AUDITORY MASKING PATTERNS
IN THE GOLDFISH (CARASSIUS AURATUS):
PSYCHOPHYSICAL TUNING CURVES

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SUMMARY

The masking effects of tones on the detection auditory signals were studied in goldfish using the psychophysical tuning-curve paradigm. For signals below 350 Hz, masking is an inverse function of the frequency separation between masker and signal; a finding consistent with previous masking studies on fishes, birds and mammals. For signals above 350 Hz, masking peaks occur both in the 350 Hz region and at the frequency of the signal. Quantitative comparisons with recent neural tuning curves for goldfish saccular neurones suggest that the filtering observed may be determined by mechanical frequency selectivity below 350 Hz, but by a neural analysis of temporal patterns above this range.

Auditory detection is a complex discrimination problem in which certain acoustic events (signals) must be differentiated from a background of both random and non-random phenomena termed ‘noise’. Clearly, the problem is not solved simply by the achievement of a certain auditory sensitivity since all acoustic input, signal and noise alike, would be subject to the same ‘gain’. Improvements in detection can occur only when mechanisms are developed which achieve an analysis of acoustic input along information-bearing dimensions. Over a century of research on mammalian hearing has identified frequency as an important information-bearing dimension, and the filtering characteristics of the cochlea as a mechanism for achieving a certain degree of frequency analysis.

Through the use of various tonal and noise-masking psychophysical paradigms (e.g. Wegel & Lane, 1924; Ehmer, 1959; Greenwood, 1961), the properties and shapes of auditory filters have been analysed in man and in other animals (McGee, Ryan & Dallos, 1976; Saunders, 1976). Quite recently, Zwicker (1974) described a masking paradigm which was designed to reveal the shapes of the most highly selective filters

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used in auditory detection. Briefly, a tonal signal is fixed in frequency and in level (just above quiet detection threshold), and then a tonal masker is introduced. The masker level necessary to just mask the signal is plotted as a function of masker frequency. This function has been termed a psychophysical equivalent of a neural tuning curve (the frequency response characteristics of a single auditory nerve fibre), since the psychophysical procedure results in a measurement which is analogous to that made in the neurophysiological experiment (e.g. Kiang et al. 1965). In the psychophysical case, the just-detectable signal restricts neural input to a small number of the most sensitive channels and thus is analogous to the microelectrode in the neural case which restricts input to a single afferent channel (fibre). The remarkable resemblance between the psychophysical curves for man (Zwicker, 1974; Vogten, 1974) and chinchilla (McGee, Ryan & Dallos, 1976), and the neural tuning curves for cat (Kiang et al., 1965) provides strong evidence that in mammals, the most highly selective filtering processes used in detection are determined peripherally at the cochlear level. Recent behavioural and neurophysiological data for birds show the same patterns (Saunders, 1976; Sachs, Young & Lewis, 1974).

The purpose of the experiments reported here is to use the above method of analysis to investigate the auditory filtering mechanisms of the goldfish. Recent psychophysical studies have illustrated the existence of filter-like processes such as a critical band phenomenon in goldfish (Tavolga, 1974) and cod (Hawkins & Chapman, 1975), 'mammal-like' critical masking ratios for the goldfish (Fay, 1974), and cod (Buerkle, 1968), and that the masking effect of a tone or noise band is confined to the frequency region of the signal to be detected in the cod (Buerkle, 1969; Hawkins & Chapman, 1975) and goldfish (Tavolga, 1974). In addition, indirect evidence for the existence of filters in the goldfish comes from 'mammal-like' frequency discrimination thresholds (Jacobs & Tavolga, 1968; Fay, 1970), studies of frequency recognition (Fay, 1972), and frequency dependent fatigue effects (Popper & Clarke, 1976).

These demonstrations of filter-like processes have led to considerable speculation over the responsible mechanisms, with some (van Bergeijk, 1967; Tavolga, 1974; Sand, 1974) maintaining that the filtering may be accomplished mechanically at the periphery, and with others (Fay, 1974, 1978; Hawkins & Chapman, 1975; Schwartzkoff, 1976) holding that a central neural analysis of temporal patterns may be responsible. Of course, this controversy is over a century old in auditory theory and is simply a restatement of the Helmholtz-von Békésy spatial coding principle versus the Rutherford-Wever temporal coding principle.

The temporal hypothesis has been the more conservative one in the fish hearing literature since the fish's otolithic ear (saccus and lagena) does not contain any obvious structures for performing a cochlea-like frequency analysis (Popper & Fay, 1973), yet neurophysiological demonstrations of phase-locking and frequency following are quite clear (e.g. Furukawa & Ishii, 1967; Grözinger, 1967; Fay, 1978). Not surprisingly, however, neurophysiological studies by themselves have not provided conclusive evidence one way or the other since some degree of peripheral tuning has also been demonstrated in several species (Furukawa & Ishii, 1967; Enge, 1963, 1967; Sand, 1974; Page, 1970; Fay, 1978). In short, neither the spatial nor the temporal hypothesis can be ruled out as possible mechanisms of frequency analysis on the basis of existing neurophysiological data.
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The present application of the psychophysical tuning curve paradigm for the goldfish is an attempt to resolve some of this ambiguity by providing psychophysical data which are, in principle, quantitatively comparable to neurophysiological data recently obtained for the same species under nearly identical acoustic conditions in this laboratory (Fay, 1978). The tuning characteristics of goldfish saccular neurones were quantitatively described in terms of both phase-locking and impulse rate modulation criteria, and were found to exhibit a certain variation in best frequency, bandwidth, and sensitivity. To the extent that the psychophysical functions are clearly similar to the neural ones, as they are in mammals, evidence will be provided that filtering in the fish auditory system is accomplished peripherally. On the other hand, to the extent that the psychophysical functions are more sharply tuned than the neural, evidence will be provided that, unlike the mammals, the most highly selective filtering processes occur centrally. While this latter result does not necessarily distinguish between a central ‘sharpening’ mechanism, and one based upon temporal pattern analysis, qualitative features of the functions may provide new insights into this question.

METHOD

Subjects

Twelve 15–18 cm goldfish (Carassius auratus) were used in these experiments. They were obtained from the Auburndale Goldfish Co. of Chicago, and were maintained in three communal 30 gal tanks.

Psychophysical thresholds were obtained under three different experimental conditions. In Expt 1 a group of four animals were conditioned to respond to noise-band signals 40 Hz wide in the presence of a continuous pure-tone masker, and psychophysical tuning curves were obtained for signals of 100, 200, 500, 600 and 700 Hz. In Expt 2 masking was measured similarly (at 100, 200, 300 and 500 Hz) in a redesigned acoustic tank for several additional animals in order to evaluate any possible effects of tank acoustics on the form of the tuning functions. In Expt 3 additional animals were conditioned to detect pure tone signals (at 300, 500 and 600 Hz) in the presence of pure tone maskers, in order to evaluate any differences between periodic and aperiodic signal detection.

Apparatus

Fig. 1 presents a schematic diagram of the acoustic tanks and plots of their frequency response characteristics used in Expt. 1 (Fig. 1A), and in Expts 2 and 3 (Fig. 1B).

In set-up A the fish was restrained in a cloth-bag holder as described by Fay (1974) within a water tank 15 cm deep, 20 cm long and 12 cm wide constructed of lucite 13 mm thick. The tank rested on foam rubber 6 cm thick within a closed air chamber (30 x 30 x 30 cm) constructed of particle board 2 cm thick. A 20 cm Realistic high compliance loudspeaker projected into the top of the air chamber, and was back-baffled by an air chamber equal in volume to the lower one. This set-up is quite similar to one previously used in studies of saccular microphics in carp (Fay, 1975), and its design was motivated by suggestions for eliminating near-field effects in small tanks (Parvelescu, 1967).

In set-up B the same restrainer was suspended in a 19 cm diam., 14 cm high
A cylindrical tank constructed of lucite 6.5 mm thick. The tank's bottom was constructed of plastic 'egg-crate' material normally used as a diffuser in lighting fixtures (a 1 cm deep grid of 1 cm squares) overlain by a rubber sheet 1 mm thick. This arrangement was meant to produce a rigid and watertight, but acoustically 'soft' bottom. The tank projected through a steel plate 13 mm thick which rested on a layer of 'air-cap' packing material, a 2.5 cm layer of particle board, another air-cap layer, and a final particle board layer. An air chamber (25 x 25 x 25 cm) filled with 'fist-sized' chunks of foam rubber packing material was formed under the tank. A Lafayette Criterion II, 20 cm speaker system projected into the air-chamber from below. This set-up is identical to that currently used in neurophysiological studies of goldfish single
auditory neurones (Fay, 1978), and its design was motivated by considerations of convenience in the neurophysiological experiments.

In both set-ups, water was continuously pumped into the tank at about 5 l per hour, and drained from an overflow port back into the 5 l reservoir from which it was pumped. Respiration of the restrained fish was measured as described by Fay (1974), by suspending a 1 cm square plastic ‘paddle’ in front of the fish’s mouth from the needleholder of a crystal phono cartridge. Respiratory water movements produced an output voltage from the cartridge which was amplified, low-pass filtered at 4 Hz, full-wave rectified, and integrated for 7 s periods immediately preceding and following the onset of the conditioned stimulus signal. Wire-screen electrodes (2 cm square) delivered a 60 Hz shock across the fish’s body. Shock causes a transient supression of respiration which can be rapidly conditioned to occur to an acoustic signal which terminates at the time of shock onset (Fay & MacKinnon, 1969). The amount of conditioned respiratory suppression is computed as the suppression ratio, \( SR = B/(A + B) \), where \( B \) is the integrated respiratory activity (voltage) occurring during the 7 s stimulus presentation, and \( A \) is the activity occurring during the 7 s period immediately preceding the stimulus onset. This number is free to vary between 0 (complete suppression) and 0.5 (no change in activity), to greater values to a maximum of 1, indicating an acceleration of respiratory activity.

Sound pressure levels were measured with a Clevite CH-17 hydrophone which replaced the fish in the restrainer. The frequency response characteristics of the two set-ups are shown in Fig. 1, and levels are expressed throughout this paper in decibels (dB) relative to 1 dyne/cm². The ambient noise spectrum level at 100 Hz was -34 dB and declined with frequency at about -12 dB/octave. The operation of the water pump augmented the ambient levels by about 4 dB between 1 and 30 Hz, and by less than 1 dB at frequencies above 30 Hz.

In Expts 1 and 2 signals were 40 Hz wide noise bands centred at 100, 200, 300, 500, 600 and 700 Hz. To generate these bands, wide band white noise was passed through a 20 Hz low-pass filter (-24 dB/octave) and then to the VCA (voltage controlled amplitude) input of a Wavetek 134 signal generator. The noise was thus used to amplitude-modulate a sinusoid, producing a noise band centred at \( f_c \) (the frequency of the sinusoidal carrier) and extending between \( f_c + f_m \) and \( f_c - f_m \), where \( f_m \) is the bandwidth of the noise input to the modulator. Note that while the bandwidth of the noise at the 3 dB-down points is the same regardless of centre frequency \( f_c \), the steepness of the noise band skirts in dB per octave grows rapidly with centre frequency (Palin & Gourevitch, 1970). The output of the Wavetek generator was led through a photo-conductive switch producing 50 ms rise times and 150 ms fall times. The signal was then led to a variable attenuator, through an active adder (for mixing with the masker), to a Dynaco S2-80 power amplifier, and then to the loudspeaker. Sinusoidal maskers were generated by an Exact 195 signal generator, and then attenuated and mixed with the noise signal. All frequencies were monitored using a Hewlett-Packard 5381-A digital frequency meter.

In Expt 3, the Wavetek generator (without VCA input) provided the sinusoidal masker while the Exact generator provided a sinusoidal signal. Maskers were never set less than 10 Hz above or below the signal frequency in Expt. 3.
Procedure

Naive goldfish were screened for ease of conditioning and only those that provided robust unconditioned suppression responses to shock and conditioning to acoustic signals in 5-10 trials were used.

After initial training of about 20 trials, threshold determinations were first determined for the detection of the noise or tonal signal in quiet (under ambient noise). A modified method of limits was used as described earlier (Fay, 1969, 1970, 1974). The signal level was attenuated in 10 dB steps until the suppression ratio (SR) remained at about 0.5 for several trials. A 10-30 dB sound pressure range was then chosen which was likely to bracket the threshold, and 5 descending stimulus series were run consisting of from 2-4 stimulus levels in 10 dB increments. Shock intensity was adjusted as necessary to keep the SR to clearly detectable signals generally below 0.25, although this was not always possible. The SR values calculated for each trial were plotted as a function of stimulus level, and straight lines were drawn between the mean of the 5 values at each stimulus level. The interpolated stimulus level corresponding to an SR of 0.4 was defined as threshold. The mean of two such determinations on separate days defined the threshold level for the signal alone. The signal level was then adjusted to be 15 dB above threshold, and the continuous tonal masker introduced.

Masked thresholds were determined similarly by plotting the SR evoked by the signal as a function of the masker level, and were defined as the masker level corresponding to an SR of 0.4. The intertrial interval averaged about 2 min. Threshold masker level plotted as a function of masker frequency defined the psychophysical tuning curves for individual animals.

In Expt. 1, 20 such curves were obtained (five signal frequency points for each of four animals), for the detection of 40 Hz noise bands in the presence of tonal maskers. In Expt 2, set-up B replaced A (Fig. 1) and seven complete and five fragmentary individual functions were obtained. In Expt. 3 a tonal signal replaced the noise and four complete and three fragmentary functions were obtained, again in set-up B.

RESULTS

The individual psychophysical tuning curves determined in Experiment 1 are presented in Fig. 1A and B. Each point is an individual threshold determination, and adjacent points are connected with straight lines. For a 100 Hz signal, the tuning functions generally show that the effectiveness of the masker varies inversely with the frequency separation between the masker and signal. For the 200 Hz signal, tuning functions have low-pass characteristics down to 100 Hz (however, see Expt 2). While the masking functions for the 500 Hz signal show band-pass characteristics, the most effective masker frequency is not 500 Hz, but is 300 Hz. The four animals tested are quite consistent in this behaviour. For the 600 Hz signal frequency, a new pattern emerges in which a masking peak occurs at 600 Hz as well as in the 300 Hz region. A third peak also occurs in the 900 Hz region. While there are large individual differences in the effectiveness of the masker, the masking peak pattern is quite consistent across the four animals tested. The 700 Hz masking functions are similar to the 600 Hz functions in that minima occur both at the signal frequency, and in the
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Fig. 2. Results of Expt 1. Individual psychophysical tuning curves for 4 animals (●, fish no. 1; ○, fish no. 2; ■, fish no. 3; □, fish no. 4) each tested at signal frequencies of 200 and 600 Hz (A), and 100, 500 and 700 Hz (B). Masker frequency is on the abscissa and masker level re: signal level is on the ordinate. The arrows indicate the signal frequency for each set of curves. The dashed and solid lines serve only to avoid confusion in differentiating the data for different signal frequencies.
300 Hz region. The possible existence and locations of tertiary masking peaks above the signal frequency could not be determined for the 700 Hz signal condition since the acoustic system was not capable of producing the sound pressure levels required to mask the 700 Hz signal with tones above 900 Hz. Note, however, that the masking effects of tones above 900 Hz could be measured for certain other signal frequencies, both above and below 700 Hz, for which the overall masking effects were greater.

In Expt 2, individual psychophysical tuning curves are presented in Figs. 3A and B for the masking of noise bands by tones in set-up B. The two functions determined
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Fig. 4. Results of Expt 3, plotted as in Fig. 2. Individual psychophysical tuning curves for four animals for signal frequencies of 300 Hz (A) (●, fish no. 10; ○, fish no. 11), and for 500 and 600 Hz (B (●, fish no. 12; ○, fish no. 13).

at 100 Hz are essentially identical to those of Expt 1. The two 200 Hz functions extend observations below 100 Hz and illustrate their essential band-pass characteristics. One 500 Hz function illustrates again that a masking peak occurs below the frequency of the signal, this time at 400 Hz. Notice here, too, the occurrence of another peak at about 1000 Hz. The two 300 Hz functions are similar in form to the 100 and 200 Hz curves except in one animal where a single elevated value at 250 Hz creates a masking peak at 200 Hz.

In Expt 3 masking functions for tones masked by tones in set-up B are shown in Fig. 4A and B. The two functions determined at 300 Hz show similar band-pass characteristics with peaks occurring near the signal frequency (290–310 Hz). Both functions show generally steeper low frequency slopes compared with the 300
Hz functions of Expt 2, but without evidence of elevated thresholds at 250 Hz. One of the functions shows an unusual degree of masking occurring within 100 Hz of the signal frequency. Whether the masking peak occurring at 700 Hz for the open circles curve in Fig. 3A is a reliable effect is not known. The 500 and 600 Hz functions show patterns typical of the 600 and 700 Hz functions of Expt. 1. That is, masking peaks occur in the 300 Hz region, at the frequency of the signal, and possibly at a frequency point above the signal. However, the 500 Hz curve departs from the pattern seen in Expts 1 and 2 where a single peak was observed in the 300 Hz region, and not at 500 Hz.

The following observations and summarizing points refer to all of the data from Expts 1–3 (Figs. 2–4):

(A) Psychophysical tuning curves determined for 100, 200 and 300 Hz signals have the form of V-shaped functions with the greatest masking occurring in the frequency region of the signal. The form of these functions does not appear to depend critically on tank acoustics, or whether tones or noise served as signals.

(B) Tuning curves for 500 Hz noise signals have a single masking peak in the 300 Hz region, while the curve for a 500 Hz tonal signal has, in addition, a pronounced peak at the signal frequency. This difference is not dependent upon tank acoustics and may be due to a difference in the resolving power of the two techniques (tone-on-tone versus tone-on-noise masking) to delineate the shapes of the filtering mechanisms operating here.

(C) Tuning functions above about 300–500 Hz always exhibit masking peaks in the 300 Hz region, at the frequency of the signal, and possibly at frequencies above the signal. This pattern does not depend upon the frequency response characteristics of the tank, or upon whether tones or noise bands served as signals.

(D) The tuning curves are generally asymmetrical on a logarithmic frequency axis with steeper slopes (in dB/octave) occurring toward the higher frequencies. In general, all curves fall off below 300 Hz with similar slopes.

(E) The masker-to-signal ratios at the point of greatest masking generally fall in the range between 15 and 25 dB.

**DISCUSSION**

These experiments suggest that the goldfish auditory system consists of frequency selective channels, with bandwidths narrower than the entire hearing range, and with best frequencies which can occur anywhere in the frequency continuum between 100 and 1000 Hz. Similar interpretations have been made for the cod (Buerkle, 1969; Hawkins & Chapman, 1975) and for the goldfish (Tavolga, 1974) from psychophysical masking data.

Buerkle (1969) studied the detection thresholds for five half-octave noise-band signals centred between 21 and 340 Hz in the presence of half-octave masker bands fixed in amplitude at 10 dB. Masking was most effective when the centre frequency of the masker and the signal coincided, and declined with the frequency separation between masker and signal. Buerkle interpreted these functions as illustrating the existence of frequency-selective detection channels in the cod.

Tavolga (1974) studied the masking of one tone by another in the goldfish. A signal was fixed in frequency (200, 500 or 1000 Hz), and a masker introduced at fixed amplitude (0 dB) at various frequencies. The elevation in signal threshold due to th
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presence of the masker was plotted as a function of masker frequency. At frequency separations greater than 5–10 Hz, Tavolga’s masking functions are broadly tuned with a single masking peak occurring where the signal and masker frequencies are most similar. These functions are qualitatively similar to the single-peaked functions of the present study.

At smaller frequency separations, however, the masking effect increases very rapidly and is ‘complete’ (in that the signal was not detected at any level used) when the frequency of the signal and masker are equal. In this case, the task simply becomes an amplitude discrimination in which the beat rate and the relative amplitudes of the two stimuli determine the detectability of the signal. Tavolga notes that the goldfish trained in a detection task at wide frequency separations between signal and masker do not generalize to an amplitude discrimination task. These rapidly rising segments of the masking functions were not evident in the present results, possibly because noise bands rather than tones served as signals in Expts 1 and 2 (leading to beat frequency bandwidths of no less than 40 Hz), and because masker and signal tone frequencies were never presented with a separation of less than 10 Hz in Expt 3.

Tavolga appears to interpret these data in terms of a mechanical ‘place’ conception, and suggests the possible existence of two filter types. One very narrow filter is postulated which would be responsible for both the very sharply rising segments of the masking functions and the frequency discrimination limen (Jacobs & Tavolga, 1968; Fay, 1970), while a second more broadly tuned filter type would be responsible for the less steep segments of the masking function. Tavolga also suggests that this latter ‘broad filter’ may be an epiphenomenon of some sort of attentional mechanism. No attempt was made to compare these masking data with the neurophysiological tuning curves for the goldfish (Furukawa & Ishii, 1967).

Hawkins & Chapman (1975) studied tonal and noise masking patterns in the cod using tones as signals (40–380 Hz) and either a tone or a 10 Hz-wide noise band (fixed in amplitude at 10 dB) as maskers. Again, functions relating the signal level necessary for detection to masker frequency showed the familiar peak at the frequency of the signal and rather sharp declines in masking with frequency separation. These authors pointed out the implausibility of a peripheral tuning mechanism being responsible for the selectivity of the psychophysical functions, and therefore interpreted their results in terms of neural filtering mechanisms operating upon temporally coded information.

The results of these three studies are consistent with the present results in illustrating that there is a broad similarity between fishes and mammals in this aspect of auditory frequency analysis. Given the additional demonstrations of the critical band phenomenon in goldfish (Tavolga, 1974) and in cod (Hawkins & Chapman, 1975) from noise-band narrowing experiments, the functional similarities between the fishes and the mammals becomes quite remarkable. These similarities have, in fact, led many to the notion that the mechanisms underlying this behaviour are the same in mammals and fishes. Some investigators have argued that this common mechanism involves a frequency-to-place transformation occurring mechanically in the periphery (van Bergeijk, 1967; Tavolga, 1974; Sand, 1974), while others have argued for a time-to-place transformation occurring neurally in the central nervous system (Fay, 1970, 1972, 1974; Hawkins & Chapman, 1975; Schwartzkopff, 1976). The present
experiment was designed to investigate the plausibility of the former hypothesis by providing psychophysical data which are directly comparable to neurophysiological measures of peripheral tuning (Fay, 1978), obtained for the same species under nearly identical conditions.

Fig. 5 presents a representative sampling of frequency response functions for single goldfish saccular neurones obtained in the acoustic stimulation set-up pictured in Figure 1B. The curves are for spontaneously active neurones which are more numerous and generally more sensitive than non-spontaneous units. The response criterion used here is the degree of synchrony, or phase-locking, between the tonal stimulus and the train of evoked neural impulses. The lines plotted connect the sound pressure levels necessary at a given frequency to produce a given degree of synchronization (see Anderson (1973) for a discussion of the measure of synchronization used). For non-spontaneous neurones, on the other hand, impulse rate criteria are more appropriate and the tuning curves for these are quite similar in shape to those shown, but generally exhibit less variation in slope and bandwidth, and show 10–15 dB less sensitivity. The dashed lines are for neurones showing positive slopes between |
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Fig. 6. A comparison of the tuning characteristics of psychophysical (●) and neural (○) (Fay, 1978) tuning curves for the goldfish with psychophysical functions for the chinchilla (●) (McGee, Ryan & Dallos, 1976), and the neural functions for the cat (△) (Kiang et al. 1965). On the abscissa is plotted the point of best sensitivity (greatest masking) and the ordinate is the $Q_{10}$ value, or the best frequency divided by bandwidth at 10 dB above best sensitivity. The goldfish neural data are from the curves of Fig. 5, and the psychophysical data include both the fragmentary and complete masking functions.

100 and 200 Hz (termed low-frequency, or LF neurones), while the solid lines are termed high-frequency, or HF neurones.

As a first attempt to compare neural and psychophysical tuning curves, Fig. 6 shows the degree of tuning ($Q_{10}$) for both types, along with neural and psychophysical tuning values for mammals. The $Q_{10}$ values are defined as the centre frequency of the function (in Hz) divided by its bandwidth (in Hz) at 10 dB above the function's best sensitivity. The goldfish neural functions are clearly broadly tuned by mammalian standards with $Q_{10}$ values generally falling in the range between 0.5 and 1.5. Data for the cat show tuning reaching $Q_{10}$ values of over 5 in the 400–500 Hz range. Note that there are no goldfish neural tuning points below about 300 Hz since the LF type neurones show simple low-pass rather than band-pass characteristics, and that no neurones are observed to be tuned above about 800 Hz.

The goldfish psychophysical curves clearly show sharper tuning than the neural (goldfish or cat), and psychophysical (chinchilla) curves, particularly in the 500–700 Hz region. The goldfish psychophysical tuning values above a $Q_{10}$ of about 4 all represent the sharp peaks of multi-peaked curves observed at frequencies above 300–500 Hz. While the $Q_{10}$ values decline sharply below this range, the mere existence of peaked psychophysical functions contrasts with the lack of any neurones observed to be tuned to a frequency below about 300 Hz. There appears to be little if any correspondence between the degree of neural and psychophysical tuning throughout the goldfish hearing range. Evidence is thus presented here that the goldfish differs from mammals in that the most highly frequency-selective mechanisms that can be demonstrated psychophysically cannot be accounted for simply by reference to peripheral neural channels with similar frequency selectivity. Some other process or mechanism must be operating for the fish.

While it is tempting at this point to suggest that a neural mechanism analysing temporally coded patterns is a plausible alternative explanation, other, possibly
Fig. 7. A comparison of the slopes of neural and psychophysical tuning curve segments for the goldfish. The abscissa plots the centre frequency of the curve segment in question, and the slope of the segment is plotted on the ordinate. The data at each frequency are plotted as a frequency distribution of slopes for both neural (open areas) and psychophysical (filled areas) curve segments. The neural data are derived from the curves of Fig. 5, and the psychophysical data include both complete and fragmentary curves of the present study.

simpler hypotheses, can be considered. In the frequency region from below 100 Hz up to 300–400 Hz, the neural functions (Fig. 5) can simply be viewed as filters with low-pass (LF) and high-pass (HF) characteristics varying somewhat in roll-off rate and gain (sensitivity). If it is assumed that the organism makes detection decisions on the basis of input from one or a small number of neurones, and that it simply 'attends' to those neurones carrying the best information [most favourable signal-to-noise ratio (S/N)], then it is possible, in principle, to account for the 'V-shaped' psychophysical functions. That is, for maskers below the signal in frequency, decisions would be made on the basis of input from the HF fibres, while for maskers above the signal in frequency, the LF fibres would be used. In this type of analysis, a masking peak would always occur at the frequency of the signal, giving the impression of the operation of a set of fixed filters with a continuous distribution of best frequencies. This idea does not appear to be an unlikely mode of operation for a neural system, and could account as well for at least the qualitative features of the masking functions for the cod (Buerkle, 1969; Hawkins & Chapman, 1975) and for the goldfish (Tavolga, 1974).

For this mechanism to account quantitatively for the psychophysical data, it appears that some correspondence between the slopes of the neural and psychophysical...
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Functions should be demonstrated. Fig. 7 presents frequency distributions of the slopes of segments of both the neural and psychophysical tuning curves as a function of the centre frequency of the curve segment. Note that the negative slopes here represent high-pass, and the positive slopes represent low-pass characteristics. While the range of psychophysical slopes is almost always greater than that for the neural, there appears to be a reasonable correspondence between the two sets of data up to about 350 Hz. It is possible, then, that below about 350 Hz where the slopes of the HF and LF neurones are of opposite sign, the psychophysical functions may simply be determined by a central neural mechanism which selects between HF and LF neurones for the most favourable S/N.

Above this frequency range, however, the psychophysical functions show slopes approaching ±180 dB per octave while there are no significant negative neural slopes at all. Thus, the sharp peaks of the multi-peaked function are probably determined by processes which are unrelated to peripheral tuning. Since the sensitivity of LF neurones falls off rapidly with frequency, and is clearly lower than for the HF neurones overall, the multi-peaked functions probably reflect the processing of information from HF neurones alone.

While we may tentatively accept the channel selection hypothesis for signal detection below about 350 Hz, the nature of the high-frequency mechanism remains unclear. Three possibilities immediately come to mind here, however, and all are based on the notion that the multi-peaked psychophysical functions are simply determined by the tuning characteristics of the HF neurones plus a mechanism which renders maskers within 100–200 Hz of the signal particularly ineffective. The first possibility is that the sharp masking peak represents the analysing capacities of a neural processor operating in the time domain (e.g. an autocorrelator) which is restricted to a rather narrow frequency band surrounding the signal. This is an intriguing hypothetical construct which often has appeared in the human psychoacoustical literature but is as yet without any empirical support. For the present, simply note that for such a process to operate in detection the signal must alter the temporal structure of the discharge pattern in saccular neurones evoked by the masker. It is not now clear how stimuli interfere with each other (how masking occurs) in terms of the modulation of these temporal patterns. Neurophysiological masking studies of this kind are now underway in this laboratory.

The second possibility is that highly detectable non-linear combination products are generated by the addition of two stimuli differing in frequency by about 100–200 Hz. It is interesting to note here that the cubic difference product $2f_1 - f_2$ (where $f_1$ is the lower frequency and $f_2$ is the higher) generated by the addition of a 500, 600 or 700 Hz tone or noise band signal with a tonal masker at about 100–200 Hz below the signal in frequency, all fall in the 300–400 Hz region where all the HF neurones phase-lock quite well. Also note that for those psychophysical tuning curves exhibiting a sharp decline in masking for maskers 100–200 Hz above the signal frequency (e.g. the 600 Hz curves of Fig. 2A), the $2f_1 - f_2$ values also fall only slightly above the 300–400 Hz region. Neural periodicities at the $2f_1 - f_2$ frequency have been observed in mammalian auditory neurones (e.g. Pfeiffer, Molnar & Cox, 1974), and are likely to occur for the fishes also. Neurophysiological investigations of the strengths of these products are underway in this laboratory.

The third possibility involves the notion that the fish is differentially sensitive to
the rate of amplitude modulation (beats) produced by signals primarily affecting the HF neurones, with the greatest sensitivity occurring in the 100–200 Hz beat frequency range. Fay (1972) has shown that goldfish are quite sensitive to a 40 Hz modulation rate at carrier frequencies of 400 and 1000 Hz, while both Tavolga (1974) and Hawkins & Chapman (1975) have observed that goldfish and cod do not respond readily to low-frequency beats (1–10 Hz). The suggestion here is that sensitivity to amplitude fluctuations increases with modulation (beat) rate. While this hypothesis makes sense qualitatively, it is difficult to see how the addition of two stimuli differing in amplitude by as much as 50 dB (see Figs. 2–4) could generate audible beats at any frequency, since the resulting intensity difference would be about 0.06 dB, a value quite a bit below the 4–5 dB intensity difference threshold measured psychophysically for the goldfish by Jacobs & Tavolga (1967). In any case, the question of the detectability of envelope periodicities is an important one in its own right, and we are presently investigating the form of the goldfish temporal modulation transfer function, both psychophysically and neurophysiologically.

SUMMARY AND CONCLUSIONS

The application of the psychophysical tuning curve procedure to the study of auditory frequency analysis in the goldfish has not been completely satisfactory in providing critical evidence bearing on the question of a peripheral versus a central mechanism. The present results are similar to those of Buerkle (1969), Hawkins & Chapman (1975) and Tavolga (1974) in illustrating that the amount of masking is an inverse function of the frequency separation between the masker and signal. However, this observation, by itself, does not clearly discriminate between a peripheral-mechanical or central-neural mechanism. Furthermore, it is pointed out that a simple system composed of overlapping high- and low-pass filters with slopes similar to those observed neurophysiologically (Fay, 1978) could account both quantitatively and qualitatively for the form of the present masking functions, up to about 350 Hz, without reference to either a temporal-neural or highly tuned mechanical mechanism. While we do not have comparable neurophysiological data for the cod, it is possible that what appear to be psychophysical band-pass filtering mechanisms (Buerkle, 1969; Hawkins & Chapman, 1975) are simply a reflection of the nervous system's selection of the high- or low-pass input channels with the most favourable S/N. At the same time, however, the present results certainly do not rule out the possibility of a temporal-neural analysis in masked signal detection in this frequency range. Through a combination of neural and psychophysical data, it is simply illustrated that the temporal hypotheses are not the only possible explanations.

Above about 350 Hz for the goldfish, however, mechanisms other than peripheral filtering must be operating to produce the very steep masking functions (up to 180 dB/octave). The overall envelopes of the multi-peaked psychophysical tuning curves produced in the 500–700 Hz range are thought to reflect the tuning characteristics of HF neurones (Fay, 1978), while the sharp peak in the region of the signal frequency is discussed in terms of mechanisms which would lead to a marked reduction of the masking effect for frequency separation of from 100 to 200 Hz. Each of these three hypothetical operations (autocorrelation, combination product detection, and hig...
Auditory masking patterns in goldfish

Auditory masking patterns (e.g., rate beat detection) is an example of a neural analysis of the temporal structure existing within input channels. Since these multi-peaked masking functions occur only when detection appears to be based solely on HF neural input, differences in neural processing between the LF and HF channels are suggested.

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