Signal-to-noise ratio for source determination and for a comodulated masker in goldfish, *Carassius auratus*

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The masking effects of white and amplitude comodulated noise were studied with respect to simple signal detection and sound source determination in goldfish. A stimulus generalization method was used to determine the signal-to-noise ratio required to completely determine the signal's characteristics. It was found that the S/N required for this determination is about 4 dB greater than that required for signal detection, or was about 4 dB greater than the critical masking ratio. This means that the potential harm to fish of a given masking noise is at least 4 dB greater than previously thought, based on critical masking ratios. However, for amplitude comodulated noise between 10 and 50 Hz modulation rate, the potential harmful effects are up to 5.3 dB less than would be predicted from the critical masking ratio for unmodulated noise. © 2011 Acoustical Society of America. [DOI: 10.1121/1.3562179]

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I. INTRODUCTION

Masked signal detection, behaviorally defined, has been extensively studied in fishes, although not for several decades (e.g., Buerkle, 1968; Chapman, 1973; Tavolga, 1974; Fay, 1974). This issue has become important again in recent years with respect to the potential harm to fishes due to anthropogenic noise (e.g., Slabbekoorn, *et al.*, 2010). It has been argued (Fay, 2010) that the critical masking ratios (CRs) obtained for many vertebrates and humans are inadequate to predict the potential harm due to anthropogenic noise because, by definition, they describe only the lowest levels at which tones may be *detected* in uniform spectrum masking noise, and do not necessarily indicate what signal levels are required for the animals to determine, segregate, or make full use of the signal source information required for further action. At detection threshold, the task for the organism is to discriminate the noise alone from the signal plus noise: The organism is not required to determine the frequency, amplitude, duration, location, or any other feature of the signal's source. In the present context with non-human animals, a precise definition of sound source determination is problematic and must be somewhat vague. For present purposes, we mean by “determination” (Yost, 1991) the acquisition of sufficient information from a signal's source so that the perception of that source is complete and essentially equivalent to the perception of a clearly audible signal (to the goldfish) presented without effective interference. In other words, a source that is “determined” transmits whatever information to the receiver that is normally transmitted when the signal is clearly audible, under interference-free conditions. One of these characteristics is known to be the signal's frequency (Fay, 1970), and while it is not certain what the other source characteristics might be, it is possible that these include its location, distance, duration, and level. Presumably, the signal would have

to be raised above the masked detection threshold (or the masking noise lowered in level) by an unknown amount for most of the signal's source characteristics to be securely transmitted, determined, or to be able to be discriminated from other signals (Lohr *et al.*, 2003). These experiments were carried out, in part, to make an estimate of the signal-to-noise ratio required for this source determination.

Closely related to this issue are the masking effects (and release-from-masking effects) caused by more naturalistic noise sources. One of the most studied release-from-masking effects is comodulation masking release (CMR) in which temporally fluctuating maskers have been shown to be less effective in masking than unmodulated Gaussian noise at the same level (e.g., Hall *et al.*, 1984). It has been argued that if this CMR effect exists in fishes, the effective signal-to-noise ratio would be smaller than that measured in the usual masked signal detection experiments conducted on fishes to the extent that typical anthropogenic and other noise may be comodulated (e.g., Branstetter and Finneran, 2008). One component of the experiments reported here was aimed at determining the relative masking effectiveness of unmodulated and comodulated noise in goldfish and if it is reduced, how much masking release takes place.

The goldfish belongs to the non-taxonomic group, the Otophysi, characterized by a specially adapted mechanical link between the swim bladder and ears known as the Weberian ossicles (e.g., von Frisch, 1938). This group also includes catfish, carps, and minnows, including zebrafish. Accompanying this adaptation is a relatively wide hearing bandwidth and an enhanced sensitivity to sound pressure (e.g., Popper and Fay, 2009) compared to many other species.

II. METHODS

A. Overview

The first question regarding the signal-to-noise ratio for sound source determination (experiment 1) is approachable using a stimulus generalization paradigm (e.g., Fay, 1992,

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2009). In stimulus generalization, the animal is first conditioned to respond to a given stimulus (the model), and then tested for response (generalization) to other novel stimuli similar to, but not identical to the conditioning stimulus. To the extent that the conditioning and test stimuli have elements in common (or cause comparable perceptions), the animal will respond (generalize) to the test stimuli. In the present experiment, the conditioning stimulus was a clearly audible at 400 Hz pure tone presented in the presence of low level masking noise (the model stimulus) and the test stimuli consisted of the same 400 Hz tone in the presence of various levels of the same masking noise. It was reasoned that a 100% response to the test stimuli (tone in noise of various levels) indicated that the test stimulus was fully “determined,” or “known,” or otherwise was equivalent to the securely audible conditioning stimulus (tone). Any response less than 100% in the generalization test can be interpreted as the test signal not being equivalent to the conditioning signal (e.g., Fay, 1992). The degree of response during the test would indicate the degree of equivalence between the conditioning (model tone) and the test stimuli. This procedure was modified slightly to estimate thresholds for masked detection and any release from masking due to comodulated noise (described below, experiments 2 and 3).

B. Animals

Animal subjects were 40 common goldfish (*Carassius auratus*) about 8 cm in length from snout to tail, maintained in communal aquaria for from 2 weeks to several months. These animals were randomly assigned to only one of the three experiments (see below). In these experiments, it was assumed that the animals detected sound pressure, and that sound pressure alone (not particle motion) determined the auditory responses and hearing capabilities measured (Dailey and Braun, 2009). This assumption was not evaluated in these or other experiments on goldfish, but it is clear that sound detection thresholds in goldfish depend on sound pressure and not particle motion. The care and use of animals in this work was approved by the Institutional Animal Care and Use Committee of Loyola University Chicago.

C. Acoustics

The experimental test chamber was a water-filled plexiglass cylinder of 23 cm in diameter and 28 cm height. A University Sound UW-30 underwater pool speaker was projected upward from the bottom of the tank, and was buried in water-saturated sand with the speaker diaphragm of about 2 cm below the sand surface.

In all experiments, conditioning and test stimuli were 6-s duration signals with 20 ms rise-fall times synthesized in advance, stored on disk, and read out of a 16-bit digital-to-analog converter (DAC1) from Tucker Davis Technologies (TDT) (Alachua, FL) at 5 kHz. The DAC1 output was low-pass filtered at 1500 Hz, led to a TDT programmable attenuator, and then to a Crown (Elkhart, IN) 100-W power amplifier and the UW-30 loudspeaker.

The acoustic signals were measured by a (Bruel and Kjaer 8103, Naerum, Denmark) calibrated miniature hydro-

phone placed in the fish restrainer (described below). In repeated measurements of the sound pressure levels existing at the position of the fish in the restrainer, levels varied by ± 2.5 dB. The hydrophone output was amplified, bandpass filtered between 10 and 2500 Hz, and digitized at 5 kHz. Samples were spectrally analyzed using the fast Fourier transform (FFT). Levels (in dB re: 1 μ Pa) at selected frequencies were also measured using an H-P 3040A wave analyzer (Palo Alto, CA). The amplitude spectrum of the noise in all experiments was approximately uniform (± 4 dB), lacking prominent peaks or tonal components in the band between 50 and 1200 Hz, beyond which it declined in amplitude irregularly. All noise levels were specified as spectrum levels, or levels per hertz. The experimental tank rested on a vibration-isolated limestone slab inside an Industrial Acoustics single-walled audiometric booth.

D. Classical conditioning and stimulus generalization

For respiratory conditioning, a goldfish was gently restrained in a cloth bag of about 2 cm from the water surface, centered in the test tank. Slits in the bag allowed respiratory movements of the gill covers and mouth. A thermistor (Quality Thermistor, Inc., Boise ID) near the mouth measured respiratory water flow which cooled the thermistor as water flowed, producing a fluctuating voltage over time. This function over time is defined as the respiratory waveform. This waveform was filtered between 1 and 4 Hz and digitized at 5 kHz. Respiratory activity was calculated as the length of the recorded waveform in arbitrary units minus the length expected without respiratory activity (flat function indicating no respiratory movement). The response during a 6-s conditioning or test stimulus was defined as the ratio of the waveform's length during the last 4 s of the stimulus to the sum of the latter and the waveform length of 4 s preceding the stimulus. Complete respiratory suppression results in a suppression ratio (SR, see below) of zero and no change in respiration results in an SR of 0.5.

Respiratory suppression lasting several seconds was an unconditioned response to a mild, 100 ms alternating current (ac) electric shock delivered through steel electrodes placed near the animal's head and tail. A single conditioning trial included a 4 s pre-trial period during which respiration was measured and a 6 s stimulus presentation that terminated with the shock. During the 4-s pre-trial period, the respiratory waveform was monitored. If no respiratory activity occurred during the 4 s pre-trial period, then the trial was delayed until there was normal respiration during the pre-trial period. Conditioned responses to sound tend to occur after 10–15 trials.

All animals in each group were conditioned and tested in two separate sessions that were between 30 min and 24 h apart.

In experiment 1 (masked signal detection), the first and second conditioning sessions consisted of 40 conditioning trials at 400 Hz, at 100 dB re: 1 μ Pa, all terminating with shock (random intertrial intervals averaging 3 min). Suppression ratios (SR) were measured on all trials. The 400-Hz signal was presented against a continuous background of broad band noise varying in level from trial-to-trial to produce eight signal-to-noise ratio (S/N) stimuli ranging from 1 to 45 dB

(noise spectrum levels between 99 and 54 dB re: 1 μ Pa) in 5 and 10 dB steps. At 1 dB S/N, the signal was inaudible (completely masked) while at 45 dB S/N, the signal was clearly audible. The programmable noise attenuator was set to the level for the subsequent trial immediately following the shock on each trial. The second session was identical to the first and resulted in estimates of performance as a function of eight masked signal levels, forming a psychometric-like function. Thus, the first session conditioned the goldfish to signals of various S/N ratios, and the second identical session served to obtain the responses that defined performance in the task. In this and in all experiments, the SR response at a given masking noise plus signal level was summarized as the median of four responses to the eight signal plus noise stimuli presented during the second test session, and the results for each experiment were averaged over the eight animals in each group.

In experiment 2 (source determination under masking), the first 40-trial conditioning session consisted of the 400 Hz signal presented against a background of continuous, low-level (spectrum level of 45 dB re 1 μ Pa), broad band masking noise at about 35 dB sensation level (100 dB re: 1 μ Pa), with signal level varying from trial-to-trial by a maximum of 15 dB. This defined the “model stimulus” as a clearly detectable 400 Hz tone that fluctuated slightly in amplitude from trial-to-trial, in the presence of low-level but audible noise. The second (generalization test) session consisted of the same 400-Hz tone presented against a background of broad band noise that varied from trial-to-trial to produce S/Ns of 1–45 dB in 5 or 10 dB steps (as in experiment 1), but without shock. Every fourth trial consisted of the conditioning stimulus terminating with shock in order to maintain the conditioned response during generalization testing (Fay, 1970). In this generalization experiment, the model stimulus (a clearly detectable 400-Hz tone) was established as the conditioning stimulus in the first 40-trial session and was compared to the stimuli with novel S/Ns in the generalization test during the second 40-trial session. A median SR was calculated for each of the stimuli presented four times during each generalization testing session. Generalization was normalized with respect to the median SR to the conditioned stimulus measured during the test session (eight trials) and expressed as a percentage. Percentage generalization was defined as

$$[(0.5 - \text{med}_T) / (0.5 - \text{med}_C)] \times 100, \quad (1)$$

where med_T is the median SR to the test stimulus and med_C is the median SR to the conditioning stimulus obtained from the eight conditioning stimulus presentations (presented with shock) during generalization testing. Generalization values above 100% occurred when suppression to a test stimulus was greater than that to the conditioning stimulus. Values below zero percent occurred when the SR was greater than 0.5, indicating an acceleration of respiratory activity during the stimulus. Generalization was estimated from the second-session responses. Responses with 100% generalization were interpreted to indicate equivalence between the model stimulus and the test stimuli. Responses of less than 100% were interpreted as indicating that the test stimuli were not equivalent to the model stimulus.

In experiment 3 (signal detection under comodulated noise masking) the conditioning and test sessions were identical, as in experiment 1. However, the background noise in both sessions was 100% amplitude-modulated by an independent noise waveform that was low-pass filtered with corner frequencies of 10, 20, and 50 Hz in the respective experiments using a Rockland model 751A (Wiltek, Inc., Ismaning, Germany) programmable elliptic filter. Wide-band Gaussian noise was multiplied by the low-pass filtered noise using a Burr-Brown (Dallas, TX) 4206K analog multiplier. This experiment compared the masking effectiveness of comodulated noise of various modulation bandwidths to that of unmodulated noise from experiment 1.

III. RESULTS

Experiment 1: The mean percent averaged SR responses for eight animals in each independent group are plotted as a function of S/N in Fig. 1. The line with open circle symbols represents the results from experiment 1 (masked signal detection) and the line with open square symbols is the results from experiment 2 (stimulus generalization). The vertical lines at each data point are standard errors over the eight animals in each group. Both of these psychometric-like functions have similar forms and slopes, and differ from each other in sensitivity by approximately 4 dB, with the generalization function (source determination) requiring a 4-dB greater S/N for performance equivalent to masked signal detection. In other words, the S/N required for sound source determination or segregation is about 4 dB above that required for simple signal detection.

Experiment 3: Figure 2 shows the psychometric-like functions for signal detection against comodulated noise at corner frequencies of noise modulation of 10, 20, and 50 Hz compared with detection under unmodulated noise from experiment 1 (masked signal detection) from Fig. 1. The corner frequency of the noise modulation results in different psychometric-like functions with the greatest S/N occurring for

FIG. 1. Psychometric-like functions for detection of a 400 Hz tone in a low-noise background (open circles) compared with source determination using a stimulus generalization method (open squares, see text). The points plotted are median SR values averaged over eight animals. S/N is the 400 Hz sound pressure level minus the noise spectrum level (lever per hertz).

FIG. 2. Detection thresholds for a 400 Hz tone masked by modulated and unmodulated noise. The unmodulated noise data (open squares) are from Fig. 1. The results for comodulated noise were obtained for random modulation with low-pass noise of 10, 20, and 50 Hz corner frequencies. The points plotted are median SR values averaged over eight animals. S/N is the 400 Hz sound pressure level minus the noise spectrum level (level per hertz).

the unmodulated noise and the least for the 10 Hz modulated noise. The range of the unmasking effect is about 5.3 dB. The intermediate corner frequency results in an intermediate S/N. The slopes and forms of these results are similar across groups and show a monotonic effect of corner frequency of noise modulation on detection performance.

IV. DISCUSSION

The present experiment assumes the validity of the generalization experiment in estimating the S/N required for a sound signal to be useful or actionable to a goldfish. There is no way to absolutely validate the use of the generalization procedure as a measure of “determination” as suggested in this paper. For example, it could possibly be the case that the shifted psychometric-like function (determination function, Fig. 1) simply results from a partial extinction of the response that occurs when reinforcement is omitted during generalization testing. Furthermore, it is possible that the differences between the functions in Fig. 1 could reflect the acquisition of a successive discrimination between the signal plus noise stimuli in the conditioning phase and the stimuli presented during the generalization tests (without shock). However, we point out that the SR response strength did not decline in generalization compared with conditioning sessions. The mean (and standard deviation) of the SRs to the conditioning stimulus during generalization testing were 0.070 (0.058), while the means (and standard deviation) for comparable trials during the detection experiment were 0.1 (0.065). Therefore, there is no evidence that extinction was responsible for the shift of the generalization curve during generalization testing (Fig. 1). In a previous generalization experiment by Fay (1992), the animals were tested identically twice and the corresponding generalization gradients did not flatten or decline as would be expected if the animals had learned to discriminate between the conditioning and generalization test stimuli. Fay (1969) attempted to condition

goldfish to successively discriminate in this way and found that it occurred only after many more test sessions than the fish received in the present experiments. Thus, it is concluded that the difference between the psychometric-like functions of Fig. 1 were not due to extinction or discrimination learning.

It seems logical that if a noise plus tone combination produces a response that is equivalent to a model stimulus comprising a low-level noise and a clearly detectable tone, the equivalence of the response suggests an equivalence of received information or perception. Guttman (1963) persuasively argued for this view in his analysis of stimulus generalization behavior in animals. In any case, stimulus generalization (or an equivalent behavioral response) is perhaps the only method that we have for judging the equivalence of perceptions in non-human animals. Several previous experiments with goldfish have used stimulus generalization methods to estimate perceptual equivalence among sounds (e.g., Fay, 1992, 2009; Fay *et al.*, 1996). It is tentatively concluded, then, that 100% generalization (perceptual equivalence) occurs when the test stimuli are “determined,” segregated, or transmitted to the receiver without any effective interference by the masker.

At face value, the effects demonstrated in this report are small. The difference in S/N between detecting and determining source characteristics amounts to about 4 dB, and the effect of masking with comodulated noise to 10 Hz modulation frequency is about 5.3 dB. There have been no other studies of the detection versus determination dichotomy in fishes with which to compare the present results. Goldfish are specially adapted to detect sound pressure over a relatively wide frequency range (e.g., Popper and Fay, 2009), and it is not clear whether other fish species, without a wide hearing bandwidth, would show the same effects, or whether these effects would be observed in goldfish at other audible frequencies. Further research on other frequencies and species is necessary to answer these questions, but it seems unlikely that the special peripheral adaptations of goldfish (Weberian ossicles), themselves, are responsible for these effects. In addition, there have been no behavioral experiments using natural or anthropogenic signals and noise sources in the laboratory or field. It is argued, however, that both the S/N differences required for detection versus determination and for the effectiveness of comodulated versus unmodulated noise are likely to exist for most fishes, with and without special adaptations for sound pressure detection. No other hearing capability other than detection sensitivity (e.g., frequency discrimination: Popper and Fay, 2009) has been shown to differ among specialized and unspecialized fishes.

Similar effects have been observed for birds (Lohr *et al.*, 2003) where S/N for a criterion detection and discrimination performance differed in the expected direction by an average of 3.3 dB for budgerigars and zebra finches responding to their own and each others calls. Their conclusion was that discrimination is more difficult than detection (requiring a larger S/N) in birds, presumably because the birds had to obtain more information from the signal in order to perform the discrimination task compared with the detection task. The same holds for human speech (Miller, 1974) and call detection

versus discrimination in anurans (Wollerman and Wiley, 2002). Thus, the 4 dB difference in S/N for detection versus determination of tones by fishes does not seem unusually small.

As pointed out by Lohr *et al.* (2003), the effective reduction in the distance over which effective communication among birds can take place (the 3.3 dB S/N) amounts to 0.685, the distance at which birds can just detect the vocalizations using their conservative model of sound attenuation with distance. The same considerations would likely apply to fishes. Thus, one certain effect of the 4 dB difference in S/N required for source determination by fishes would be a significant reduction in the distance required for fishes to acquire sufficient information about a sound source to behave appropriately. This limitation has previously been assumed to be determined by the S/N required for mere signal detection, using the several CRs that have been published for fishes (e.g., Chapman, 1973; Tavalga, 1974; Fay, 1974; summarized in Fay, 1988). Now we know that, at least for the goldfish, this limitation is 4 dB greater (at a minimum) than the critical masking ratio for tone detection. It is not known whether this sort of experiment on goldfish would result in the same conclusion for other fish species, but it seems likely. Therefore, to be precautionary, we should assume that the levels of noise that would interfere realistically with sound communication by fishes are about the CR +4 dB below the measured masking noise spectrum levels.

The 5.3 dB release from masking caused by coherent amplitude modulation of the noise masker is similar to the effects in human and animal hearing known as comodulation masking release (CMR) (Hall *et al.*, 1984; Klump and Langemann, 1995). The present demonstration of masking release cannot properly be termed as CMR, however. Proper CMR depends on the demonstration that extending the comodulated noise band beyond the critical bandwidth results in a reduction of the masking effect. Nevertheless, the present results demonstrate that a comodulated noise has a reduced masking effect compared with an unmodulated noise, both noises having bandwidths wider than the critical band. The effect observed in the present experiments is small, however. Figure 3 shows the present masking thresholds for goldfish compared with the CMR values determined for the European starling (Klump and Langemann, 1995). Both species show a similar effect of noise modulation frequency, with higher frequency bandwidths resulting in a smaller masking release effect. However, the maximum effect for the starling is about 18 dB while the maximum effect for goldfish is just over 5 dB.

Mechanistic explanations for these effects focus on (1) the opportunity to “listen in the valleys” of the modulated noise (limited by temporal resolution: Buus, 1985), and (2) the processing of across-channel (critical bandwidth) cues or differences caused by the addition of the tone signal and the modulated noise (Schooneveldt and Moore, 1989) in one or more critical bands. The goldfish results do not help distinguish between these two accounts because both potential explanations may still apply for fishes (e.g., Tavalga, 1974; Fay and Passow, 1982). Although there are few data for a range of fish species, it appears that at least goldfish, cod

FIG. 3. The masking effect of comodulated noise with various low-pass noise modulation bandwidths compared with unmodulated noise for goldfish (open circles with an indication of standard error) and for the European starling (*Sturnus vulgaris*) (filled squares) from Klump and Langemann (1995).

(*Gadus morhua*: Hawkins and Chapman, 1975) and toadfish (*Opsanus tau*: Fay and Edds-Walton, 1997) parse the auditory spectrum into several frequency bands, a condition presumably required for CMR. However, as has been demonstrated repeatedly, human and goldfish psychoacoustics show many commonalities in spite of quite different peripheral auditory structures (e.g., Fay and Coombs, 1992; Fay *et al.*, 1996). The present masking release results are an additional example, further indicating that vertebrate auditory systems have many processing phenomena in common.

A. The effects of anthropogenic noise on fishes

These masking experiments were motivated, in part, by considerations of the potentially harmful effects on fishes of increased levels of noise in the environment caused by human activity. The first two experiments suggest that masking by the classical definition provided by behaviorally measured CRs underestimates the potential harmful effects of noise in interfering with sound source determination as defined here. A noise level that is more than one CR below the level causing any masking at all (the animal's detection threshold in quiet) is presently assumed to be completely harmless to fish (i.e., will not affect sound detection in any way). The present results show, on the other hand, that this noise level still can interfere with sound source determination, even though it may not raise the signal detection threshold. To be completely harmless, the noise level must be at least the CR +4 dB below the signal detection threshold measured in quiet, or an additional 4 dB below the level that just causes any masking at all.

The comodulation noise masking results are relevant to the question of the masking effects expected in the field for natural and anthropogenic noise sources, which are unlike typical white noise maskers used in the laboratory, may have arbitrary spectral and temporal characteristics that can determine their effectiveness as maskers. In general, the predicted masking effectiveness of these more natural maskers would be less than that of white noise maskers if the more natural maskers were effectively comodulated, either due to source characteristics or due to complex transmission pathways. The temporal modulations in environmental noise have generally not been noted, but at least one report has described many of these noises as comodulated (Branstetter and Finneran, 2008) and having a large effect on masking in dolphins (up to 17 dB). Klump and Langemann (1995) have noted, in addition, some of the factors that may cause amplitude fluctuations in the natural terrestrial soundscape. Therefore, not all noises of equal level and spectral profile are equally effective as maskers, and to the extent they are comodulated, they may be less effective as maskers by up to 5.3 dB for fishes, depending on the temporal modulation rate. For noise surveys assessing potential harm to fishes or other aquatic life, the degree and bandwidth of amplitude comodulation should be noted.

V. SUMMARY AND CONCLUSIONS

The masking effects of white and amplitude comodulated noise were studied with respect to simple signal detection and sound source determination in goldfish. Using a stimulus generalization method, it was found that the S/N required for source determination is about 4 dB greater than that required for mere signal detection. This means that the potential harm to fish of a given masking noise is at least 4 dB greater than previously thought. However, for amplitude comodulated noise between 10 and 50 Hz modulation rate, the potential harmful effects are up to 5.3 dB less than previously thought. These facts should be considered in future noise surveys assessing the potential harmful effects of noise on fishes.

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