

## Chapter 43

# Detection Thresholds for Amplitude Modulations of Tones in Budgerigar, Rabbit, and Human

Laurel H. Carney, Angela D. Ketterer, Kristina S. Abrams, Douglas M. Schwarz, and Fabio Idrobo

**Abstract** Envelope fluctuations of complex sounds carry information that is essential for many types of discrimination and for detection in noise. To study the neural representation of envelope information and mechanisms for processing of this temporal aspect of sounds, it is useful to identify an animal model that can sensitively detect amplitude modulations (AM). Low modulation frequencies, which dominate speech sounds, are of particular interest. Yet, most animal models studied previously are relatively insensitive to AM at low modulation frequencies. Rabbits have high thresholds for low-frequency modulations, especially for tone carriers. Rhesus macaques are less sensitive than humans to low-frequency modulations of wideband noise (O’Conner et al. *Hear Res* 277, 37–43, 2011). Rats and chinchilla also have higher thresholds than humans for amplitude modulations of noise (Kelly et al. *J Comp Psychol* 120, 98–105, 2006; Henderson et al. *J Acoust Soc Am* 75, 1177–1183, 1984). In contrast, the budgerigar has thresholds for AM detection of wideband noise similar to those of human listeners at low modulation frequencies (Dooling and Searcy. *Percept Psychophys* 46, 65–71, 1981). A one-interval, two-alternative operant conditioning procedure was used to estimate AM detection thresholds for 4-kHz tone carriers at low modulation frequencies (4–256 Hz). Budgerigar thresholds are comparable to those of human subjects in a comparable task. Implications of these comparative results for temporal coding of complex sounds are discussed. Comparative results for masked AM detection are also presented.

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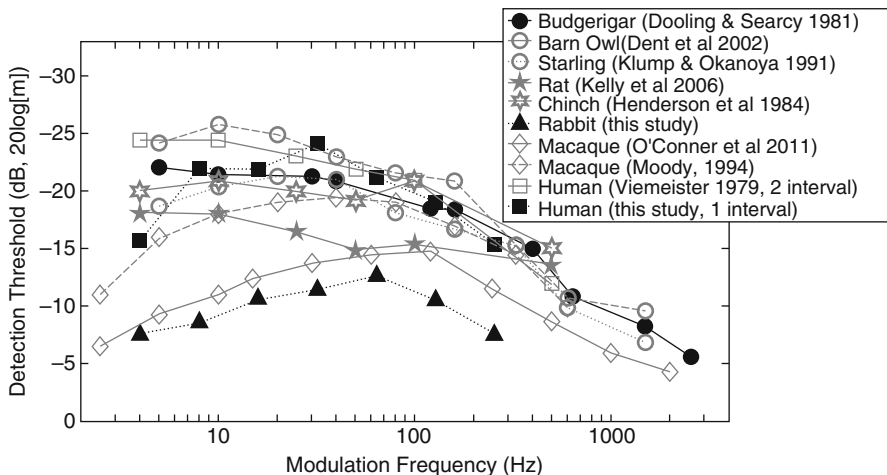
L.H. Carney, PhD (✉) • A.D. Ketterer • K.S. Abrams • D.M. Schwarz  
Departments of Biomedical Engineering and Neurobiology & Anatomy,  
University of Rochester, 601 Elmwood Ave, Box 603, Rochester, NY, USA  
e-mail: laurel.carney@Rochester.edu

F. Idrobo  
Department of Psychology, Boston University,  
Boston, MA, USA

## 1 Introduction

The importance of amplitude modulations (AM) for carrying information in complex sounds has motivated numerous psychophysical, behavioral, and physiological studies of AM detection and discrimination. Humans and birds are sensitive to sinusoidal amplitude modulation (SAM) depths as low as  $-25$  dB (in terms of  $20 \log m$ , where  $m$  is the modulation index), whereas several other species studied are less sensitive (Fig. 43.1). In particular, a study of AM detection in rabbits has shown that they are insensitive to low-frequency modulations of tone carriers (Carney et al. 2009). Gourevitch and Eggermont (2010) found, in a physiological study of auditory cortex in cat, that low-frequency AM is most effectively coded by the timing of discharges, whereas high-frequency AM is effectively coded in terms of average discharge rates. Thus, differences across species in the ability to detect low-frequency AM may indicate differences in the ability to make use of temporal information in neural responses. A goal of this study was to identify an animal model that is able to detect low-frequency modulations of narrowband sounds.

In this study, AM detection thresholds for narrowband stimuli were estimated for the budgerigar, a vocal learner that has been used in a number of previous behavioral studies (e.g., Dooling and Searcy 1981; Dooling et al. 1989; Dent et al. 2002). Amplitude modulation detection thresholds for wideband noise stimuli (Dooling and Searcy 1981) suggested that the budgerigar's sensitivity for SAM noise is comparable to that of human. Therefore, it was hypothesized that the budgerigar would be sensitive to low-frequency amplitude-modulated tones.



**Fig. 43.1** Comparison of AM detection thresholds for sinusoidally amplitude-modulated (SAM) wideband noise across several species. More sensitive thresholds appear higher on the plot. Thresholds in three bird species (*circles*) are generally comparable to human thresholds (*squares*). Rabbits and macaques are less sensitive to AM for wideband SAM stimuli similar to those used in the human studies. Thresholds in a one-interval task for human, budgerigar, and rabbit are highlighted by the *solid symbols*

In addition to estimating AM detection thresholds, performance of the budgerigar in a masked modulation detection task was studied. Responses were compared to results using the same stimuli in human and rabbit. This experiment was motivated by previous studies of masked modulation in human listeners (e.g., Strickland and Viemeister 1996; Ewert and Dau 2000; Ewert et al. 2002; Nelson and Carney 2006). However, the use of reproducible narrowband noises as modulation maskers allows detailed comparisons of hit and false-alarm rates across masker waveforms as a means of identifying cues used in this detection task.

## 2 Methods

AM detection thresholds of budgerigar were estimated for SAM tones. Four English budgerigars were tested using a 4-kHz tone carrier modulated at frequencies ranging from 4 to 256 Hz. Stimuli were presented at 50 dB SPL.

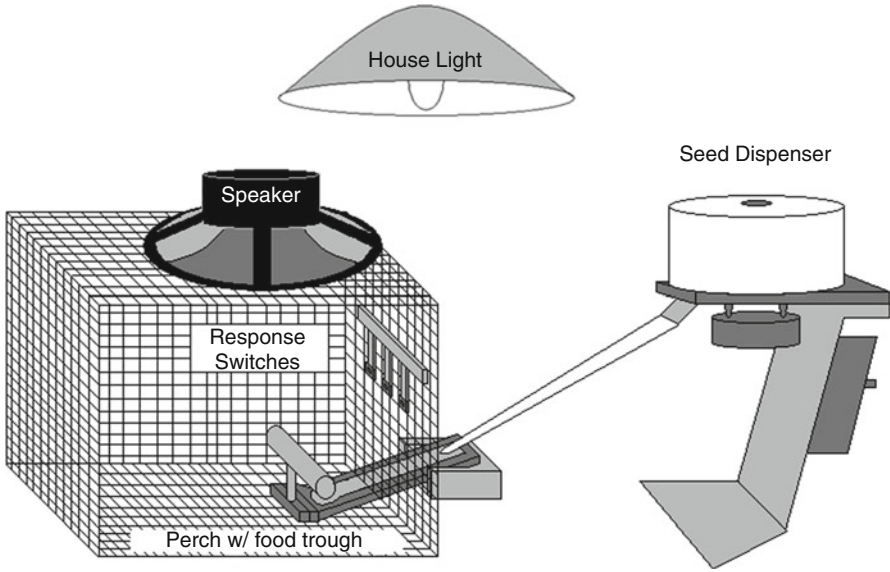
Operant methods were used with a single-interval two-down, one-up (2D1U) adaptive tracking procedure (Levitt 1971) to estimate AM detection thresholds. Correct responses were reinforced by delivery of a single hulled millet seed. Incorrect responses were followed by a 5-s timeout with the house light extinguished. Bias was monitored throughout each session and was controlled by the delivery of two seeds for the responses on the side that was biased against for a percentage of trials that depended on the degree of bias. Sessions of approximately 250 trials were typically 10–20 min in duration and were conducted twice a day. Threshold estimates were based on the average of an even number of reversals over the last half of each track that had bias less than 0.3 and a standard deviation of modulation depth less than 3 dB.

The operant testing was done in the behavioral setup shown in Fig. 43.2. A row of three switches was mounted on the end of the enclosure. The speaker was mounted overhead. The bird started each trial by making an observing response on the center switch which initiated an acoustic stimulus. A correct reporting response for the standard stimulus was a peck on the left switch, and for the target stimulus, on the right switch. Each block of ten trials consisted of a random sequence of five modulated and five unmodulated trials, to avoid long runs of either trial type that could result in short-term bias.

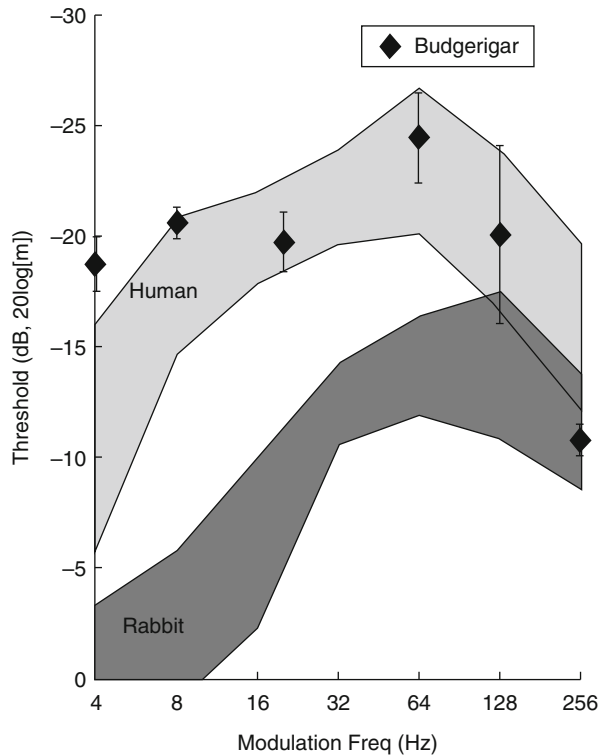
## 3 Results

### 3.1 AM Detection Thresholds

At low modulation frequencies, the average AM detection thresholds for budgerigar were comparable to those of human listeners in a matched task (Fig. 43.3). At these frequencies, rabbits had the most difficulty in detecting modulation.



**Fig. 43.2** Schematic diagram of behavioral test setup. The dimensions of the enclosure are 23 cm on each side. This apparatus was housed in a small sound-proof booth, the inner walls of which were lined with sound-absorbing foam



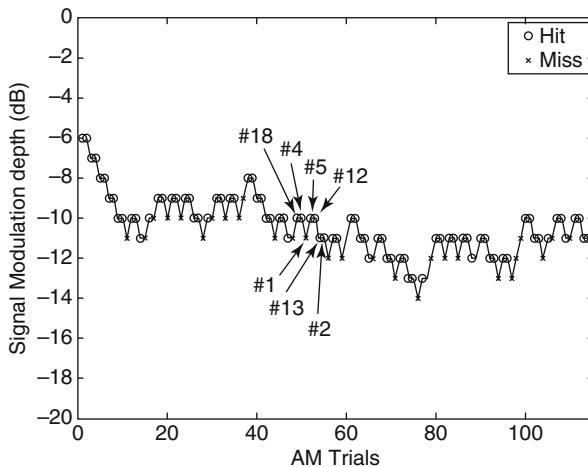
**Fig. 43.3** AM detection thresholds of budgerigar ( $n=4$ , for 4–64 Hz;  $n=2$  for 128 and 256 Hz). Budgerigar (diamonds) thresholds for SAM tones with 4 kHz carriers are superimposed on threshold ranges for humans ( $n=3$ ) and Dutch-belted rabbits ( $n=5$ ) using matched stimuli and methods. Thresholds are plotted as  $20 \log(m)$ ; more sensitive thresholds appear at the top of the plot. Means across birds  $\pm$  standard deviation are plotted. All stimuli were presented at 50 dB SPL

### 3.2 Masked Modulation Detection

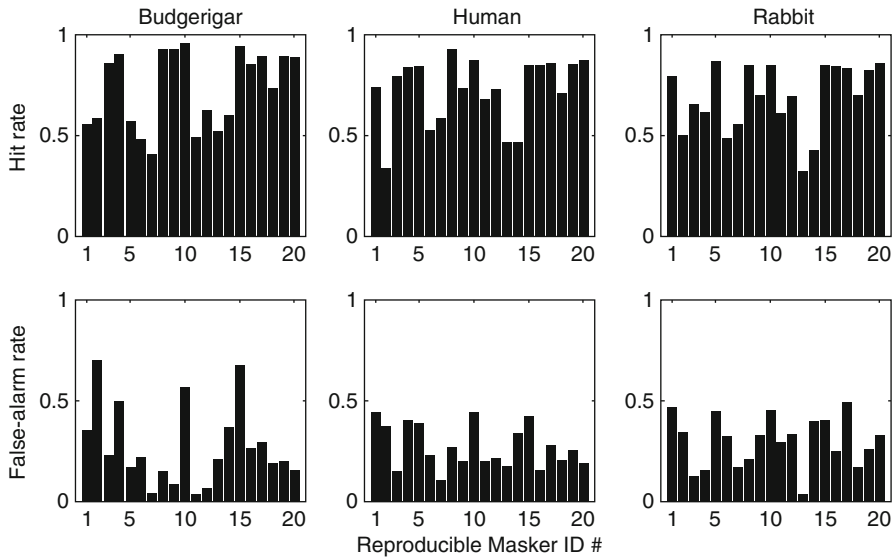
Masked AM detection was studied using reproducible noises as modulation maskers. Stimuli were matched to those in a previous study of human listeners (Nelson and Carney 2006). The target modulation was 64-Hz SAM. Stimuli were generated by adding a 64-Hz sinusoid to a noise masker that was then used to modulate a 4-kHz tone carrier. The noise maskers consisted of a set of 20 reproducible (“frozen”) noises, created using a 32-Hz wide Gaussian noise centered at 64 Hz. The root mean square, RMS, level of the modulation masker was 13 dB below the RMS level of a tone modulator giving 100 % modulation. This level was selected to elevate modulation detection thresholds approximately 6 dB with respect to unmasked thresholds. Stimulus level was 65 dB SPL. Masker waveforms were randomly selected for each trial from the ensemble of 20 maskers, while the AM detection threshold was estimated using a 2DIU paradigm. The combined reproducible noise and 2DIU tracking test procedures are illustrated in Fig. 43.4.

Estimated detection patterns (Fig. 43.5) consist of hit and false-alarm rates for each of the noise waveforms in the ensemble. Average detection patterns are shown in Fig. 43.5 for budgerigars, in comparison to rabbit and human results tested with matched stimuli and similar procedures. Masked modulation detection thresholds for the 64-Hz SAM were 0–1 dB SNR for birds, humans, and rabbits.

Patterns were consistent within each subject, as evidenced by 1st-half, 2nd-half correlations (Table 43.1) and  $\chi^2$  analyses (not shown) for both hits and false alarms.



**Fig. 43.4** Illustration of a 2DIU track with reproducible noise masker. Noise IDs are indicated for a few of the trials. Trials near threshold were sorted by noise ID to compute hit and false-alarm rates for each masker noise waveform in the ensemble, as follows: The distribution of modulation depths (omitting the initial 1/3 of the track) was computed for each animal. Hit rates (correct detections) and false-alarm rates were computed for each reproducible masker based on trials that had modulation depths within one standard deviation of the mean depth over the latter 2/3 of the track. False-alarm trials were assigned to the modulation depth of the nearest preceding modulated trial



**Fig. 43.5** Average reproducible noise results for three species are shown as “detection patterns,” which consist of hit and false-alarm rates for each of the noise masker waveforms used

**Table 43.1** 1st-half, 2nd-half correlations show the consistency in individual birds of detection patterns computed from reproducible noise results (*left*). Across-subject correlations show consistency of the detection patterns across birds (*middle*). Cross-species correlations show the similarity of detection patterns across species (*right*)

1st-half, 2nd-half correlations			Across-subject correlations			Cross-species correlations		
	H	FA		H	FA		H	FA
B1	0.84	0.83	B1–B2	0.79	0.74	Bird-human	0.73	0.75
B2	0.95	0.92	B1–B3	0.67	0.51	Bird-rabbit	0.63	0.32
B3	0.97	0.95	B1–B4	0.84	0.83	Human-rabbit	0.89	0.62
B4	0.92	0.92	B2–B3	0.86	0.86			
			B2–B4	0.93	0.82			
			B3–B4	0.87	0.82			

Detection patterns were strongly correlated across birds, as is true for humans. The average patterns for birds, rabbits, and humans were used to make comparisons across species (Table 43.1).

The stimuli used for the above experiment were equalized for overall energy. Envelope energy was equalized across maskers, but energy varied across the masker+target stimuli due to interactions between the target 64-Hz modulation and the 32-Hz bandwidth masker noise, which was centered at 64 Hz. The budgerigar detection patterns for hits were significantly correlated to envelope energy ( $r=0.60$ ; 36 % of the variance in the patterns was explained by energy). Envelope energy did

not vary across unmodulated waveforms; thus, variations in the false-alarm rates across waveforms cannot be explained by envelope energy.

## 4 Discussion

Amplitude modulation detection thresholds for SAM tones in the budgerigar were comparable to those of human listeners tested with a similar one-interval paradigm (Fig. 43.3). This result was especially interesting for low modulation frequencies, where some mammalian species, such as rabbits and macaques, have relatively high detection thresholds. The shape of the modulation transfer function (MTFs) for tone carriers in budgerigar is similar to that of human. The overall shape of the MTFs in bird and human are notably different from that of rabbit, especially for low modulation frequencies. The thresholds and MTFs in budgerigar suggest that this species is a good model for human AM processing, for both wideband and narrowband carriers.

In a masked modulation detection task using reproducible envelope maskers, detection performance varied significantly and consistently across masker waveforms in all three species tested (Fig. 43.5). Masked modulation thresholds for all species were tested at 64 Hz because this was a favorable modulation frequency for all three species (Fig. 43.1). Performance differences across masker waveforms were consistent within individual subjects. Variations in hit and false-alarm rates from waveform to waveform were significantly correlated across individuals within a species and across species. Masked modulation thresholds across species were within approximately 1 dB. These results suggest that similar strategies are used across these species for masked modulation detection of a 64-Hz sinusoidal amplitude modulation. Envelope energy differences in the masker-plus-target stimuli were correlated to the hit rates; however, consistent differences across maskers were also observed for false-alarm trials, which had identical envelope energy. Ongoing studies are investigating cues that can explain both hit and false-alarm rates in the masked modulation task.

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