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NON-SIMULTANEOUS AUDITORY MASKING IN THE GOLDFISH, *CARASSIUS AURATUS*

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SUMMARY

Auditory thresholds were determined for 500 Hz pure tone pulses of 15, 25 and 50 ms duration presented leading, following or simultaneously with noise pulses of 50 or 250 ms duration. Masking by the noise decreased: (i) with an increase in tone pulse duration; (ii) with a shortening of the noise pulse duration; and (iii) as the interval between tone and noise pulses was increased from 0 to 350 ms. The effect of the noise was independent of whether the noise led or followed the pure tone. It is suggested that the most significant factor affecting masking was the duration of the interval between tone and noise, and that the site for the interactions between signals is central to the inner ear.

INTRODUCTION

Recent behavioural and physiological investigations have shown that a number of teleosts can detect auditory signals over a wide range of frequencies, and that several species can also perform frequency and intensity discrimination (see Tavolga, 1971; Popper & Fay, 1973; Fay, 1978*a*, for reviews). In most studies of auditory sensitivity, thresholds have been determined in a quiet environment very atypical of the noisier environments in which fishes live. To study sensitivity in a more 'normal' environment, and to provide comparison with the masking and critical band phenomena found in mammals, a number of investigators have recently explored auditory sensitivity in the presence of another (masking) signal (e.g. Tavolga, 1967, 1974; Buerkle, 1969; Chapman & Johnstone, 1974; Fay, 1974; Fay, Ahroon & Orawski, 1978). While these workers have demonstrated several functions in the teleost auditory system that hold striking parallels to functions found in mammals, they have been careful to note that the physiological basis for masking and the critical band-like mechanisms in fishes and mammals may be strikingly different, particularly in light of the marked differences in the anatomy of the auditory structures peripheral to the central nervous system in fishes and mammals (see Popper, 1977, 1978 for a discussion of the anatomy of the teleost auditory system).

In addition to the studies of masking in mammals using signals presented simultaneously, there is a growing body of literature that shows that masking (or interf[illegible]ence) occurs even when the test signal and masker are presented non-simultaneously.

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In general, the degree of masking in mammals decreases with increases in the interval between signal and masker up to about 100 ms, and the level of masking depends upon whether the signal leads or follows the masker (e.g. Wilson & Carhart, 1971; Druifhuis, 1973; Penner, 1974; Lynn & Small, 1977). The mechanisms involved in non-simultaneous masking are less clear than those involved in simultaneous masking. Some workers have suggested that the non-simultaneous masking data reflect responses at the level of the peripheral auditory system (e.g. Druifhuis, 1973) while others argue that the whole process occurs centrally (e.g. Elliot, 1962; Wilson & Carhart, 1971). Still other investigators have suggested that whether the process is central or peripheral depends upon whether the masker leads or follows the test signal (e.g. Simlarowski & Carhart, 1975; Weber, 1978).

Experiments on non-simultaneous masking have not, to date, been performed with teleost fishes. However, physiological experiments on goldfish (*Carassius auratus*) have shown that presentation of one signal will adversely affect the response to the second signal, indicating that interactions between signals are occurring over time in the auditory system (Piddington, 1971; Fay, 1978*b*). Interactions of non-simultaneous signals may tell something about the function of the teleost auditory system and also have considerable relevance in understanding signal detection by a fish with a background of sporadically produced noises such as those produced by snapping shrimp or the breaking of waves.

The experiments reported here were designed to measure the ability of goldfish to detect pure tone signals of differing durations presented simultaneously with a noise signal, or before or after it at different time intervals.

MATERIALS AND METHODS

The experimental paradigm involved training *Carassius auratus* to suppress respiration when they detected a pulsed pure tone, by pairing the pure tone with a mild shock. The general experimental procedure involved restraining the fish in a holder of cheesecloth on a plastic frame and placing it in a small aquarium located in a soundproof chamber (Popper, Chan & Clarke, 1973). Sounds were presented to the animal from a speaker just outside the aquarium. Masking noise pulses (white noise bandpass filtered at 500 Hz) were presented once per second during the whole time the animal was in the test chamber, while the pure tone pulses were only presented during a 10-s test period. Respiration rate and amplitude were measured during and just prior to the test period, and the difference was used as a criterion of detection of the pure tone signals (see below).

Experimental variables were the interval between the noise and pure tone signal (0–350 ms), the duration of the pure tone signal (15, 25 or 50 ms), the duration of the noise pulses (250 or 50 ms) and whether the pure tone signal preceded or followed the noise. In all cases the interval between noise and masker is defined as the time between termination of the leading sound and the start of the following. During one day's trials each variable was kept constant. Tables 1–4 indicate the various combinations of parameters used during the course of these experiments.

Threshold determination

Thresholds were determined for 500 Hz pure tone pulses. This frequency was selected since it is within the frequency range of best detectability by goldfish (Jacobs & Tavolga, 1967).

If the animal detected the pure tone there would be a statistically significant decrease in the respiration rate and/or amplitude during the signal presentation while there would be no change in respiration if the animal did not detect the tone. The animal's threshold for a signal was determined using the up–down staircase method (e.g. see Tavolga & Wodinsky, 1963; Jacobs & Tavolga, 1967; Popper, 1972 for details).

Respiration rate measurement

Respiration was measured with a strain gauge (Kistler–Morse DSK) placed by the fish's operculum. The analogue output of the strain gauge was directly proportional to the amplitude of the movement of the operculum. This signal was integrated and digitized and this value indicated the rate, duration, and amplitude of all opercular movements during a given period. These parameters were then interpreted as 'respiration rate'.

The animal's response to the pure tone signal was determined by measuring rate during the 10-s test period (T) and comparing this with the level in a 10-s pre-trial period (P) which immediately preceded the trial, during which time only the masker was presented. The degree of respiration change, or the suppression ratio (SR), was determined by dividing respiration rate in period T by the sum of the rates in P and T ($SR = T/(P+T)$). The SR would be 0·5 if no respiration suppression occurred and 0 if total suppression occurred throughout the test period. To take account of variability inherent in the animal's respiration, an SR level at which the animal was considered to have detected the sound was calculated by determining the mean and standard deviation of the SR for 500 trials without sound presentation ($\bar{X} = 0{\cdot}53$; S.D. = 0·045) (Popper *et al.* 1973) and selecting an SR of 0·44 which was two standard deviations (95% confidence level) below the mean value as the response threshold level ($SR < 0{\cdot}44$). To ensure that the variability in the animal's normal respiration rate did not bring the SR below 0·44 by chance, test periods were alternated with periods identical except for the absence of pure tone. An SR of 0·44 was almost never reached in the 'blank' periods.

Training

Training of respiration suppression to the pure tone was done by initially presenting the fish with the signal in the presence of the masker, followed, after 10 s, by a single 25-ms alternating current shock that varied from 6 to 10 V in amplitude at the source, depending on the particular animal. The normal response of a goldfish to shock is to stop respiration for several seconds. After approximately ten trials, the fish start to suppress respiration following the onset of the sound and before the shock. After 25 trials, animals would suppress respiration in at least 80% of all trials. Training continued for several days beyond the time that the fish first reached 80% correct response so that they would be 'overtrained' prior to taking data. Shock was continued throughout the experiments, but to minimize the trauma, it was presented

in only 50% of the sound trials. Presentation of shocks in fewer trials would have been preferable, but this was found to cause extinction of the conditioned response.

Experimental control and sound presentation

A minicomputer system (PDP 11/10) was used for control of all aspects of the experiments. The computer was used to time signal presentations and inter-signal intervals (using an internal programmable clock), calculate suppression ratios, control sound levels, and monitor the responses of the test animals. A running check on the animal's current threshold was kept by having thresholds displayed on an oscilloscope or printed on the terminal.

Sounds were presented through an air loudspeaker placed near the test tank. The wavelength of the sound was larger than that of the tank, ensuring good transfer of sound from air to water (Parvulescu, 1964; Hawkins & MacLennan, 1976). The nature of the sound stimulus detected by the fish was not of particular concern in these experiments. However, it is likely that the sound was only being detected by the inner ear rather than the lateral-line (Popper & Fay, 1973).

Signals were produced with an audio oscillator (Wavetek, model 114B) or noise source (Grason–Stadler, model 455c), gated with an electronic switch to produce a 5 ms rise and decay time so as to prevent on and off transients, attenuated (Hewlett–Packard, model 350D) and filtered (Krohn–Hite, model 3200).

The sound pressure levels in the experimental tank were calibrated by placing a hydrophone at the position of the fish and measuring the voltage to the power amplifier necessary to produce a desired sound level. Variation in sound levels along the length of the holding apparatus was no more than 1 or 2 dB, a value well within the standard deviation of our results.

Ambient sound levels were measured in the test tank and sound spectrum levels calculated. These were at least 30 dB below thresholds for pure tone signals without noise, indicating that masking by ambient noise, which has been reported in goldfish and other species, did not affect thresholds (see Buerkle, 1969; Tavolga, 1967, 1974; Fay, 1974).

Experimental animals

The experimental animals were comet goldfish (*Carassius auratus*) (6–8 cm in length) obtained from a single supplier on the island of Oahu, Hawaii.

RESULTS

The experiments were directed to determining the change in the sensitivity threshold for a pure tone resulting from the presence of noise at different times relative to the pure tone. Thresholds in the absence of noise (Tables 1–4) were essentially the same as those determined earlier for sounds of similar pulse durations (Popper, 1972).

The amount of threshold change produced by noises at different times relative to pure tone signals of varying duration are shown in Tables 1–3. In all but a few cases the data represent determinations with at least four animals, each of which was tested a minimum of three times for each test parameter.

Table 1. *Amount of threshold change for a 15 ms pure tone with a 250 ms noise*

(Threshold changes were calculated by subtracting the masked threshold from the absolute threshold. For example, the masked threshold for a signal presented 350 ms before the noise was −19·7 dB, *re*: 1 μbar. This was subtracted from the absolute threshold of −36·2 dB, *re*: 1 μbar to give a threshold change of 16·5 dB.)

	Signal: before noise			Signal: after noise		
Interval (ms)	Threshold change (dB)*	S.D.	N	Threshold change (dB)*	S.D.	N
0	30·5	3·9	20	29·7	3·8	20
5	29·1	4·3	16	27·6	4·1	11
15	30·5	4·0	18	24·5	5·9	14
50	24·7	5·3	20	17·2	8·4	30
75	—	—	—	15·4	7·3	20
100	19·7	4·3	20 †	14·6	7·5	24
	18·3	4·9	10 †			
125	—	—	—	10·8	8·9	18
150	—	—	—	11·6	7·5	20
160	9·7	8·2	17	—	—	—
200	—	—	—	12·7	10·7	15
225	15·9	6·6	20	—	—	—
300	18·4	5·0	21	14·9	9·8	23
350	16·5	8·1	15	19·0	5·9	16

* Threshold without noise −3·62 dB, *re*: 1 μbar (S.D. = 3·93 dB; N = 18).
† Replications at least 1 year apart.

Table 2. *Amount of threshold for a 25 ms pure tone with 250 ms noise*

	Signal: before noise			Signal: after noise		
Interval (ms)	Threshold change (dB)*	S.D.	N	Threshold change (dB)*	S.D.	N
0	34·6	3·2	23	36·2	3·6	23 †
	32·6	5·2	28	29·6	6·0	24 †
5	28·9	4·9	20	27·0	5·4	20
15	26·6	3·3	11	22·2	6·2	10
25	—	—	—	19·0	7·3	21
50	18·1	5·9	23	17·2	8·2	22
63	—	—	—	13·3	5·6	15
75	12·3	5·7	14	8·5	8·5	16
83	—	—	—	13·7	9·5	17
90	—	—	—	18·4	8·2	13
100	21·6	6·0	25	24·9	5·2	20
110	—	—	—	25·6	6·8	14
125	13·4	5·7	13	14·5	9·2	12
150	17·7	8·2	20	14·5	8·2	24
300	15·7	8·5	22	13·1	10·8	22

* Threshold without noise 40·1 dB, *re*: 1 μbar (S.D. = 4·01 dB; N = 18).
† Replications at least 1 year apart.

Table 3. *Threshold change for a 50 ms pure tone with a 250 ms noise*

Interval (ms)	Signal: before noise — Threshold change (dB)*	s.d.	N	Signal: after noise — Threshold change (dB)*	s.d.	N
0	17·9	10·0	23	28·4	4·0	15
15	10·3	10·5	18	15·3	7·3	23 †
				15·0	6·5	11 †
25	5·9	7·7	13	12·7	5·8	19
50	13·3	7·5	22 †	5·0	6·6	23
	11·1	7·3	22 †			
75	−1·1	7·6	17	—	—	—
100	0·3	6·0	20	4·9	5·4	19
150	4·1	7·3	38	5·7	8·2	21
300	2·1	7·3	27	—	—	—

* Threshold without noise −37·6 dB, *re*: 1 μbar (s.d. = 3·89 dB; N = 19).
† Replications at least 1 year apart.

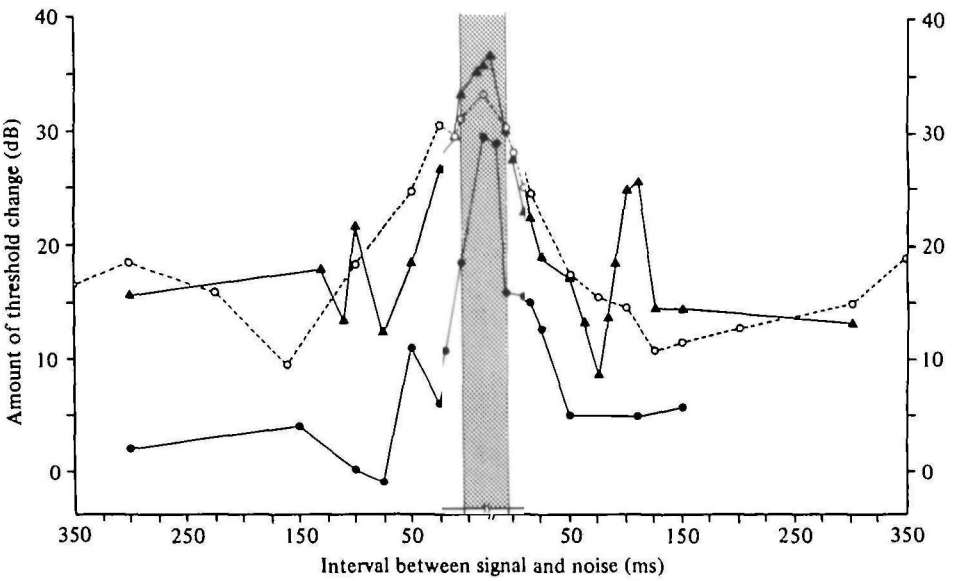

Fig. 1. Mean threshold changes (*re*: absolute threshold for each duration signal) as a function of pure tone duration and time between pure tone and noise. The noise, indicated by the hatched area, was 250 ms in duration and the interval is the time between the end of the leading signal and the start of the following. Signal duration: ○---○, 15 ms; ▲—▲, 25 ms; ●—●, 50 ms. Noise duration: 250 ms.

The data in Tables 1–3 are summarized and compared in Fig. 1. It is apparent that as the pure tone was presented at a longer interval from the noise there was a substantial improvement in the detectability of low level signals. The amount of interference for each interval depended upon the pure tone duration. The poorest detection occurred for the shorter pure tone signals (15 and 25 ms duration). This is further illustrated in Fig. 2 which shows the amount of threshold change with different pure tone durations for each interval. The greatest amount of threshold

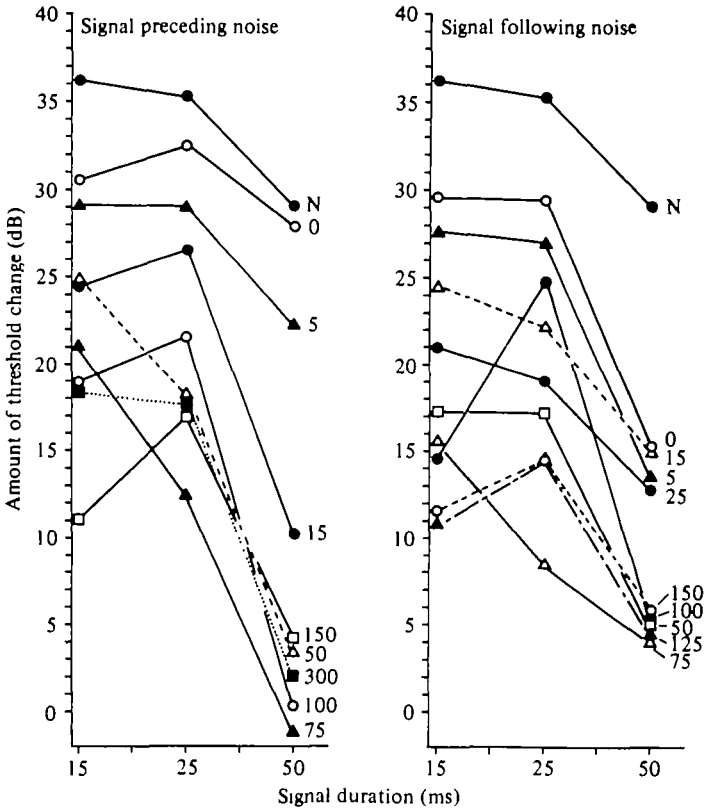

Fig. 2. Amount of threshold change for different signal durations with the signal preceding and following the 250 ms noise. Data are for different intervals between signal and noise and for signals presented during the noise (N).

change occurred, as would be expected, when the signal was totally embedded in the noise masker. The precise position of the signal in the noise did not significantly alter the amount of threshold change. Further, the degree of threshold change, or the amount of masking, did not differ significantly for the three durations of pure tone when they were presented within the noise (analysis of variance). However, when the signals were presented sequentially with an interval of 0 s there was far less masking for the 50 ms signal than for the 15 and 25 ms signals, leading to the suggestion that the longer duration signal had more energy outside of the region of major effect of the noise.

Examination of Fig. 1 shows that the most significant decrement in sensitivity to the pure tones occurred when the interval between signal and noise was 50 ms duration or less. The only exception to this finding is for the 25 ms pure tone preceding or following the noise and, possibly, for the 50 ms pure tone that preceded the noise. In the case of the 25 ms signal the amount of threshold change decreased as the interval increased to 75 ms before and after the noise. This was followed by a sharp, and statistically significant ($P < 0{\cdot}01$), increase in the threshold change until an interval of 150 ms and then another drop in the threshold change that was essentially

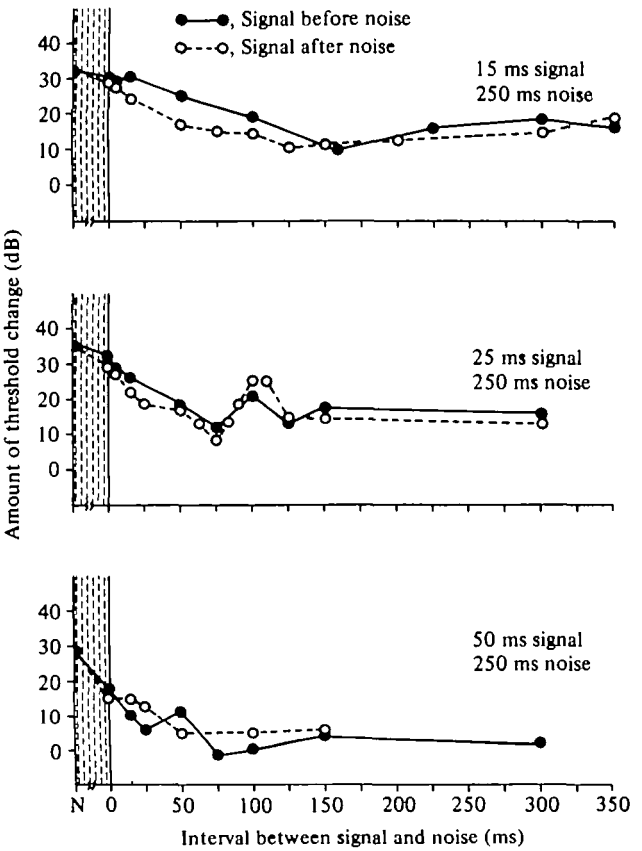

Fig. 3. Threshold change for signals presented before and after the 250 ms noise (hatched area) overlapped on one another to show similarity between the two groups of data.

flat through to the longest interval of 350 ms. This sharp increase in threshold change was carefully explored for the 25 ms signal following the noise by determining the threshold changes for intervals of 83, 90, 100, 110 and 125 ms (Table 2), and it was clear that the shift was not an experimental artifact. This unexpected decrease in detectability of the pure tone when the interval was greater than 75 ms was not found for the 15 ms probe signal and was very small when the 50 ms probe led the noise by 50 ms. However, exploratory studies of other intervals around the 50 ms period did not indicate that this decrease in detectability of the pure tone was as clear-cut as the changes for the 25 ms signal.

It is also of interest to note that while the amount of threshold change decreased as the pure tone was moved further from the noise for all three signal durations, only the 50 ms signal reached 0 dB threshold change. Even for the longest interval, the 15 and 25 ms signals showed some threshold change, indicating that their detection was still being affected by the noise. Due to equipment limitations, it was not possible to extend the interval beyond 350 ms, but it should be noted that when the 15 ms signal was tested with a 50 ms noise the amount of threshold change came close to 0 dB with an interval of 50 ms (Fig. 4).

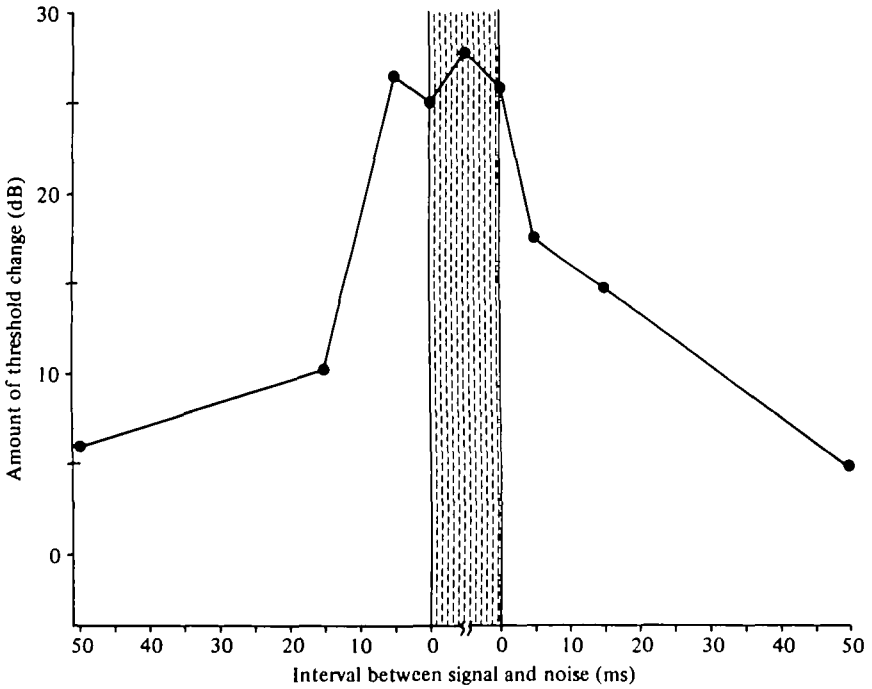

Fig. 4. Threshold changes for a 15 ms signal presented before and after a 50 ms noise (hatched area).

Table 4. *Threshold change for a 15 ms pure tone with a 50 ms noise*

	Signal: before noise			Signal: after noise		
Interval (ms)	Threshold change (dB)	S.D.	N	Threshold change (dB)	S.D.	N
0	24·9	4·4	23	25·8	5·9	23
5	26·5	4·8	19	17·6	8·9	20
15	10·2	9·2	15	12·7	7·4	18
50	5·9	8·2	19	4·8	5·6	23

It is also significant to compare the threshold changes with the probe presented before and after the noise for the same intervals. These comparisons are shown in Fig. 3 which overlaps the threshold changes for probes presented before and after a 250 ms noise. While several of the differences between thresholds for signals leading and following the masker are statistically significant, ($P < 0{\cdot}05$), there is no clear pattern with either the leading or following signal having a consistently higher or lower threshold than the other.

To test the effects of noise duration on the degree of threshold change, an additional series of experiments were run with a 15 ms pure tone and a 50 ms noise signal (Table 4 and Fig. 4). The degree of threshold change with the 50 and 250 ms noise is considerable (compare with Fig. 1). However, the shape of the threshold change with the two different duration noise signals and the 15 ms probe is essentially the

same, with there being slightly more threshold change when the probe was presented before than after the noise in both experiments, although the difference was not statistically significant. As with the 250 ms noise, there was slightly more threshold shift when the 15 ms probe preceded the noise than when it followed.

Controls

Several different controls were run to ensure that the results stayed stable over changes in fish and over the course of the experiments. In several cases data were replicated with different animals up to one year after the original data were taken. Data for a 15 ms signal and 250 ms masker with an interval of 100 ms had mean threshold changes of 19·7 dB (S.D. 4·3 dB) and 18·3 (dB (S.D. 4·9 dB) 1 year apart (Table 1). Thresholds of 50 ms signal, 250 ms masker and an interval of 50 ms were 13·4 dB (S.D. 7·5 dB) and 11·1 dB (S.D. 7·3 dB) (Table 3), again taken 1 year apart. In several other instances data for the same test conditions were taken for the same animal with a year or more time interval in between and again there was close replication of results.

DISCUSSION

The goldfish data show that interactions occur between a pure tone signal and a noise when the two signals are presented simultaneously and at different times. It is apparent that the duration of the signals as well as the time between signal and noise are significant in controlling the amount of interference in the detection of the pure tone. The duration of the noise clearly affected the threshold as is evident in comparing the amount of threshold change for the 15 ms pure tone that was tested with the 50 and 250 ms noises. The duration of the pure tone also affected thresholds, particularly when comparing the amount of threshold change for the 50 ms signal with the 15 and 25 ms signals. The lesser threshold change for the 50 ms signal could have resulted from the longer signal having more energy at a time further from the noise than did the shorter duration signals. However, it is more likely that the absolute duration of the pure tone is not responsible for the differences in threshold change, and that the significant factor is the time relationship of the signal to the noise. One reason for suggesting this is that the amount of threshold change for the different durations of signal did not differ greatly when the signals were totally embedded in noise. Thus it is unlikely that total energy in the signals altered thresholds when they were separated from the noise by a silent interval. Further, thresholds for pure tones of different durations were similar to one another as in an earlier study (Popper, 1972), again indicating that total energy may not be important in some facets of goldfish signal detection. Instead it is likely that the temporal relationship between signal and noise was the dominant factor in obtaining the present results. This argument is also supported by the findings that the length of the inter-signal interval affected the degree of threshold change since thresholds were higher with shorter intervals between signal and noise.

It is also important to note that the greatest degree of threshold change occurred for intervals of 50 ms or less, with the exception of humps in the data for the 25 ms signal with an interval of 100 ms. Perhaps most importantly, the data for the signals

that led and followed the noises did not vary significantly. This is opposed to some of the mammalian data in which either the leading or following signal will consistently have greater threshold change than the other signal (e.g. Small *et al.* 1972).

It is clear from these data that there must be interaction over time between noise and signal in the teleost auditory system. We might hypothesize that when the noise leads the pure tone there is some auditory fatigue to the noise which decreases with time. If the noise is then followed by the pure tone, the detection of the probe would depend upon the amount of release from fatigue that has already occurred in the auditory system. Consequently, the detection of the pure tone would depend upon the signal:noise ratio between the two signals and the ratio would increase with longer duration inter-signal intervals. If there has been considerable delay in the response to the noise, a small change in threshold to the pure tone would be predicted, while a small decay would have a large effect on sensitivity to the pure tone. Indeed, the experimental results correlate with what would be expected in this type of system where: (*a*) there would be less threshold change for a long inter-signal interval since the response to the noise would have had a greater opportunity to decay before the start of the signal; (*b*) a long signal, having more summed energy, would be easier to detect, all other parameters being equal, since the total energy in the signal would be higher so that the signal:noise ratio in the system would be high; and (*c*) longer noise durations would result in more threshold change than a shorter noise.

A mechanism for the result obtained with the pure tone leading the noise masker is more difficult to explain, particularly when considering that the thresholds for tones presented before and after the masker are relatively similar and that there are identical 'humps' in the data for the 25 ms pure tones for the leading and following situations. Two possible functions may be hypothesized. One hypothesis is that the animal takes a long time to make a decision regarding the presence of the signal and so, essentially, waits for the two signals to be interacting in the auditory system. In such a case, the signal:noise ratio would be lower than for the same with signal following the masker after the same interval since the signal response would start to decay before the presentation of the noise. Consequently, the identical leading and following thresholds should not have occurred. Another, more likely hypothesis, is that the animal makes some threshold judgement on the basis of the pure tone but the presence of the following noise creates some interference with detection or signal processing, resulting in poorer thresholds than were the noise not present (e.g. Massaro, 1975; Sparks, 1976). If such interaction did not occur, we might expect identical thresholds at all intervals. It is possible in forward masking in the goldfish that the actual mechanism might include both hypotheses, with interactions present for short intervals and no interactions for longer (beyond 50 ms) periods. In any case, we do not yet know enough about the function of the teleost auditory system to propose a final hypothesis regarding the mechanism for non-simultaneous masking, nor is it possible to explain the similarity in thresholds for signals presented before and after the masker. Perhaps even more difficult to explain will be the 'humps' in the data for the 25 ms signal presented about 100 ms before and after the 250 ms noise. These data lead to a suggestion that some combination of the

intervals and signal durations used caused a unique interaction in the auditory system found with no other signal combinations. However, what these interactions are remain to be seen.

A further consideration is the site or sites of interaction of the signal and noise in the auditory system involved in non-simultaneous masking. There is considerable discussion in the literature as to the mechanisms of acoustic analysis by fishes (e.g. Fay, 1978*a*; Popper, 1978; Sand & Michelsen, 1978) but we do not yet know whether fishes do some processing in the ear or whether all processing occurs in the central nervous system. While not directly comparable due to differences in the auditory system morphology, there is some suggestion that non-simultaneous masking in mammals occurs in the central nervous system (Small *et al.* 1972; Druifhuis, 1973; Lynn & Small, 1977). Studies with goldfish have also shown evidence of signal summation and interference in the auditory C.N.S. (Piddington, 1971) and that there may be long-duration fatigue in the eighth nerve (Fay, 1978*b*). Since both signal interference and fatigue could be involved in non-simultaneous masking, it is possible to make a preliminary suggestion that such masking may occur central to the inner ear.

It is of some interest to consider the functional significance of non-simultaneous masking in fish. However, rather than thinking of non-simultaneous masking as being adaptively significant in its own right, it may be more correct to think of it as an indication of a relatively rapid release from masking when a signal and noise do not occur together. Thus, the data obtained for non-simultaneous masking may indicate that goldfish have evolved mechanisms to detect sounds that occur in close temporal relationship to other sounds. While the present data indicate that there may be masking up to an interval between signal and noise of 5 or 10 ms (Fig. 4), release may actually be faster if the noise were of shorter duration than 50 ms. However, it was difficult to use shorter duration signals, and shorter intervals, in the present experiments since it was necessary to use air loud-speakers. Some human studies have demonstrated total release from interference in non-simultaneous masking when intervals between signals and noise were only several milliseconds, but in these experiments it was possible to use earphones, thus eliminating problems of acoustic transients and room acoustics (e.g. Wilson & Carhart, 1971; Penner, 1974; Smiarowski & Carhart, 1975).

Finally, it is necessary to point out that these data for non-simultaneous masking in the goldfish may not apply to all teleost species. Comparative data on auditory functions in fishes, other than for hearing thresholds, are minimal and it is too early to know whether the analysis mechanism for sounds that might result in data such as those found here, or by other workers studying other auditory functions as simultaneous masking (e.g. Buerkle, 1969; Fay, 1974; Tavolga, 1974) or discrimination (e.g. Jacobs & Tavolga, 1967; Chapman & Johnstone, 1974), would be the same in all species. There are substantial inter-specific morphological differences in the auditory regions of the inner ear and yet we have no data on the functional significance of such differences (e.g. Popper, 1978). Less is known about the anatomy and function of the central auditory system in fishes and until such data are available it will not be reasonable to speculate about the applicability of data for goldfish to other species.

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