

MASKING OF AUDITORY RESPONSES IN THE MEDULLA OBLONGATA OF GOLDFISH

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INTRODUCTION

Most studies on fish hearing have dealt with responses to pure tones, and only few investigations have been concerned with the response to noise or with the ability of fish to detect signals in the presence of background noise (Buerkle, 1968, 1969; Tavalga, 1967).

Information about the response to noise is of interest if one wants to compare the auditory thresholds to pure tones with values for sound pressure measured in the sea. These are usually given either as the spectrum level (i.e. in 1 Hz bandwidths) or in bandwidths of one- or one-third octave. According to the way of reading, the pressure levels are very different. For example, a white noise recording measured through a 250 Hz octave filter is 5 dB higher than through a 1/3 octave filter, which again is 17 dB above the spectrum level. It is not known which of these pressure values—if any—should be used for a comparison with known thresholds to pure tones in fish, because the bandwidth over which the fish integrates the sound energy is not known. The present study deals with this question before proceeding to detection of signals in the presence of background noise.

The masking effect of background noise on the auditory threshold has been studied by Tavalga (1967) and Buerkle (1968), but only in so far as the effect of noise bands centred around the test frequency was concerned. To the author's knowledge Buerkle's report from 1969 is the only one dealing with masking of a given sound with noise bands of different frequencies. In the present paper responses of auditory neurones in the goldfish brain have been recorded when pure tone stimuli were presented either alone or together with noise bands of various centre frequencies.

MATERIAL AND METHODS

Experimental. Thirty-eight specimens of goldfish 6-10 cm long were used, 24 of which gave successful recordings from one single unit each only, while in the rest two or more units were obtained. The fish was initially anaesthetized with tricaine methanesulphonate (MS-222, Sandoz) (1 part per 15000) and curarized by intramuscular injection of 0.05-0.1 mg tubocurarine chloride, and clamped in a holder which held the fish above the eyes and at two more points along its back. Except for the dorsal part of the head, the fish was held submerged in water in a trough 80 cm long made of half of a 30 cm diameter polyethylene cylinder. The gills of the fish were ventilated with running water through a plastic tubing put into its mouth. The

water was held at room temperature. The dorsal part of the brain was exposed and access to the acoustic lobes was made by reflecting the cerebellum rostrally.

Recording of nervous activity. Micropipettes filled with 4 M-NaCl were used for extracellular recording of single-unit activity. During the first phase of the study metal-filled pipettes (Gesteland *et al.* 1959) with tip diameters of about 5 μm were used for a general localization of the acoustic area. The micropipettes were connected to a high-impedance pre-amplifier (Medistor, Model 140) and further to a dual-beam oscilloscope (Tektronix 565). Signals were photographed on running film (Grass Kymograph Camera, model C 4).

Sound stimulation and recording. Sound stimuli were delivered from a low-frequency loudspeaker (Philips AD 5201 S) hanging in the air about 30 cm above the experimental container. The diaphragm was covered with cotton gauze to eliminate possible gross air movements during sound stimulation. Stimuli were of two types: (1) pure tones from a beat-frequency oscillator (type 1022) and (2) noise stimuli from a random-noise generator (type 1402) either applied directly or filtered through a band-pass filter set (type 1612) to give noise bands of one- or one-third octave widths (equipment from Brüel & Kjaer, Copenhagen). Signals were amplified by a 10 W power amplifier (Quad II) driving the loudspeaker. Sound pressures were measured by a calibrated hydrophone (LC 34, Atlantic Research Corp.) placed in the same position as the fish occupied during the experiments. Signals from the hydrophone were amplified by an a.c. amplifier with 100 M Ω input impedance and a linear gain from 10 Hz to 100 kHz (built by the Central Institute for Industrial Research, Oslo) and either displayed on the oscilloscope or measured with a vacuum tube a.c. voltmeter directly through a one-octave filter (Brüel & Kjaer type 1613). Sound pressures are given in decibels (dB) referred to 1 $\mu\text{bar}_{\text{rms}}$. For any given frequency and position in the container sound pressures were reproducible within 1 dB and the broadband, unfiltered background noise level in the experimental container was -6 to 0 dB.

RESULTS

General. Neural units responding to acoustic stimulation were located in the ventral half of the acoustic lobes of the medulla oblongata. The area was at the level of the eighth nerve root at a depth of 1000-1800 μm below the dorsal surface of the acoustic lobes. Although the area was large, any one penetration with the microelectrode had only a small chance of recording unitary nervous responses. Most often either no response was obtained or the response was multi-unitary with spikes of low amplitudes. Eventually, on advancing the electrode the spike amplitude of presumably 1 unit could increase smoothly and reach a maximum at a certain electrode position. Of the unitary responses obtained, only few lasted for more than 1-2 min. The results presented in this paper are based on records from 57 single units lasting more than about 5 min. Units responding to low sound frequencies (below 350 Hz) were most readily obtained in the dorsal and lateral parts of the acoustic region of the acoustic lobes. Units responding to higher frequencies seemed to be localized in the ventral and medial parts of the lobes, but were obtained less frequently than low-frequency units.

The response to acoustic stimulation in most cases consisted of an increase in

Discharge rate above the low 'spontaneous' rate of 0-30/sec. Among units responding to high frequencies, however, cases were observed in which the 'spontaneous' discharge rate was inhibited by the higher and excited by the lower sound frequencies. The findings were rather similar to those reported for medullary auditory units in herring (Enger, 1967), but an additional finding was units (two only) which responded to noise stimulation and not to pure tones.

Responses were measured by counting numbers of impulses in $\frac{1}{8}$ sec periods. In order not to include the initial transient phase, the first 100 msec of the responses were not counted.

Responses to pure tones and noise. Fig. 1 gives an example of the response to three types of acoustic stimuli, namely a pure tone and noise of one-third octave and one-octave bandwidths, respectively, of the same centre frequency as the pure tone. This unit had its lowest threshold for frequencies of 200-300 Hz, and it is seen that the response, measured as the average discharge rate, is about the same for equal sound pressures of the three stimuli, except at intensities close to threshold where the responses to noise is a little stronger than to the pure tone. This is more clearly illustrated in Fig. 2, which shows the results from two different units. In Fig. 2A are plotted the data from a unit which responded somewhat better to a pure 250 Hz tone and the narrowest noise band of one-third octave than to the one-octave noise band, probably because this unit was rather insensitive to frequencies above 315 Hz. More often, the responses to the two noise bands were equal, as shown in Fig. 2B. On the other hand, this unit discharged at a much higher rate in response to the 250 Hz pure tone than to noise. This is due to the tendency in many units (but not all) to discharge at the same rate as the frequency of the tone—at low pitch and relatively high intensities.

It was a consistent finding in all auditory units obtained that the threshold was 3-4 dB higher for a pure tone than for a band of noise of the same centre frequency. This is probably due to the large fluctuations in sound pressure in the noise bands (Fig. 1). When the average sound pressure is close to threshold, the pressures above the average elicit neuronal discharges according to the actual instantaneous pressure, whereas pressures below the average will be non-stimulatory regardless of whether the pressure is just a little or far below threshold. As a result of this, the number of discharges will be less in response to a pure tone at threshold value than to a noise band of the same average intensity.

The response to white noise is also plotted in Fig. 2A, and it is seen that in order to obtain a response to white noise of the same magnitude as to a 250 Hz tone or a one-third octave noise-band, the sound pressure had to be 15-17 dB higher. For the noise band of one-octave width the corresponding value was 13-15 dB. Since this unit was insensitive to frequencies above 350 Hz, the response to white noise is produced only by sound of frequencies below this value.

Measurements of the white noise through an octave filter (see Methods) revealed that the octave band centred at 250 Hz had an average pressure of 17-19 dB below the total pressure of the white noise, indicating that the response has been caused by a somewhat broader frequency range than the one-octave band. The average sound pressure of the octave band centred at 125 Hz was 3-5 dB lower than that at 250 Hz. The pressure of these two octave bands combined therefore, will be some 16-17 dB below the white noise pressure (Albers, 1965). Due to fluctuations in the sound

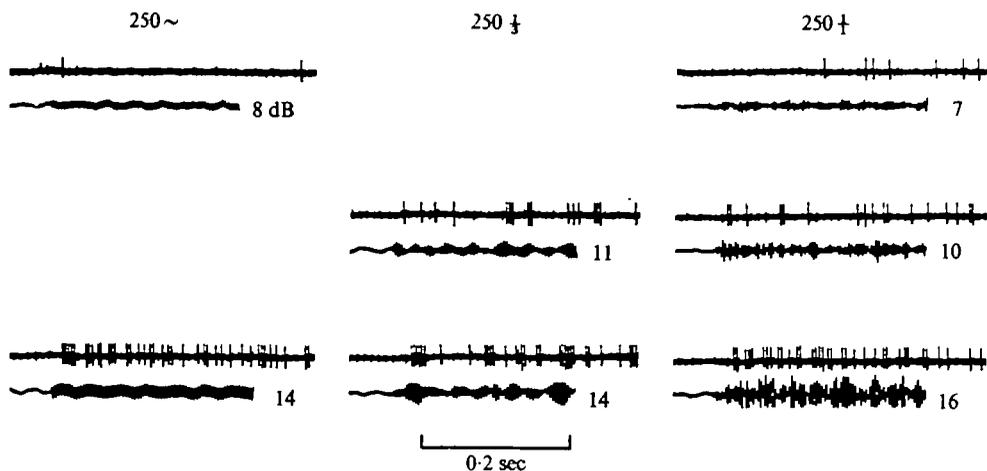


Fig. 1. Discharges of single auditory neurones in response to a 250 Hz pure tone (left column), a 250 Hz one-third octave noise band (middle) and 250 Hz one-octave noise band (right column). Sound recordings are on lower trace and sound pressures (in dB re $1 \mu\text{bar}$) are given on each record. Note large fluctuations in sound pressure in the noise recordings. Values given are the average pressures.

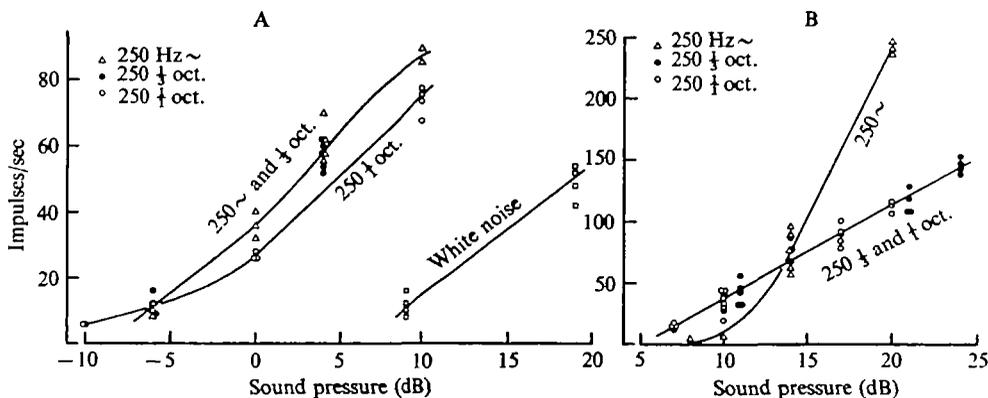


Fig. 2. Relation between the discharge rate of a single unit and sound pressure for a pure tone and bands of noise in two different units (A and B). The threshold to a pure tone in both cases is higher than two noise bands with the same centre frequency.

pressure at these low frequencies, however, one cannot state with certainty that the width of the noise band contributing to the response is two full octaves, although it is certainly more than one.

Units responding to high frequencies often displayed an inhibitory response to the higher frequencies and an excitatory response to the lower. Consequently, their response to bands of noise was often very complicated. Those rather rare units (three) with their threshold minima to sound frequencies of 500–1000 Hz, responded to one-octave and one-third octave bands with the same discharge rate as to pure tones.

Masking of pure tones with noise. The response to a pure tone may or may not be influenced by the presence of background noise. In Fig. 3 are shown results from an

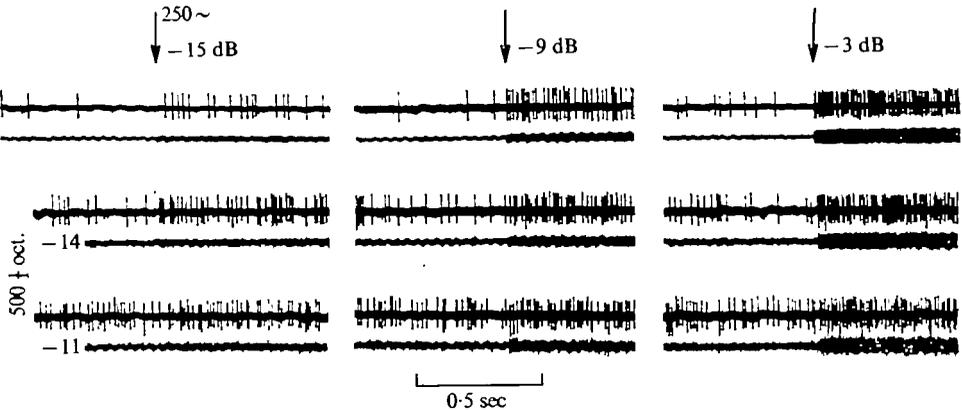


Fig. 3. Discharges from a single unit during stimulation with a 250 Hz pure tone of -15 , -9 and -3 dB intensities presented either alone (top row) or in the presence of one-octave band noise centred at 500 Hz of -14 and -11 dB intensities (two lower rows). The arrows indicate start of 250 Hz tone stimulation. Lower trace in each record gives the sound recording.

experiment in which the response to a 250 Hz tone was recorded alone (top row) or in the presence of a one-third octave noise band of 500 Hz centre frequency. It is quite clear that the tone response is added to the noise response at low and medium tone intensities. At higher tone intensities, when the response seems to level off and approach a maximal discharge rate, however, the presence of background noise has little or no additional effect on the response. The results are shown also in Fig. 4B, and one can see that the auditory threshold to the 250 Hz tone is not influenced by the presence of moderately intense noise of one-third octave bandwidth around 500 Hz. The threshold for individual units is defined here on the graph as the pressure at which the response curve intersects either the abscissa (in units without 'spontaneous' discharge) or the level of discharges produced 'spontaneously' or by masking sound stimuli. In the example given in Fig. 4B the threshold for the 250 Hz tone is about -17 dB (indicated by arrow) when presented alone as well as in the presence of 500 Hz one-third octave background noise. When the pure tone was in the same frequency range as the noise, however, no additive effect of the two sound stimuli was observed. Fig. 4A illustrates how the response to the 250 Hz pure tone was masked by the noise band centred at 250 Hz, and the threshold for the pure tone rose by exactly as much as the noise level; when the noise level increased from -15 dB to -9 dB, the pure tone threshold also rose by 6 dB.

The degree of masking has been studied systematically for two pure tone frequencies only, namely 250 and 500 Hz. The reason for this is purely technical as most single units lasted a relatively short time, and the procedure was rather time-consuming. The response curves of the types shown in Fig. 4 have been determined for 250 and 500 Hz in the absence and presence of background noise presented in one-third octave bands at various intensities and frequencies. The result from one such experiment is given in Fig. 5, where the increase in threshold, i.e. masking, for a 250 Hz (A) and a 500 Hz tone (B) versus the centre frequency of one-third octave noise bands is plotted. The number at each point gives the sound pressure (in dB) of the noise band.

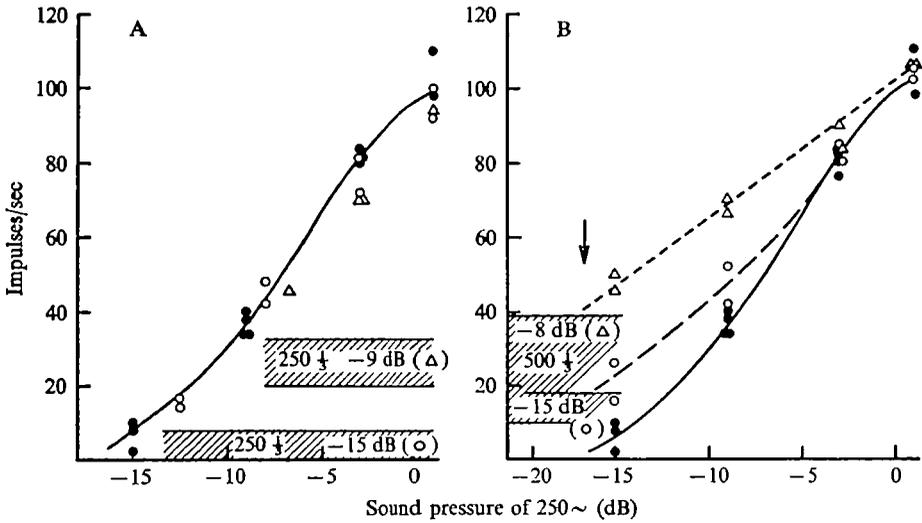


Fig. 4. Discharge rates versus sound pressure during stimulation with a 250 Hz pure tone. In (A) the tone was applied either alone (●) or in the presence of background one third octave noise bands, centred at 250 Hz, of intensities -15 dB (○) and -9 dB (▲). The discharge rates during noise stimulation before tone was introduced are indicated by hatched areas. In (B) the 250 Hz tone was presented either alone (●) or with one-third octave noise bands centred at 500 Hz, of -15 dB (○) and -8 dB (Δ) intensities. Note that threshold increases by 6 dB (from -15 to -9) in (A) when background noise increases from -15 to -9 dB. In (B) threshold is constant at -17 dB (indicated by arrow) when background noise increases from below measurable through -15 to -8 dB.

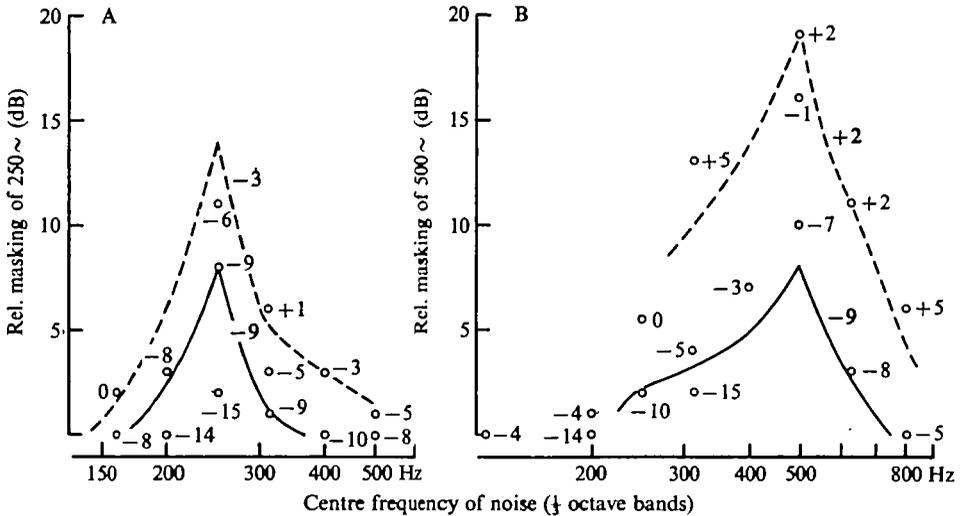


Fig. 5. Relation between noise bands of various centre frequencies and their masking effect on 250 Hz (A) and 500 Hz (B) pure tones. Each point is a threshold determination obtained from curves of the type given in Fig. 4 (cf. legend to Fig. 4). Number at each point gives sound pressure of noise, and threshold increase is plotted along the ordinate. Curves are drawn by eye through points of equal sound pressure thresholds for pure tones in presence of noise. Solid curves represent -9 dB in both (A) and (B).

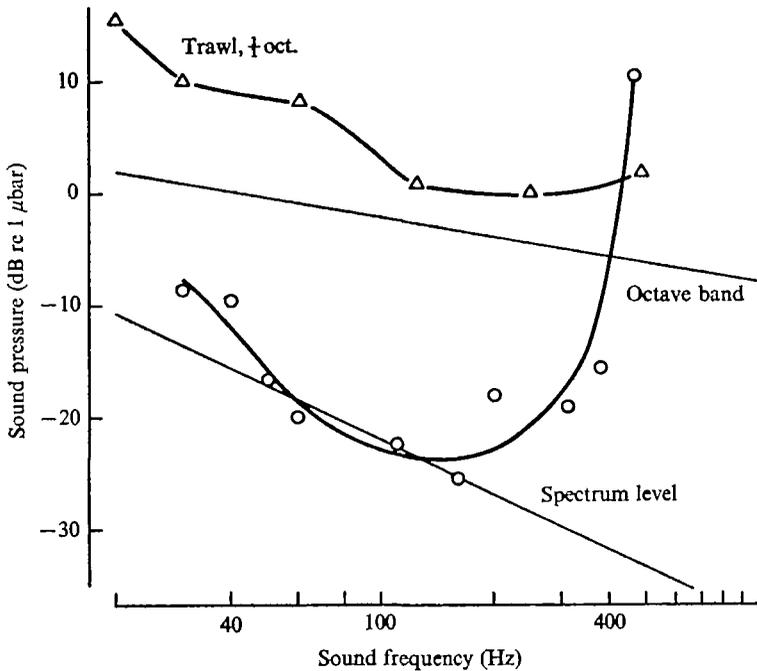


Fig. 6. Cod audiogram (from Chapman & Hawkins, 1973) compared to noise level at sea state No. 2, given both as spectrum level (lower curve) and as one-octave band level (upper curve). Noise from a trawl recorded at minimum distance of 75 m, measured through one-octave filters, plotted for comparison (Anon. 1965).

The solid curves in both figures represent the masking produced by a -9 dB pressure of the one-third octave noise bands and are drawn by hand through the points determined experimentally. The broken curves represent the masking at higher noise intensity, but because of scarcity of data these curves are more suggestive than factual. The masking is strongest at identical frequencies of tone and noise. As noise frequency deviates from the tone, the masking effect decreases at a rate which for the tone of 250 Hz is different from the tone of 500 Hz. Scarcity of points on the graph prohibits a detailed description, but one gets the impression that the 250 Hz tone is masked equally well by lower and higher noise frequencies, whereas the 500 Hz tone is better masked by lower than by higher noise frequencies. Thus in both instances the masking effect decreases by some 20–22 dB/octave for the first one-third octave for noise frequencies above the test tones. This value also applies to the masking of the 250 Hz tone with lower noise frequencies, but the masking of the 500 Hz tone with noise of lower frequencies falls off at a rate which may be roughly 9 dB/octave for the first one-third octave. It is readily seen that at the intensities used there is practically no masking of the 250 Hz tone by noise bands centred one octave apart from the test tone, whereas the 500 Hz tone is somewhat masked by noise centred at 250 Hz.

DISCUSSION

Response to noise. It has been shown that the neural responses to pure tones and to bands of noise of one-third octave and one octave bandwidths, respectively, are essentially the same. This statement is true only as far as the average discharge rates are concerned, but there can be little doubt that the response is caused by the total acoustic power integrated over a large span of frequencies. By comparing the responses to band noise and white noise, the present results suggest that, at low frequencies at least, the actual bandwidth over which such integration takes place is more than one octave. Since all fish are sensitive to low frequencies, this result is probably generally applicable, and a comparison of auditory thresholds with values from noise measurements should be made on the basis of the total sound pressure of at least one, perhaps two octaves in the frequency band below 300 Hz.

This conclusion may seem at variance with the result obtained from the masking experiments, in which virtually no effect on the threshold of a test tone was observed when the masking noise was separated from the tone by one octave. In that case therefore the acoustic power was integrated over less than one octave. It is to be remembered, however, that masking concerns the interaction in the nervous system of two different acoustic responses, whereas signal detection concerns the ability of sensory cells to respond to acoustic energy over a given frequency spectrum.

The finding that the threshold noise-bands is some 3–4 dB lower than of pure tones is true also for units in the cochlear nucleus of the cat (Greenwood & Goldberg, 1970), and should be kept in mind when one compares pure tone thresholds found for fish in the laboratory with noise recordings in the sea.

It has not yet been established what a fish can hear of the natural background noise. According to the present results it would definitely be wrong to compare the auditory thresholds as determined by pure tone testing with the spectral noise level. This is illustrated in Fig. 6, where the cod audiogram—obtained by Chapman & Hawkins (1973) under very good acoustic conditions in the sea—is compared with the background noise in the sea at sea-state number 2*. The lower curve in the diagram gives the spectrum level of the background noise, according to which one would expect the cod to be just able to perceive this noise level. The upper noise curve gives the noise level measured in one-octave bands. Taking into account that the fish ear probably integrates the acoustic power over more than one octave, it is obvious that this background noise level is far above the auditory threshold for cod. As an example of man-made noise in the sea, the measured pressure values of a trawl passing sound recording equipment at a minimum distance of 75 m has also been plotted. The bandwidth used was one octave, and it is seen that this noise level also is well within the audible range of codfish.

Masking. Tavalga (1967) and Buerkle (1968) have shown in behavioural studies on three species of teleost fishes that the auditory thresholds rise with the same value as the increase in background noise of the same frequency. The same was found to hold true for single auditory neurones in the present study. Later, Buerkle (1969)

* Noise-level values in the sea can be calculated from the so-called Knudsen curves giving the noise level versus sound frequency. The noise level varies with sea state, i.e. wave height and wind strength. At sea state No. 2 the wave height is 2–3 ft.

was also studied masking in experiments where the test sound and the masking noise were of equal as well as of different frequencies. He studied codfish and used noise bands both as test sound and as masking sound. From his data it appears that the masking effect decreases by 13–20 dB when the signal frequency is removed one octave from the centre frequency of the masking noise. The present study gave a reduction in masking effect of 20–22 dB/octave for the first one-third octave, but measured over one full octave the value appears to be 13–15 dB. The comparison is made for low frequencies (masking of 250 Hz tone in goldfish) since the upper limit of sound perception in cod is about 400 Hz and the data obtained from behavioural studies on cod and the electrophysiological data from goldfish are in remarkably good agreement. Chapman and Hawkins (1973) in a study on cod found a 25–35 dB reduction in masking effect at one-octave separation of masking and test signal, but their masking bandwidth was only 10 Hz. Buerkle used half-octave filters and in the present study one-third octave filters were used. The differences reported may therefore be a consequence of the various techniques employed.

The present results have indicated that a given tone may be better masked by noise of lower than of higher frequencies. This is consistent with previous neurophysiological results on fish (Enger, 1963, 1967). All auditory neurones perceive low frequencies, but as frequency increases fewer and fewer units will respond. Thus, a medullary neurone responding to a tone of 500 Hz most definitely will be influenced by noise of lower pitch because all neurones responding to 500 Hz also respond to lower frequencies. On the other hand, a unit responding to a 250 Hz tone will not necessarily be influenced by higher frequencies unless there are primary neurones responding to higher frequencies which synapse on this unit in the medulla oblongata.

SUMMARY

1. The nervous activity of single auditory neurones in goldfish brain have been measured.
2. Four types of acoustic stimuli were used, (1) pure tones, (2) noise of one-third octave band width, (3) noise of one-octave band width with centre frequency equal to the pure tone, and (4) white noise.
3. Except for white noise, these stimuli produced the same response to equal sound pressures. The white noise response was less, presumably because the frequency range covered by a single neurone is far narrower than the range of white noise.
4. The conclusion has been reached that for low-frequency acoustic signals, the acoustic power over a frequency band of one to two octaves is integrated by the nervous system.
5. The masking effect of background noise on the acoustic threshold of single units to pure tones is strongest when the noise band has the same centre frequency as the test tone. In this case the tone threshold increases linearly with the background noise level.
6. When the noise band was centred at a different frequency from the tone, the masking effect decreased at a rate of 20–22 dB/octave for the first one-third octave for a tone frequency of 250 Hz. For a tone of 500 Hz the masking effect of lower

frequencies was stronger and was reduced by only some 9 dB/octave for the first one-third octave.

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