above criterion on all six songs, the masking experiments were
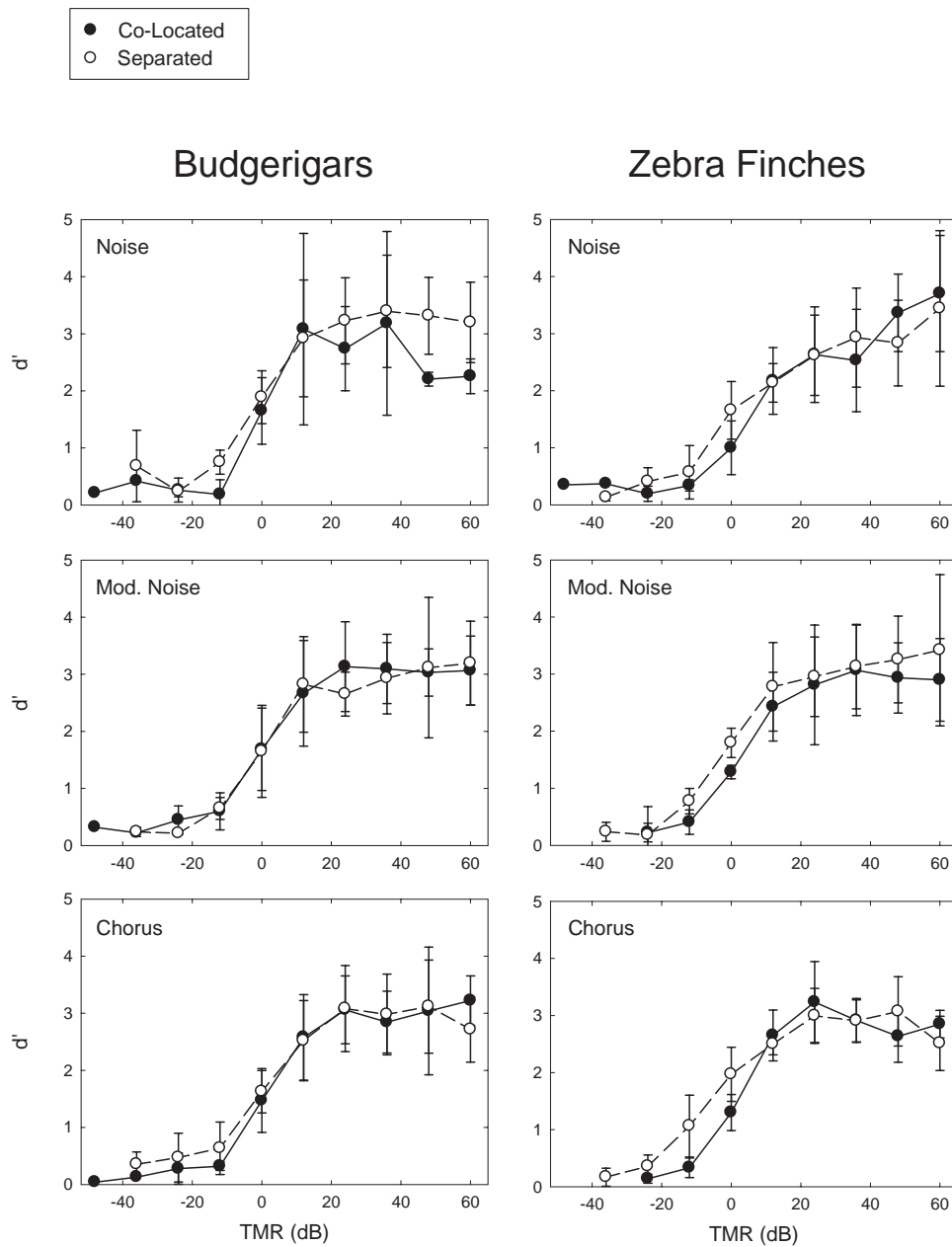
Figure 2. Mean psychometric functions for budgerigars (left column) and zebra finches (right column) for targets embedded in three noises (top row), modulated noises (middle row), and choruses (bottom row). *d′* values are shown as a function of TMR for the colocated (black circles) and separated (white circles) speaker conditions. Error bars represent between-subjects standard deviations. The birds were tested at slightly different TMRs, resulting in offset psychometric functions.

conducted. The average identification performance at the end of training for all songs was approximately 90%.

In the masking experiment, the task for the birds remained the same: to correctly classify the song and to respond with the appropriate key peck. Training differed from testing in that the songs were now embedded in maskers, and the TMRs of the maskers and songs varied randomly within a session according to the psychophysical Method of Constant Stimuli. The maskers were either presented from the same speaker as the target (colocated condition) directly behind the bird, or from a speaker to the right of the bird (separated condition). An additional condition in Experiment 1 was conducted on the zebra finches, where the masker was presented from the right of the bird and the target was presented to the left of the bird (180° condition).

Data Collection and Analysis

Percent correct performance was measured for each bird on each rendition (three total) of each target (six total) embedded in each masker (three total) at each TMR (eight total) and each speaker configuration (two total). Only one masker type/speaker configuration was presented per session and each bird was tested in a different order on those six conditions. For every one of the

target/masker/TMR combinations, between 18 and 22 trials were collected for each subject.

To calculate threshold for a particular masker type/speaker configuration, percent correct scores were transformed into d-primes and a $d' = 1.5$ threshold was obtained for each condition. To do this, percent correct scores were first calculated for each of the six songs at each TMR. The mean "left" and "right" hits and false alarms were then calculated for each TMR, averaged across the song renditions. Hits were simply the percent correct values for the three songs. False alarms were the percent incorrect scores for the opposite side. That is, a 90% hit rate for a given TMR to the left also yielded a 10% false alarm rate for that same TMR to the right. The mean "left" and the mean "right" hits and false alarms at each TMR were next transformed into z-scores. Those z-scores were transformed into d-primes, and then a d' of 1.5 threshold was calculated. Transforming the percent correct values into d' removed any left-right response biases.

For the first experiment, a four-way between-subjects analysis of variance (ANOVA) was conducted (Species × Speaker condition × Masker type × Masker rendition). For the second experiment, a three-way ANOVA was conducted (Species × Masker
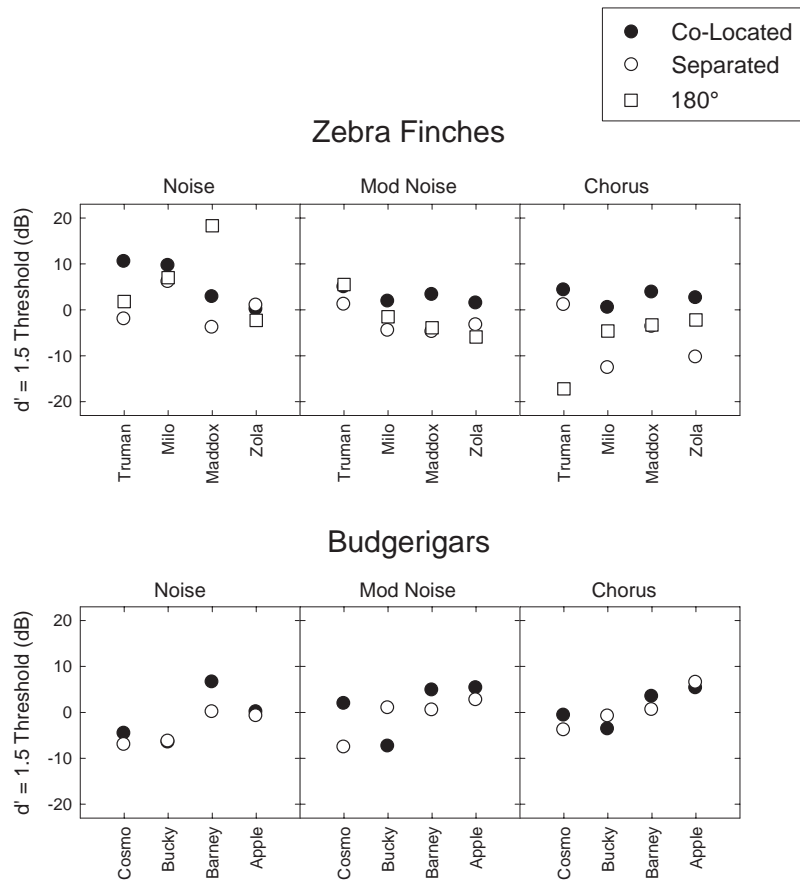

Figure 3. Individual d' thresholds for the zebra finches (top row) and budgerigars (bottom row) for the noise (left panels), modulated noise (center panels), and chorus (right panels). Thresholds are shown as black circles for the colocated conditions and as white circles for the separated conditions. Zebra finches were run on an additional 180° speaker separation condition. Those thresholds are shown as white squares.

type × Speaker configuration). When ANOVA main effects yielded significance, we also ran paired *t* tests to determine if the differences between the speaker configurations showed a value significantly different from 0.

Results

Experiment 1

In Experiment 1, where the targets and maskers were initiated at the same time, both species of birds showed poor identification performance for low TMRs and increasingly better identification performance as TMR increased (see Figure 2). The *d'* values for all three masker types started at chance levels for the lowest TMRs of −48 to −24 dB and reached identification-in-quiet levels at TMRs greater than +24 dB. The trends were similar for all three masker types and both speaker configurations.

The mean individual thresholds of *d'* = 1.5 (averaged across three motif renditions) for broadband noise, the modulated noise, and the chorus maskers (Figure 3 left, middle, and right panels, respectively) show quite a bit of variability (Figure 3: top row, zebra finches; bottom row, budgerigars; black circles, colocated; white circles, separated). The ANOVA revealed no significant differences in thresholds between the masker types, masker renditions, or species but there was a significant main effect of speaker configuration (see Table 1).

There were also two significant interaction effects. The first was between species and speaker configuration and the second was between species and masker type. Post hoc comparisons based on these interactions showed that the zebra finches performed better on the separated speaker configuration than the coincident configuration (a threshold difference of about 6.8 dB), suggesting that spatial unmasking occurred, but the average difference of 1.6 dB for the budgerigars did not reach statistical significance. When the zebra finches were tested in an additional condition with the target and masker separated by 180° (Figure 3, white squares), there was no consistent improvement in thresholds. Post hoc comparisons of masker types showed no significant patterns for either species.

For both species, there was a substantial variation across subjects in the amount of spatial unmasking (difference between 90° separated and colocated thresholds), ranging from +13 dB to −8 dB. As a whole, this experiment suggests that budgerigars exhibit little spatial unmasking for zebra finch song, with similar thresholds across masker renditions and types, and that zebra finches exhibit small but significant spatial unmasking, but again with no differences across masker renditions or masker types.

Experiment 2

Experiment 1 revealed no consistent differences in unmasking for the different masker types or renditions for the birds. The very small amount of unmasking with the broadband noise maskers (Figure 2, top panels) was especially surprising given that previous experiments with budgerigars demonstrated substantial spatial unmasking for the detection of pure tones embedded in broadband

Table 1

Summary of ANOVA Results for Experiments 1 (Short Masker) and 2 (Continuous Masker) and for Comparisons of Thresholds Across the Two Experiments

Dependent variable	Source	df	F	p
Short masker (Exp 1)	Masker type	2, 108	0.17	>0.05
	Masker rendition	2, 108	1.25	>0.05
	Species	1, 108	0.52	>0.05
	Speaker configuration	**1, 108**	**12.77**	**<0.05**
	Species × Speaker config.	**1, 108**	**4.74**	**<0.05**
	Species × Masker type	**2, 108**	**3.98**	**<0.05**
	Species × Masker rend.	2, 108	0.79	>0.05
	Speaker config. × Masker type	2, 108	0.07	>0.05
	Speaker config. × Masker rend.	2, 108	1.80	>0.05
	Masker rend. × Masker type	4, 108	0.53	>0.05
Continuous masker (Exp 2)	Masker type	2, 30	0.20	>0.05
	Species	**1, 30**	**48.75**	**<0.05**
	Speaker configuration	**1, 30**	**90.09**	**<0.05**
	Masker type × Species	2, 30	3.12	>0.05
	Masker type × Speaker config.	2, 30	0.02	>0.05
	Species × Speaker config.	1, 30	3.45	>0.05
ZFs	**Masker length**	**1, 3**	**13.00**	**<0.05**
Co-located speaker configuration	Masker type	2, 6	3.18	>0.05
	Length × Type	2, 6	4.22	>0.05
ZFs	**Masker length**	**1, 3**	**11.47**	**<0.05**
Separated speaker configuration	Masker type	2, 6	0.59	>0.05
	Length × Type	2, 6	1.90	>0.05
Budgerigars	**Masker length**	**1, 3**	**59.02**	**<0.05**
Co-located speaker configuration	Masker type	2, 6	0.05	>0.05
	Length × Type	2, 6	1.81	>0.05
Budgerigars	**Masker length**	**1, 3**	**48.05**	**<0.05**
Separated speaker configuration	Masker type	2, 6	0.47	>0.05
	Length × Type	2, 6	0.74	>0.05

maskers (Dent et al., 1997). We suspected that the task difficulty might be a factor; thus, in Experiment 2 we attempted to simplify the task by playing the masker continuously throughout the session. We hoped that this would reduce any automatic "grouping" of the target and masker that may have occurred based on common onset times, making the task of identifying the target easier.

Psychometric functions for the continuous masker conditions show that, as in Experiment 1, d' values increased as a function of TMR (see Figure 4). The between-subjects errors were larger for

Experiment 2 than Experiment 1, and there were also larger differences between the colocated and separated functions in this experiment, especially for the zebra finches. The $d' = 1.5$ thresholds support this observation (see Figure 5); thresholds for the colocated condition were higher in almost every instance than the thresholds for the separated conditions (black circles higher than the white circles). In Experiment two, the ANOVA revealed significant effects of species and speaker configuration, but no significant effect of masker type and no significant
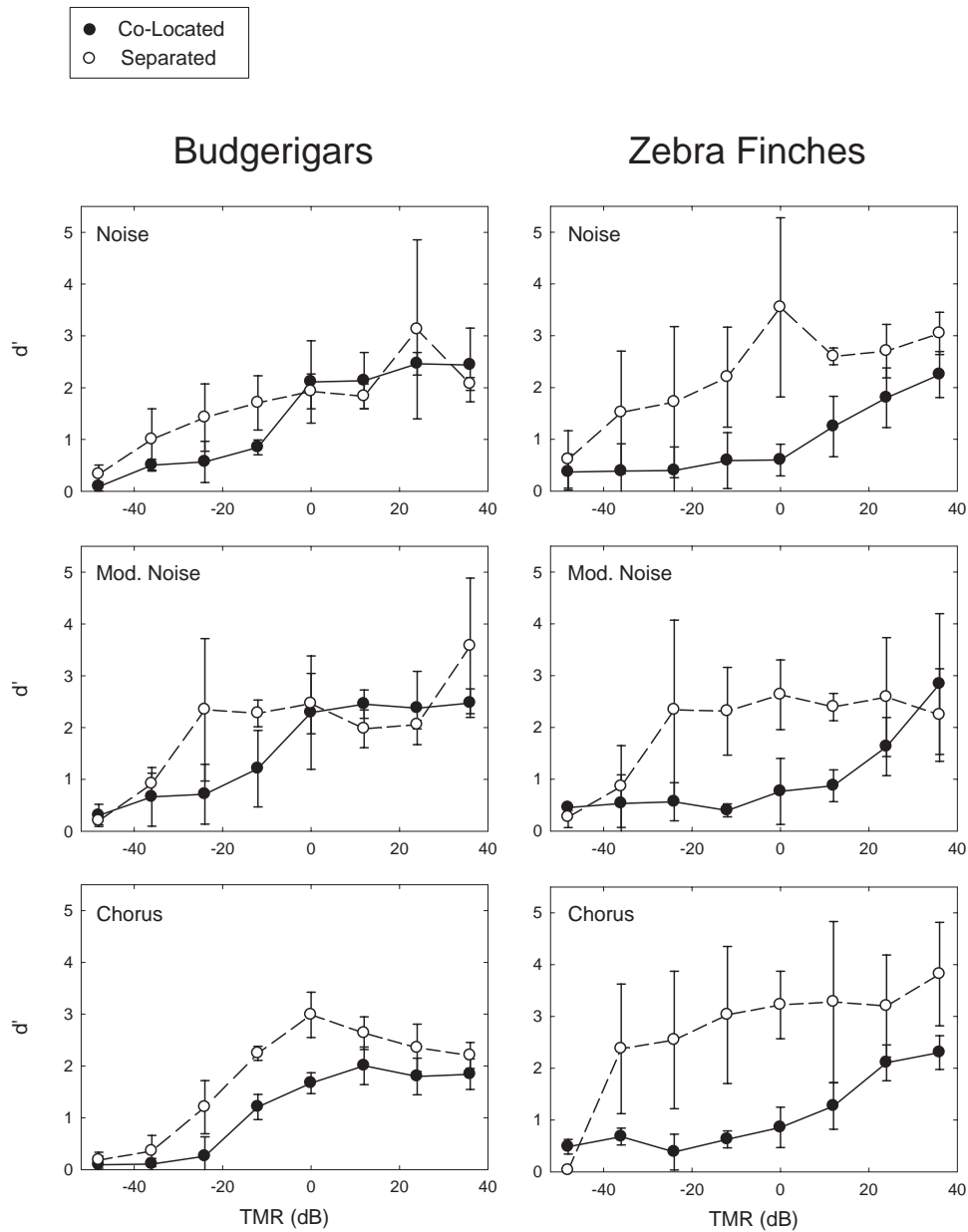

Figure 4.   Mean psychometric functions for budgerigars (left column) and zebra finches (right column) for targets embedded in continuous noise (top row), continuous modulated noise (middle row), and a continuous chorus (bottom row). d' values are shown as a function of TMR for the colocated (black circles) and separated (white circles) speaker conditions. Error bars represent between-subjects standard deviations. The birds were tested at slightly different TMRs, resulting in offset psychometric functions.
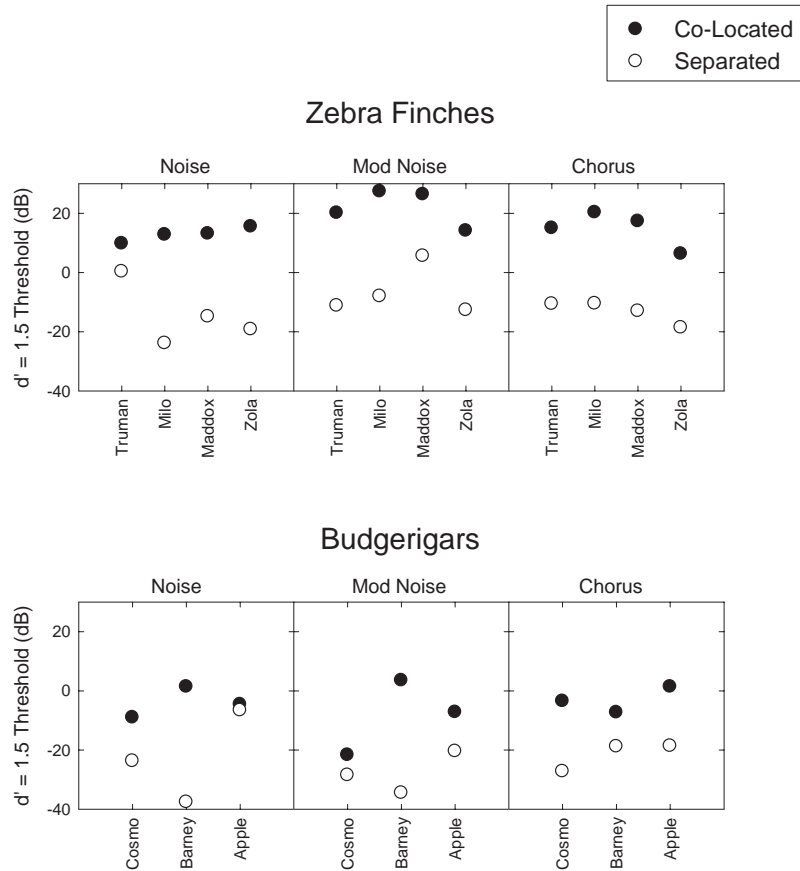
Figure 5. Individual *d'* thresholds for the four zebra finches (top row) and three budgerigars (bottom row) for the continuous noise (left panels), continuous modulated noise (center panels), and a continuous chorus (right panels). Thresholds are shown as black circles for the colocated conditions and as white circles for the separated conditions.

interactions (see Table 1). The budgerigars had significantly lower thresholds than the zebra finches, and the colocated thresholds were significantly higher than the separated thresholds. The amount of unmasking for each bird and each of the three masker types in Experiment 2 ranged from 2 dB to 39 dB overall.

In general, playing the masker continuously not only lowered the overall thresholds (see Figure 6), but also significantly increased the amount of spatial unmasking (see Figure 7). The three budgerigars that completed both experiments showed lower thresholds in all conditions when the masker was lengthened (see Figure 6). The zebra finches showed lower thresholds in the separated configuration for all three maskers, but interestingly, higher thresholds for at least two of the masker types in the colocated condition (see Figure 6). Two-way repeated measures ANOVAs were conducted for each species and each speaker configuration for the one masker used in both experiments and results revealed significant differences for the masker lengths but not the masker types (see Table 1). Unmasking was small for the brief maskers, but averaged about 28 dB for all three maskers in the finches and about 20 dB for all three maskers in the budgerigars (see Figure 7).

Discussion

Noise is an increasing problem for animals communicating in the wild. Knowing how well animals can hear in different kinds of noise and what mechanisms they have available to help them more effectively communicate despite loud noise levels is important for determining the ecological impact of noise, and for increasing our overall understanding of animal communication.

Differences in spatial location are used by humans and other animals to reduce the deleterious effects of noise and interference on the reception of a signal of interest. In birds, the first measurements of spatial unmasking (Dent et al., 1997) showed that despite very poor absolute sound localization abilities, spatial unmasking of tones approached that found in humans under similar conditions (Saberi et al., 1991): about 11 dB. In the present study, even larger benefits of spatial separation (20–30 dB) were measured in zebra finches and budgerigars when target zebra finch songs were masked by a chorus of similar songs or by broadband noise.

In a previous study using human subjects but identical stimuli to those used here, Best et al. (2005) also found large amounts of spatial release from masking. In that study, Best et al. also included a monaural control condition, which enabled them to attribute a
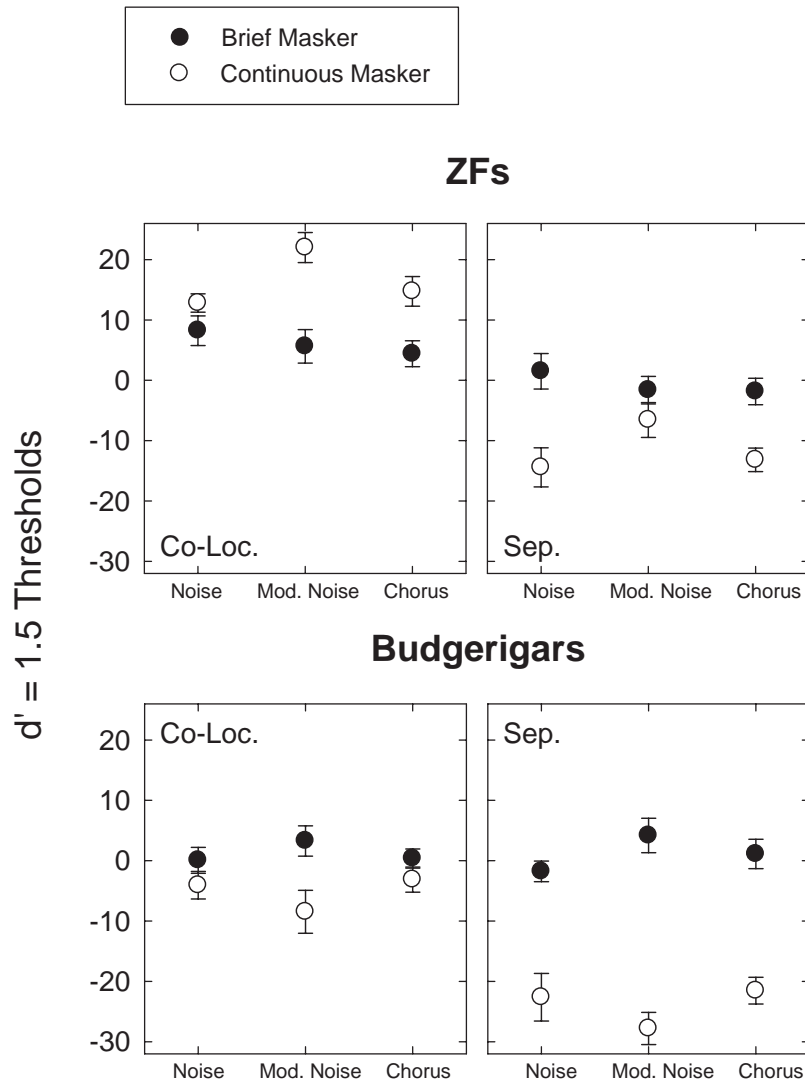
Figure 6. Mean thresholds for zebra finches (top panels) and budgerigars (bottom panels) with the colocated (left panels) and separated (right panels) speaker conditions. Thresholds for the brief masker are in black and thresholds for the continuous masker are in white. Error bars represent between-subjects standard deviations.

part of the spatial benefit to an improvement in signal-to-noise ratio at one ear in the case of spatial separation. Since the birds were not tested under monaural conditions, we do not know at this time how much this "better ear advantage" contributed to the improvement in identification of the target song when it was separated from the maskers. However, given that the signal-to-noise ratio changes largely as a result of the shadowing effect of the head, the small head size of the birds leads us to predict that any acoustic advantage would be very small. The idea that the head-shadow benefit is likely small in birds is also supported by the fact that spatial separation caused little change in performance in Experiment 1, where the head-shadow would also yield a better-ear benefit. Once the acoustic advantage was accounted for, Best et al. noted that the remaining benefit of spatial separation was far greater for the spectro-temporally complex chorus masker than for the other two maskers, which had a very distinct spectro-

temporal structure from that of the target. They attributed this to a release from informational masking, whereby the perceived differences in sound source position reduced confusion about which elements of the mixture belonged to the target (see also Arbogast, Mason, & Kidd, 2002; Freyman et al., 1999). Consistent with this, performance in the colocated condition was especially poor with the chorus masker, as would be expected if informational masking were high in this condition.

In contrast to the results of Best et al. (2005) in humans, we did not find any differences between the masker types in our experiment in terms of the amount of masking (or the amount of spatial unmasking). We see two possible explanations for this. First, it is possible that the difficulty of the task caused very high levels of masking for all three maskers. The birds were required to detect the signal embedded in the masker (one of 30 targets), identify the correct category for that signal (one of two), and respond appro-
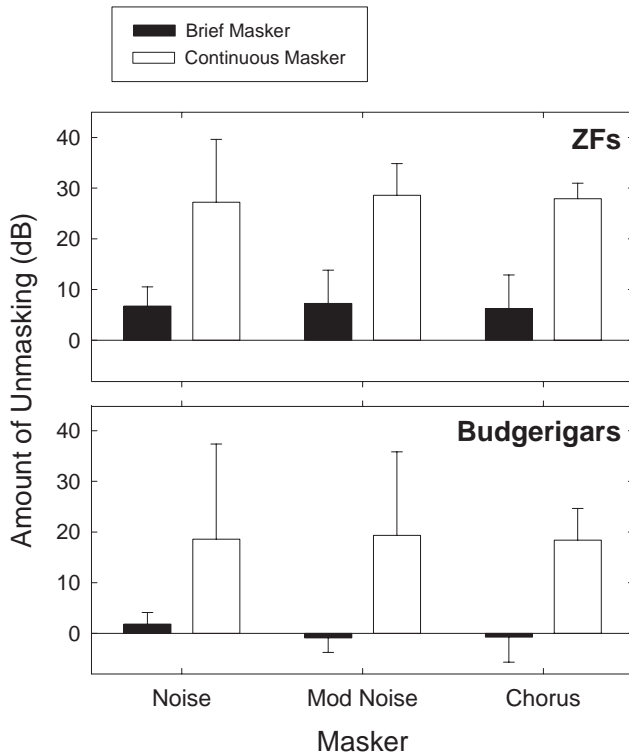
Figure 7. Mean spatial unmasking for zebra finches (top panel) and budgerigars (bottom panel) for the three masker types. Unmasking for the brief masker is shown in black and for the continuous masker is shown in white. Error bars represent between-subjects standard deviations.

priately to that category within less than 2 seconds. This task was made even more difficult with the simultaneous onset and offset of the targets and maskers, which may have caused grouping of the target and masker into a single perceptual object. In contrast, evidence from humans listening to the same stimuli suggests that target and masker only group together when the masker has similar spectro-temporal structure to the target (i.e., only for the chorus masker; see Best et al., 2005). Based on the interpretation of the human results for similar tasks, we would not expect to see differences in the amount of unmasking produced by the avian subjects if the target and masker tend to group together for all three types of maskers. Consistent with this view, Appletants et al. (2005) also found no difference in masking between song maskers and noise makers for canaries (doing a different task). Thus, it may be that the avian subjects have difficulty segregating the target from the sound mixture whenever the target and mixture have common onsets and offsets, regardless of the type of masker present in the mixture, whereas human listeners only have such difficulty when the masker is a birdsong chorus.

A second possible explanation for the differences between how spatial separation affected human and avian subjects may be that chorus maskers pose *less* of a problem for birds than they do for humans. It may be that the birds' superior spectro-temporal resolution allows them to make subtle distinctions between simultaneous birdsongs that humans cannot make. Interestingly, however, our post hoc *t* tests revealed more unmasking for the zebra finches

than for the budgerigars. Since the stimuli were derived from zebra finch vocalizations, perhaps species-specific auditory processing is contributing to the effects seen here. Both zebra finches and budgerigars are known to have species-specific advantages in identifying and discriminating among their own vocalizations relative to the vocalizations of other species (Benney & Braaten, 2000; Dooling, Brown, Klump, & Okanoya, 1992), and perhaps this advantage extends to spatial unmasking tasks, too.

In evaluating the possible alternative explanations for differences in how unmasking plays out for human and avian subjects, it is important to consider the differences in the results for Experiments 1 and 2. Specifically, in Experiment 2, more consistent and substantial spatial unmasking was observed. The only difference between the experiments was that the masker in Experiment 2 was on continuously, which should have made segregation of the target and masker easier (if segregation were an issue in Experiment 1, where target and masker had simultaneous onsets and offsets). This difference strongly supports the idea that the avian subjects had difficulty in perceptually segregating the targets from the maskers in Experiment 1 compared to in Experiment 2 (especially the zebra finches, who were listening to conspecific target signals). This result, in turn, suggests that avian and human subjects differ in how they weigh the various acoustic cues that contribute to perceptual segregation: for the humans, common onsets and offsets are not sufficient to cause a birdsong target to group with a noise masker, whereas they seem to be sufficient to cause difficulties for the avian subjects.

Overall, our experiments demonstrated for the first time in controlled laboratory conditions that spatial unmasking occurs for natural complex signals in two animals, budgerigars and zebra finches. We found more spatial unmasking with these stimuli than was previously found with pure tones masked by broadband noise in budgerigars (Dent et al., 1997), suggesting that factors beyond energetic masking may be involved here. Even though these stimuli are not necessarily meaningful or "information carrying" to the budgerigars, informational masking may have occurred due to similarity and confusion between the target and maskers, as is seen in human listeners (Best et al., 2005). Since the spatial unmasking of pure tones in broadband noise has not been measured in zebra finches, we do not know whether spatial unmasking differs between simple and complex stimuli for them. Regardless, the fact that both species showed similar amounts of spatial unmasking is surprising given that sound location limens of zebra finches are more than three times greater than those of budgerigars (Park & Dooling, 1991). Consistent with the idea that informational masking occurred for the birds in this experiment, across-subject variability in thresholds and spatial unmasking was high, a phenomenon seen in humans when complex stimuli and tasks are involved (for review see Kidd et al., 2007).

In the wild, animals trying to communicate may adopt a number of strategies to boost the effectiveness of information transfer when conditions become noisy. Both humans and animals can increase the intensity of their vocalizations, vocalize during quiet periods, or move to a location that separates signals from noise. The experiments here demonstrate that differences in spatial location are salient and useful cues for allowing birds to segregate competing sounds and improve the reception of a target when the target and masker have distinct onsets and offsets (as they will in natural environments). These improvements appear to be more pronounced for the complex vocalizations used here than has been observed previously for simpler signals. In future research, the use of natural stimuli might provide a

clearer picture of what animals may be doing in their natural ecological niche.

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