

UC Davis

UC Davis Previously Published Works

Title

Amplitude modulation detection as a function of modulation frequency and stimulus duration: Comparisons between macaques and humans

Permalink

<https://escholarship.org/uc/item/0kv355v0>

Journal

Hearing Research, 277(1-2)

ISSN

0378-5955

Authors

O'Connor, Kevin N
Johnson, Jeffrey S
Niwa, Mamiko
et al.

Publication Date

2011-07-01

DOI

10.1016/j.heares.2011.03.014

Peer reviewed



Research paper

Amplitude modulation detection as a function of modulation frequency and stimulus duration: Comparisons between macaques and humans

Kevin N. O'Connor^{a,b,*}, Jeffrey S. Johnson^a, Mamiko Niwa^a, Nigel C. Noriega^{a,b}, Elizabeth A. Marshall^a, Mitchell L. Sutter^{a,b}

^a Center for Neuroscience, UC Davis, 1544 Newton Ct. Davis, CA 95616, USA

^b Department of Neurobiology, Physiology and Behavior, UC Davis, CA 95616, USA

ARTICLE INFO

Article history:

Received 14 January 2011

Received in revised form

16 March 2011

Accepted 22 March 2011

Available online 30 March 2011

ABSTRACT

Previous observations show that humans outperform non-human primates on some temporally-based auditory discrimination tasks, suggesting there are species differences in the proficiency of auditory temporal processing among primates. To further resolve these differences we compared the abilities of rhesus macaques and humans to detect sine-amplitude modulation (AM) of a broad-band noise carrier as a function of both AM frequency (2.5 Hz–2 kHz) and signal duration (50–800 ms), under similar testing conditions. Using a go/no-go AM detection task, we found that macaques were less sensitive than humans at the lower frequencies and shorter durations tested but were as, or slightly more, sensitive at higher frequencies and longer durations. Humans had broader AM tuning functions, with lower frequency regions of peak sensitivity (10–60 Hz) than macaques (30–120 Hz). These results support the notion that there are species differences in temporal processing among primates, and underscore the importance of stimulus duration when making cross-species comparisons for temporally-based tasks.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

In recent years, the rhesus macaque has become increasingly popular for research on the neurophysiology of hearing. This popularity rests, in part, on the expectation that this primate model will be useful for understanding human audition. To successfully extend sensory neurophysiological findings from non-humans to humans, however, it is important that we understand the performance of the system as a whole, and not just the parts it comprises. Psychophysical studies using rhesus and other macaque species have revealed some significant differences in spectral and temporal processing between these monkeys and humans.

Evidence for human and macaque differences in the temporal domain comes from several lines of research. Studies of temporal integration for pure tones in the rhesus macaque suggest that their rates of temporal integration (summation near threshold) are slightly slower than those for humans (Clack, 1966; O'Connor et al., 1999). Difference limens (Weber fractions) for detecting changes in tone duration are ~2–2.5 times higher in several macaque species compared to human subjects (Sinnott et al., 1987). Pure-tone frequency-difference limens decrease more rapidly for humans than

macaques as a function of increasing tone duration (Sinnott and Brown, 1993). Using vocalizations, Sinnott and colleagues have shown that sensitivity to temporal variations such as spectral peak position, and changes in the phonemic/ra-la/continuum, is higher in humans than macaques (Hopp et al., 1992; Sinnott and Brown, 1997). Although comparisons of species sensory capacities should be made with caution due to possible dissimilarities in psychophysical methods, Sinnott, O'Connor and colleagues tested both macaque and human subjects under the same conditions and were careful to control for response biases that might have affected accuracy.

Perhaps the most common way of assessing temporal processing is to measure sensitivity to sinusoidally varying amplitude modulation (AM) of broad-band noise. Because these signals do not vary in spectral information, detection of changes in the envelope of the noise carrier must rest only on time. These stimuli would, therefore, seem ideal for species comparisons of temporal processing, controlling for possible spectral processing differences. Somewhat surprisingly—given the findings above—the few studies comparing human and macaque detection of sine-AM noise have not reported significant species differences. An early study, however, shows graphical evidence for lower macaque sensitivity for low-frequency AM, in both gated and continuous noise carriers (Moody, 1994; Fig. 2). A later study found a similar result for gated carriers, though this difference was not statistically significant (O'Connor et al., 2000).

* Corresponding author. Center for Neuroscience, UC Davis, 1544 Newton Ct. Davis, CA 95616, USA.

E-mail address: knoconnor@gmail.com (K.N. O'Connor).

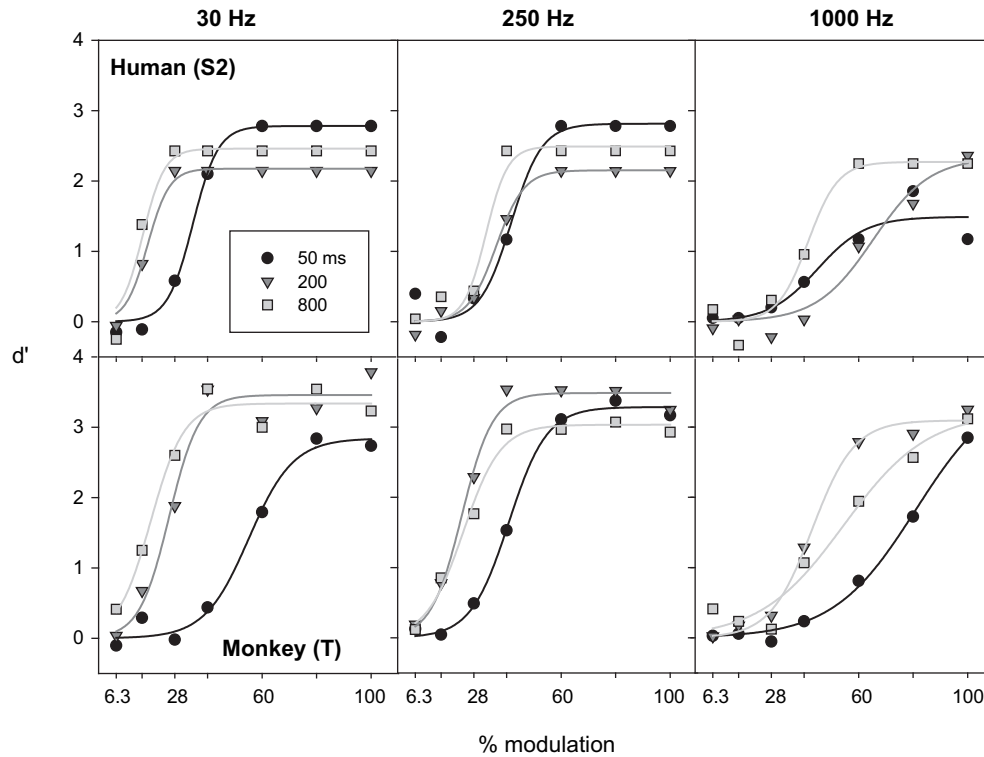


Fig. 1. Accuracy (d') plotted as a function of modulation depth at three modulation frequencies and three durations for two subjects, one human (*top panels*) and one monkey (*bottom panels*). Thresholds ($d' = 1$) were taken from best fitting logistic functions ($p < 0.005$), $y = a/[1 + \exp[-(x_m - x_0)/b]]$, where x_m is the level of modulation and a , x_0 and b are free parameters.

We thought these findings deserved further investigation, particularly given the importance of noise AM for electrophysiological studies of temporal coding in macaques (and other species) as well as for computational modeling work. Because human detection thresholds for AM in noise are strongly dependent on stimulus duration (Lee and Bacon, 1997; Sheft and Yost, 1990; Viemeister, 1979), we included duration as an independent variable. Given evidence for human and macaque differences in temporal processing, we thought it possible that species differences in AM detection would depend on AM duration as well as frequency.

In this study we examined sine-AM detection in macaques and humans as a function of both modulation frequency and stimulus duration, and found that the relationship between AM detection, AM frequency and duration was strongly species dependent.

2. Materials and methods

2.1. Subjects

The macaque subjects were three adult rhesus (*Macaca mulatta*), one male and two females (7–16 yrs of age) maintained under a restricted liquid protocol. Two monkeys (X and T) were screened for hearing impairment using auditory brainstem response (ABR) measurements; their ABR thresholds were within the range of previously reported results from rhesus macaques (Dai et al., 2010; Fowler et al., 2002; Torre et al., 2004). The male macaque (X) had previously undergone testing in experiments using complex spectral stimuli (O'Connor et al., 2000). The human subjects were three adult males (25–57 yrs), none reporting any history of hearing impairment. One human subject was a naïve paid participant (S3) and the others were authors on this paper. All procedures using

macaques conformed to the PHS policy on experimental animal care and were approved by the UC Davis animal care and use committee. The procedures using humans were approved by the UC Davis human subject committee; in accordance with their guidelines, none of the human subjects are identified in this report.

2.2. Behavioral task and experimental conditions

The general testing methods have been described in detail (O'Connor et al., 1999; O'Connor et al., 2000), but are briefly summarized here. We used a 'go/no-go' task for AM detection. Testing was done in two double-walled, foam-lined booths; one large (IAC: 9.5' × 10.5' × 6.5'), the other smaller (IAC: 4' × 3' × 6.5'). All of the human subjects were tested only in the large booth, and one of the monkeys (T) was tested only in the small booth. The other monkeys (W and X) were tested in both booths. Monkeys sat in an "acoustically transparent" primate chair, humans in an office chair. Subjects began each trial by pressing down a response lever, initiating the presentation of two noise bursts separated by a silent 400-ms interval. The second sound was either identical to the one preceding it (a "non-target"), or sine-amplitude modulated (a "target"). Subjects were trained or instructed to release the lever after hearing a modulated sound. Responses (lever releases) were recorded as "hits" or "false alarms" depending on whether they followed the target or non-target sound within 800 ms. Monkeys' hits and "correct rejections" (withheld responses to non-targets) were rewarded with water or diluted juice while their false alarms were followed by a time-out period. The sound of solenoid operation served as an accuracy cue for humans. Stimulus presentation, experimental control and data collection were accomplished using an Intel Quad-processor microcomputer controlling solid-state interface equipment and software (CED).

2.3. Acoustic stimuli

We examined modulation in gated rather than continuous noise, because we have used gated AM stimuli in parallel, past and ongoing electrophysiological macaque work (Yin et al., 2011). The amplitude modulated (AM) stimuli consisted of broad-band (white) Gaussian noise bursts, “frozen” on a trial, created from four different random seeds using Matlab software (MathWorks). Target stimuli were sine-modulated at 11 frequencies: 2.5, 5, 10, 15, 30, 60, 120, 250, 500, 1000 and 2000 Hz. Non-target stimuli were repetitions of the identical, preceding noise burst. The ratio of target to non-target trials was 7:2.

Five stimulus durations were used: 50 (at 30–2000 Hz), 100 (at 5–2000 Hz), 200, 400 and 800 ms. The lower AM frequencies were excluded from the 50- and 100-ms stimuli because we required that at least one half cycle of modulation be present for testing. Targets were presented at seven levels of modulation: 6.3, 16, 28, 40, 60, 80 and 100%. The various stimulus (AM frequency, duration and depth) and trial (target vs. non-target) conditions were presented in completely randomized order, within blocks, over sessions.

The acoustic signals were generated using a digital-to-analog converter (CED Power 1401) with 16-bit output resolution, passed through a programmable attenuator (TDT PA5) and then through a passive attenuator (Leader LAT-45). The signal was then amplified (Radio Shack MPA-200) and delivered through a speaker at 65 dB (Bruel & Kjaer, A-scale). In the large booth, the speaker was a Radio Shack PA-110 (10-in woofer and piezo horn tweeter, 38–27,000 Hz) positioned at ear level 1.5 m in front of the subject; in the small booth the speaker was a Radio Shack Optimus Pro-7AV (4-in woofer and 1 in dome tweeter, 120–20,000 Hz) positioned 0.8 m in front of the subject.

2.4. Data analysis

Humans were tested on 30 daily sessions of 300 trials each. Monkeys W and X were tested on 20 sessions with all conditions presented in randomized order as noted above (randomized design), as well as on 20 sessions in which only one stimulus duration/session was presented (blocked design), with duration and design-type counterbalanced over sessions. No significant difference was found between the thresholds obtained under the two presentation conditions, but only the data from the randomized design (as was used with humans) is included in this report. The absence of significant differences between the two methods of stimulus presentation argues against a role for stimulus uncertainty in our results. Monkey T was tested on a total of 100 sessions using the randomized design only. Monkeys worked each day until satiated, typically from ~300 to 1200 trials/session. Only data from sessions for which performance was asymptotic and stable was included for analysis.

We evaluated performance using signal detection theory (Green and Swets, 1974; O'Connor et al., 2000). We calculated d' , a measure of accuracy, using the proportions of hits and false alarms from each stimulus condition for each subject. d' provides a measure of accuracy that is that is unbiased (independent of response criterion) under the usual assumptions of signal detection theory.¹ This is important because our human subjects exhibited both higher

average hit (0.78 vs. 0.53) and false alarm (0.45 vs. 0.14) rates, suggesting that they were operating with lower response criteria than the monkeys on this task. d' scores were plotted against modulation level and a logistic equation was fit to each set of points (Luce, 1959; O'Connor et al., 2000). Thresholds for modulation detection, the proportion of modulation at $d' = 1$, were then estimated from these fitted functions given that the fits reached a criterion significance level ($p < 0.005$). For further analysis, modulation depth at threshold was converted to a sensitivity (peak-to-trough) AM measure using the equation $s = 20 \log m$, where m is the proportion of modulation at threshold and s is expressed in units of (relative) dB. Here we followed the convention of multiplying s by -1 when plotting data, so that a larger value means higher sensitivity. (The values of % modulation depth used in these experiments map onto $-s$ as follows: 6.3% = 24.0, 16% = 15.9, 28% = 11.1, 40% = 8.0, 60% = 4.4, 80% = 1.9 and 100% = 0.) Values of s , when plotted as a function of modulation frequency (f_m), yield a traditional measure of temporal processing ability, the temporal modulation transfer function (tMTF) (Viemeister, 1979). We performed curve fits, and assessed the statistical significance of experimental effects with analysis of variance (ANOVA) tests, using Matlab functions (“lsqcurvefit” and “anovan”).

3. Results

Threshold sensitivity (s) was found to be, on average, slightly higher in the small booth for both monkeys tested there, but because these differences were quite small (mean \pm SD over stimulus conditions: W = 0.48 ± 1.27 ; X = 0.77 ± 1.03), the data from the small and large booth were pooled for threshold determination and further analysis.

Fig. 1 shows several psychometric function examples from one human (top panels) and one monkey subject. Each panel displays d' as a function of modulation depth for one AM frequency (30, 250 or 1000 Hz), at three durations (50, 200 and 800 ms). Though showing only a subset of all the threshold data collected, this figure illustrates the dependence of accuracy on both f_m and stimulus duration that was found in all subjects.

Fig. 2 illustrates the main results of the experiment. The top and middle panels show tMTFs at each duration for humans and monkeys, respectively (each point is the mean across subjects). The bottom panel displays difference functions; the monkey tMTF has been subtracted from the human tMTF at each duration. It seems clear from this figure that the relationship between AM sensitivity, stimulus duration and f_m is strongly species dependent. Overall, the region of highest sensitivity is lower for humans (10–60 Hz) than macaques (30–120 Hz). The difference functions show that macaques are less sensitive than humans at the lower frequencies and shorter durations tested but are as, or slightly more, sensitive at higher frequencies and longer durations. tMTFs derived from gated noise typically have a bandpass characteristic (Sheft and Yost, 1990; Viemeister, 1979), and the tMTFs of both species exhibit this form, though it is more pronounced for macaques due to their higher thresholds at low f_m .

Because our experimental design was not ‘balanced’ (the 50- and 100-ms duration stimuli did not include all f_m), we performed two three-factor (mixed design) ANOVAs on the sensitivity data. One test was performed across all durations at 30–1000 Hz² (omitting 2.5–15 Hz), and the other across f_m (2.5–1000 Hz) at 200–800 ms (omitting 50 and 100 ms). Sensitivity values at 2000 Hz were excluded from these analyses because of the relatively large

¹ These well-known assumptions are that the underlying sensory or evidence distributions are normal and have equal variance. Technically, in order for d' to be unbiased, the shape of the receiver operating characteristic relating the proportions of hits and false alarms must be symmetrical about the negative diagonal, though this was not examined in our study.

² The test at 30–1000 Hz was performed with two missing scores (no thresholds) from monkey X (50-ms stimulus, at 500 and 1000 Hz).

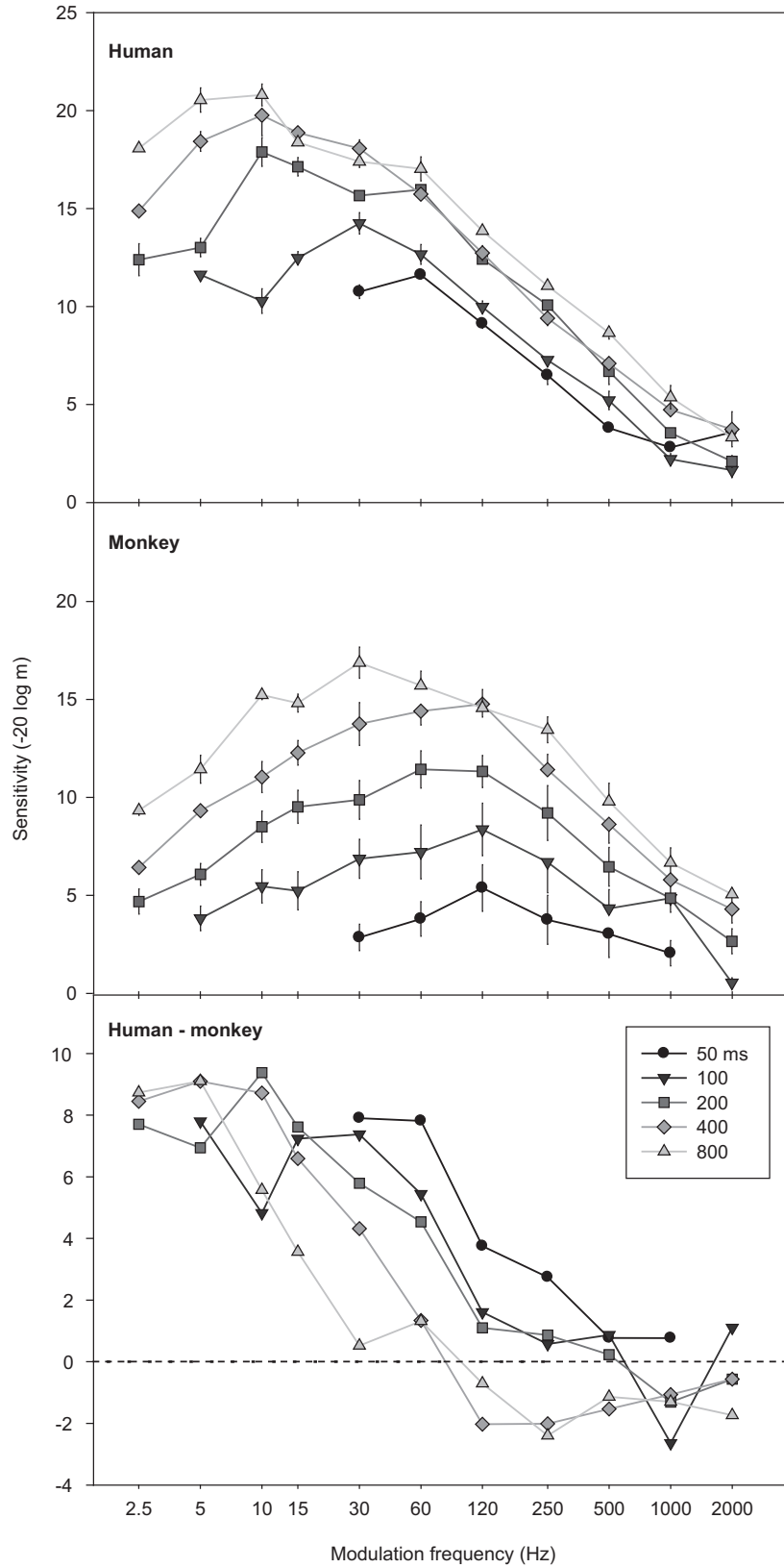


Fig. 2. Sensitivity at threshold plotted as a function of duration and modulation frequency, giving the temporal modulation transfer functions (tMTFs) for humans (*top*) and monkeys (*middle*). Each point is the mean for three subjects. Vertical bars = 1 standard error of the mean (in some cases the top or bottom portion of the bar was removed to improve clarity). Sensitivity is expressed as $-20 \log m$, where m is the proportion of modulation at threshold. The maximum mean sensitivity for humans (800 ms at 10 Hz) is 20.8 corresponding to 9.12% modulation depth; for monkeys the maximum (800 ms at 30 Hz) is 16.9 corresponding to 15.4% depth. The differences between the species tMTFs at each duration are shown in the *bottom* panel.

Table 1

The results of two three-factor, mixed design (one group factor and two repeated measures factors) ANOVAs are shown for AM sensitivity values at threshold (see Results for additional explanation and discussion). Asterisks indicate $p < 0.05$.

Source	'Across duration' (50–800 ms)			'Across f_m ' (2.5–1000 Hz)		
	df	F	p	df	F	p
species	1	0.47	0.53	1	5.33	0.0821
duration	4	51.16	<0.0001*	2	16.60	0.0014*
f_m	5	128.14	<0.0001*	9	55.81	<0.0001*
species \times duration	4	5.88	0.0041*	2	1.10	0.3771
species \times f_m	5	16.75	<0.0001*	9	21.16	<0.0001*
duration \times f_m	20	3.89	<0.0001*	18	3.99	<0.0001*
species \times duration \times f_m	20	1.75	0.0906	18	2.87	0.0014*

proportion of missing thresholds from both species at this frequency. Table 1 summarizes the results of these tests. Both tests revealed main effects of duration and f_m on AM sensitivity, and both also showed interactions between these variables implying that their effects were interdependent. Both tests also revealed an interaction between species and f_m , though only the test across duration showed an interaction between species and duration: perhaps not surprising given that some of the largest species differences were found for the shorter duration stimuli and these observations were absent in the 'across f_m ' test. The test across f_m was the only one to show a three-way interaction, however, indicating that—across this large frequency range—the effects of both f_m and stimulus duration on AM sensitivity depended on species. The overall sensitivity difference between species was not large; species differences depended strongly on both duration and f_m , underscored by the fact that a significant species main effect for sensitivity was not found.

The mean tMTFs plotted in Fig. 2 suggest that tuning for AM detection is symmetrical and bell-shaped (on a log scale); this is most obvious for monkeys where sensitivity falls markedly at lower f_m . To examine this relationship more closely and quantify the sensitivity tuning functions for individuals of both species, we plotted each subject's tMTF at each duration and fit log-normal curves to the points, which provided reasonably good fits (all were significant at $p < 0.05$). Examples of these functions and fits are presented in Fig. 3 for one human (left) and one monkey. Peak sensitivity (amplitude) values, AM tuning widths (σ in octaves), and the AM frequencies corresponding to these peaks (mean f_m) were then estimated from the fitted functions.

The parameters from these fits are plotted for all subjects in Fig. 4 as a function of (log) duration, and best-fitting functions fit to the group (species) means. In both groups, peak sensitivity (top panel) increases as a function of stimulus duration ($F_{(4)} = 59.87$; $p < 0.001$). Though, on average, peak sensitivity is higher in humans than macaques, this difference is not significant ($F_{(1)} = 6.23$; $p = 0.067$), likely due to the performance of one monkey (T) that was on a par with humans. The sigmoid functions fit to the group-mean values are nearly parallel, indicating that peak sensitivity increases at roughly the same rate for humans and monkeys, an observation supported by the absence of an interaction between species and duration.

AM tuning widths (middle panel) also increase with duration ($F_{(4)} = 38.17$; $p < 0.001$), at the rate of about half an octave for each doubling in duration, and tend to be larger in humans ($F_{(1)} = 9.49$; $p < 0.05$). Again, there was no interaction between species and duration implying that the rate of increase in tuning width is about equal for both species.

Best (peak) f_m values (bottom panel) decline as a function of duration ($F_{(4)} = 44.06$; $p < 0.001$) and are lower in humans than macaques ($F_{(1)} = 24.13$; $p < 0.01$), supporting observations from the group data (Fig. 2). The log-log plot suggests that this decline is greater in humans than monkeys, which is confirmed by the presence of an interaction between species and duration ($F_{(4)} = 3.60$; $p < 0.05$). This decline appears to be roughly twice as large in humans as macaques: a decrease of ~ 2 octaves (~ 40 to 10 Hz) relative to ~ 1 octave (~ 100 to 50 Hz), from 50 to 800 ms.

4. Discussion

This study examined sensitivity to AM in rhesus macaques and humans and found that it was strongly dependent on modulation frequency (f_m), stimulus duration and species, with humans showing higher sensitivity at lower f_m . Overall, humans showed broader AM tuning than macaques, likely due to their higher sensitivity at low f_m . Best f_m sensitivity was dependent on stimulus duration, with larger species differences appearing at longer durations.

Our results are congruent with previous findings using relatively long duration stimuli. Humans show maximum sensitivity values of ~ 20 – 25 for AM in gated noise carriers of up to 1.5 s (Viemeister, 1979). A previous study showed macaques to have slightly lower maximum sensitivities for similar stimuli, ~ 15 – 20

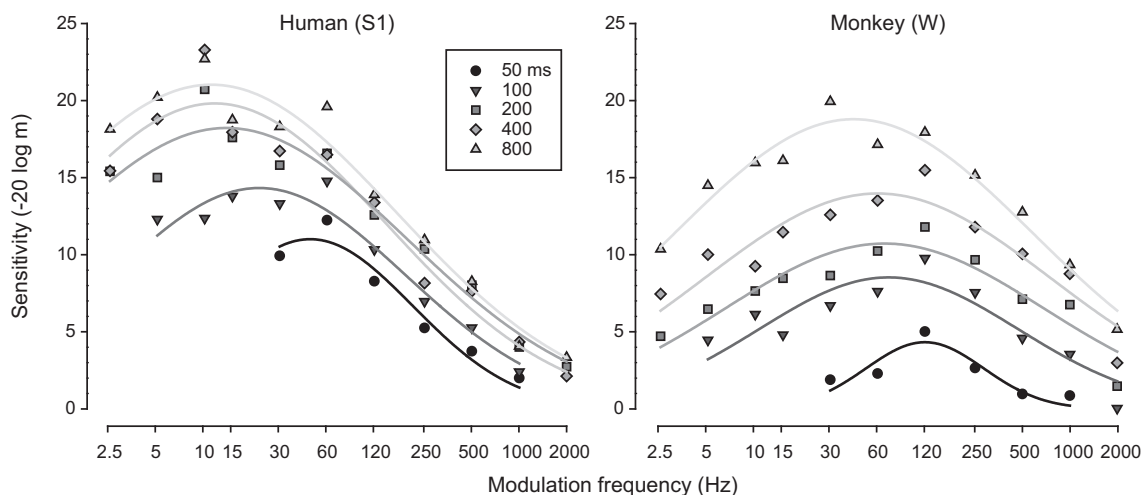


Fig. 3. Temporal modulation transfer functions (tMTFs) for one human (left) and one monkey (right). Parameters from best fitting log-normal functions (lines; $p < 0.05$), $a \cdot \exp\{-0.5 [\ln(f_m/\mu)]^2/\sigma^2\}$, were used to estimate peak sensitivity (a), AM tuning width (σ) and best AM frequency (μ) for each subject, at each duration.

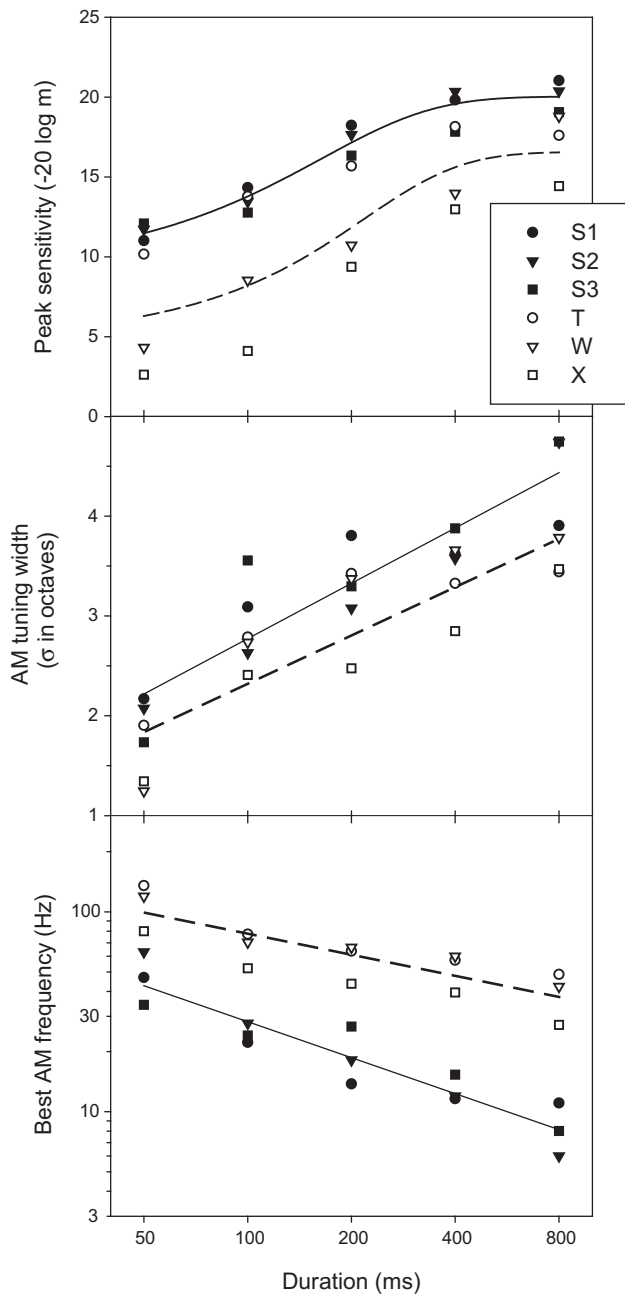


Fig. 4. Peak sensitivity (*top*), AM tuning widths (*middle*) and best AM frequency (*bottom*) as a function of stimulus duration. Each symbol represents a parameter estimated from log-normal fits of the type shown in Fig. 3, for each subject; humans (S1–S3) by closed symbols. Sigmoid functions (*top*: logistic functions as in Fig. 1), or (log-transformed) linear regressions (*middle* and *bottom*) are fit to the group means ($p < 0.01$ for all fits).

(Moody, 1994). Our plot of peak AM sensitivity as a function of duration (Fig. 4, top), shows that human and macaque peak values tend to asymptote within these ranges. The peak sensitivity decline and upward shift in best f_m found here, with decreasing stimulus duration, are also similar to those of previous studies on AM detection and duration in humans (Sheft and Yost, 1990; Viemeister, 1979). For example, the tMTFs for 250- and 500-ms gated noise in Viemeister's study display peaks (16 and 8 Hz) quite close to those in our human 200- and 400-ms tMTFs (~ 20 and 10 Hz; Fig. 4 bottom).

An obvious issue is whether the species differences we found in AM noise sensitivity and tuning are unique to macaques or just one

instance of a general temporal processing disparity between humans and other species. This is a difficult question to address because of methodological differences between studies. AM sensitivity depends on stimulus duration, as this and previous investigations with humans show (Lee and Bacon, 1997; Sheft and Yost, 1990; Viemeister, 1979), and there is little constancy in AM signal duration across studies (for example, several animal studies have used a shock avoidance technique which presents AM at relatively long (>1 s) and sometimes variable durations). Nonetheless, some comparisons are possible. Starlings show mean best sensitivity values at ~ 20 – 60 Hz for 800-ms noise carriers, close to the values found for our macaques and those in Moody's study (Klump and Okanoya, 1991). Barn owls exhibit best sensitivity values between macaques and humans, at 10–20 Hz, for noise carriers of the same duration (Dent et al., 2002). These studies using birds suggest that AM tuning in macaques is within the range of variation found in other species.

Whether or not there exists a definitive difference in AM tuning between humans and other species, one result does stand out from cross-species comparisons: Threshold differences for AM detection appear most obvious at lower f_m , with humans exhibiting noticeably higher sensitivities below ~ 100 Hz (Dooling et al., 2000; Dooling and Searcy, 1985; Kelly et al., 2006; Klump and Okanoya, 1991; Moody, 1994; Salvi et al., 1982). Again, because of possible methodological differences this conclusion must be made with caution, but it is a prevalent result and one that is supported by our study. tMTFs are usually obtained in order to assess temporal acuity (high f_m sensitivity), and the results of these studies generally show most species to have slightly higher acuity than humans. The tMTF may be as effective or better, however, at revealing species differences at low f_m . While species differences in temporal acuity may be ascribed to variation in peripheral and central physiological limitations in resolving rapid acoustic changes, a possible explanation for the relatively large species differences at low frequencies seems less obvious. The poorer sensitivity of non-human species at low f_m has been attributed to the limiting, higher intensity-difference limens generally found in animals, for example: birds (Dooling and Saunders, 1975; Hienz et al., 1980), fish (Chapman and Johnstone, 1974; Fay, 1985; Jacobs and Tavolga, 1967) and mammals, including monkeys (Ehret, 1975; Hack, 1971; Rosenzweig, 1946; Sinnott et al., 1985; Terman, 1970). These differences are typically quite small (~ 1 – 2 dB) at moderate intensities, however, as seen in the one study using rhesus macaques (Clopton, 1972) showing thresholds <1 dB higher than humans at >20 dB sensation level (Fay, 1988). It is not clear, therefore, that greater intensity-difference limens in non-humans can account for the species disparity.

A better explanation for this disparity may be species differences in rates of temporal integration for AM detection. As this and several previous studies show, the particular tMTF derived from AM detection depends on the duration of the AM signal. The form of the tMTF also depends on the nature of signal presentation, that is, whether it is gated or embedded in a continuous background (Klump and Okanoya, 1991; Sheft and Yost, 1990; Viemeister, 1979). Whereas gated signals typically result in bandpass tMTFs, detection of AM in continuous noise produces tMTFs that are more low-pass in form. The dependence of the tMTF on duration and type of presentation has led to the hypothesis that these variables affect temporal integration rates for AM detection and to the development of several types of model to explain these effects. One of these, the "multiple looks" model, posits that the improvement in performance found with longer durations is due to the increase in number of possible detections of a peak-to-trough difference a listener can make as the signal lengthens (Lee and Bacon, 1997; Sheft and Yost, 1990; Viemeister, 1979). Another model is based

on a “leaky integrator” or low-pass filter, and so directly incorporates a rate constant in its dynamics (Forrest and Green, 1987; Sheft and Yost, 1990; Viemeister, 1979). The third type of model is based on a “modulation filterbank” (Kay and Matthews, 1972), a bank of bandpass filters that can be adjusted to simulate the AM sensitivity of human observers (Dau et al., 1997a, 1997b). It may be possible to identify species differences in temporal integration for AM with one or more parameters in these models, and the addition of across-species comparisons may provide valuable constraints on model operation.

Though these models may be computationally sufficient in describing duration-related effects in AM detection, a causal explanation for species-based AM sensitivity and tuning differences must come from neurophysiology. The neural basis for behavioral AM sensitivity is most likely to come from studies in which neuronal responses to the depth of modulated, as well as unmodulated, noise are examined—ideally from behaving animals—in conjunction with computational modeling.

In summary, we found differences in the sensitivities of rhesus macaques and humans for detection of AM noise that depended on both modulation frequency and signal duration. The poorer sensitivity of macaques to low-frequency AM is qualitatively similar to results that have been found for relatively long duration stimuli in a variety of other species, though there may be some quantitative differences. The greater sensitivity found in humans is intriguing. It is tempting to think that it might be due to the particular demands of amplitude envelope processing in speech. Amplitude modulation spectra taken from samples of human speech peak at ~5 Hz (likely related to syllable duration in human languages)—and experiments show that modulation in the region of ~3–10 Hz is critical for speech intelligibility (Greenberg and Arai, 2004; Steeneken and Houtgast, 1980)—which may account for higher human sensitivity. A close examination and comparison of the envelope information-carrying capacity of the vocalizations of other species, with particular regard to the duration of ‘meaningful’ acoustic units, will be needed to test this hypothesis.

Acknowledgments

We thank Zachary Cline-Egri for assistance in testing macaque subjects, and James Engle and Xochi Navarro for performing the ABR tests. This work was supported by the NIH: NIDCD Grant DCO2514 and T32 DC008072.

References

- Chapman, C.J., Johnstone, A.D., 1974. Some auditory discrimination experiments on marine fish. *J. Exp. Biol.* 61, 521–528.
- Clack, T.D., 1966. Effect of signal duration on the auditory sensitivity of humans and monkeys (*Macaca mulatta*). *J. Acoust. Soc. Am.* 40, 1140–1146.
- Clopton, B.M., 1972. Detection of increments in noise intensity by monkeys. *J. Exp. Anal. Behav.* 17, 473–481.
- Dai, C., Fridman, G.Y., Della Santina, C.C., 2010. Effects of vestibular prosthesis electrode implantation and stimulation on hearing in rhesus monkeys. *Hear. Res.*
- Dau, T., Kollmeier, B., Kohlrausch, A., 1997a. Modeling auditory processing of amplitude modulation. I. Detection and masking with narrow-band carriers. *J. Acoust. Soc. Am.* 102, 2892–2905.
- Dau, T., Kollmeier, B., Kohlrausch, A., 1997b. Modeling auditory processing of amplitude modulation. II. Spectral and temporal integration. *J. Acoust. Soc. Am.* 102, 2906–2919.
- Dent, M.L., Klump, G.M., Schwenzfeier, C., 2002. Temporal modulation transfer functions in the barn owl (*Tyto alba*). *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* 187, 937–943.
- Dooling, R.J., Saunders, J.C., 1975. Auditory intensity discrimination in the parakeet (*Melospittacus undulatus*). *J. Acoust. Soc. Am.* 58, 1308–1310.
- Dooling, R.J., Searcy, M.H., 1985. Temporal integration of acoustic signals by the budgerigar (*Melospittacus undulatus*). *J. Acoust. Soc. Am.* 77, 1917–1920.
- Dooling, R.J., Lohr, B., Dent, M.L., 2000. Hearing in birds and reptiles. In: *Comparative Hearing: Birds and Reptiles*. Springer-Verlag, New York, pp. 308–359.
- Ehret, G., 1975. Frequency and intensity difference limens and nonlinearities in the ear of the housemouse (*Mus musculus*). *J. Comp. Physiol.* 102, 321–336.
- Fay, R.R., 1985. Sound intensity processing by the goldfish. *J. Acoust. Soc. Am.* 78, 1296–1309.
- Fay, R.R., 1988. *Hearing in Vertebrates: a Psychophysics Databook*. Hill-Fay Associates, Winnetka, IL.
- Forrest, T.G., Green, D.M., 1987. Detection of partially filled gaps in noise and the temporal modulation transfer function. *J. Acoust. Soc. Am.* 82, 1933–1943.
- Fowler, C.G., Torre 3rd, P., Kemnitz, J.W., 2002. Effects of caloric restriction and aging on the auditory function of rhesus monkeys (*Macaca mulatta*): the University of Wisconsin study. *Hear. Res.* 169, 24–35.
- Green, D., Swets, J., 1974. *Signal Detection Theory and Psychophysics*. Wiley, New York.
- Greenberg, S., Arai, T., 2004. What are the essential cues for understanding spoken language? *IECE Trans. Inf. Sys* E87-D, 1059–1070.
- Hack, M.H., 1971. Auditory intensity discrimination in the rat. *J. Comp. Physiol. Psychol.* 74, 315–318.
- Hienz, R.D., Sinnott, J.M., Sachs, M.B., 1980. Auditory intensity discrimination in blackbirds and pigeons. *J. Comp. Physiol. Psychol.* 94, 993–1002.
- Hopp, S.L., Sinnott, J.M., Owren, M.J., Petersen, M.R., 1992. Differential sensitivity of Japanese macaques (*Macaca fuscata*) and humans (*Homo sapiens*) to peak position along a synthetic coo call continuum. *J. Comp. Psychol.* 106, 128–136.
- Jacobs, D.W., Tavolga, W.N., 1967. Acoustic intensity limens in the goldfish. *Anim. Behav.* 15, 324–335.
- Kay, R.H., Matthews, D.R., 1972. On the existence in human auditory pathways of channels selectively tuned to the modulation present in frequency-modulated tones. *J. Physiol.* 225, 657–677.
- Kelly, J.B., Cooke, J.E., Gilbride, P.C., Mitchell, C., Zhang, H., 2006. Behavioral limits of auditory temporal resolution in the rat: amplitude modulation and duration discrimination. *J. Comp. Psychol.* 120, 98–105.
- Klump, G.M., Okanoya, K., 1991. Temporal modulation transfer functions in the European starling (*Sturnus vulgaris*): I. Psychophysical modulation detection thresholds. *Hear Res.* 52, 1–11.
- Lee, J., Bacon, S.P., 1997. Amplitude modulation depth discrimination of a sinusoidal carrier: effect of stimulus duration. *J. Acoust. Soc. Am.* 101, 3688–3693.
- Luce, D., 1959. *Individual Choice Behavior: a Theoretical Analysis*. Wiley, New York.
- Moody, D.B., 1994. Detection and discrimination of amplitude-modulated signals by macaque monkeys. *J. Acoust. Soc. Am.* 95, 3499–3510.
- O'Connor, K.N., Barruel, P., Hajalilou, R., Sutter, M.L., 1999. Auditory temporal integration in the rhesus macaque (*Macaca mulatta*). *J. Acoust. Soc. Am.* 106, 954–965.
- O'Connor, K.N., Barruel, P., Sutter, M.L., 2000. Global processing of spectrally complex sounds in macaques (*Macaca mulatta*) and humans. *J. Comp. Physiol. A* 186, 903–912.
- Rosenzweig, M., 1946. Discrimination of auditory intensities in the cat. *Am. J. Psychol.* 59, 127–136.
- Salvi, R.J., Giraudi, D.M., Henderson, D., Hamernik, R.P., 1982. Detection of sinusoidally amplitude modulated noise by the chinchilla. *J. Acoust. Soc. Am.* 71, 424–429.
- Sheft, S., Yost, W.A., 1990. Temporal integration in amplitude modulation detection. *J. Acoust. Soc. Am.* 88, 796–805.
- Sinnott, J.M., Brown, C.H., 1993. Effects of varying signal duration on pure-tone frequency discrimination in humans and monkeys. *J. Acoust. Soc. Am.* 93, 1541–1546.
- Sinnott, J.M., Brown, C.H., 1997. Perception of the American English liquid /ra-la/ contrast by humans and monkeys. *J. Acoust. Soc. Am.* 102, 588–602.
- Sinnott, J.M., Petersen, M.R., Hopp, S.L., 1985. Frequency and intensity discrimination in humans and monkeys. *J. Acoust. Soc. Am.* 78, 1977–1985.
- Sinnott, J.M., Owren, M.J., Petersen, M.R., 1987. Auditory duration discrimination in Old World monkeys (*Macaca, Cercopithecus*) and humans. *J. Acoust. Soc. Am.* 82, 465–470.
- Steeneken, H.J., Houtgast, T., 1980. A physical method for measuring speech-transmission quality. *J. Acoust. Soc. Am.* 67, 318–326.
- Terman, M., 1970. Discrimination of auditory intensities by rats. *J. Exp. Anal. Behav.* 13, 145–160.
- Torre 3rd, P., Mattison, J.A., Fowler, C.G., Lane, M.A., Roth, G.S., Ingram, D.K., 2004. Assessment of auditory function in rhesus monkeys (*Macaca mulatta*): effects of age and caloric restriction. *Neurobiol. Aging* 25, 945–954.
- Viemeister, N.F., 1979. Temporal modulation transfer functions based upon modulation thresholds. *J. Acoust. Soc. Am.* 66, 1364–1380.
- Yin, P., Johnson, J.S., O'Connor, K.N., Sutter, M.L., 2011. Coding of amplitude modulation in primary auditory cortex. *J. Neurophysiol.* 105, 582–600.