4th Quarterly Progress Report
July 1 to September 30, 2001

Fundamental Neurosciences Contract N01-DC-0-2108

Protective Effects of Patterned Electrical Stimulation on the Deafened Auditory System

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ABSTRACT

This Quarterly Progress Report presents a summary of some of the findings from psychophysical studies conducted in neonatally deafened cats to examine auditory detection and discrimination thresholds for complex signals. A detailed report and full discussion of these and other findings is currently *in press* in the Journal of Neurophysiology. To explore the basic mechanisms underlying the success of contemporary speech processing strategies for cochlear implant recipients, this work examined how specific complex electrical stimuli delivered by intracochlear electrodes are processed in the central auditory system. Sinusoidal amplitude modulated (SAM) and unmodulated pulse trains were used to investigate behavioral and central neuronal thresholds in the same deaf cats. Some animals were trained in a *discrimination* task to respond to changes in the modulation frequency of successive SAM signals. The study had four primary objectives: 1) to estimate *psychophysical* thresholds for SAM and unmodulated pulse trains in the same trained animals; 2) to determine *neural* thresholds for SAM and unmodulated pulse trains; 3) to compare psychophysical and neural thresholds in the same animal; and 4) to evaluate the ability of animals to discriminate changes in the modulation frequency of SAM signals delivered by a cochlear implant.

INTRODUCTION

Using unmodulated pulse trains, a number of behavioral studies have described the influence of simple electrical stimulus parameters (e.g. phase duration, stimulus frequency, stimulus duration) on detection thresholds (e.g. Beitel et al. 2000a, Pfingst and Morris 1993, Shannon 1985, Smith and Finley 1997). However, speech information for CI listeners in contemporary speech processing strategies is conveyed by high frequency, amplitude modulated stimuli (Brill et al. 1997, McDermott et al. 1992, Wilson et al. 1991). To study the effects of these temporally more complex electrical signals on detection threshold, we have developed a behavioral model for deaf cats implanted with a cochlear prosthesis that allows collection of both psychophysical and electrophysiological data from the same animal (Beitel et al. 2000a, b, Vollmer et al., in press). One important question concerning the processing of SAM pulse trains is whether detection threshold for these signals is based exclusively on detection of the peak amplitude of the modulated pulse train or whether threshold is significantly influenced by temporal integration of the modulated carrier pulses. In preliminary studies, Beitel and colleagues (2000b) have hypothesized that the detection of unmodulated and SAM pulse trains is based on the amplitude of unmodulated current pulses or the maximum amplitude of the pulses in the modulated carrier, respectively. However, in these studies only two different SAM signals with identical modulation frequency were used, and detection thresholds were compared between *different* groups of animals. The research presented here extends the combinations of SAM carrier and modulation frequencies examined and estimates behavioral thresholds for unmodulated and SAM pulse trains in the *same* animals, thus, eliminating the influence of inter-individual variability on threshold detection.

Further, we investigated the relationship between psychophysical detection of intracochlear electrical stimulation and the underlying activity of neural elements. Pfingst (1988) has compared psychophysical thresholds in macaque monkeys and humans with auditory nerve thresholds in cats or squirrel monkeys. These *indirect* comparisons among different species and different laboratories showed that neural thresholds were consistently higher than psychophysical thresholds. However, we have previously reported (Beitel et al., 2000a, b) that the lowest neural thresholds recorded in the IC or the A1 were essentially the same as the psychophysical detection thresholds measured in the same deaf cats. The present study confirms these findings and extends them by determining *electrophysiological* thresholds for unmodulated and SAM pulse trains in the *same* isolated single neurons in the IC.

Finally, using a successive discrimination paradigm we estimated the ability of deafened cats to discriminate an increase in the modulation frequency of electrical pulse trains with different carrier frequencies (Vollmer et al., in press). An important goal in this study was to investigate whether the discrimination of SAM signals was based only on differences in the modulation frequency or whether the rate of *suprathreshold* SAM carrier pulses had an additional influence on discriminative performance. To our knowledge, the current study is the first behavioral investigation of temporal resolution in a deaf animal model.

METHODS

Cats were deafened neonatally (n=11; Table 1) by systemic administration of ototoxic drugs and implanted chronically with feline intracochlear electrodes, which consisted of four electrode contacts driven as 2 bipolar pairs. After recovery from implant surgery, cats were behaviorally trained in a conditioned avoidance paradigm to lick a metal spoon on "safe" trials to obtain a preferred food reward (meat puree) and to

HISTORIES OF EXPERIMENTAL ANIMALS

#cat	Age @ Implantation (wk)	Age@ Initial Behavioral Stim. (wk)	Behavioral Training Period (wk)	Behavioral Task(s)
K98	7	10	19	Detect., Discrim. (SAM)
K99	7.4	19	25	Detect., Discrim. (SAM)
K146	7.5	12.5	20	Detect., Discrim. (SAM)
K148	6.3	10	19	Detect., Discrim. (SAM)
K107	7	8.3	22	Detect. (Unmod., SAM)
K108	6.4	20.4	11	Detect. (Unmod., SAM)
K109	6.5	21	12	Detect. (Unmod., SAM)
K117	6	13.3	16	Detect. (Unmod., SAM)
K119	7	12.7	28	Detect. (Unmod., SAM)
CH618	4.3 yr	4.3 yr	34	Detect. (Unmod., SAM)
K55	6.5 yr	6.7 yr	17	Detect. (SAM)

Table 1: Behavioral training histories for all neonatally deafened animals included in this study. Training was initiated at an average of 14 wk in the kittens and at age >4 yr in the long-term deafened cats, CH618 and K55. Detect.=Threshold detection. Discrim.=Successive Discrimination.

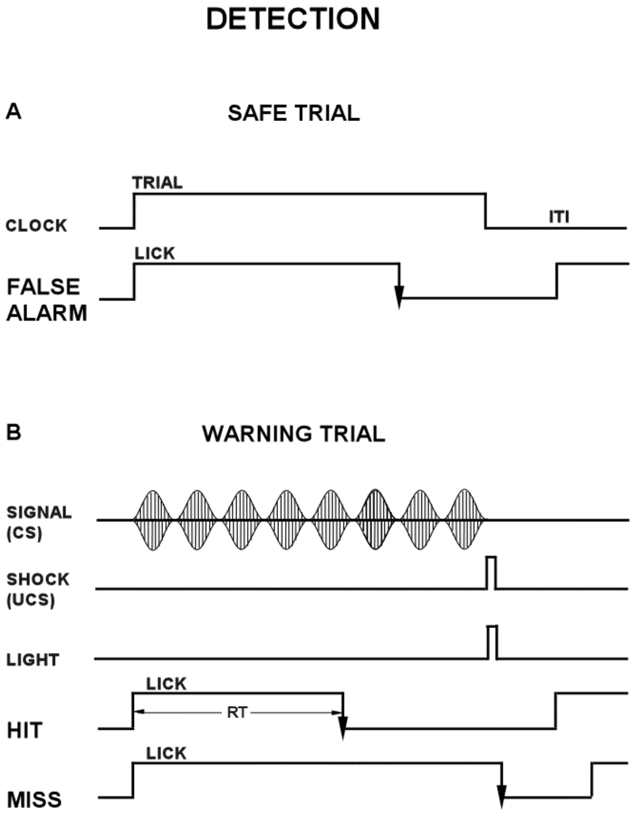

Fig. 1. A, B: Conditioned avoidance paradigm (CAR) for detection of SAM signals. Line traces illustrate events that would result in a FALSE ALARM during a safe trial (A), and either a HIT (correct detection) or a MISS (no detection) on a warning trial (B). Trials and intertrial intervals (ITI) are 1-s duration. LICK: Cat is consuming reward. RT: Reaction Time. CS: Conditioned stimulus. UCS: Unconditioned stimulus.

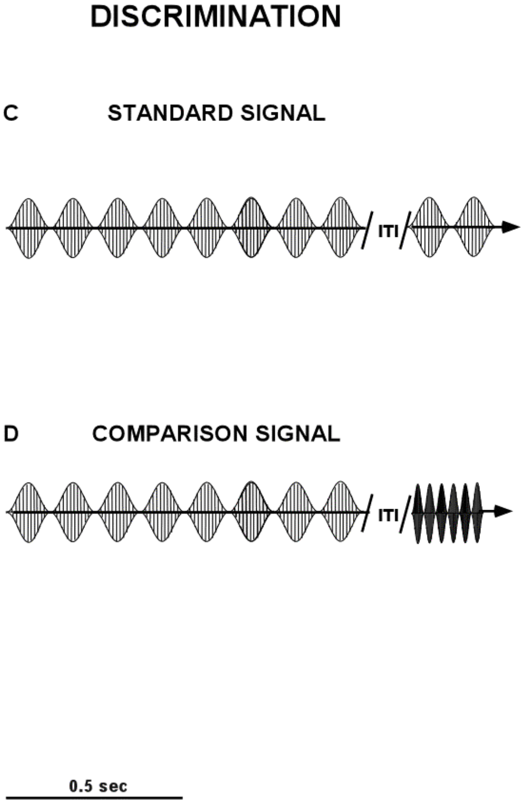

Fig. 1. C, D: CAR paradigm for successive discrimination. Successive SAM waveforms (1-second duration) for Standard (C) and Comparison (D) trials. Unconditioned stimulus.

interrupt licking on "warning" trials to avoid a mild electrocutaneous shock (Fig. 1A, B). Detection thresholds were estimated using either unmodulated trains of biphasic current pulses (0.2 ms/ph; 30 or 100 pps) or SAM pulse trains (carrier: 100, 300, or 500 pps; modulation frequency: 8 or 30 Hz; modulation depth= 100%; 0.2 ms/ph; Fig. 2).

Some animals (n=4) were trained subsequently in a *discrimination* task to respond to changes in the modulation frequency of successive SAM signals (Fig. 1C, D). During standard trials (70%), a SAM signal was delivered at a constant modulation frequency of 8 Hz and a constant carrier rate of 100, 300, 500, 1000 or 1500 pps. On comparison trials (30%), only the modulation frequency was changed (range of SAM=10-48 Hz, with a 2-8 Hz increment between adjacent envelope frequencies). In acute electrophysiological experiments, response thresholds to unmodulated and SAM trains of biphasic current pulses (0.2 ms/ph) were estimated from neurons in the inferior colliculus (IC) and primary auditory cortex (A1). From all recording locations in the IC and A1 of a given cat, the *minimum* neuronal threshold was determined.

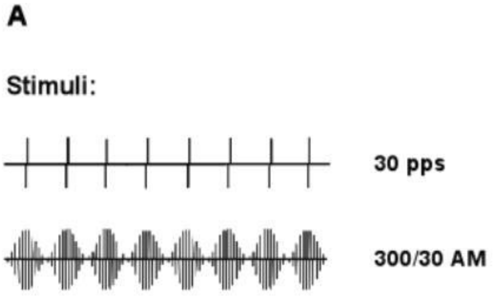

Fig. 2. A: Examples of unmodulated (30 pps) and SAM (carrier/modulation=300pps/30Hz AM) signals used in this study.

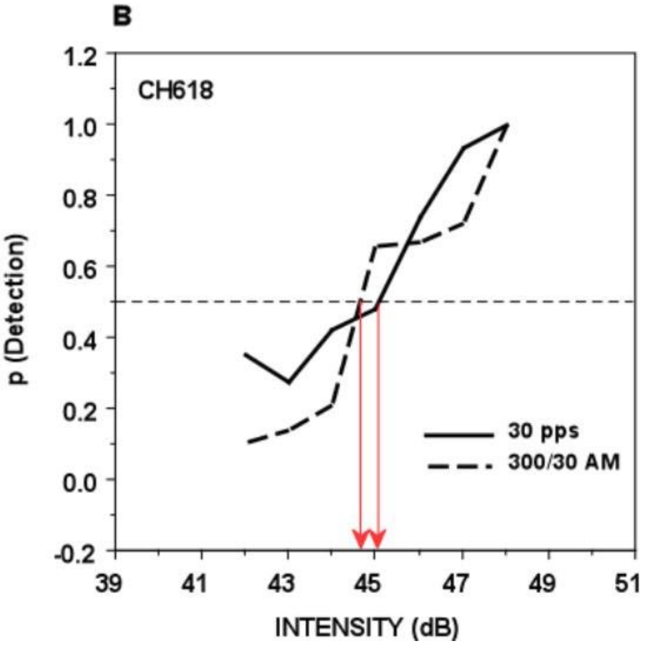

Fig. 2. B: Psychometric functions showing probability of detection as a function of the intensity for unmodulated (30 pps) and SAM (300/30 AM) warning signals in cat CH618. Dashed line: 50% detection. Detection thresholds determined by linear interpolation for the two signals are indicated by arrows.

RESULTS

1. BEHAVIORAL THRESHOLDS FOR SAM AND UNMODULATED PULSE TRAINS

Figure 3A shows a plot of psychophysical thresholds for SAM signals (100/30 AM or 300/30 AM) as a function of psychophysical thresholds for unmodulated, low frequency pulse trains (30 pps or 100 pps) estimated in six animals. The thresholds for SAM and unmodulated pulse trains ranged from 29.5 to 46.1 dB, and 28.5 to 45.1 dB, respectively. The corresponding mean SAM and unmodulated thresholds were 37.2±2.9 (SE) dB and 36.9±2.9 (SE) dB, and the thresholds were strongly correlated (r=0.99).

Figure 3B illustrates the differences between detection thresholds for unmodulated and SAM signals for the single animals. The mean threshold difference between the two signals was 0.3±0.4 (SE) dB, a difference that was not significant (paired t-test; p>0.5). These results suggest that, compared to unmodulated pulse trains (e.g. 30 pps), the high pulse rate carriers of the SAM signals (e.g. 300/30 AM) do not convey additional information for the detection of the warning signal.

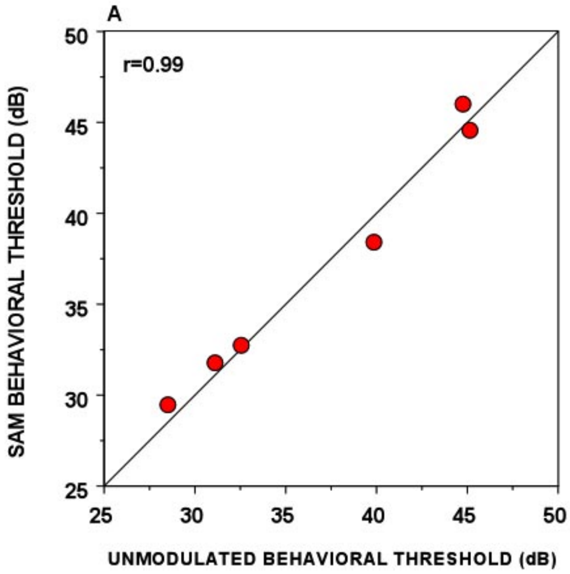

Fig. 3. A: Detection thresholds for SAM pulse trains (100/30 AM or 300/30 AM) versus unmodulated pulse trains (30 pps or 100 pps) estimated for 6 cats. Line is x=y.

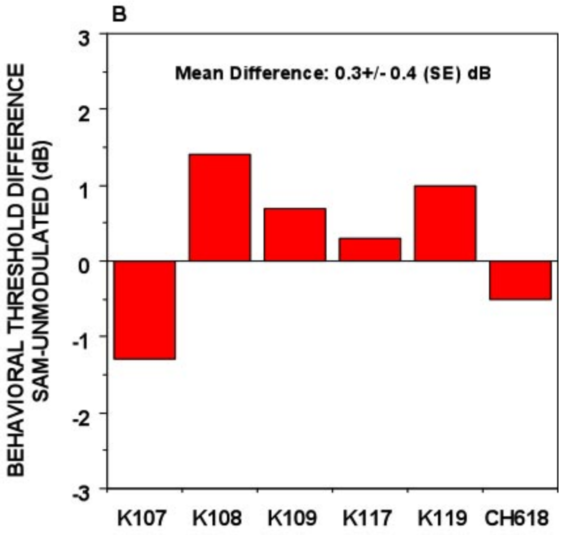

Fig. 3. B: Behavioral threshold differences (SAM threshold minus unmodulated threshold). The results show that psychophysical thresholds for SAM and unmodulated pulse trains are virtually identical (paired t-test; p>0.5).

2. SINGLE NEURON THRESHOLDS FOR SAM AND UNMODULATED PULSE TRAINS IN THE IC

Neuronal response thresholds for SAM signals (300/30 AM) and unmodulated pulse trains were measured and compared in 127 single IC neurons (Fig. 4). The stimulus frequencies used to determine neural thresholds for unmodulated pulse trains ranged from 3 to 30 pps. Over this range, single neuron response thresholds were not affected by the frequency of the unmodulated pulse train.

As illustrated in Figure 4, neural thresholds for both SAM and unmodulated pulse trains cover a broad range of intensities (39 to 60 dB and 39 to 59 dB, respectively). The dispersion or scatter observed for the two threshold measures increases slightly at intensities of 49 dB or above. At these higher intensities, the standard step size of 1 dB is a larger step in absolute current than the current step at lower intensities. As a result, estimation of neural thresholds is less precise at higher intensities.

For the data illustrated in Figure 4, the mean thresholds for SAM and unmodulated signals were 51.1 dB (359 µA) and 50.7 dB (343 µA), respectively, and neural thresholds for the two kinds of signals were strongly correlated (r=0.96). The mean threshold difference for the two signals is relatively small (0.4 dB or 15.5 µA), but this difference was significant (paired t-test; t=4.04; df=126; p<0.001).

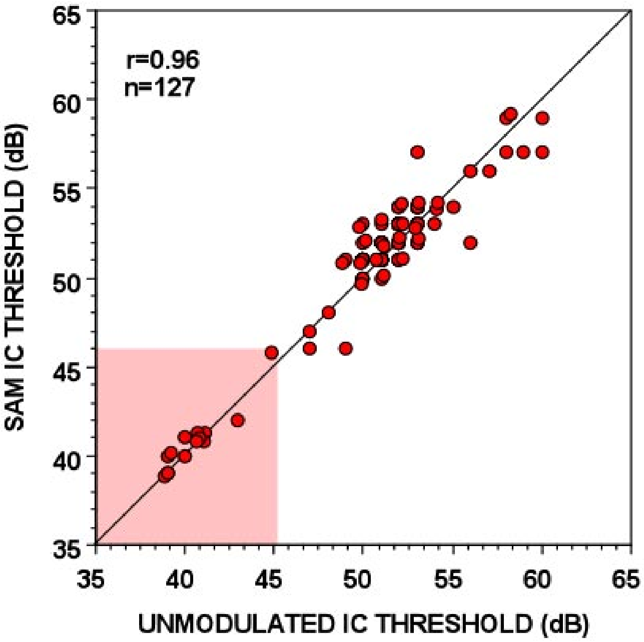

Fig. 4: Single neuronal thresholds in the IC for SAM pulse trains (300/30 AM) versus unmodulated pulse trains (2-30 pps; 0.2 ms/ph). When measured within the range of psychophysical thresholds (shaded area), the mean IC neural thresholds for SAM (40.9 dB) and unmodulated (40.7 dB) pulse trains are virtually identical. At intensities above the psychophysical range, the neuronal thresholds for SAM signals are slightly, but significantly, higher (0.4 dB) than thresholds for unmodulated pulse trains (p<0.01). Line is x=y. n=Number of neurons.

When the comparison of neural thresholds was limited to stimulus intensities that fell within the range of psychophysical thresholds (cf. Fig. 3A and 5A), a different result was obtained. The psychophysically-relevant threshold ranges are depicted by the shaded area in the lower left of Figure 4. The average neural thresholds (n=13 pairs) were 40.9±0.5 (SE) dB for SAM pulses and 40.7±0.5 (SE) dB for unmodulated pulse trains, and the threshold difference was only 0.2 dB or 3.2 µA. This threshold difference was not significant (paired t-test; p>0.2). These results are consistent with the psychophysical finding reported above that detection thresholds for SAM and unmodulated pulse trains are equivalent for the two kinds of signals (Figs. 2B, 3A and B). However, we cannot rule out the possibility that the identical IC neural thresholds are due to the small sample size (n=13 pairs), because seven out of ten comparisons of 13 randomly selected pairs of SAM and unmodulated thresholds outside the psychophysical threshold range were also not significant (p>0.05).

3. COMPARISON OF BEHAVIORAL AND NEURAL THRESHOLDS

Figure 5A and B shows the comparisons of minimum neural thresholds for unmodulated, low frequency pulse trains and psychophysical thresholds for SAM signals for six cats. Due to incomplete sampling of IC thresholds for pulses in K98 and due to electrode failure before the IC experiment in K109, only the A1 thresholds recorded in these cats have been included in the analysis. In the remaining four cats, pulse thresholds were determined in both the IC and the A1. The average number of IC thresholds obtained in each experiment was 141. In each cortical experiment, neuronal thresholds were obtained from 52 to 160 recording sites (average: 107 per experiment).

The six minimum neural thresholds (see Methods) shown in Figure 5A were obtained from a total of 1005 thresholds (IC: n=562; A1: n=443) recorded in the six animals. Two of the minimum neural thresholds shown in the figure were recorded in the IC (open symbols) and four in the A1 (closed symbols). In order to minimize the influence of changes in detection threshold over time, only the psychophysical thresholds estimated closest to the time of the acute electrophysiological experiment (i.e., SAM thresholds) were included in the comparison with minimum neural thresholds. Because psychophysical detection thresholds for SAM and unmodulated pulses were virtually identical (Fig. 3A and B), a comparison of minimum neural thresholds and behavioral thresholds for low frequency unmodulated pulses would have demonstrated essentially identical results to those presented in Figure 5.

Figure 5A illustrates the strong correlation (r=0.93) obtained between the behavioral and minimum neural thresholds. Minimum neural thresholds from either the IC or the A1 were not consistently located below or above psychophysical thresholds. Psychophysical thresholds ranged from 30.6 dB (K98) to 47.8 dB (CH618); neural thresholds ranged from 29 dB (K98) to 51 dB (CH618). The mean values for psychophysical and minimum neural thresholds were 36.7±2.5 (SE) dB and 36.5±3.2 (SE) dB, respectively. It should be noted that the highest threshold values shown in Figure 5A were obtained from a long deafened cat with very poor nerve survival (CH618; >4 yr of deafness, spiral ganglion cell density 1.3% of normal). Figure 5B shows the threshold differences between behavioral and neural thresholds among the six animals. These threshold differences ranged from -3.3 dB (K109) to 3.5 dB (K107). The average threshold difference [0.3±1.1 (SE) dB] was not statistically significant (paired t-test; p>0.8).

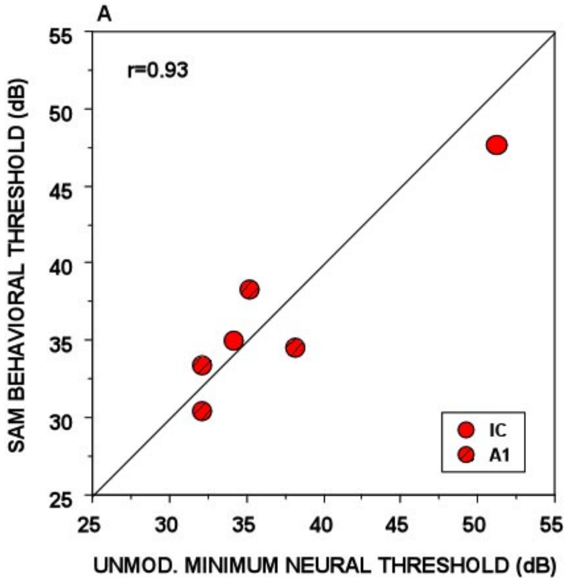

Fig. 5. A: Behavioral thresholds for SAM pulse trains versus *minimum* neural thresholds for unmodulated pulse trains estimated for six cats. For each cat the lowest neural threshold measured in the IC (plain symbols) or the A1 (striped symbols) is shown. Line is x=y.

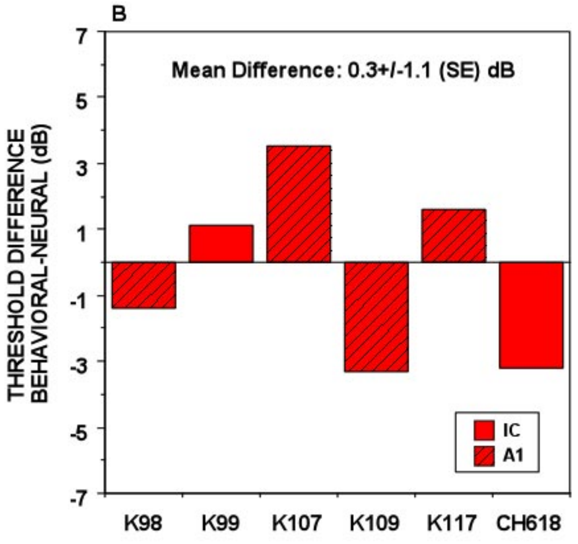

Fig. 5. B: **Threshold differences** (behavioral threshold minus neural threshold). The results from Figsures 4 and 6 indicate that *minimum* neural thresholds for low frequency unmodu-lated pulse trains are virtually identical to behavioral thresholds for either SAM or low frequency unmodulated pulse trains. Plain bars=IC. Striped bars=A1.

In summary, the results from Figures 3 and 5 indicate that minimum neural thresholds for low frequency unmodulated pulse trains are virtually identical to behavioral thresholds for either SAM or low frequency unmodulated pulse trains. These findings suggest that the most sensitive neurons in the IC and the primary auditory cortex contribute to psychophysical detection of electrical stimulation of surviving ganglion cells in the deaf cochlea.

4. EFFECTS OF SAM CARRIER AND ENVELOPE FREQUENCIES ON PSYCHOPHYSICAL THRESHOLDS

An important issue in the current study was to determine whether psychophysical thresholds for SAM signals were affected by the carrier frequency, the modulation frequency, or both when measured in the same animal. For example, interactions between carrier and modulation frequencies might influence behavioral detection of SAM pulse trains. In Figure 6 psychometric functions for two animals (K119, K55) show the probability of detection as a function of the intensity of SAM warning signals with different modulation and carrier frequencies. The slopes for the linear portion of the functions indicate that the probability of detection between 0.25 and 0.75 occurred within 2 to 3 dB. Thus, the slopes of the psychometric functions for SAM pulses (0.2 ms/ph) are comparable to the slopes of psychometric functions reported for 0.2 ms/ph unmodulated pulses (Beitel et al. 2000a). The slopes of these curves represent the range of slopes for all psychometric functions obtained in the cats included in this study (cf. Fig. 2B).

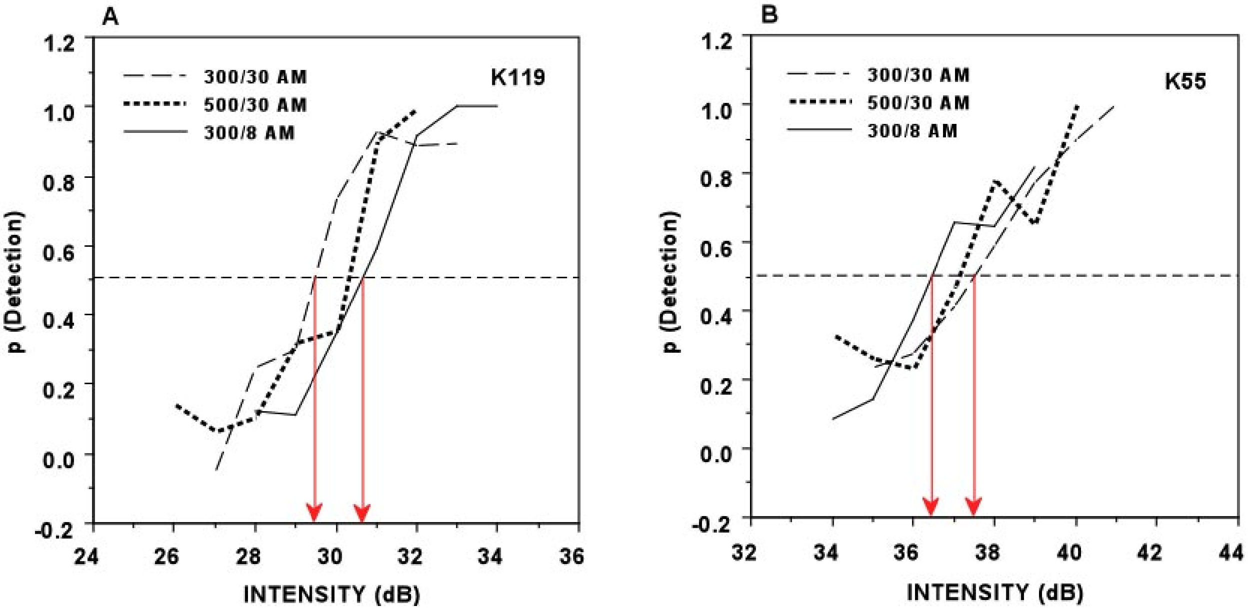

Fig. 6: **Psychometric functions** showing probability of detection as a function of the intensity for SAM warning signals in 2 cats, K119 (A) and K55 (B). Data are shown for 3 different signals. Dashed lines: 50% detection. The arrows indicate the range of thresholds. Within the range of tested frequencies, the rank order of the detection thresholds does not change systematically with the parameters (carrier or envelope frequency) of the SAM signals. The range of modulation frequencies roughly corresponds to the range of modulation frequencies used for the discrimination task (Fig. 7).

The ranges of thresholds for the different signals are indicated by the arrows on the abscissae. Figure 6A illustrates psychometric functions for cat K119 for three different SAM signal combinations of 300/30 AM, 500/30 AM and 300/8 AM. The lowest threshold was observed for 300/30 AM (29.5 dB), and the highest threshold was observed for 300/8 AM (30.6 dB). Thus, in this animal the maximum threshold difference for the SAM signals was 1.1 dB.

Figure 6B depicts psychometric functions for cat K55 for the same three SAM signal combinations. The lowest threshold was obtained for 300/8 AM (36.5 dB) and the highest for 300/30 AM (37.5 dB), i.e., thresholds for the given SAM signals were within 1 dB.

An examination of the results shown in Figures 6A and B indicate that the rank order of the detection thresholds did not change systematically with the parameters (carrier or envelope frequency) of the SAM signals. Thus, these results indicate that *within the range of tested frequencies*, detection thresholds are independent of the carrier and modulation frequencies.

5. TEMPORAL DISCRIMINATION OF SAM SIGNALS

The results in the preceding section provided essential information that guided our choice of stimuli used for training and testing cats on a successive discrimination task. Because our results show that detection thresholds and psychometric functions for different modulation frequencies are equivalent at a particular carrier rate, we reasoned that discrimination of a change in the envelope or modulation frequency should be based on temporal rather than amplitude or intensity cues. Thus, SAM signals with modulation and carrier frequencies similar to those reported in the preceding section were used to train four deaf cats on a successive discrimination task. Three cats were trained to discriminate SAM signals with carrier frequencies of 100 pps, 300 pps and 500 pps. In addition, two of these animals were trained to discriminate SAM signals with higher carrier frequencies of 1000 and 1500 pps.

The immediate goals of our discrimination experiment were 1) to investigate whether deaf cats could be trained to discriminate SAM signals; 2) if so, to estimate the differences limens for successful discrimination; and 3) to determine whether a cat’s ability to discriminate SAM signals was exclusively dependent on the animal’s ability to resolve differences in the temporal structure of the modulating envelope or whether the animal’s performance was influenced, as well, by the carrier frequencies.

Note that the standard and comparison signals always had the *same* carrier rate in a given testing session, and the modulation frequency of the standard signal was 8 Hz throughout *all* of the behavioral testing. Figure 7A, C and E show performance functions for discrimination of the envelope frequencies of the comparison signals by cats K99, K148 and K146. The carrier rates of the signals varied between 100-1500 pps. For cat K99, discrimination testing was concluded after training on three carrier frequencies (100, 300 and 500 pps). An animal’s discrimination thresholds [p (Discrimination)=50%] for the envelope or modulation frequency of the comparison signal were determined by linear interpolation from the dashed lines to the abscissae in Figures 7A, C and E, and the ranges of thresholds are depicted by the arrows in each plot. In each animal, threshold testing was conducted within a 4 weeks period, and each performance function for a given carrier frequency includes 3.6±0.3 (SE) threshold sessions.

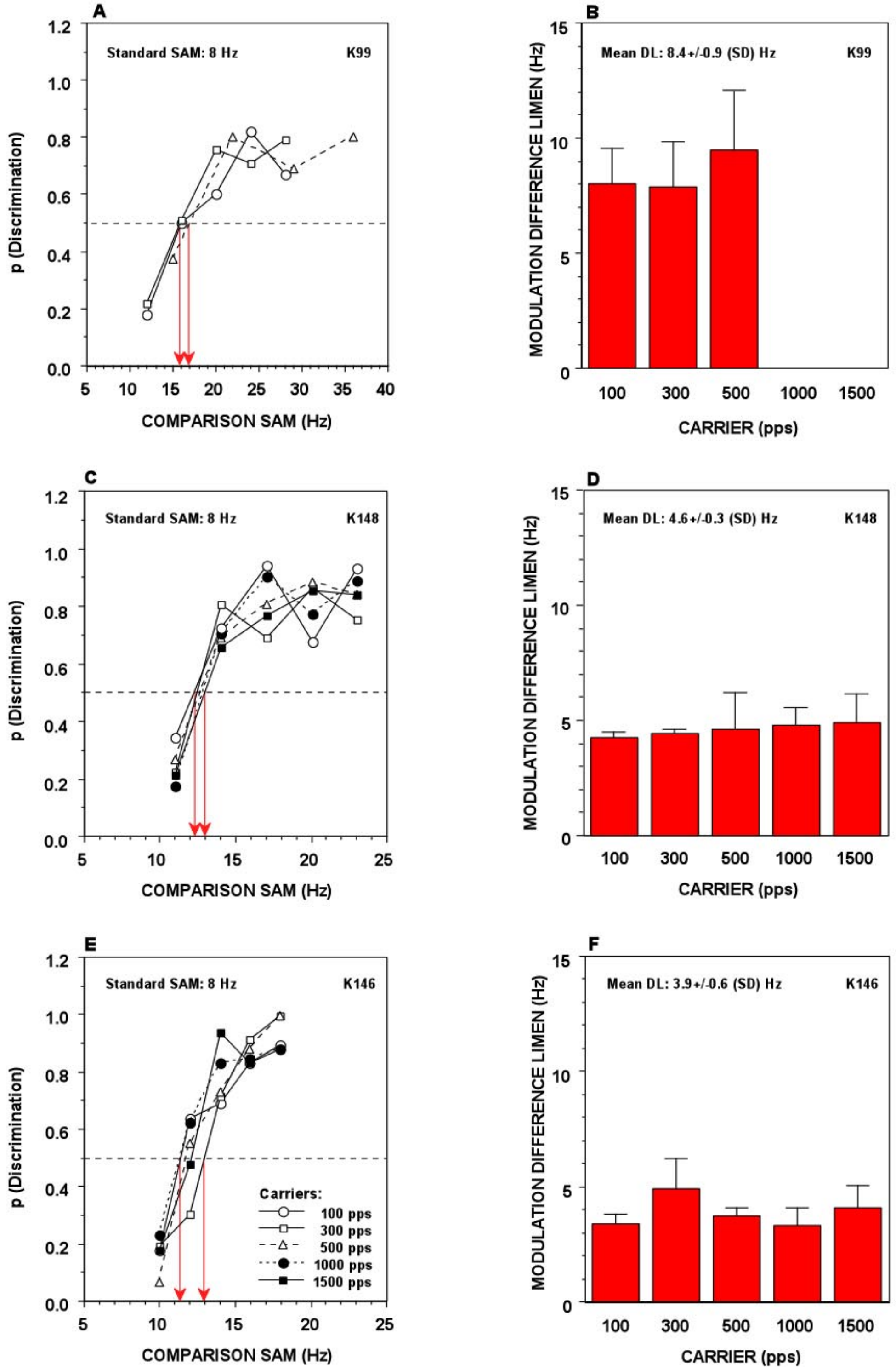

Fig. 7: Successive discrimination of SAM pulse trains for three cats. A, C and E: Psychometric functions showing probability of discrimination as a function of the modulation frequency of comparison SAM signals. Parameter varied was carrier frequency. The Standard SAM signal was constant (8 Hz). Note the different scale on the abscissa in A. Thresholds (50% discrimination) were determined by linear interpolation from the dashed lines to the abscissae. Arrows indicate threshold ranges for different carrier frequencies. **B, D and F:** Modulation difference limens (DL) in Hz versus signal carrier rate (pps). The animals' performance was based exclusively on the discrimination of changes in the envelope of the SAM signal, whereas changes in the carrier had no obvious effect on performance.

During the time of testing, an animal's general behavior and various factors with possible influence on behavioral performance (e.g. device integrity, EABR thresholds, electrode impedances) remained stable.

For modulated signals with different carrier frequencies, the difference limens (DL= Comparison SAM frequency minus the Standard SAM frequency) for successive discrimination of changes in the SAM envelope are illustrated in Fig. 7B, D and F. In cat K99 (Fig. 7A and B), the estimated modulation frequencies required for discrimination of comparison signals with carrier frequencies of 100 pps, 300 pps and 500 pps were 16.0 Hz, 15.9 Hz and 17.5 Hz, respectively, which are equivalent to DLs of 8 Hz, 7.9 Hz and 9.5 Hz. The mean DL was 8.4±0.9 (SD) Hz, and all DLs were within 1.5 Hz. In cat K148 (Fig. 10C and D), the DLs for comparison signals with carrier frequencies of 100 pps, 300 pps, 500 pps, 1000 pps and 1500 pps were 4.2 Hz, 4.4 Hz, 4.7 Hz, 4.8 Hz and 5.0 Hz, respectively. The mean DL was 4.6±0.3 (SD) Hz, and all DLs were within 1 Hz. In cat K146 (Fig. 7E and F), the DLs for comparison signals with the same carrier frequencies were 3.4 Hz, 4.9 Hz, 3.8 Hz, 3.3 Hz and 4.1 Hz, respectively. All DLs were within 1.7 Hz with a mean DL of 3.9±0.6 (SD) Hz. Although discriminative performance varied across animals, there was no effect of carrier frequency on discrimination thresholds in any of the trained cats (t-tests; $p>0.05$).

For each cat, the slopes [p (Discrimination)/Comparison SAM (Hz)] of the discriminative functions between p (Discrimination) 0.25 and 0.75 were estimated by linear regression for the linear portion of the function. The animal with the poorest discriminative performance across all carrier frequencies (K99) had discriminative functions with the shallowest slopes, whereas the animal with the best performance (K146) had discriminative functions with the steepest slopes. However, the slopes did not change systematically with the carrier frequencies in any of the cats.

These results suggest that an animal's performance was based exclusively on the discrimination of changes in the envelope of the SAM signals, whereas changes in the carrier rate had no obvious effect on performance.

SUMMARY AND CONCLUSIONS

The results of presented herein indicate that:

- Behavioral and neuronal response thresholds are based on detection of the peak pulse amplitudes of the modulated and unmodulated signals rather than the carrier frequency.
- The most sensitive neurons in the IC and A1 contribute to psychophysical detection of electrical stimulation of surviving ganglion cells in the deaf cochlea.
- Discrimination of successive SAM pulse trains is based on temporal resolution of the envelope frequencies. Performance on the discrimination task was not affected by carrier rate.

Overall, our animal model provides a robust framework for future studies of behavioral discrimination and central neural temporal processing of electrical signals applied to the deaf cochlea by a cochlear implant.

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Work Planned for the Next Quarter

1) Chronic stimulation will be completed and the acute electrophysiological experiment will be conducted in the final animal in our "long-deafened" experimental series. This study is designed to examine the consequences of severe neural degeneration upon electrophysiological thresholds, dynamic range and the effects of chronic stimulation in this model of severe cochlear pathology.

2) Chronic stimulation will be completed and final experiments conducted in 2 animals in a new chronic series in which profound hearing losses are induced at 1 month of age using acute administration of kanamycin/ethacrynic acid, rather than the neonatal prolonged administration of neomycin used in most prior studies.

3) Preliminary multichannel recording experiments examining spatial selectivity of electrical stimulation in guinea pigs using the 16 electrode Michigan probe will continue, as software development progresses.