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AUDITORY SENSITIVITY OF THE GOLDFISH
WITHIN THE NEAR ACOUSTIC FIELD

by

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AUDITORY SENSITIVITY OF THE GOLDFISH
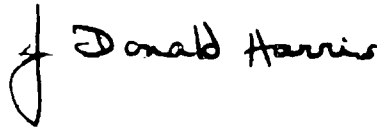# WITHIN THE NEAR ACOUSTIC FIELD

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Richard R. Fay

SUBMARINE MEDICAL RESEARCH LABORATORY

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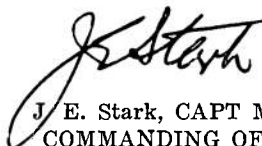
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SUMMARY PAGE

THE PROBLEM

To study auditory sensitivity and discrimination within the acoustic near field for goldfish.

FINDINGS

The sensitivity of goldfish to a low frequency sound source varies with distance of the fish from the source and is not a simple function of sound pressure. Goldfish are able to discriminate small changes in the frequency of a sound. Sensitivity of fish can not be inferred from measurements of ambient sound pressure levels. Goldfish are sensitive to the direction from which a sound arrives.

APPLICATION

These findings contribute to the general understanding of the mechanism of sensitivity of goldfish to low frequency acoustic energy. This information will be useful in studies of underwater acoustic insult using goldfish as experimental subjects.

ABSTRACT

Four experiments were conducted on auditory sensitivity and discrimination of goldfish within the acoustic near field. Experiment I studied the effects of the near field on sound pressure thresholds. The sensitivity of goldfish in terms of sound pressure appeared to vary with distance from the sound source. Experiment II studied stimulus generalization and frequency discrimination within the near field. A generalization gradient was observed which indicated that goldfish can discriminate a frequency change as small as 12.5% without explicit differential training. Experiment III studied the effects of far field noise or near field thresholds. A masking effect was observed which appeared to be a negatively accelerated function of masker spectrum level. Experiment IV tested the ability of goldfish to localize a sound source within the near field. It was shown that goldfish could discriminate between right 45° and left 45° stimulus directions. Discussion is presented concerning the implications of the results of the four experiments and their relevance to the study of underwater communication.

AUDITORY SENSITIVITY OF THE GOLDFISH
WITHIN THE NEAR ACOUSTIC FIELD

I. INTRODUCTION

In recent decades, the study of the acoustic behavior of marine animals has received a new vigor. Researchers in the area of sonar technology and underwater communications have turned to animals for possible mechanical and electronic models in an effort to solve problems involved with human communication (Dreher[1], Kuroki[2]). In addition, research in the evolution of vertebrate hearing is pointing farther down the evolutionary scale for the origin of a structure capable of frequency analysis (van Bergeijk[3]). In recent years, for example, behavioral evidence has accumulated (Tavolga[4]), that the fish's inner ear may, in fact, analyze frequency in a manner analogous to the mechanical action of the coiled basilar membrane of the more advanced vertebrates (van Bergeijk[5]). This finding was not predicted from what is known about the structure of the teleostean ear.

Classical research in fish hearing has been concerned with whether or not certain species can hear, and what bands of frequencies are relevant. Almost all studies done prior to 1960 have been questioned on a number of issues due to inadequate control and measurement of the sound stimulus and to high and unspecified levels of ambient noise. For example, Harris[6] reviewed the physics of underwater sound sources and introduced the concept of the "near field" to the ichthyologists. Harris' discussion indicated first, that sound generated underwater behaves in a complex way that is difficult to measure. Any moving object not only generates acoustic pressure waves and their concomitant particle displacements, but also hydrodynamic particle displacement activity known as near field energy. These fluid displacement effects are negligible to terrestrial animals due to the low acoustic impedance of air. In water, however, where the acoustic impedance is about 3000 times greater, these near field displacements may make up most of the displacement energy up to one wavelength away from the source, and attenuate as the cube of the distance from the source. Thus, these effects are most important at the low frequencies, due to the relatively longer wavelengths, and at distances close to the source. Unfortunately, the standard pressure sensitive hydrophone is inadequate in measuring this energy. Evidence exists (Enger[7]), for the role of the inner ear in direct displacement sensitivity: a behavioral separation between responses to a stimulus with a high amplitude near field component and a stimulus with a low amplitude near field component can be shown electrophysiologically by recording from single units of the medulla near the entrance of the VIIIth nerve.

Thus, it is probably true if we say that within the near field, either or both receptors may function to transmit frequency, intensity and directional information to the brain. For high frequencies at greater source distances, where purely pressure waves predominate (far field), the ears stimulated via the air bladder seem to be the relevant receptors. All this, of course, depends upon frequency, intensity, the type of source and its distance.

The general approach taken by most investigators has been to eliminate near field effects by either generating the stimulus in air or by lengthening the distance between the source and the fish. The result of both procedures is that the stimulus is necessarily made somewhat artificial. An alternative approach to the problem is to study the near field phenomena themselves.

Several of the physical factors may be controlled by generating the stimulus in air, above the water surface (Parvalescu[8, 9]). In this case, near field effects may be minimized so long as the pressure waves to not add out of phase at the surface of the water. Enger[7] used this method in conjunction with an underwater loudspeaker in order to obtain two distinct audiograms for the goldfish. It appeared that the near field effect was evident up to 700 Hz at distances as great as several meters. As Jacobs and Tavolga[10] and von Bekesy[11] have observed, however, one cannot

simply assume that this method completely eliminates near field effects.

The present series of experiments was designed to study auditory sensitivity and discrimination within the acoustic near field for the common goldfish, using conditioned inhibition of respiration. Experiment I studied the effects of the near field on sound pressure thresholds. Experiment II studied stimulus generalization and frequency discrimination within the near field. Experiment III studied the effects of far field noise on near field thresholds. Experiment IV tested ability of the goldfish to localize the sound source with the near field.

II. GENERAL PROCEDURE AND RESULTS

A full account is found in Fay[12]. Four young, common goldfish about five to six inches long were used throughout the four experiments. For Experiments I and IV, the experimental tank was a 4 x 4 x 1-ft wood box supported by four 16-in heavy duty, rubber inner tubes to reduce noise and vibration from the floor. In Experiment I, where more sound-proof conditions were desirable, the tank was placed on a concrete floor in a small basement room. For Experiments II and III a 23-gallon glass aquarium served, supported by a 16-in inner tube on the floor. The fish was held in a plexiglas and sponge restrainer approximately 6 inches above the floor of the tank. The fish could be shocked through tin electrodes.

The respiration response was recorded by a mechanical connection between the fish's lower lip and the needle of a phonograph crystal cartridge. Fish, restrainer, shock electrodes, and cartridge were all rigidly constructed as a single unit that could be taken in and out of the tank together.

The electrical signal (see Fig. 1) was transduced by a 5-in Lafayette acoustic suspension loud speaker; most of the loudspeaker cone was removed so that its sound pressure generating capabilities were minimized, while still retaining its rigid structure. A 1 x ¼-in styrofoam cylinder was glued to the center of the speaker cone. A large plastic soda straw was then imbedded

in the styrofoam and a ping-pong ball, filled with water, served as the dipole sound source. Only the ball and most of the straw were in the water.

The conditioned stimulus (CS) and unconditioned stimulus (UCS) durations and the interstimulus intervals were controlled by timers. The CS was of course acoustic energy, the UCS electric shock. The "white" masking noise of Experiment III was transduced by a 10-in acoustic suspension loudspeaker located 21 in above the water. The sound monitoring equipment was an Atlantic Research Corp., Model LC32 transducer, the output of which was amplified, filtered, and measured with a vacuum tube volt meter (VTVM).

Details of maintaining and handling the fish and of preliminary studies which led to the pattern and strength of stimulus parameters have been given (Fay[12]). To summarize the conditioning procedures: CS frequency was 40 Hz; CS-UCS interval was 4 sec, intertrial interval was 2 min; UCS duration was 1 sec. Figure 2 is a tracing of the typical conditioned and unconditioned responses after 20 trials.

EXPERIMENT I. Effect of the Near Field on Sound Pressure Thresholds.

In this experiment the amplitude of the near field was controlled by varying the distance between the source and the subject. It was hypothesized that if the fish responded to some aspect of near field energy, the threshold in terms of sound pressure would appear to increase with distance, due to the rapid attenuation of the near field. If, on the other hand, the fish responded to pressure fluctuations as measured by a standard hydrophone, the threshold should remain constant regardless of distance.

Procedure.

The dipole source was positioned either 13, 18, 23, 28, 33, 38, or 43 cm from the center of the subject's head at 0° azimuth. Threshold was determined by a method of limits in steps of 3 db. When the determination was completed, the source was moved to a new
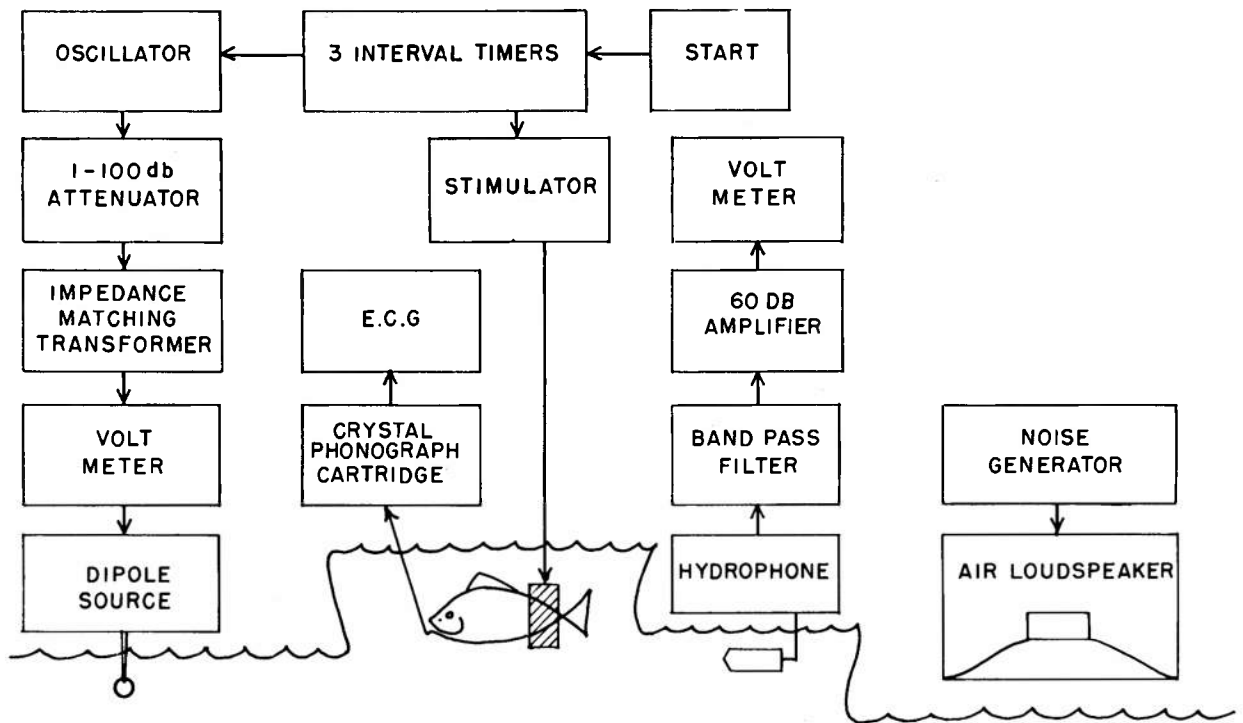
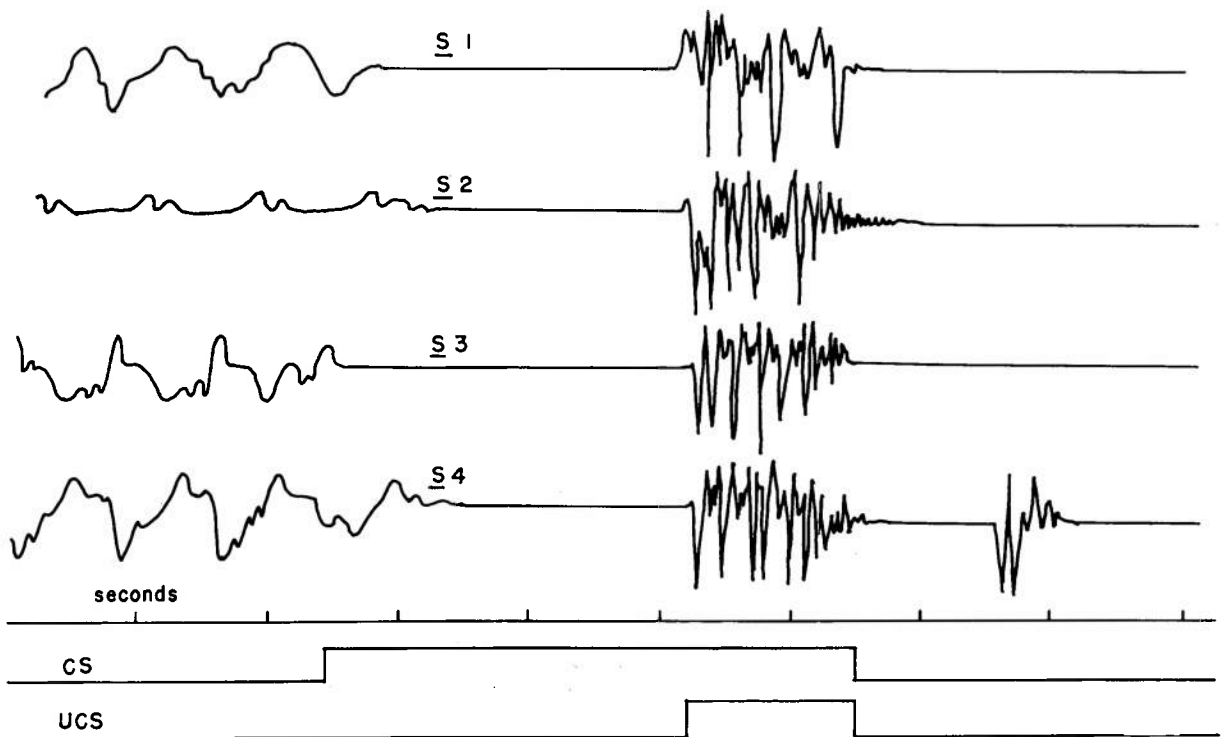Fig. 1.   Block diagram of the electronic equipment.

Fig. 2.   Typical conditioned and unconditioned inhibition of respiration responses for each subject after approximately 20 conditioning trials.

position and a new threshold series started. No more than three determinations were attempted for any subject in a single session. The experiment was completed after four subjects were tested twice at each distance.

In determining threshold in db/1 microbar, the hydrophone was placed in the restrainer in place of the fish and several measurements were taken at each source distance. Two runs taken with the hydrophone in a vertical orientation, and two taken in a horizontal orientation, were averaged to give mean sound pressure values in db/1 volt.

Results.

The results of this experiment appear in Figure 3. Data were converted to db/1 microbar by measuring the sound pressure at 0 db attenuation and subtracting from this the attenuator setting corresponding to each threshold value. The following is the formula used in this conversion:

Fig. 3. **Sound pressure thresholds as a function of distance between the source and the fish. The points are means for each S.**

rements would confirm the phenomenon of true conditioning and would rule out the possibilities that sensitization, pseudo-conditioning, or conditioning to experimental arti-

Sound Pressure in db/1μ bar	=	Amplified Hydrophone Output	—	60 db Amp. Factor	+	hydrophone sensitivity (— 104 db/1 volt/ 1 μ bar/40 Hz.)	—	attenuator setting (db/ .5 volt)

It is clear from Figure 3 that the increase in source distance from 13 cm. to 28 cm. had the apparent effect of raising sound pressure thresholds. This effect, however, was complex in that thresholds were lowest when the source was at its most extreme positions. Threshold values systematically decreased as the source was moved from 28 cm to 43 cm from the fish, yielding the U-shaped function in Figure 3. This trend appeared to be reliable across all fish. The sensitivity of the fish in terms of threshold sound pressure, therefore, appeared to change with distance from the source.

EXPERIMENT II. Stimulus Generalization.

A number of factors combined to suggest that a test of stimulus generalization over several frequencies surrounding 40 Hz would yield valuable information. Particularly, the appearance of consistant generalization dec-
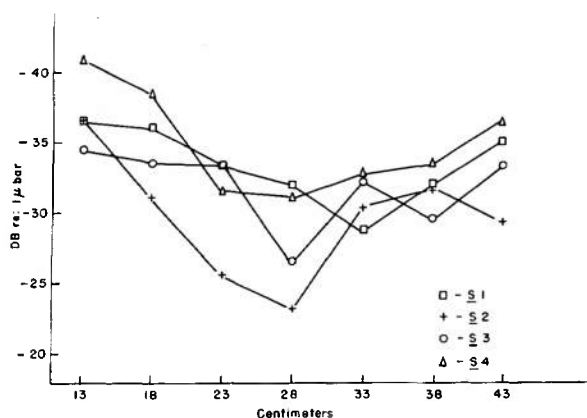
facts, such as mechanical transients in the transducer, were responsible for the thresholds determined in Experiment I.

Procedure.

The four fish used in Experiment I were run once in a series of 24 massed generalization trials where responses were recorded to eight frequencies (20, 25, 30, 35, 40, 45, 50, 60, 70 Hz) presented three times each, in random order. On each trial, the stimulus was presented without shock. Every fifth trial was a conditioning trial at 40 Hz. The inter-trial interval was approximately 1 min and the stimulus intensity remained high throughout the test. Sound pressure was not controlled, but was found to increase with frequency through subsequent measurements. Percent generalization was analyzed in terms of both amplitude and rate of breathing.

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Results.

Mean percent generalization at each frequency appears in Figure 4 for both amplitude and rate. It is evident that a sharp generalization gradient (decrement) did occur for the frequencies tested, and that a change as small as 12.5% could be discriminated without explicit differential training. That is, the response measures indicate that 25 Hz, and 45 Hz were perceived as different from 40 Hz. All specimens behaved essentially alike, in that generalization was slightly asymmetrical, with the steepest decrement occurring toward the lower frequencies.
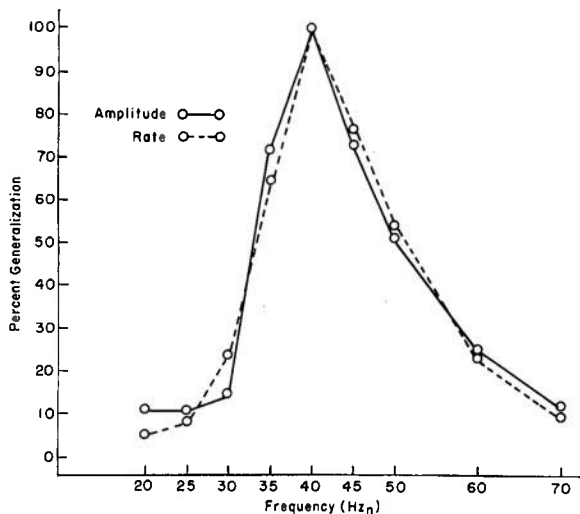

Fig. 4. Mean percent stimulus generalization for several test frequencies for all Ss, in terms of both amplitude and rate change.

EXPERIMENT III. Masking.

This experiment studied the effects of broad band noise on tonal thresholds. It was thought that if the detected signal was predominantly far field pressure fluctuations, then the noise would have differential effects depending on the receptor system responsible for the detection of the signal. That is, if the ear were directly responsive to the near field generated by the dipole source, then the far field noise would efficiently mask the signal through the activity of the air bladder. If, on the other hand, the lateral line system was responsible for mediating responses to the near field, then relatively high intensities

of noise would be necessary to produce significant masking effects.

Procedure.

Three noise level conditions in 10-db steps were created by generating white noise through the air loudspeaker. Thresholds at 40 Hz in these noises were determined exactly as in Experiment I, including the ambient condition (air loudspeaker "off"). Also, thresholds for the 40-Hz tone generated in air were determined under ambient noise. During the masked threshold determinations, the noise was on constantly.

Results.

The masking effects of the noise levels are shown in Figure 5. An increment in the noise level induced an increment in threshold value. The relationships between these two
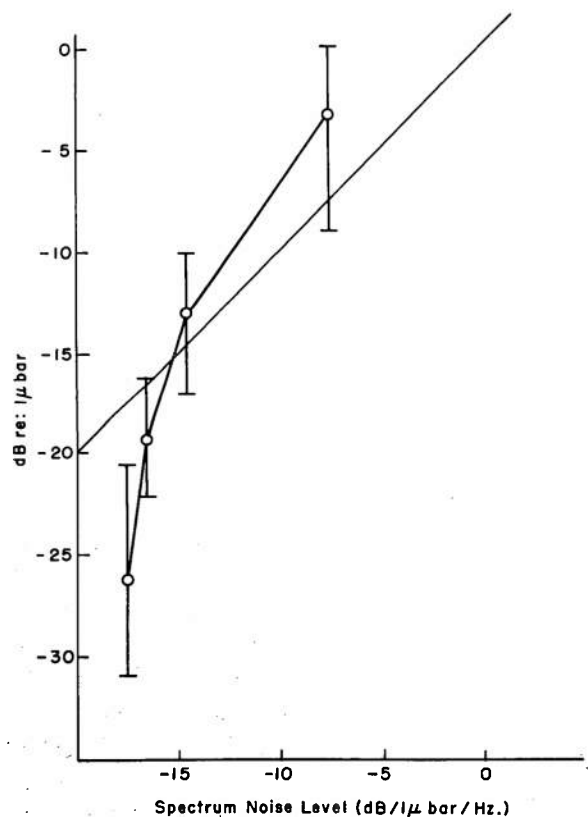

Fig. 5. Mean masked thresholds as a function of spectrum noise level at 40 Hz compared to the ideal function for humans in air. The vertical lines indicate the ranges of threshold values.

increments, however, are complex. A 1-db increment of the noise spectrum level at 40 Hz over the ambient noise level produced a 7-db increment in threshold. This trend continues in what appears to be a negatively accelerating function. All subjects behaved similarly. Thresholds under ambient noise were 8.8 db below the spectrum level at 40 Hz (S/N = —8.8 db). With a 1-db noise increment, the S/N rose to —2.8. As the noise level rose further in 10-db steps, the S/N rose to +1.5 and then to +4.3.

Of interest was the finding that the sound pressure threshold for the dipole source was within 2.4 db of the threshold for the air loudspeaker.

EXPERIMENT IV: Discrimination of Location.

This experiment attempted to condition a discrimination between the stimulus patterns generated by the dipole source in different positions relative to the fish, the sound pressure level remaining constant. In effect, this experiment tested the ability of the fish to discriminate different acoustic patterns without additional sound pressure or frequency differences cues. It was assumed that any receptor system involved in making this pattern discrimination would have to be sensitive to either time or intensity differences within the near field, and that the central nervous system would have to be able to process this information.

Procedure.

The subject was restrained in the center of the large wooden tank as in Experiment I. An opaque screen was placed around the fish so that no visual cues regarding the location of the source were available. The dipole source could be moved to any position around a circle (15 cm radius) with the fish's head at its center.

Training sessions consisted of 60 massed trials at 1-min intertrial intervals. Differential classical conditioning was used such that a USC (shock) always followed the CS onset by 4 sec when the source was 45° to the right (positive trial). Shock was withheld when the source was 45° to the left (neutral trial). Positive and neutral trials were presented in alternating order.

Testing trials consisted of presenting the stimulus on the left or right for 6 sec in either LRRL or RLLR order without shock to either stimulus. Testing began immediately after training and consisted of 16 trials, eight to the positive stimulus, and eight to the neutral stimulus.

Discrimination in terms of both amplitude and rate was analyzed. Rate was measured in the number of respirations during the 5 sec before and after the stimulus onset. Amplitude was measured in cm during the 5 sec before and after the stimulus onset. A difference in response rate deceleration or in response amplitude decrease between responses to the positive and neutral stimuli indicated the ability to discriminate.

Results.

Measurements of amplitude and rate before and after the CS onset are presented in Figures 6 and 7 respectively.

Although there were large individual differences in terms of both amplitude and rate measures, it is evident that discrimination was demonstrated in all subjects. Inspection of the raw data revealed the nature of these individual differences. Of particular interest are the responses of Subject No. 1 to the positive stimulus both early and late in testing. Early in testing, there appears to be a component of the reflexive jerking of the mouth which always accompanied shock. This fish was the only one which showed the conditioning of this response component. Later in testing, this component dropped out, and the conditioned inhibition of respiration appeared more normal.

The nature of the differential responding to the positive and neutral stimuli is particularly significant. If a measurable rate or amplitude supression did occur following the neutral stimulus, it occurred within the first three or four sec. In most cases, respiration started to resume its normal course within the last two or three sec of the stimulus presentation. This is to be contrasted with re-
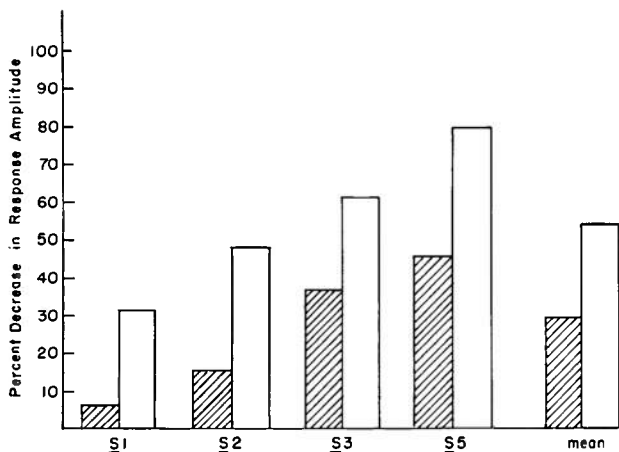
Fig. 6. Percent decrease in response amplitude following neutral (shaded) stimulus onset, and following positive (unshaded) stimulus onset in discrimination of location test trials. Each bar represents the mean of 8 trials.

sponses to the positive stimulus for which response supression became greater at the end of the CS presentation. Thus, the differences between the responses to the positive and neutral stimuli are most evident during the last two or three sec of the stimulus presentation.

III. GENERAL DISCUSSION

The most striking aspect of the conditioning procedure is that inhibition of respiration is conditioned very rapidly. All four fish showed a clear anticipatory conditioned response within eight conditioning trials These responses were clear and unambiguous, especially at high intensities of the CS. During threshold determinations, however, the conditioned response tended to become more ambiguous as the threshold was approached. At times, and depending on the subject, the response was evident more as a rate and amplitude decrease rather than a complete suppression. Often, too, the latency of the response would become greater, possibly indicating that the total acoustic energy summated over time has some effect on threshold in fish, (Offutt[13]). For other subjects, however, the responses near threshold were quite clear.

The usefulness of the respiration suppression response is indicated dramatically in Experiments II and IV, where subtle discriminations were measured with relatively

few test trials. In Experiment II, for example, stimulus generalization could be quantitatively measured on the basis of one trial at each stimulus value rather than on the frequency of response occurrence over a number of trials. In Experiment IV, the two response measures, rate and amplitude change, correlated well to indicate a classically conditioned discrimination that was measured in terms of reliable but quite subtle response differences.

In summary then, the classically conditioned inhibition of respiration has been shown to be a reliable and useful response in a variety of psychophysical experiments with goldfish. The response is quickly conditioned, easily measured, and is particularly useful in discrimination learning, where quantitative measures can be made on a single response sequence. The results of the four experi-
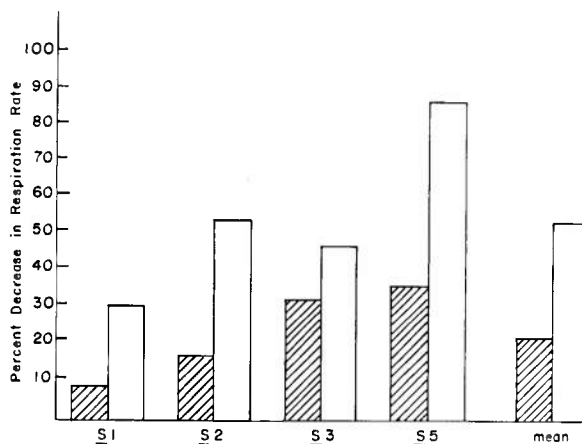
Fig. 7. Percent decrease in respiration rate following neutral (shaded) stimulus onset, and following positive (unshaded) stimulus onset in discrimination of location test trials. Each bar represents the mean of 8 trials.

ments can now be interpreted and discussed in terms of near field auditory sensitivity.

Experiment I indicated that the amplitude of the near field generated by a dipole source had an effect on sound pressure thresholds. More simply stated, the goldfish did not behave like a hydrophone. This indicates that some aspect of the stimulus, not adequately measured by a pressure sensing device, contributed to the energy responsible for the observed thresholds. It is assumed for two reasons, that this energy is near field particle displacement activity. First, the dipole source

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is an efficient near field generator, for which displacement energy predominates up to about one wavelength away from the source (about 125 ft at 40 Hz). Second, displacement activity, as such, is not adequately measured by the standard hydrophone.

It would appear reasonable, therefore, that the apparent dip in pressure sensitivity as the source was moved away from the fish was due to the attenuation of the near field which occurs with distance. Enger[7] has observed this same phenomenon with goldfish using an underwater loudspeaker. At 50 Hz, he found a 29-db difference between thresholds determined at 2 and at 20 cm from the source. This result had been predicted by Harris and van Bergeijk[14], on the assumption that the fish's responses would be mediated through the lateral line system. On the basis of the physiological work by Enger[7], Moulton and Dixon[15], however, it cannot be assumed that the lateral line system is responsible for the behavioral thresholds determined in the present experiment. It is equally likely that direct, near field stimulation of the inner ear may have mediated these responses.

The results of Experiment I are complicated, however, by the finding that as the distance between the fish and the transducer increased beyond 28 cm, the pressure sensitivity appeared to rise. Subsequent sound pressure measurements indicated that pressure did not attenuate with distance as predicted. It is evident, then, that the experimental tank did not approximate free field conditions. These unpredicted acoustic effects, therefore, were most probably due to complex reflection patterns from the tank walls. It is significant that the highest thresholds were observed when the transducer was placed halfway between the fish and the tank wall. It appears that as the transducer was moved toward the wall, more of the acoustic energy was reflected, or even amplified by the "acoustically soft" wall (Parvalescu[8]), which may have acted as a secondary sound source generating near field effects of its own. If this were the case, the closer the transducer was to the wall, the greater would be the acoustic energy radiated back into the tank. In the absence of direct physical measurements,

however, speculations of this kind have limited value. It is enough to say that the upward turn of the threshold curve in Figure 3 was probably a result of unpredicted acoustic effects.

The results of Experiment II indicate that the conditioned respiration suppression response does not readily generalize to other CS frequencies. While this is not critical to the specification of the receptor system involved, these results demonstrate that frequency discrimination around 40 Hz is quite sharp. Furthermore, it is evident that the thresholds determined in Experiments I and III were not a result of conditioning to extraneous cues such as mechanical and electrical switching transients. The possibility that the responses were merely the result of sensitization was also ruled out.

Due to the procedures involved, these results cannot be held as direct evidence on frequency discrimination ability in the goldfish. First, the limits of this ability were not necessarily approached because differential training was not explicitly used. Using a discrimination learning paradigm, frequency discrimination would probably have appeared more sharp. Second, intensity was not controlled. Subsequent sound pressure measurements showed that as the frequency increased from 20 Hz, the test tones increased about 25 db. These intensity differences do not predict the overall shape of the generalization curves, however. First, it is rare for an increased CS intensity to cause a generalization decrement (Kimble[16]). Second, it was observed in Experiment I that a drastic intensity decrease (20 db) did not cause a generalization decrement at 40 Hz as long as the stimuli were above threshold.

The consistent asymmetry of the generalization curves may be a result of these intensity diffrences, however. Where the intensities were low (20-35 Hz), the decrement was quite steep. Where the intensities increased (45-70 Hz), there was greater generalization. At any rate, it is significant that the response allowed the measurement of this steep generalization decrement, and that some amount of frequency discrimination exists for near field stimulation.

The results of Experiment III indicate that at low noise levels, thresholds within the near field were below the spectrum level of the noise, while for higher noise levels, the thresholds were shifted up above the noise (Fig. 5). These results are unlike results for human hearing in two ways. First, the signal to noise ratio (S/N) at threshold is never a negative quantity for humans, as long as noise is expressed in spectrum level. Second, the S/N does not change as the noise intensity is increased. Further, Tavolga[4] has shown that these human results agree well with masking data he has collected on two species of fish.

A possible explanation for the failure of the present experiment to reproduce these findings for the goldfish is that sound pressure S/N measurements may be irrelevant in describing masking within the near field. Thus, while the sound pressure S/N at threshold changed over the various noise conditions, the displacement amplitude S/N may have remained the same. That is, under ambient noise, the threshold appeared to be below the noise because the behavioral threshold was a function of displacement activity rather than of sound pressure. As a new source of noise was introduced above the tank, the particle displacement activity may have increased in some unpredictable manner in relation to the increment in sound pressure. This phenomenon may be explained by assuming that the presence of the loudspeaker added near field activity of its own, which, while not measured by the hydrophone, produced a significant masking effect on near field thresholds. In the absence of direct physical measurements, however, this question cannot be answered. It seems reasonable, though, that this non-linear masking effect was due to some complicated acoustic effects rather than to non-linear characteristics of the receptor system.

Further evidence for this kind of near field effect comes from the second part of Experiment III, where thresholds were determined for tones generated above the water. In this case, too, the detected signal was below the spectrum level of the noise at 40 Hz. Further, the threshold value was very close to that determined under ambient noise for the

dipole source. This finding was unpredicted in that it does not agree with the double audiogram found by Enger[7]. The most plausible explanation is that the conditions were such that a near field effect was generated at the surface of the water by the out of phase addition of acoustic energy.

In summary, then, the results of Experiment III indicate that a pressure measurement does not seem adequate to specify the total acoustic energy to which goldfish may respond. The masking curves probably represent the relation between unpredicted near field effects and the sound pressure levels which accompany them, rather than a true relation between sound pressure increments and masking effects. What is most interesting is that the thresholds determined under ambient noise were lower than most audiograms for the fish indicate (Weiss[10], Jacobs[17], Tavolga[18]). The thresholds determined in this experiment, even under relatively high ambient noise conditions, are more similar to those reported by Enger[7] for an underwater source with a high near field component. Under more optimal but unspecified noise conditions (Experiment I), the thresholds were generally below those reported by Enger, which are the lowest reported to date. It is probably safe to say, then, that all the thresholds determined in these experiments were masked thresholds, and that the absolute sensitivity of the receptors involved have not been experimentally approached.

The results of Experiment IV indicate that goldfish can be trained to discriminate between two auditory stimuli differing only as a result of their source location relative to the fish. These results do not indicate that fish will orient to a sound source, and they do not mean that the fish necessarily localized the sound source in this experiment. These results simply mean that the fish could discriminate the differences which exist between the pattern of near field energy as it was generated 45° to the left of the subject in one case, and 45° to the right in the other.

It is assumed that the major physical difference between these two patterns of stimulation was the direction of the near field intensity gradient. First, visual and sound pressure intensity cues were eliminated. Sec-

ond, the near field intensity gradient conveys a great amount of directional information (van Bergeijk[3]).

There has been an alternative explanation for this phenomenon which has appeared in the recent literature. Kuroki[2] combined a mechanical and electrical analysis of the lateral line system to postulate that localization is a result of the processing of time of arrival differences among the various receptor organs. This view has been criticized by Harris[6] on the grounds that the speed of sound in water is too great, and the nervous system of the fish is too primitive to allow complex neural interactions to take place on the basis of time differences. Moulton and Dixon[15] have also interpreted their localization results in terms of interaural time differences, but van Bergeijk[19] has provided a reasonable explanation based, again, on near field intensity gradient information processed through the inner ears. The neural processing, here, is assumed to start at the level of the medulla in the Mauthner cells.

The results of the present experiment, however, do not necessarily support either of these explanations. At best, these results demonstrate that it is possible for a goldfish to discriminate two stimuli, on the basis of the source location, without moving within the sound field. In order to do this, the receptor system involved must be sufficiently complex to process either time or intensity difference information. In either case, at least a two dimensional receptor array is required. Inner ear stimulation through pressure fluctuations acting on the air bladder is not adequate to account for these results.

IV. CONCLUSIONS

The results of this series of four experiments can be combined to provide a preliminary examination of the functional properties of the receptor systems involved in near field sensitivity of the goldfish.

First, the receptors appear to be sensitive to direct displacement activity. That is, the air bladder is not principally involved, as it is in long range, high-frequency hearing. Second, there is some process for frequency analysis which allows fine frequency discrim-

inations to be made. Whether the receptor here is the ear or the lateral line, synchronous neural firing is assumed to be the mechanism of analysis, at least for the low frequencies. Third, broad band noise masks these near field thresholds to some extent, but general sensitivity is greater for the detection of nearby objects than for far field pressure-producing sources. This means that ambient noise levels do not necessarily limit the sensitivity of the fish to those stimuli which are produced at close range. This assumption, therefore, that sound pressure measurements of ambient noise levels will determine the hearing sensitivity of species living under those conditions is not valid. Fourth, the detector system responsible for mediating these responses is capable of processing subtle directional information. It appears that sensitivity within the near field may be quite important in the life of the fish, and probably plays a role in sexual, agonistic, and schooling behavior where proximity to other fish is of prime importance. Sensitivity in the far field, where directional information is not available, and where ambient sea noise is likely to play a greater role in masking, therefore, may not be as biologically important as the experimental literature tends to indicate.

On the basis of these results, unequivocal statements about ear or lateral line involvement are not possible. Previously, many investigators have assumed that low frequency displacement sensitivity was mediated by the lateral line system. The important and interesting work of Enger[7] and Moulton and Dixon[15] has shown, however, that the ear is definitely involved in direct displacement sensitivity, even to the point of providing directional information. What is necessary in future studies, in order to resolve some of these complications, is the rigorous combination of adequate behavioral, physiological, and physical techniques. Physiologists have been advised to take a controlled look at the behavior of the intact organism. Behaviorists have been advised to consult the biologists for adequate ablation techniques. Everyone involved in the area of underwater acoustics and hearing has been advised to consult the engineers for the development of

a device that will measure acoustic energy in terms of particle displacement or velocity. Too much speculation and mathematical calculation is based on shaky assumptions for the present biological problems to be completely resolved. It is quite obvious that fish and other underwater animals hear things that a hydrophone cannot hear. The measurement of this energy is a necessity for the full understanding of the acoustic behavior of marine animals.

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13. ABSTRACT

Four experiments were conducted on auditory sensitivity and discrimination of goldfish within the acoustic near field. Experiment I studies the effects of the near field on sound pressure thresholds. The sensitivity of goldfish in terms of sound pressure appeared to vary with distance from the sound source. Experiment II studied stimulus generalization and frequency discrimination within the near field. A generalization gradient was observed which indicated that goldfish can discriminate a frequency change as small as 12.5% without explicit differential training. Experiment III studied the effects of far field noise on near field thresholds. A masking effect was observed which appeared to be a negatively accelerated function of masker spectrum level. Experiment IV tested the ability of goldfish to localize a sound source within the near field. It was shown that goldfish could discriminate between right 45° and left 45° stimulus directions. Implications of the results of the four experiments are discussed.

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