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A STUDY OF TEMPORAL INTEGRATION IN THE AUDITORY SYSTEM
OF THE GOLDFISH (Carassius auratus)

by

Marian L. Patricoski

A Thesis Submitted to the Faculty of the Graduate School
of Loyola University of Chicago in Partial Fulfillment
of the Requirements for the Degree of

Master of Arts

April

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VITA

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	ii
VITAiii
LIST OF FIGURES	iv
REVIEW OF RELEVANT LITERATURE	1
RATIONALE FOR THE CURRENT STUDY	19
METHOD	21
Subjects	21
Apparatus	21
Procedure	22
RESULTS	26
DISCUSSION	30
Temporal Integration	30
Critical Ratio and Critical Band	34
Neural Model	38
Summary	41
REFERENCES	44

LIST OF FIGURES

Figure	Page
1. Fourier Analysis of 5.1 and 8.2 msec Signals	5
2. Fourier Analysis of 13.8 and 25 msec Signals	6
3. Fourier Analysis of 45 and 85 msec Signals	7
4. Selected Results From Papers on Temporal Integration in the Goldfish	17
5. Stimuli for the Present Experiment	23
6. Spectral Analysis of Noise Background	25
7. Experimental Results of the 100 msec Repetition Period	27
8. Experimental Results of the 1000 msec Repetition Period	29
9. Comparison of Results for Offutt (1967), Popper (1972), Hawkins and Horner (1980), and the Present Study	32
10. Results From the Critical Ratio Study by Fay (1974)	35
11. Critical Ratio as a Function of Signal Duration	36
12. Critical Bandwidth as a Function of Signal Duration	39

REVIEW OF THE RELEVANT LITERATURE

The dependence of sensory magnitude on stimulus duration, or more precisely, the averaging of sensation over a short duration, is often termed temporal summation or integration. Temporal integration occurs in most if not all sensory systems. Generally, sensory magnitude increases as stimulus duration increases, with some temporal limits. In the visual system, when the duration of a flash of light is very brief, a high level of luminance (intensity) is needed in order to detect the stimulus, but as the duration increases, the level of luminance required for threshold depends on the product of luminance (intensity) and duration (time). It is well established that a functional relation exists between the duration of acoustic stimulation and the auditory response. That is, the expenditure of acoustic intensity may not produce a response unless it occurs over some minimum length of time. This relationship between time and intensity is referred to as auditory temporal integration or summation.

In the course of human auditory research, several theories have been advanced to describe the process of temporal summation. These theories will be discussed in chronological order and will include mathematical models of the integrator when applicable.

One of the earliest experiments in this area, performed by Hughes (1946), studied the absolute hearing threshold as a function of the duration (63-739 msec) of single tone pulses presented at frequencies of 250, 500, 1000, 2000, and 4000 Hz. If the ear were to act as a perfect integrator of acoustic intensity, where the change in threshold level was directly proportional to the change in stimulus duration, then the relationship between threshold and stimulus duration could be expressed as

$$Ixt = \text{constant} \quad (1)$$

This relationship assumes that the auditory threshold depends only upon the total amount of energy (Ixt) in the stimulus and not on the distribution of that energy over time. This expression is analogous to Bloch's Law for the visual system. The resulting threshold-duration curve of the Hughes (1946) experiment was best described by the equation

$$I/I_{\infty} = 1 + (\mathcal{T}/t) \quad (2)$$

or

$$(I/I_{\infty})t = I_{\infty}\mathcal{T} = \text{constant} \quad (3)$$

with (I) equal to threshold intensity of a tone pulse of duration (t); (I_{∞}) equal to threshold intensity of a continuous tone, and (\mathcal{T}) a time constant. Notice in equation (3) it is not (Ixt) which is constant, but the product

of time and the amount by which the stimulus intensity exceeds the value I_{∞} .

The Hughes experiment measured temporal summation at the threshold of hearing. A later study by Garner and Miller (1947) determined the masked threshold for stimulus frequencies of 400, 670, 1000 and 1900 Hz at durations between 12.5 msec and 2 sec. The slope of the threshold function of duration suggests a linear integration of acoustic energy up to durations of 200 msec. Beyond 200 msec, the curve gradually flattens out until there is relatively little change in the signal-to-noise ratio necessary for threshold performance. Garner and Miller (1947) proposed several interpretations of these data. The principal interpretation was that there is a certain stimulus intensity minimum above which the ear will summate energy in a perfectly linear manner, but below which summation will not occur. This idea concurs with equation (3) of Hughes (1946).

A subsequent investigation by Garner (1947) studied the effect of the frequency spectrum on the integration of acoustic energy. Garner hypothesized that the rate of temporal integration of energy in the ear is dependent on the distribution of that energy in the frequency spectrum. Before discussing the results of the Garner (1947) experiment, it is essential to examine more closely the changes in the frequency spectra of signals that accompany changes

in duration.

A problem with the physical characteristics of the stimulus is encountered when tones of extremely short durations, especially those employed in studies of temporal summation, are used. An analysis of the frequency spectrum of such a tone would reveal the presence of the signal frequency component and other frequency components, sometimes called sidebands. For short tones, this spread of energy across the spectrum is related to tone duration, with the bandwidth of the energy surrounding the signal frequency being proportional to the reciprocal of signal duration. For example, the spectrum of a 10 msec 800 Hz tone pulse would have a primary energy band surrounding 800 Hz that will drop off from a maximum energy level near 800 Hz to zero energy levels at about 790 Hz and 810 Hz. In addition, other frequency bands both above and below the primary will occur. The short duration tone spectra presented in Figures 1, 2 and 3 provide a general illustration of this phenomenon. These spectra were calculated from signals used in the present study and will be discussed more extensively in a later section. However, it is important to note that as the duration of the tone decreases, the width of the primary energy band increases and its amplitude decreases as more energy is scattered into other bands.

Given these changes in the physical characteristics of the stimulus, Garner (1947) proposed that a change in

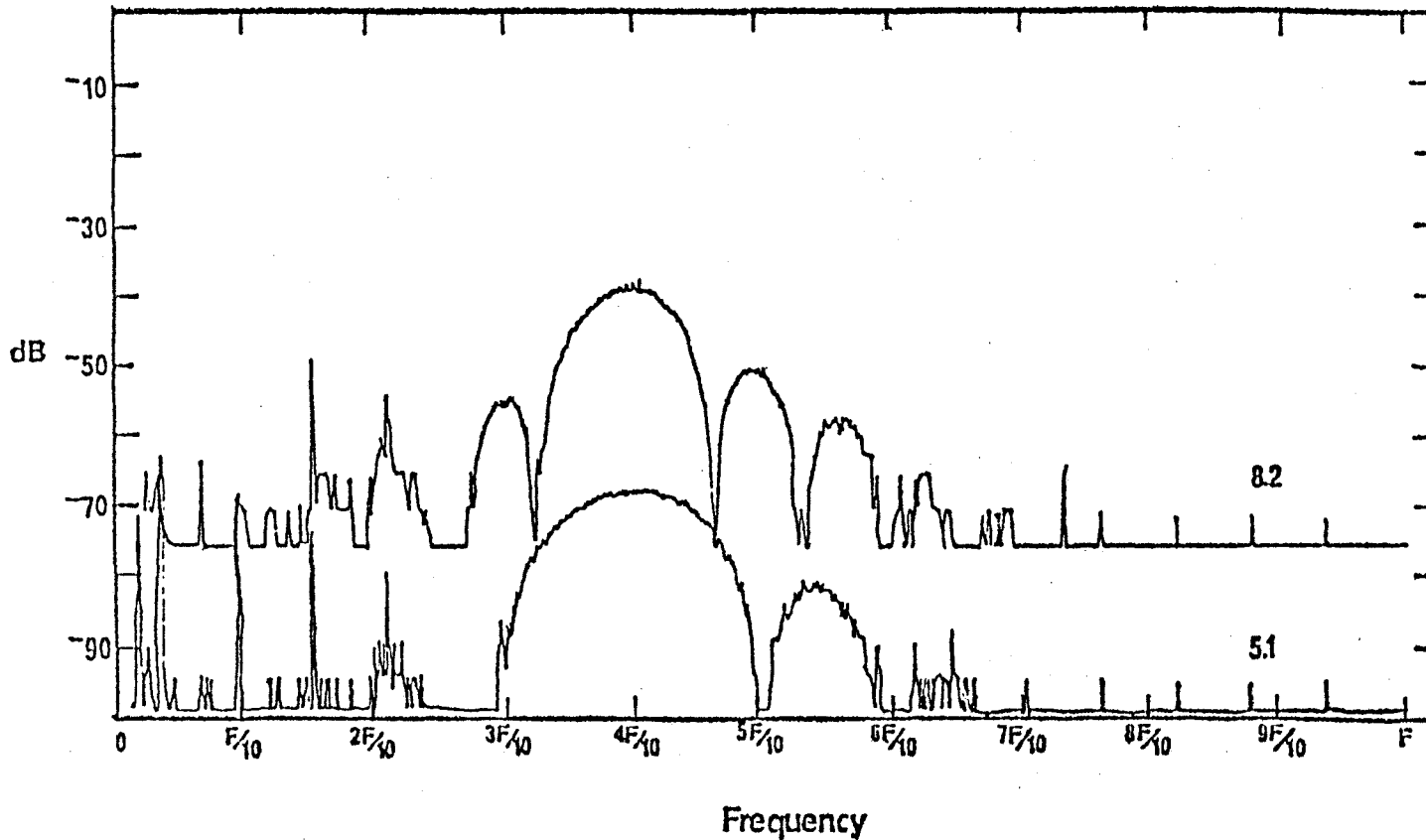


Figure 1: Fourier analysis of 5.1 and 8.2 msec signals used in this study. Signal durations are effective durations. ($F=2000$)

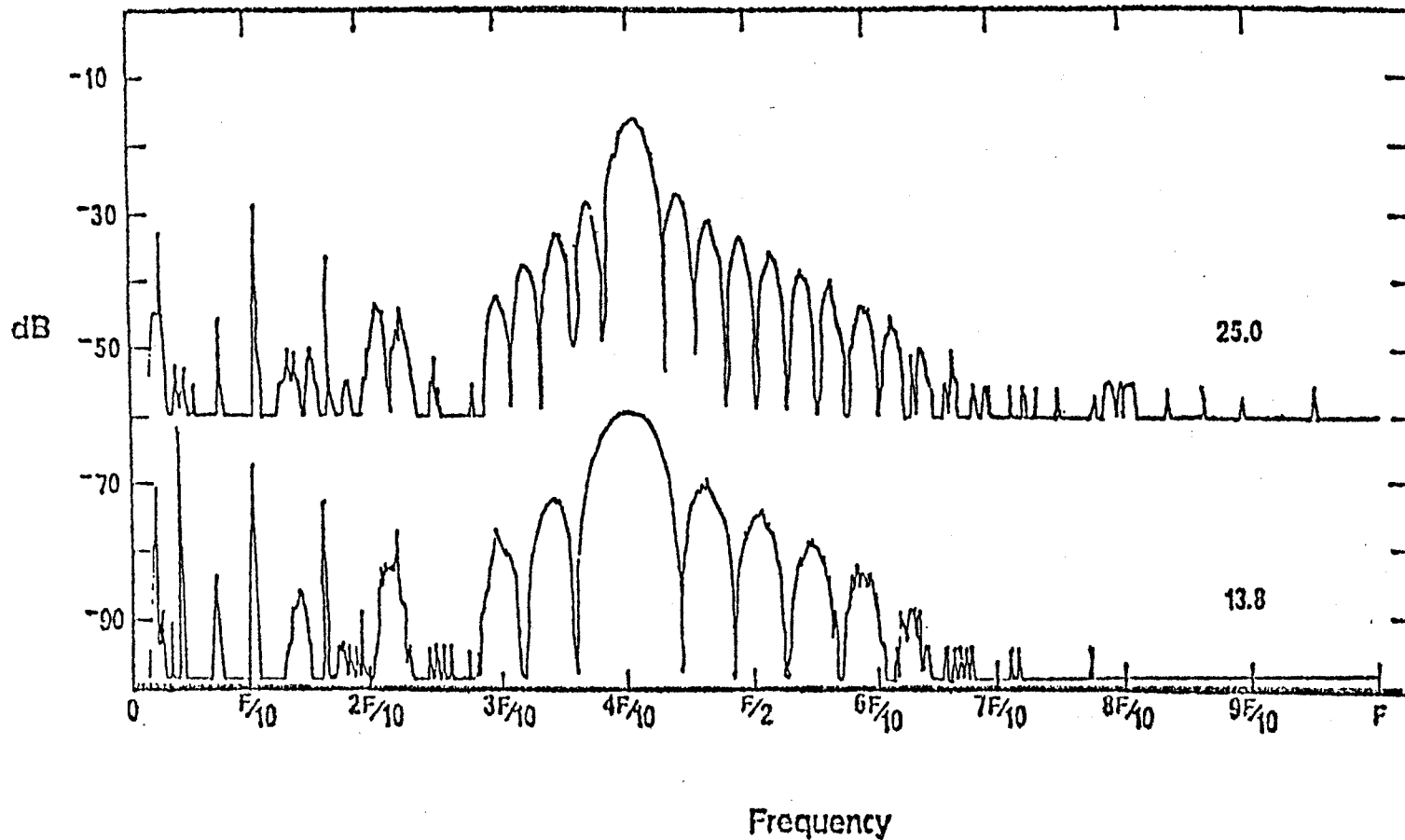


Figure 2: Fourier analysis of 13.8 and 25 msec signals used in this study. Signal durations are effective durations. ($F=2000$)

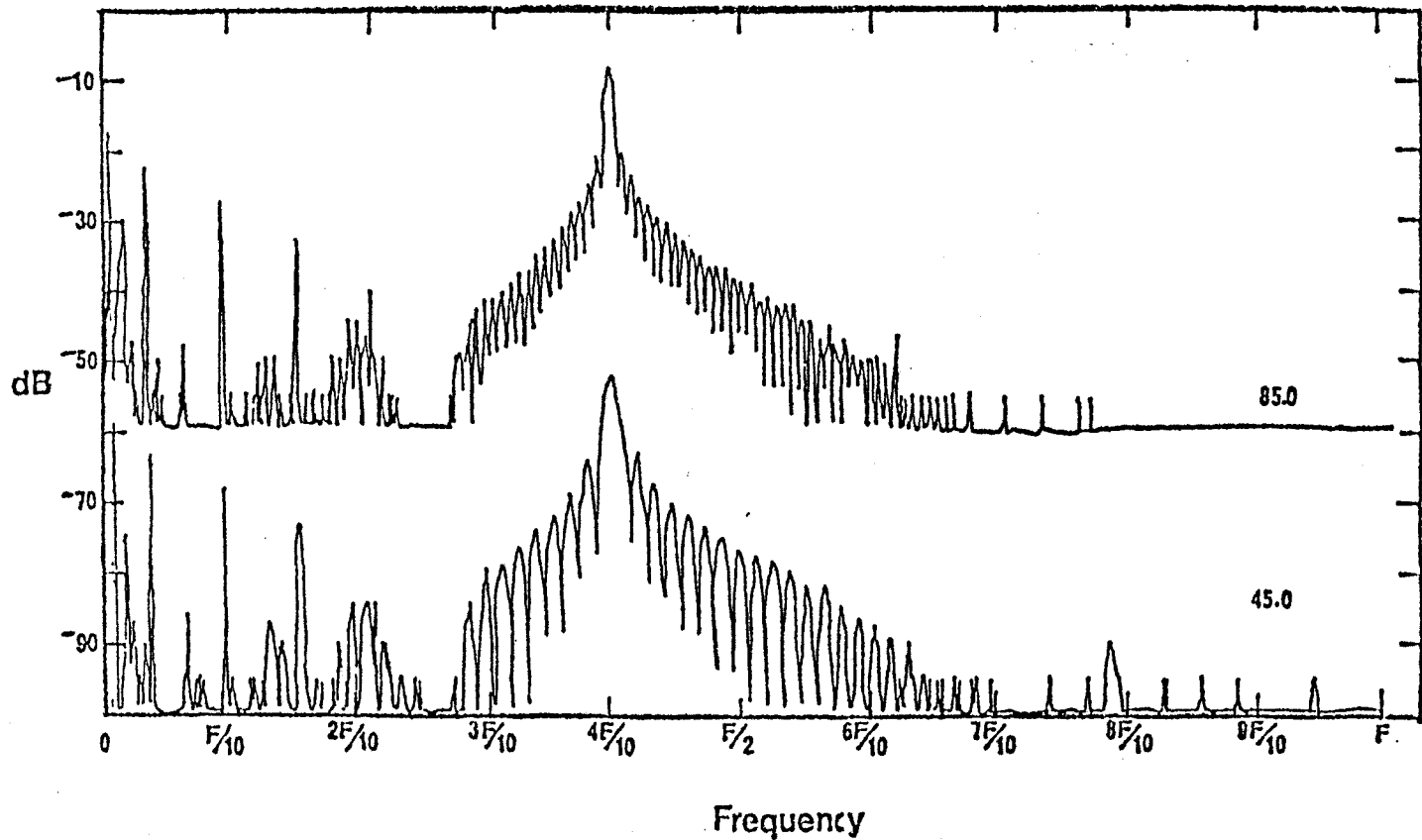


Figure 3: Fourier analysis of 45 and 85 msec signals used in this study. Signal durations are effective durations. (F=2000)

duration can be equivalent to a change in intensity only if all of the energy to be integrated is within a narrow band of frequencies or what might be termed a critical "integration" bandwidth. If the energy is located throughout a wider band of frequencies, as is the case with short duration stimuli, integration will occur, but the change in threshold cannot be equivalent to the change in duration.

In the Garner (1947) experiment, the absolute hearing threshold was measured at frequencies of 250, 1000 and 4000 Hz for pulse durations between 1 and 100 msec. The results were in concordance with the earlier proposal that a linear integration of intensity occurs only for that energy within a certain band of frequencies.

Several years later a paper by Plomp and Bouman (1959) proposed a hypothetical model of temporal integration in the human ear. The hypothesis of temporal integration proposed by Plomp and Bouman (1959) simply states that the occurrence of a tone pulse of intensity (I) results in an effect (s) somewhere in the auditory system, that approaches its end value according to an exponential function, with the end value proportional to (I). Perception results when (s) exceeds the critical value (s_0).

The following equation describes the predicted relationship between the intensity (I) at threshold and the tone duration (t) for single tone pulses.

$$I/I_{\infty} = 1 / (1 - e^{-t/\mathcal{T}}) \quad (4)$$

Here the variable (\mathcal{T}) is a time constant which determines the rate at which (s) increases with time. Taking the log of both sides of equation (4) and multiplying by 10 yields the threshold in decibels above the continuous tone threshold.

$$10 \log(I/I_{\infty}) = -10 \log(1 - e^{-t/\mathcal{T}}) \quad (5)$$

In the experiment, tone pulse durations varied between 1 msec and 10 sec at frequencies of 250, 500, 1000, 2000, 4000 and 8000 Hz. The masked threshold was determined at a fixed noise level as a function of tone duration, using a descending series of limits.

The results indicate that the Plomp and Bouman (1959) hypothesis accurately predicts threshold as measured, except at very short durations. At shorter durations the threshold curve rose more sharply than predicted. This implies that only part of the total energy contributes to detection. This notion would be consistent with Garner's (1947) proposal that only energy within a certain bandwidth is integrated. If a mathematical correction is made for the shorter durations then a (\mathcal{T}) of about 0.20 sec results.

The hypothesis proposed by Plomp and Bouman (1959) and its associated mathematical model appear to accurately describe the data for temporal integration of single tone pulses. To account for threshold experiments with repet-

itive tone pulses it is necessary to derive an extension of equation (4). In a later study, Plomp (1961) provided a model that predicts threshold for repetitive tone pulses.

Recall that for single tone pulses, only the increase of (s) was important to establish the relation between threshold and tone duration. When using repetitive pulses it is necessary to also account for the decrease of (s) in the intervals between the pulses. Plomp proposes the equation

$$10\log(I/I_{\infty}) = 10\log \left\{ 1 - e^{-[(t_0 + t_1)/\mathcal{T}]} \right\} - 10\log \left[1 - e^{-(t_0/\mathcal{T})} \right] \quad (6)$$

to predict the threshold intensity in decibels above that for a continuous tone. Tone pulse duration equals (t_0) and the interval between the pulses is represented as (t_1). The repetition period would be equivalent to the expression ($t_0 + t_1$).

The primary intention of the Plomp (1961) study was to examine the relation between threshold intensity and repetition time. However, if the data are plotted as a function of duration, the threshold curves are in close agreement with those predicted by equation (6). The course of threshold curves for very short durations may again be related to changing bandwidths of energy. In this experiment a time constant (\mathcal{T}) of 0.20 sec was also reported.

In general, human threshold curves for experiments of temporal summation describe the response of the auditory system to duration changes as a decrease in threshold as signal length increases up to 150-225 msec. After about 225 msec, the threshold equals that of a continuous tone. Auditory thresholds for signals shorter than 150 msec increase exponentially, with even steeper slopes at durations less than 10 msec. The auditory system's response to very short duration stimuli may be attributable to, as Garner (1947) proposed, the spread of energy outside of some critical "integration" bandwidth. With these observed changes in threshold as a function of tone duration, it can be assumed that temporal integration occurs. In addition, the mathematical models proposed by Plomp and Bouman (1959) for single tone pulses and Plomp (1961) for periodic tone pulses appear to be reasonable descriptors of the integration process in the human auditory system. Estimates of the integration time derived from these investigations range between 100 and 300 msec depending on stimulus frequency.

More recent studies have challenged these conclusions. It appears that it is not the validity of the results themselves that are in question, but rather the concept of a simple, single integration time. Green (1971, 1973) proposes this thought experiment to test the notion of a single integration time. If 100 msec (Plomp and Bouman,

1959) is the shortest estimated integration time of the system, then a psychophysical task requiring detection of a very short click (100 μ sec) centered in noise should yield rather poor observer performance. Actual observer performance for this task, however, is better than might be predicted given the 100 msec integration time. Green (1971, 1973) suggests that the auditory system may employ both a maximum and a minimum integration time. Maximum or long integration times, such as those obtained in the Plomp and Bouman (1959) study, would be appropriate in situations requiring long temporal averaging such as detection of tones of different durations. A short or minimum integration time would be advantageous for tasks of detecting brief stimuli presented in noise. It is the minimum integration time, in fact, which describes the temporal acuity of the auditory system (Green, 1971).

The stimulus conditions used in early studies of temporal integration have usually confounded changes in the signal's temporal characteristics (duration) with changes in spectral features (energy splatter). Stimuli employed to measure the minimum integration time carefully control the energy spectrum and permit changes only in the temporal aspects of the signal (Green, 1973). Investigations of the minimum integration time include tasks which require discrimination between Huffman sequences (Patterson and Green,

1970); the detection of a click in sinusoidally modulated noise (Viemeister, 1977); the detection of sinusoidally amplitude modulated signals (Viemeister, 1979); and the detection of a click centered in a rectangular noise burst (Penner, Robinson, and Green, 1972). The first three techniques estimate the minimum integration time at approximately 1 to 3 msec. The last procedure estimates the integration time to be about 20 msec or ten times longer than the previous estimate. At present, there is no hypothesis to explain this discrepancy (Green, 1973).

In our review of the human literature it is clear that the auditory system performs a temporal integration of acoustic energy. Early investigations have estimated the integration time of the system at about 100 to 300 msec, a value that varies inversely with signal frequency. More recent research has suggested the addition of a shorter or minimum integration time of about 1 to 3 msec which may be utilized to preserve more of the variation in extremely brief stimuli than the previously measured maximum integration time. The next point of review for this discussion regards other species: Does temporal integration occur in the auditory system of other species? If so, is the integrative process similar to human models?

Investigations of other species have, in fact, indicated that temporal integration occurs in the auditory

system of the monkey (Clack, 1966); the bottlenose porpoise (Johnson, 1968); the house mouse (Ehret, 1976); the chinchilla (Clark, 1980) and the parakeet and field sparrow (Dooling, 1979).

Several of these comparative studies have applied the mathematical models discussed above. Experiments by Johnson (1968) with the bottlenose porpoise, Ehret (1976) on the house mouse and the chinchilla (Clark, 1980) note that the variation in threshold intensity as a function of duration can be approximated by equation (2). Temporal summation in the auditory systems of these animals can be described as a proportion between (I) and (t) which assumes a linear integration of energy. The avian experiments of Dooling (1979) with the parakeet and field sparrow produced threshold curves best described by the exponential model of Plomp and Bouman (1959). Using equation (4) these results indicate a time constant (\mathcal{T}) of 0.23 sec.

Reptilian and amphibian studies of temporal integration are absent. However, among the lower vertebrates, three studies of temporal integration in the goldfish (Carassius auratus) have been reported. A study by Fay (1980) used amplitude modulated signals similar to Viemeister (1979) to measure the minimum integration time for the goldfish auditory system. The results suggest that the minimum integration time for the goldfish may be very short, perhaps less than 0.4 msec. Two previous investigations of

the maximum integration time in the same species have been performed (Offutt, 1967; Popper, 1972). Unfortunately, as the ensuing discussion concludes, the results are conflicting and we are left without a clear picture of temporal integration in fishes.

In the Offutt (1967) experiment, four goldfish were classically conditioned to decrease heart rate upon presentation of an acoustic stimulus. Stimuli were repetitive 400 Hz tones with pulse periods from 50 to 500 msec and rise-fall times of 2.5 to 25 msec. Signal durations in the experiment were defined as time at peak intensity. The duty cycle, of percent of time that the signal was on during any period, varied from 10 to 90 percent. Actual pulse durations varied between 2.5 and 445 msec. Each test series had a constant period and rise-fall time while the duty cycle and intensity (in 2 dB increments) were varied.

Offutt's results indicate that the animals tested had higher thresholds for short duration tone pulses with a slight enhancement of auditory sensitivity as pulse-length increased. Nearly perfect integration of about 3 dB per octave was found for long duration signals at each repetition period. However, at very short durations (less than 100 msec) and very small duty cycles (less than 20%) there is a very rapid fall-off in threshold. The data of the Offutt (1967) study are not consistent with Plomp's model (1961) and are unlike any other description of temporal integra-

tion as we know it. An illustration (Fig. 1) of the results emphasizes the effect of duration upon threshold, which does not occur independently of duty cycle. This deviation of results from Plomp's model (1961) may be due to signal energy splatter as Garner (1947) suggested of a possible effect of repetition period. At present, there is no explanation for these findings.

Popper (1972) conducted a two-part experiment to study the relation between auditory threshold and duration. The second experiment followed the procedure of the earlier Offutt (1967) paper. Twelve goldfish were conditioned to cross a barrier when a pulsed sound was presented. Thresholds were determined for pulse periods ranging from 100 to 1000 msec, with duty cycles of 1 to 90 percent. Signal durations varied between 10 and 500 msec at a frequency of 500 Hz. Signal duration in this experiment was defined by the equation

$$T=3r/(3+P) \quad (7)$$

where r is the rise-fall time and P is the peak time of the signal. The data indicate that the auditory thresholds in goldfish for tone pulses as short as 10 msec are not significantly different from thresholds for continuous tones (Fig. 1). It was concluded that temporal summation did not occur in the goldfish auditory system or that it might occur at durations significantly less than 10 msec.

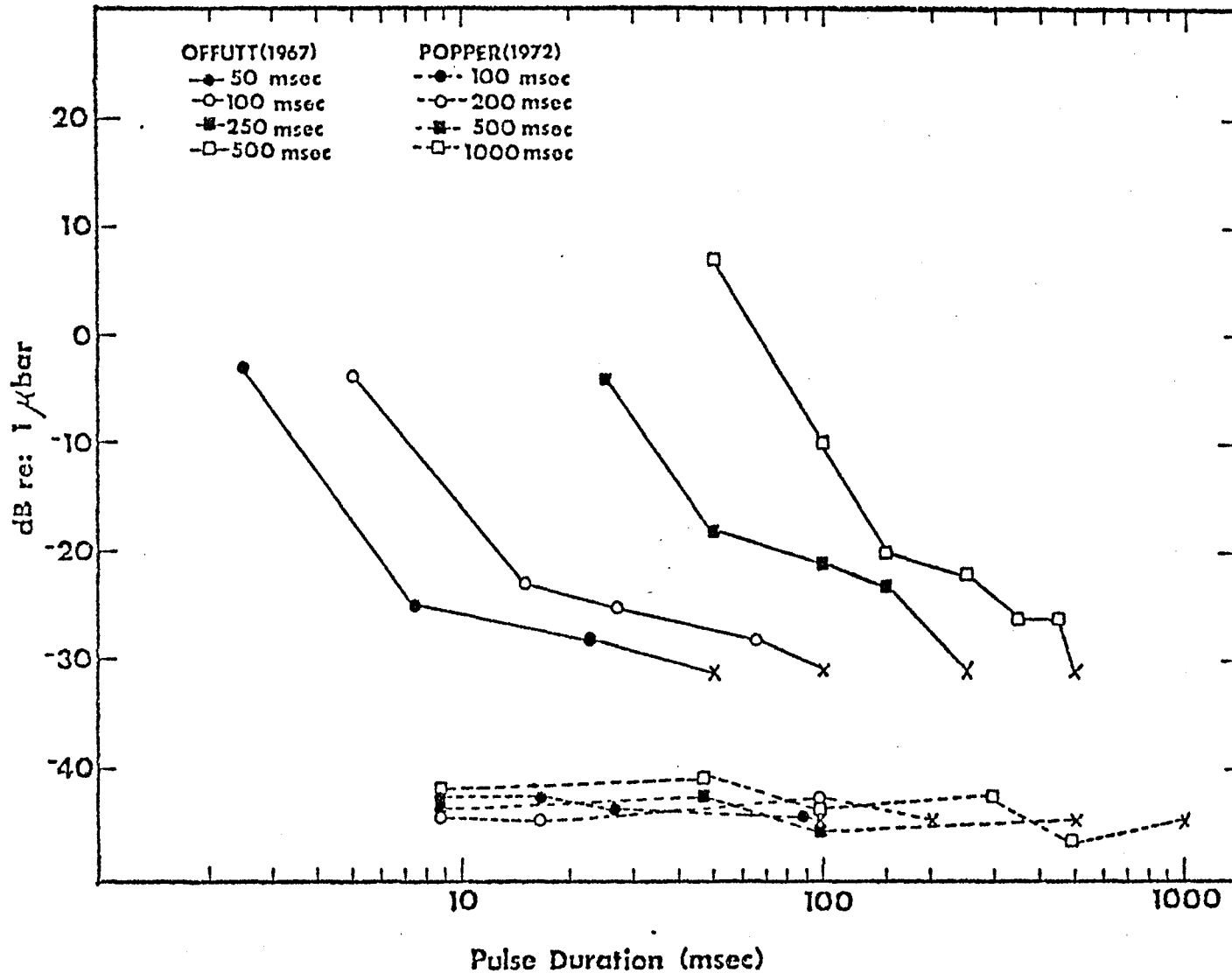


Figure 4: Results of selected repetition periods from papers on temporal integration in the goldfish. (X=continuous tone thresholds).

Before leaving this discussion it is important to note that although Offutt (1967) and Popper (1972) did arrive at different conclusions about the temporal integration issue, their threshold functions differed only in two respects. First, the Popper (1972) results are overall about 10 to 15 dB more sensitive than Offutt's (1967). Secondly, if the sensitivity differences are ignored the slope of Offutt's (1967) threshold functions only deviate markedly from Popper's (1972) at small duty cycles (less than 20%) and short durations (less than 100 msec).

RATIONALE FOR THE CURRENT STUDY

The Offutt (1967) and Popper (1972) experiments are essentially similar, yet their results are in conflict. A clear difference in conditions between the two studies appears to be the ambient noise levels. Offutt (1967) reported a 12 dB re: 1 μ bar background noise produced by the electronic switch. The Popper (1972) experiment was conducted in an acoustic chamber with the ambient noise levels well below any thresholds found in the experiment.

It is proposed that the different temporal integration results obtained in these two studies may be attributable to the ambient noise levels of the test situation. In the Offutt experiment, the short duration pulses were less detectable and required an increase in intensity for detection. If the level of the ambient noise present in the experiment was a factor, its presence might reduce the detectability of the short tone pulses.

The present study proposes to examine several questions surrounding the issue of temporal integration in the goldfish auditory system. First, can the conflicting results be attributed to the ambient noise levels of the test conditions? It is proposed that a psychophysical experiment replicating representative conditions from the two papers be performed with and without an added noise back-

ground. It is important to define the added noise background concept. Within the context of this paper the terms quiet or ambient may be used interchangeably but will always refer to the thresholds collected under the ambient noise levels of the acoustic chamber. The noise condition will refer to the thresholds collected with the addition of a wide-band noise.

Secondly, if the results indicate temporal integration in the noise and/or the ambient condition, can the integration processes be described by any of the mathematical models? Finally, given the psychophysical results, what are the neurophysiological correlates? This will be discussed based on current neurophysiological knowledge of the goldfish auditory system.

METHOD

Subjects

Three common goldfish (Carassius auratus) obtained locally and maintained in communal tanks.

Apparatus

An 800 Hz sine-wave stimulus was generated by a Wavetek 136 VCG/VCA Generator and was switched through a computer controlled electronic timer which determined the duration and repetition period of the stimulus. The pulsed signal was mixed, attenuated, amplified and presented through an underwater loudspeaker. A noise generator (General Radio Model 1390-TA) was added or deleted from the system by altering the settings of a second attenuator (General Radio Model 1450-TA).

The animals were restrained in a cloth bag suspended in a tank of water above the loudspeaker. The restraining apparatus and respiratory monitoring device were previously described by Fay, Ahroon and Orawski (1978). The test tank consisted of a 1 gallon plastic pail, equipped with an underwater loudspeaker immersed in 4 inches of sand. The upper portion of the pail was lined with plastic and filled with tank water. The tank was located within an IAC sound attenuated room.

Procedure

Animals were classically conditioned to suppress respiration upon presentation of acoustic stimulation. Thresholds were obtained using a modified method of limits, whereby the signal level was attenuated in 5 dB increments. A duration detection threshold was defined as the intensity value producing a median respiratory suppression ratio of 0.4 (Fay, 1974). Thresholds were determined three times for each of the animals in each of the conditions.

Stimulus conditions consisted of repeated tone pulses presented at a repetition period of 100 msec with a rise-fall time of 2.5 msec. Thresholds were measured for pulse durations of 2.5, 5, 10, 20, 40, 80 msec and continuous (Fig. 5). The pulse duration was defined as the time at peak intensity. The stimulus interval was 7 sec in length. For each of the pulse durations there was both an added noise and as ambient condition. The order of conditions was randomly determined. Additional data were obtained in quiet at a 1000 msec repetition period at 20 and 100 msec pulse durations using identical procedures.

The investigations by Popper (1972) and Offutt (1967) presented stimuli at signal frequencies of 500 Hz and 400 Hz respectively. The present experiment instead, generated signals at 800 Hz since the frequency characteristics of the test tank did not allow simple ogival rise-fall envelopes at the lower frequencies. There is no reason to believe that

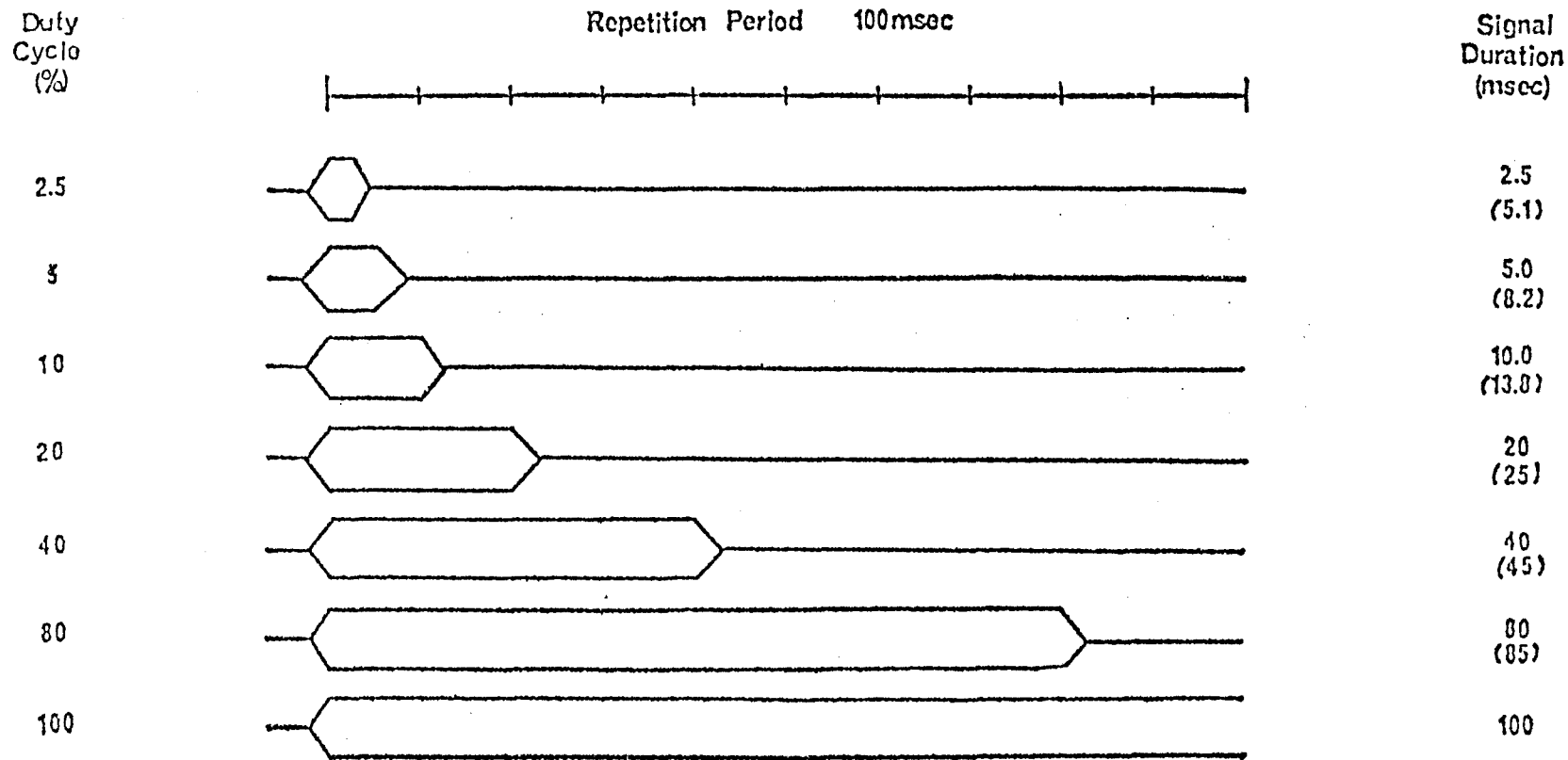


Figure 5: Stimuli from the present experiment.

this change in stimulus frequency should significantly alter the results since tuning curve data suggest that the neural channels responding at the lower frequencies are the same as those responding at 800 Hz (Fay, 1978; Furukawa and Ishii, 1967).

The stimuli used in this study were Fourier analyzed to produce the spectra in Figures 1, 2 and 3. It is evident that as the duration of the pulse decreases the width of the main energy peak ($1/T$) increases and its amplitude decreases. The energy peaks present at the lower frequencies represent 60 Hz interference and its harmonics. Calculations of signal durations based on the width of the main energy peak yield effective durations of 5.1, 8.2, 13.8, 25, 45 and 85 msec. These durations will be used for all calculations and plotting of data.

The spectrum of the wide-band noise used in the experiment can be seen in Figure 6. The noise level at 800 Hz was -44 dB re: 1 dyne/cm^2 .

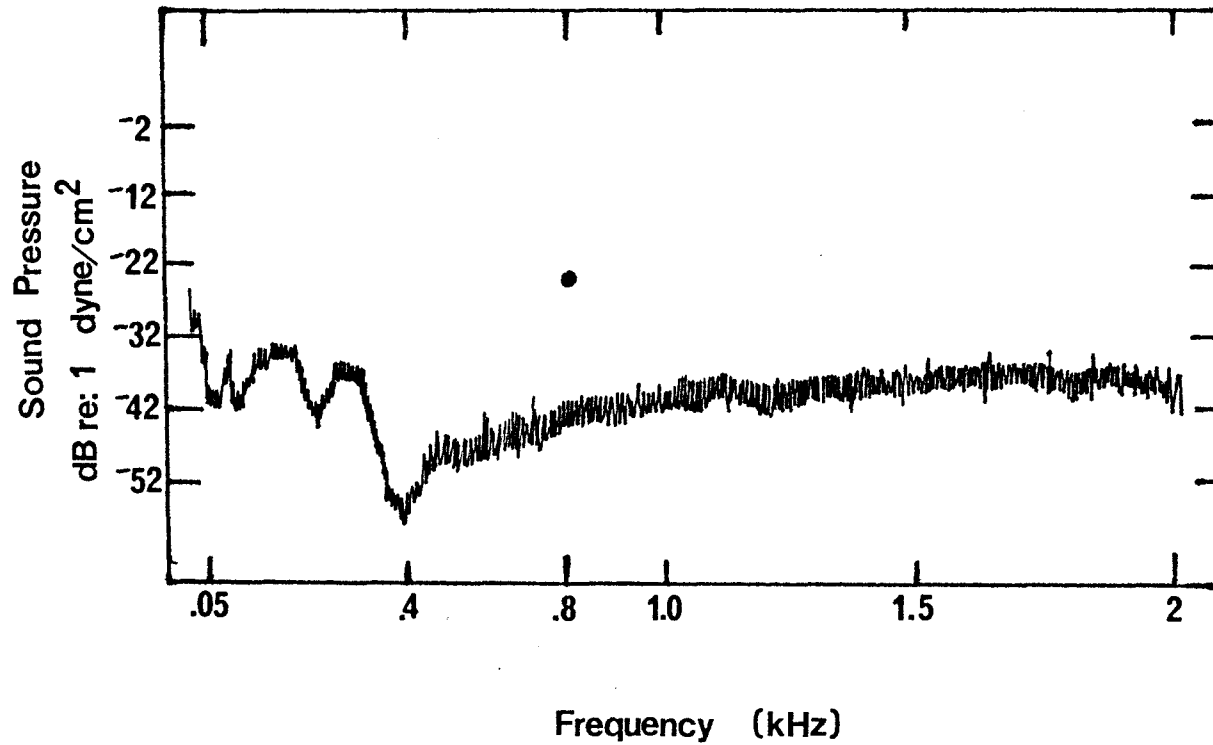


Figure 6: Spectrum of the noise background for the present study. The dot represents the masked threshold.

RESULTS

Three threshold estimates were made for each fish for each tone duration, giving a total of 108 measurements. Seven threshold estimates were made for each animal in the continuous tone conditions, resulting in an additional 42 measurements. The data points are plotted in Figure 7 with straight lines connecting the median threshold values at each stimulus duration. The ambient (quiet) and noise conditions are presented as separate functions.

In quiet, there was no consistent effect of signal duration on threshold ($p > 0.05$). In the noise condition, a significant effect (repeated measures analysis of variance) among thresholds and across signal durations was found ($p < 0.01$). An expanded analysis of variance measured a significant interaction ($p < 0.05$) between quiet, noise and signal duration. A significant difference between the noise and quiet conditions across signal duration ($p < 0.01$) was also noted. The difference between the continuous tone threshold in quiet and the same measurement in noise indicates 11 dB of masking. The threshold function of signal duration under noise showed nearly perfect integration, about a 3 dB threshold decrease per doubling of duration. There is a notable difference between pulsed and continuous thresholds in quiet, except for the 85 msec condition.

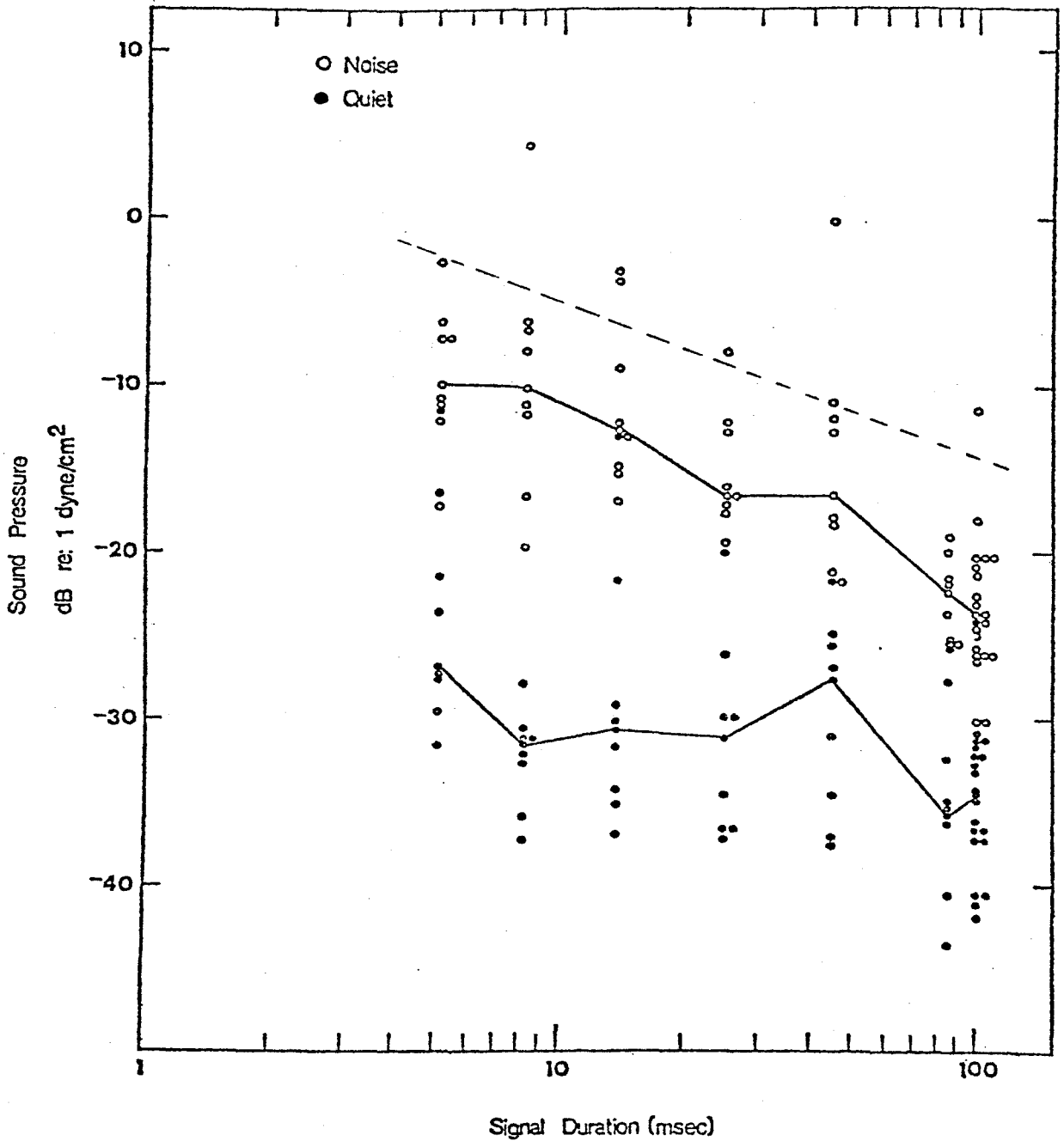


Figure 7: Experimental results from the 100 msec repetition period. The dashed line represents a 3 dB/octave slope.

A plot of the data collected at the 1000 msec repetition period (Fig. 8) shows essentially no difference in threshold as a function of duration. Again, it should be noted that a substantial difference between pulsed and continuous thresholds was observed. The majority of the data collected for the 1000 msec repetition period was with the original animals. However, one additional animal was trained to complete the needed data and did not exhibit any unusual threshold responses.

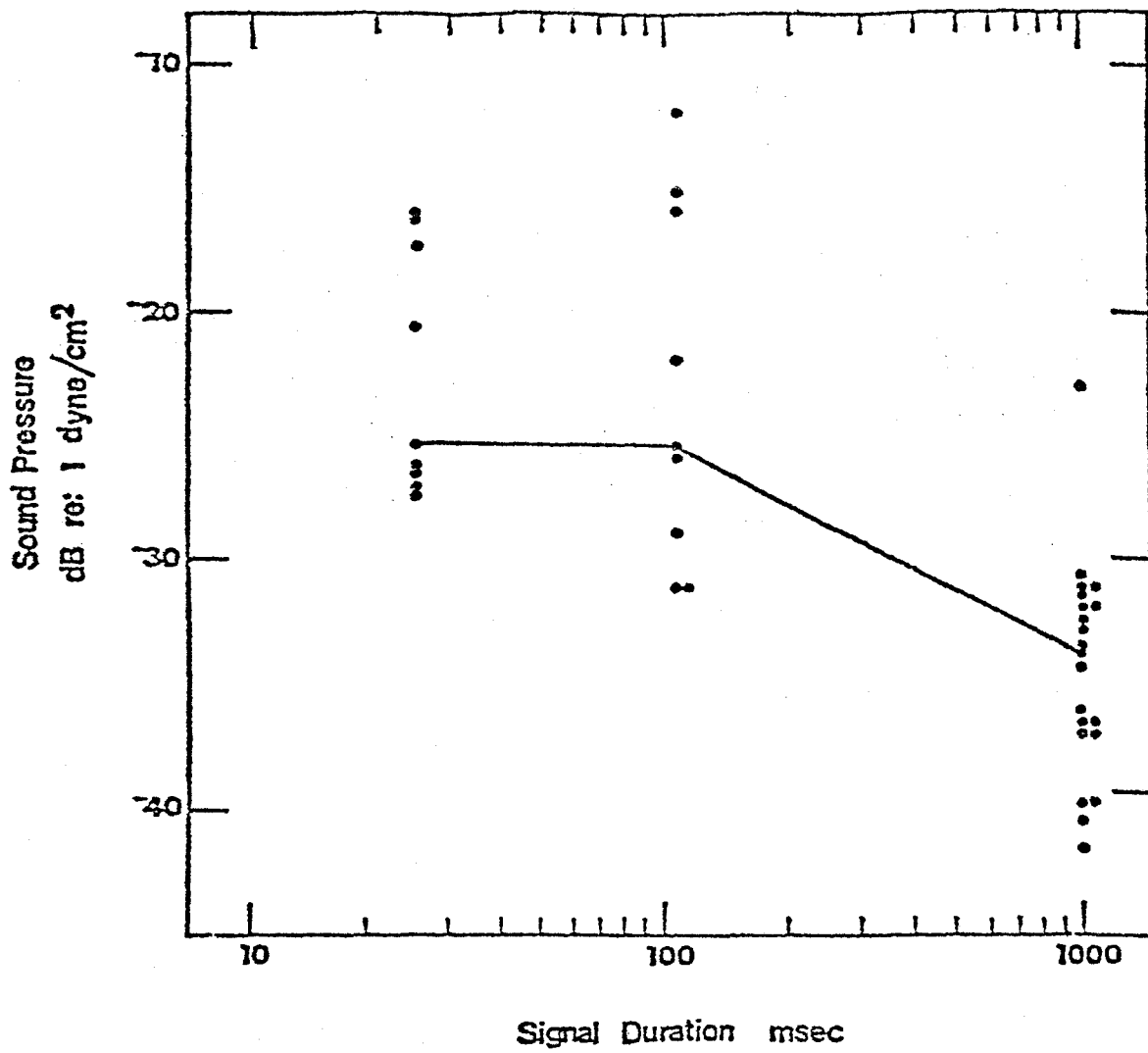


Figure 8: Experimental results from the 1000 msec repetition period.

DISCUSSION

Temporal Integration

The review of the literature concluded that temporal integration is performed in the auditory systems of man (Plomp and Bouman, 1959), other mammals (Ehret, 1976), and avian species (Dooling, 1979). It was noted, however, that previous investigations (Offutt, 1967; Popper, 1972) of temporal integration in the goldfish have presented conflicting results. One of the differences between these two studies was the level of a noise background. The present study sought to clarify this controversy for the species by re-examining the thresholds of stimulus conditions selected from both papers and tested under ambient and noise backgrounds.

The results (Fig. 7) of the present study indicate a behavioral difference between the noise and quiet conditions across signal duration. The results of the noise condition clearly show an effect of duration on threshold. The threshold function for the noise condition describes a temporal integration function where threshold decreases 3 dB for each doubling of signal duration. On the other hand, the results of the ambient condition at the 100 and 1000 msec repetition periods (Figs. 7 and 8) fail to show any discernable effect for signal duration.

Before discussing the significance of these results for the goldfish auditory system it may be worthwhile to note the results of a similar investigation on the cod (Gadus morrhua). The Hawkins and Horner (1980) experiment obtained masked auditory thresholds for single pulses of different durations and pulse sequences of varied duty cycles. A comparison of their results, reported as critical ratios, with those of the noise condition suggest that the auditory system of the cod also performs a temporal integration of brief duration stimuli (Fig. 9). The slope of the temporal integration function for the cod at the 100 msec repetition period is also about 3 dB per octave. Thresholds were not measured in quiet for this species.

A comparison of the continuous thresholds of Offutt (1967) and Popper (1972) indicate about 10 to 15 dB of masking, a possible result of the presence of a noise background (Fig. 9). Recall the present study exhibited 11 dB of masking. The results of the 100 and 1000 msec repetition periods in quiet and the Popper (1972) study all fail to show any clear effect of signal duration on threshold and thus lead to the conclusion that there is no evidence to support temporal integration in quiet in the auditory system of the goldfish. The results of the present noise condition and those of Offutt (1967) clearly indicate temporal integration. Apparently, the presence or absence of a background masking noise may account for the previously

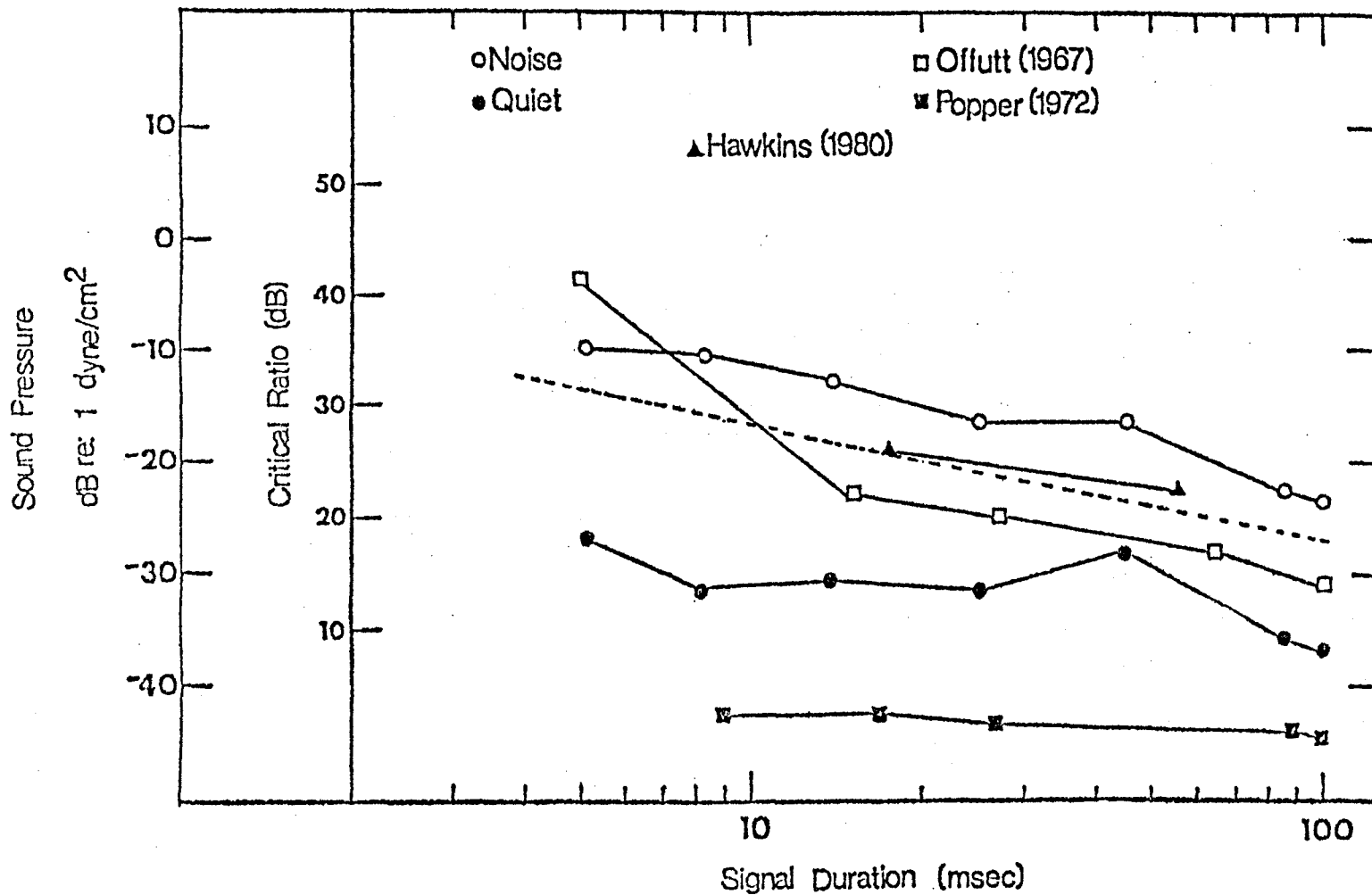


Figure 9: Comparison of results for Offutt (1967), Popper (1972), Hawkins and Horner (1980) and the present study. The dashed line represents a 3 dB/octave slope.



conflicting results for this species. It is also apparent from these conclusions that the goldfish auditory system employs different detection processes under noise and quiet conditions. A possible neural model dealing with these processes will be presented later.

It is difficult to make a complete statement about the effect of duty cycle on threshold because it is confounded with signal duration at the 100 msec repetition period. The effects of duty cycle, may explain the thresholds at 85 msec. In both the noise and quiet conditions the thresholds for 85 msec signals were noticeably different from the other pulsed stimuli, but similar to continuous thresholds. This is probably a result of the signal's duty cycle rather than duration.

Since the threshold-duration function in noise exhibited nearly perfect integration (3 dB/octave) throughout the durations used, it is impossible to calculate the integration time (\mathcal{T}) for this function. Although a (\mathcal{T}) cannot be calculated, a large portion of the results of the present study are consistent with Plomp's (1961) model, while most of the Offutt (1967) effects cannot be modelled. Given the limitations of the present experiment, however, it can be stated that the integration time or (\mathcal{T}) for the noise condition is significantly larger than 100 msec. Further, it is possible that temporal integration exists under quiet conditions but that the time constant may be

very small.

Critical Ratio and Critical Band

The main purpose of this experiment was to understand the issue of temporal integration in the goldfish auditory system. However, a brief examination of auditory masking in this species may also be accomplished. In masking studies the measurement of the critical ratio or difference in decibels between the level of the pure tone at threshold and the spectrum level of the noise is essential. A critical ratio (CR) of 15 dB would indicate that the signal at threshold is 15 dB above the power of the noise centered at the signal frequency. The data from the noise condition of this study were converted to critical ratios for this analysis.

An earlier psychophysical study by Fay (1974) measured the critical ratio for Carassius auratus at 5 frequencies between 100 and 1200 Hz. Although thresholds were not obtained at 800 Hz, an interpolation of the critical ratio function at this frequency equals about 22.5 dB (Fig. 10). The converted thresholds of the noise condition produce the critical ratio function presented in Figure 11. The median critical ratio value of 20.77 dB obtained for the masked continuous tone is about 2 dB below the critical ratio measured by Fay (1974) for the same species.

A comparison of the critical ratio function obtained

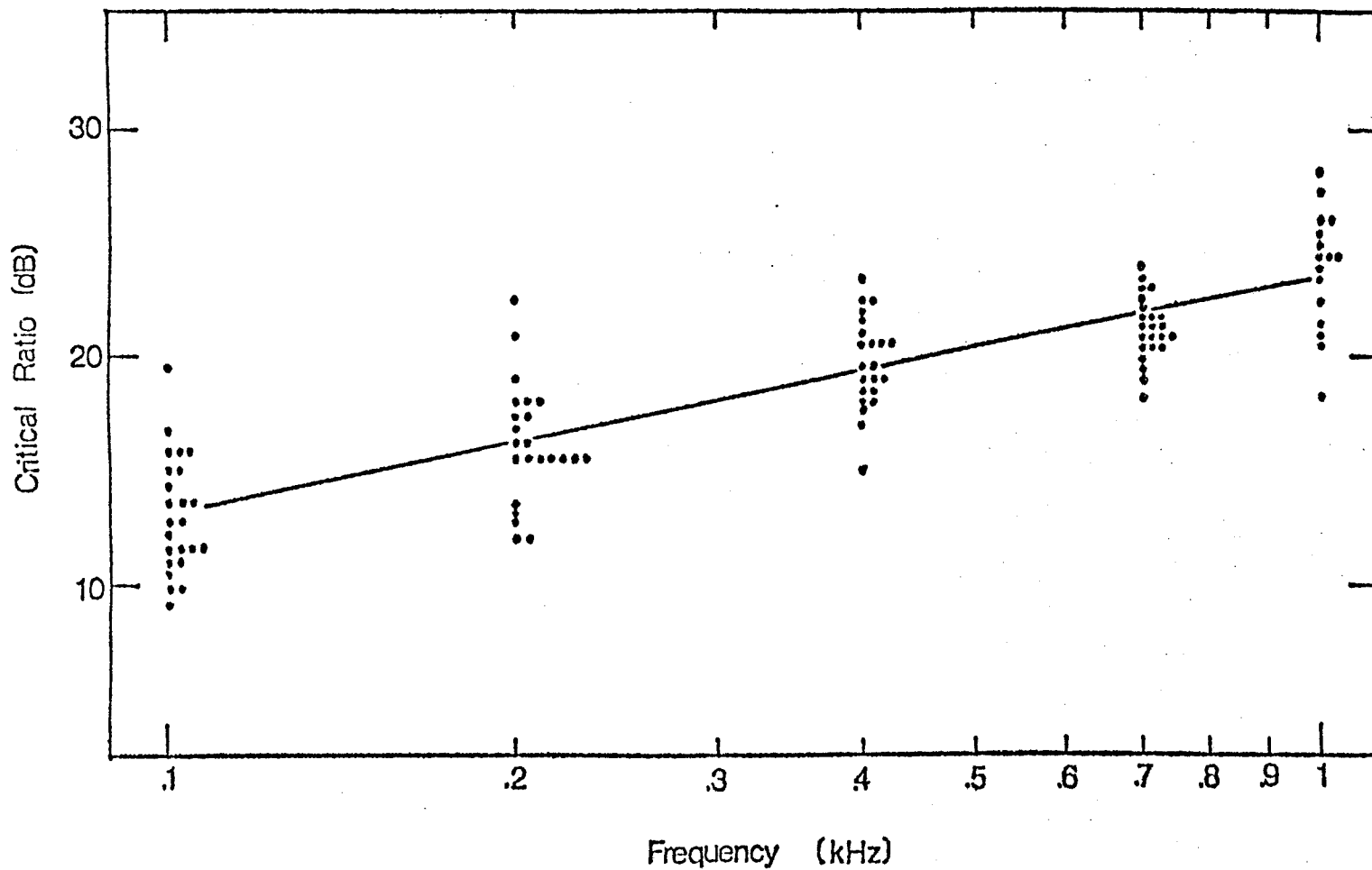


Figure 10: Results of the critical ratio study by Fay (1974).

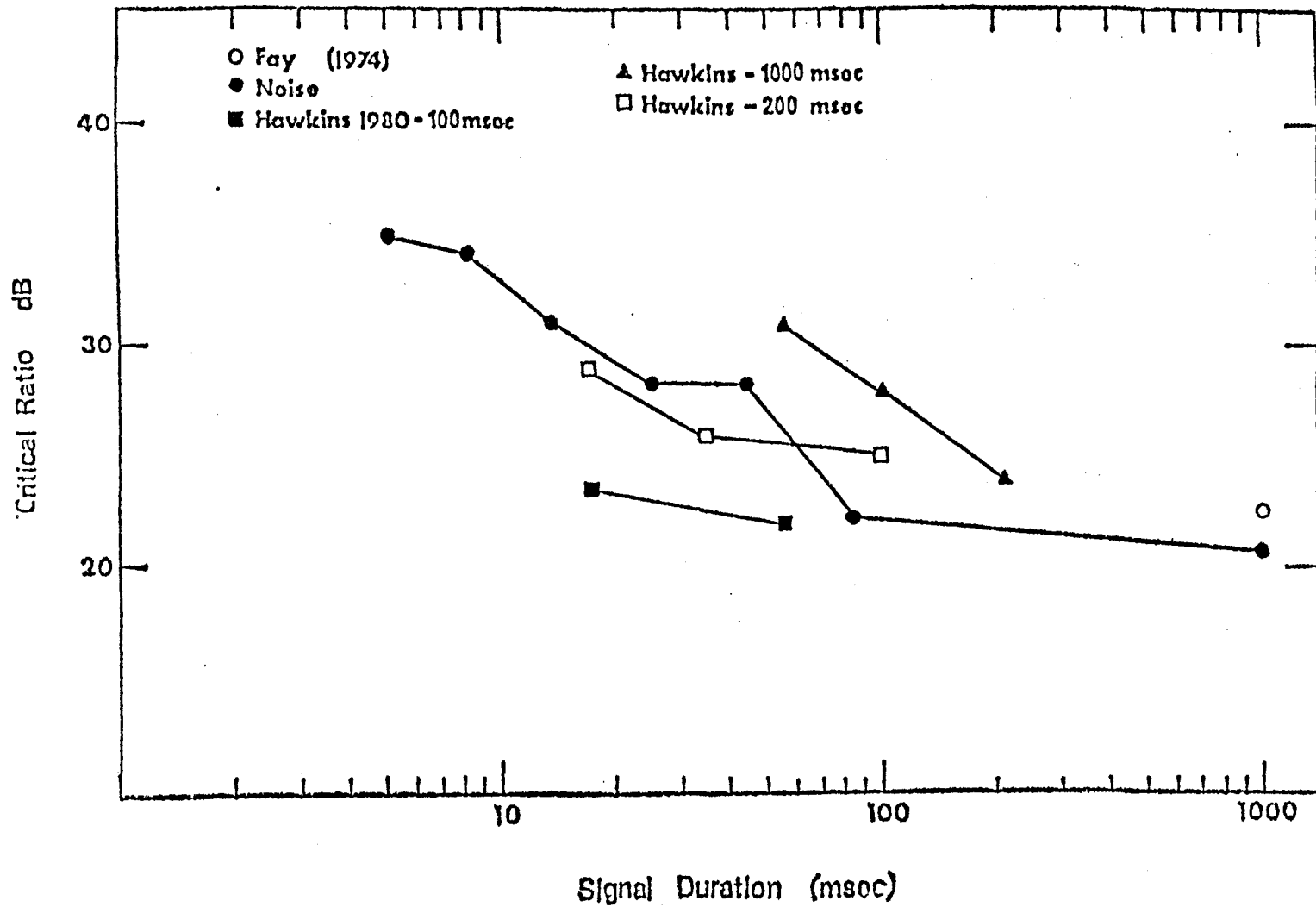


Figure 11: Critical ratio as a function of signal duration.

from the present experiment (Fig. 11) with that measured by Hawkins and Horner (1980) for the cod (Gadus morhua) exhibit similar slopes at repetition periods of 100, 200, and 1000 msec. Both functions suggest increasing critical ratios with decreasing signal durations. This growth of critical ratio with a decrease in signal duration implies that the frequency resolving abilities of the system may decline when analysis is required at shorter durations.

One of the early masking studies in man, Fletcher (1940), employed critical ratios to advance the understanding of the frequency selectivity of the auditory system. The experiment consisted of a wide-band noise masking a sinusoidal signal. The frequency spectrum of the noise was varied and its effect on the detection of a signal centered in the noise band was observed. It was found that a signal will be most easily masked by a masker having frequency components close to those of the signal. The frequency components in a flat masking noise effective in masking a pure tone located at the center of the noise band comprises the critical band (CB). The previously measured critical ratio can be converted into estimates of the critical noise bandwidth effective in masking a pure tone signal by making two assumptions. First, only a rectangular band of noise centering on the signal frequency produces masking. Second, the power of the signal is equal to the power of the noise band when the signal is at threshold. A change in duration

as was the case with the critical ratio would suggest changing frequency selectivity.

$$CB = 10 \left[\left(CR/10 \right) \right] \quad (8)$$

Using the above equation, the critical ratio bandwidths for the median threshold values were calculated. Figure 12 presents the CB values as a function of duration. While it is apparent that CB increases with decreasing signal duration, the values are unreasonable. At stimulus durations less than 20 msec the CB exceeds or nearly exceeds the hearing bandwidth for this species. The CB is more than 10 times larger than the measured bandwidth of the main spectral energy peak of the signal. It is conceivable that the critical bandwidth for the goldfish may vary with signal duration to accommodate the corresponding changes in spectral energy. It is impossible to conclude from these results if the critical band is changing with duration or if the critical band remains fixed and the animal is temporally integrating. A study designed for this purpose may be more conclusive.

Neural Model

The results of this study indicate that the goldfish auditory system processes short duration signals differently in noisy and quiet conditions. With a noise background the system appears to be performing temporal integration, while in an ambient condition, pulse durations have no ef-

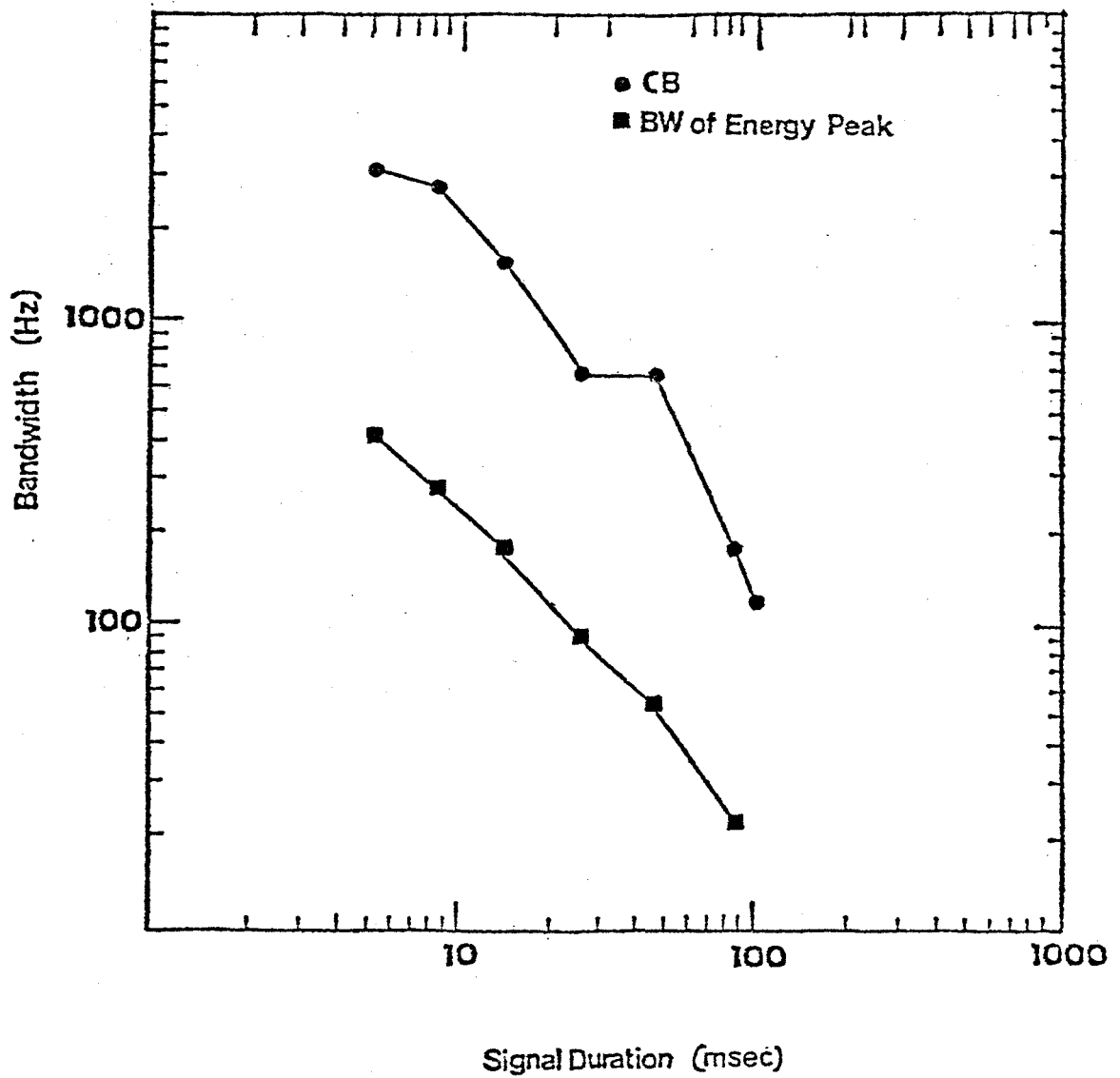


Figure 12: Variation in the critical bandwidth as a function of duration.

fect on threshold. Furthermore, it is interesting to note that this dual processing has not been observed in any other vertebrates.

On the basis of present neurophysiological evidence for the goldfish auditory system (Furukawa and Ishii, 1967; Fay, 1978), it is possible to propose an explanation for the psychophysical results just described by examining the properties of non-spontaneous neural fibers. Non-spontaneous or Saccular Type I (Furukawa and Ishii, 1967) fibers in this species have steep input-output functions and marked sensitivity at high frequencies (i.e. 800 Hz). It is possible that the thresholds in quiet are determined by non-spontaneous neurons which respond to stimulation with rapid changes in spike rate. In this case neural detection decisions would be based on the presence or absence of neural activity in normally silent channels. When noise is added to the acoustic environment, the non-spontaneous neurons are no longer silent and may now "behave" like spontaneous units. Spontaneous fibers respond to stimuli with gradually changing spike rates and are not as sensitive as their non-spontaneous counterparts. In the noise situation detection decisions may result from a statistical analysis of neural activity changing over time. If detection occurs in this manner, then the different psychophysical results may be due to the fact that detection of signals in noise and in quiet are two qualitatively dif-

ferent situations. Detection in quiet requires the presence of neural activity in non-spontaneous fibers, while detection in a noise background asks the system to analyze changes which may be more easily detected through a temporal averaging process.

It is important to make the assumption that non-spontaneous neurons are responsible for the detection of signals in quiet for the goldfish. Investigations of the avian auditory nerve (Sachs, Lewis and Young, 1974) note the complete absence of non-spontaneous fibers in these auditory systems. On the other hand, studies on the cat (Liberman, 1978) note that a large class of fibers in the auditory nerve are non-spontaneous fibers with generally poor sensitivity. Given this evidence it is possible that the temporal integration of acoustic energy occurring in the noise condition for the goldfish and in other species may be performed by spontaneously active or noise driven fibers. The highly sensitive non-spontaneous neurons observed only in the goldfish auditory nerve may be responsible for detection of short duration signals in quiet and thus account for the lack of temporal summation observed psychophysically in this experiment.

Summary

The results of this study suggest that the detection of brief stimuli by the goldfish auditory system may be per-

formed by different underlying processes depending on whether detection is required in a noisy or a quiet environment. It is possible that the temporal integration functions obtained by Offutt (1967) and those of the noise condition were due to the levels of background noise. On the other hand, the absence of temporal integration in the Popper (1972) study and the ambient thresholds of this experiment suggest that in quiet conditions, the goldfish may be able to detect short duration signals as easily as long duration signals. The previously conflicting results may have been caused by the noise levels of the test situations, a point that should be considered in future experiments of this nature.

The data of the noise condition also permitted the measurement of the critical masking ratio and the critical band for the goldfish. The critical ratios obtained from this study were within 2 dB of ratios measured for this species by Fay (1974). The critical ratio function across signal duration for the goldfish compared favorably with the identical function for the cod (Hawkins and Horner, 1980). The calculated critical bandwidths were observed to increase with decreasing signal duration. However, the validity of the critical band is questionable because of the extreme values.

Finally, a hypothetical neurophysiological model was proposed which may qualitatively account for the different

processing of signals in noise and quiet. It is thought that the detection of signals in quiet for the goldfish may be performed by the non-spontaneous fibers. Detection of signals in noise backgrounds may be performed by the spontaneously active or noise driven fibers. Detection decisions in quiet may be based on the presence or absence of neural activity in normally silent channels. While in noise, the decision results from a statistical analysis of neural activity over time.

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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Arts.

April 20, 1981
Date

Richard R. Fay
Director's Signature