

SINGLE UNIT RESPONSES RECORDED FROM THE FIRST ORDER NEURON OF THE PIGEON AUDITORY SYSTEM

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SUMMARY

Intracochlear recordings from the first order neurons in the eighth nerve of the pigeon were made with microelectrodes. The basic response characteristics of the single units were similar to those recorded from mammalian first order auditory neurons with the following exceptions: units responding solely to 'sweep frequencies' were found and one unit was found for which the rate of discharge decreased with increased intensity. Suppression of spontaneous activity during tonal stimulation was found within the response curve of the unit and for frequencies beyond the boundaries of the response curve. In addition, suppression of spontaneous activity was found after the termination of the tone. The amount of suppression and the recovery process varied considerably from unit to unit. The controlling variables were intensity and duration of the stimulus.

INTRODUCTION

Information concerning the discharge characteristics of the first order auditory neuron in the pigeon has recently been reported by Sachs *et al.*¹⁷. They present information concerning the response curves, thresholds, etc. of these primary afferent neurons. It is the purpose of this report to present additional information concerning the discharge characteristics of these neurons in the pigeon. The first section will deal with the response of single neurons during stimulation. Evidence will be presented to show that the discharge pattern for a unit at the higher and lower extremes of the response curve frequently differs from that at the most sensitive frequency. Evidence of suppression of spontaneous activity during stimulation will be presented. Information concerning the suppression of spontaneous activity after the termination of the tone will also be presented.

METHODS

Surgical procedures. Mature White Carneaux pigeons (*Columba livia*) were anesthetized with a combination of Vetelar (Parke Davis) and Nembutal (Abbott) or with a combination of Vetelar and urethane (1.0 g/kg)³. The animal was placed in a specially designed head holder in the supine position and the head fixed with the aid of acrylic cement. The trachea was cannulated and the musculature covering the ventral surface of the skull was removed. A portion of the skull and the bony trabeculae surrounding the cochlea-lagena were removed by curettage. The nerve could be then visualized as a white line through the translucent cochlear wall. A small hole was made in the cochlear wall over the nerve to permit the entry of the electrode.

Electrodes. Micropipettes filled with 3 M NaCl with impedances ranging between 20–30 M Ω were used for recording purposes. The electrodes were held and advanced by a mechanical manipulator.

Recording system. The microelectrode was connected to a preamplifier (Grass P-15) which in turn was linked to an oscilloscope (Tektronix 565). The oscilloscope served to provide a visual display of the neural response wave form, to discriminate the neural events from the background noise and to normalize the signal amplitude. The discriminated events were fed to a real-time clock (KW-12) and then to the computer (PDP-12) where they were displayed as dot patterns or in the form of response histograms. The analogue signals were simultaneously recorded on a direct-record channel of an instrumentation tape recorder (H.P. 3960) for permanent storage and later reprocessing. One FM channel of the tape recorder was reserved for stimulus markers which were used for data analysis. A second direct-record channel was used to preserve stimulus phase and voice protocol.

Stimulating equipment. The stimuli were generated by a function generator (Wavetek model 115) and these signals were controlled for 'on-off' times and for duration by appropriate timing circuitry. The tones had a rise-fall time of 5 msec and were approximately 250 msec in duration. The signals were then fed to an attenuator network and finally to an earphone (PDR-600) which was enclosed and connected to a speculum by a plastic tube. The speculum was placed as close to the ear drum as possible without touching the skull. The speculum, during the experiment, contained a dummy sound calibration tube.

Intensity calibrations were made with the aid of a calibrated condenser microphone (Brüel and Kjaer 4134) probe tube combination which was designed to measure sound pressure level (SPL) at the speculum opening. The output of the microphone was fed to a wave analyzer (General Radio 1900-A) which was in turn linked to the computer through a logarithmic converter. A calibration curve from 0.1 to 25.6 kHz was the final product.

Data acquisition. The animal was positioned in a sound-isolated room during recordings. When a unit was encountered, usually detected by an irregular discharge of spontaneous activity, the adequate stimulus was then determined. During the experiment, response dot-pattern or histogram displays were available to aid in the selection of the frequencies and intensities to be used.

At a later time the analogue tapes were used for data analysis. The histograms were computed and then drawn with the aid of a digital incremental plotter (Calcomp 565).

RESULTS

Responses during stimulation. Data were obtained from 82 units. Detailed information was obtained from about one-third this number. The adequate stimulus for all units recorded was not the same nor were the response patterns uniform from unit to unit. Examples will be presented to illustrate these differences.

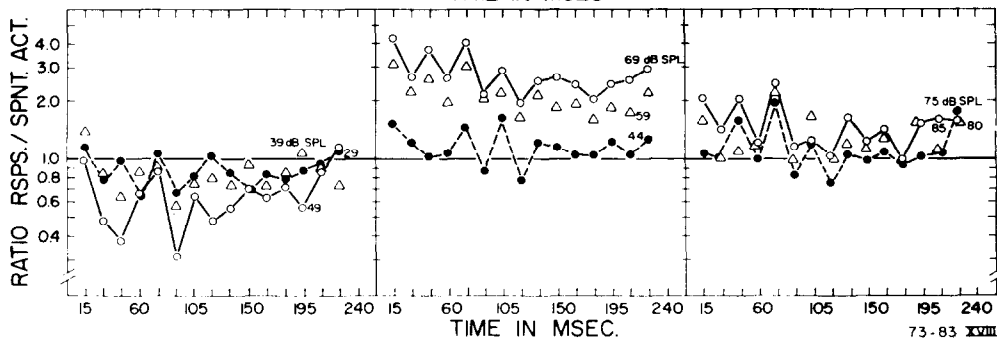
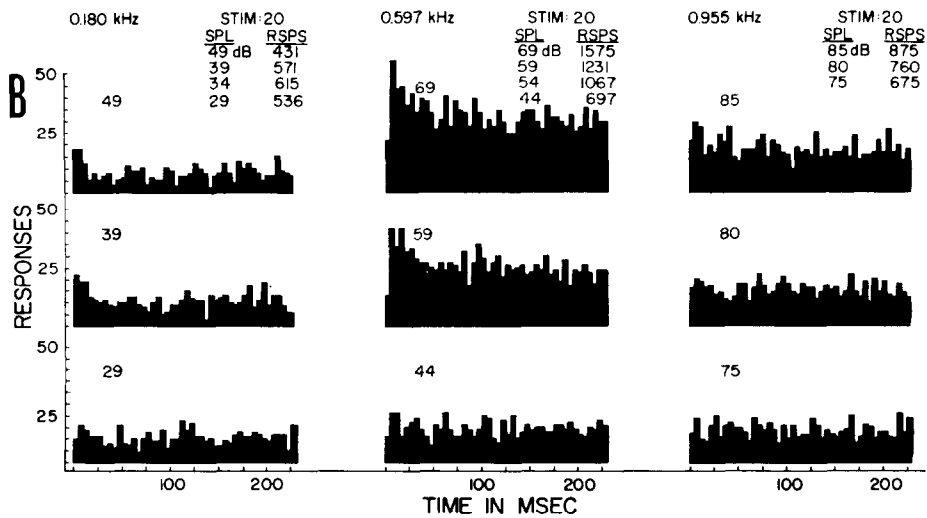
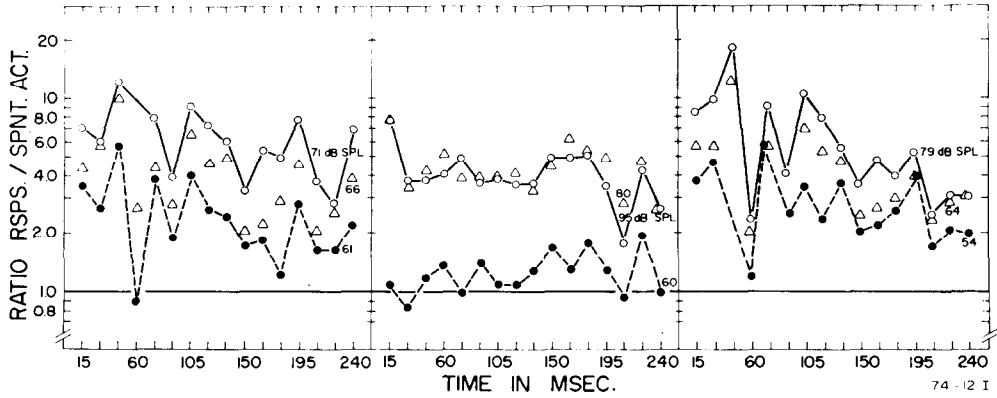
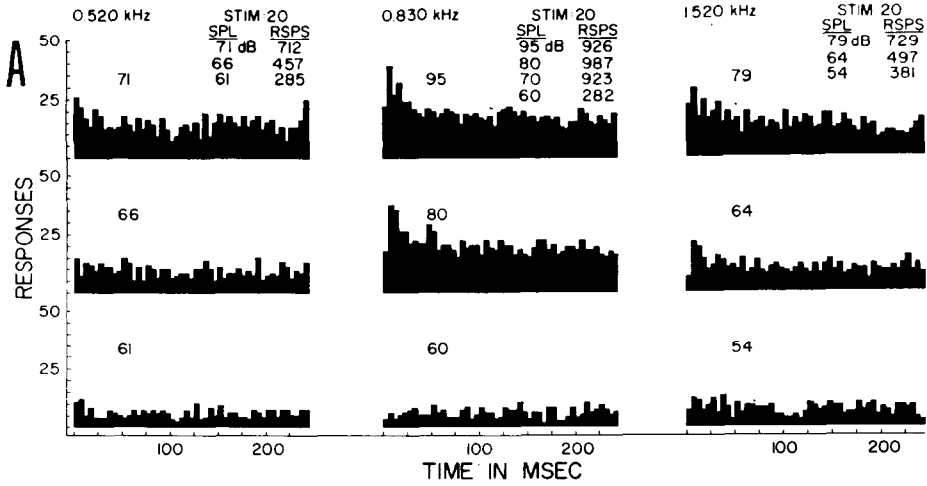
Two units were encountered which responded exclusively to 'sweep frequencies'. Both units had their best frequency (BF) around 0.6 kHz and responded when the stimulus was increased in frequency. One neuron was encountered which, at its BF, demonstrated a progressive reduction in the rate of discharge with increased stimulus intensity. At 35 dB SPL total discharge was 1517 responses for 20 stimuli while at 65 dB SPL the rate was reduced to 149 — a 10-fold reduction. The BF for this unit was 1.347 kHz.

Except for the units cited above and one additional case to be discussed later the discharge pattern at the BF for all units showed common features. At low intensity the discharge rate was uniform throughout the duration of the tone. At higher stimulus intensities there was an initial high rate of discharge followed by a gradual reduction in the rate of discharge which reached a steady state at different times after the onset of the tone depending upon the strength of the tone. This pattern was found for a number of frequencies above and below the BF within the response curve.

In some cases the pattern of discharge at the extreme ends of the response curve differed significantly from that at the BF. The histogram in Fig. 1A presents the data obtained from unit 74-12:I at its BF (0.830 kHz, threshold = 32 dB SPL) at 3 different intensity levels. The histograms were constructed by summing the number of neural impulses generated during consecutive periods of 5 msec of the stimulus period. In addition the total number responses at 4 intensity levels are presented in the table above the histograms. It can be seen that the total number of responses increased very rapidly with an intensity increase of 10 dB and reached a plateau after this initial rise. The histograms show that at the higher intensities there was an initial transient of high discharge rate with a reduction in time to a uniform rate. This pattern of discharge was found for frequencies between 0.650 and 1.520 kHz.

The discharge rate is related to the spontaneous activity of the unit in the graphs below the histograms. The ratio of the number of neural discharges obtained during successive 15 msec periods of stimulation to the number of neural discharges obtained during equivalent 15 msec periods of spontaneous activity were determined at 3 intensities. At the BF and at 60 dB SPL the ratios are about 1.0 while at 80 and 95 dB SPL the ratios are greater than 1.0 and are about the same at both intensities. The ratios at the onset of the tone are the highest and a uniform value is reached at 30 msec after the onset of the tone.

At the high frequency end of the response curve (1.520 kHz) the general trend is



for the ratios to be highest immediately after the onset of the tone and the ratios then gradually fall throughout the period of stimulation. The trend is not quite as discernible in the response histograms.

At the low frequency end of the response curve (0.520 kHz) the same trend as observed at the high frequency end of the response curve was also present. The ratios are highest at the onset of the tone at the lowest intensity (61 dB SPL) and gradually become smaller with time. At the intermediate intensity (66 dB SPL) the variability precludes any generalization. The trend is again observed at the highest intensity (71 dB SPL) but at the end of the stimulus period, as can be seen both in the histogram and the graphs, there is a transient increase in the rate of discharge — an ‘off’ response.

The data obtained from another unit (73-83:XVIII) illustrate a variation in the discharge pattern (see Fig. 1B). The pattern of discharge was similar for the range of 0.250–0.874 kHz and is illustrated by the data obtained at 0.597 kHz. The relation between discharge rate and intensity increases monotonically within this range. The ratio data show that at the lowest intensity used (44 dB SPL) there is little or no excitation since the ratios hover around 1.0. At the two highest intensities (59 and 69 dB SPL) the ratios are highest after the onset of the tone followed by a slight reduction in the ratios with time. At the high frequency end of the response curve the rate of discharge is less but the trend is similar to that at 0.597 kHz.

At 0.180 kHz there is a significant change in the discharge pattern. At the lowest intensity levels (29 and 39 dB SPL) the ratios hover around 1.0. Raising the tone 10 dB produces a marked change. Again during the initial 15 msec the ratio is about 1.0. The ratio is reduced to 0.4 during the next 30 msec followed by a gradual return of the ratio to 1.0. Suppression of the spontaneous activity, then, took time to develop but it gradually dissipated with time.

The data from unit 73-40:V (Fig. 2A) is also of interest since the pattern of discharge differs both at the low and high frequencies from that at the BF. The histograms and the ratio curves at the BF reflect an excitatory process and this pattern of discharge extended from 0.650 to 1.0 kHz.

At 3.98 kHz the pattern of discharge is similar to that described for the low tone response in the previous case (unit 73-83:XVIII). At 66 dB SPL the rate of discharge differed little from that of the spontaneous activity as seen in the ratio data. However, with increased intensity the spontaneous activity was reduced. At 71 dB SPL the spontaneous rate of discharge after 15 msec of stimulation is reduced from a ratio of 1.0 to 0.5 and was uniform for the remainder of the stimulus period. At 81 dB SPL there was an immediate reduction in spontaneous activity (the ratio is about 0.5).

Fig. 1. Responses from two neurons. In each case the stimulus frequency, the number of stimuli (Stim.), the sound pressure level (SPL) and the number of responses are presented above the histograms. The histograms represent the number of responses for consecutive periods of 5 msec after the onset of the tone for 20 stimuli. The intensity of stimulation is given above each histogram. The ratio data, presented below, are based on the number of responses for consecutive time periods of 12 msec of tone to the number of responses for equivalent intervals of spontaneous activity.

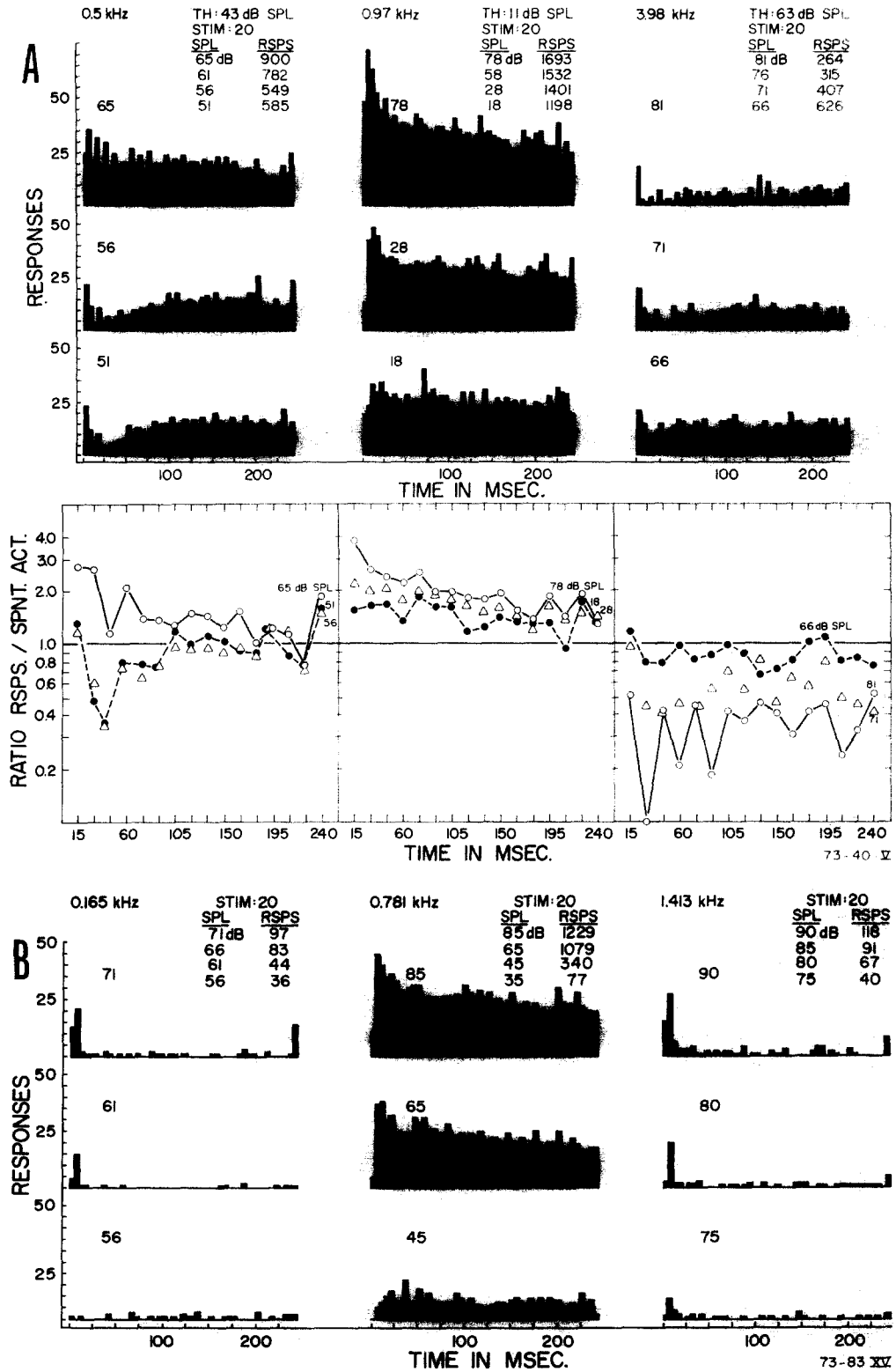


Fig. 2. Responses from two additional neurons. The histograms and ratios were obtained as in the previous figure.

Suppression then increases (the ratio is 0.1) and there follows a slow recovery to a ratio of about 0.5 at the termination of the tone, 240 msec after the onset.

At 0.5 kHz the discharge pattern changes with the intensity of stimulation in a different way. At the lowest intensity (51 dB SPL) the ratio of discharge during the first 15 msec of stimulation is about 1.0. The rate of discharge immediately decreased and reached its lowest ratio (about 0.4) 45 msec after the start of stimulation. The ratio then slowly returns to 1.0 about 105 msec after the onset stimulation. At the termination of the stimulus the ratio increases to about 1.5. The data at 56 dB SPL is essentially the same. An increase in the ratio occurs again after the tone.

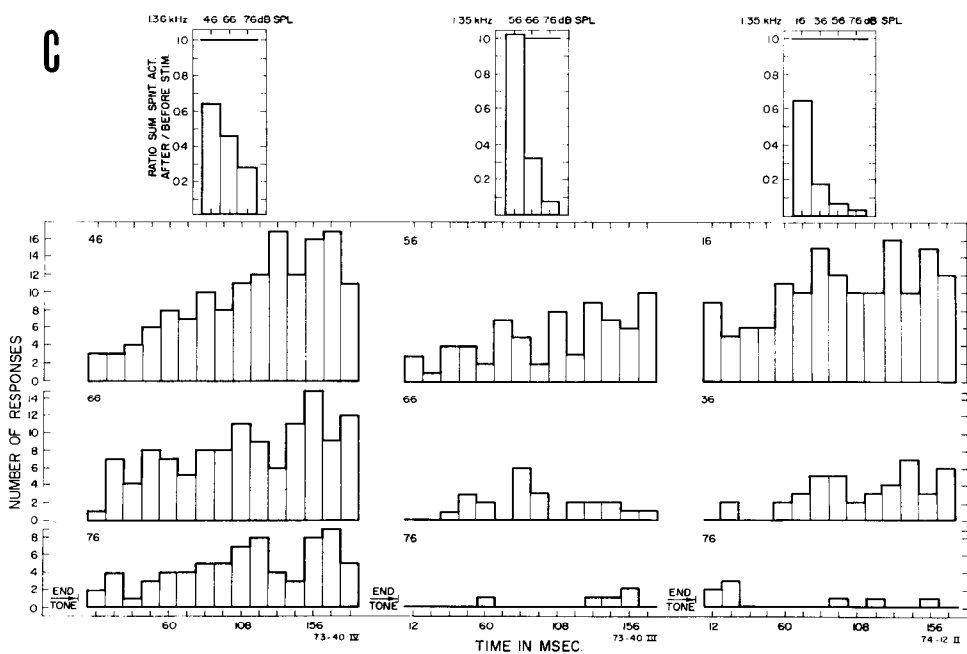
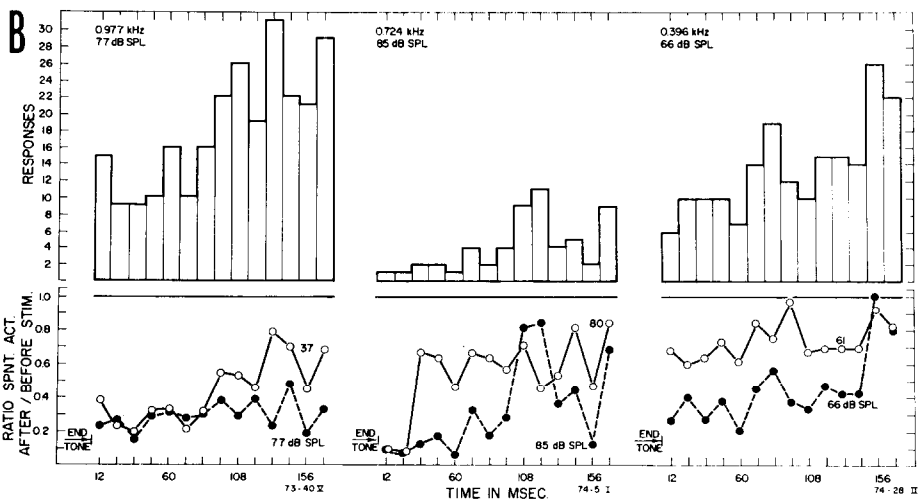
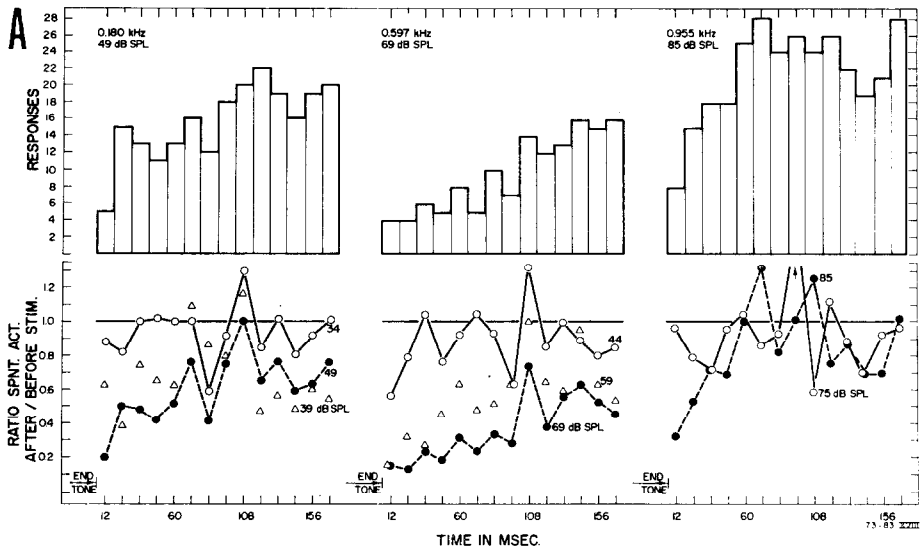
The pattern of response changes from suppression to excitation when the tone was raised another 5 dB (65 dB SPL). The ratio at the onset is about 2.7 and the ratios decrease with time. There is again an increase discharge after the tone.

The data provided by unit 73-83:XV (Fig. 2B) is of interest because it illustrates a still different pattern of discharge as a function of frequency and intensity. At the BF (0.781 kHz) the discharge rate *vs.* intensity resembled the general trend of the previous units at their BF's. At both the high frequency end of the response curve (1.43 kHz) and at the low frequency end of the response curve (0.165 kHz) the response patterns differed from that at the BF but were alike in their discharge patterns. In this case the rate of spontaneous activity was too low to have meaningful reciprocals. The main features, however, are observable in the histograms. At low intensities the discharge was delayed by about 5 msec after the onset of the tone. This initial discharge increased with intensity. There was also a discharge at the termination of the tone if the intensity was sufficiently high.

Spontaneous discharge after stimulation. In this section the changes in neural activity after termination of the tone will be discussed. The general finding is that given sufficient tonal intensity the rate of post-stimulus discharge is suppressed maximally immediately after the termination of the tone and the rate of discharge recovers to the spontaneous level with time. The length of the tone is also an important variable.

Some features of suppression and recovery from suppression of the neural activity after the termination of the tone are illustrated by the data obtained from unit 73-83:XVIII. In Fig. 3A the histogram at 0.597 kHz shows the rate of spontaneous discharge in successive 12 msec units of time *after* the termination of the tone at the highest intensity used — 69 dB SPL. It can be seen that immediately after the termination of the stimulus, the rate of discharge was 4/12 msec for 20 stimuli and at 168 msec the rate has gradually increased to 16.

These data plus data for two less intense tones, at the BF, are expressed as ratios in the graph below. The ratio of the rate of discharge *after* stimulation to the rate of spontaneous activity *before* stimulation for successive 12 msec units of time have been calculated. At 44 dB SPL, there is an initial suppression of activity below the spontaneous activity rate immediately after the termination of the tone and recovery after 36 msec. Raising the intensity 15 dB produced a dramatic reduction in the ratio to 0.2 immediately after the termination of the tone and the ratios increased gradually to 0.5 after 178 msec of post-stimulus time. Increasing the intensity of the tone another 10 dB increased the amount of suppression very little.



At the high frequency end of the response curve (0.955 kHz) suppression of the rate of discharge can be seen both in the response histogram and the ratio data. Suppression was most marked during the first 12 msec after the termination of the tone at the highest intensity (85 dB SPL). Despite the variability in the data there appears to be a gradual recovery which was complete about 60 msec after the termination of the tone. Suppression lasts a shorter length of time than at the BF.

Suppression of rate of spontaneous activity was also in evidence at the low frequency end of the response curve (0.180 kHz). At 34 dB SPL the ratios are essentially 1.0. The tone was then increased 10 dB and ratio is reduced to around 0.625 and there is little change throughout the period of measurement. The tone was increased another 10 dB and the ratio is reduced initially to 0.2. There is progressive recovery during the initial 60 msec but then the ratios reached a plateau of about 0.7. Suppression was less marked and the recovery was faster at this frequency than at the BF. Note that this frequency is beyond the limits of the response curve since the tone is not excitatory (see Fig. 1B).

The amount of suppression (neural activity) after the termination of the tone and the recovery period was not always the same even at BFs as is illustrated by the data presented in Fig. 3B. The data are for the BFs for 3 different units from different animals. In each case the response histograms at the highest intensity and the ratio data at 2 intensity levels are presented. The common feature again is that the number of responses per 12 msec periods after the termination of the tone increases with time even though there is considerable variability in the data.

Differences in recovery are more evident in the ratio data. In Fig. 3B at 0.977 kHz at 77 dB SPL there is considerable suppression (the ratio is 0.225) and there is very little recovery. Decreasing the intensity 10 dB produced initially the same amount of suppression which lasted for 84 msec, followed by partial recovery which reaches a plateau at a ratio of 0.6, 120 msec after the termination of the tone. The next unit had a BF of 0.724 kHz. The initial ratio for both intensities is the same (0.1). The ratios at 85 dB SPL increased gradually and peaked at the end of the test period at about 0.5. Decreasing the intensity 5 dB results in a response ratio of 0.1 for the first 24 msec followed by an increase in the ratio to 0.65 which is maintained for the remaining time. For the third unit with a BF of 0.396 kHz, at the highest intensity (66 dB SPL) the ratios starts at 0.3 and remains unchanged for 136 msec and then rises steeply.

Fig. 3. Neural discharge after the termination of the stimulus. In A, data are presented at the BF and at the high end of the response curve. Data were also obtained at 0.180 kHz. The histograms are based on the number of neural responses for consecutive periods of 12 msec after the termination of the stimulus, at the highest intensity of stimulation. The ratio data were obtained for two intensities of the tone. In B, data are presented from 3 neurons from 3 different animals at the BF for each neuron. The histograms are based on the highest tonal intensity and the ratio data are based on two intensities of stimulation. In C, data are presented from 3 neurons having the same BF from 3 different animals. The histograms are based on 3 different intensity levels of stimulation. The ratios are based on the total number of response for 168 msec after the stimulation to the total number of responses for an equivalent period of spontaneous activity.

When the tone was decreased by 5 dB the initial ratio is initially about 0.6 and remains essentially the same for the remainder of the test period.

Suppression of spontaneous activity following the termination of the stimulus always occurred but the depth of the suppression and the course of recovery were not always the same even for the same BF (Fig. 3C). In all 3 animals the rate of spontaneous discharge was low, therefore the data are expressed as the ratio of the sum of the neural discharges after stimulation to the sum of spontaneous discharges before stimulation.

The histograms presented in the lower part of each figure are based on the number of discharges per 12 msec of successive intervals after the termination of the stimulus. In the case of the first unit, it can be seen that the discharge rate in the first 12 msec was about the same regardless of the intensity of stimulation. There followed a progressive increase in the number of neural discharges per unit of time. The recovery was least at the highest tonal intensity and greatest at the lowest intensity. The ratio data presented in the graph above are based on the total number of unit discharges for 178 msec after the termination of the tone to the total number of responses for an equivalent period of spontaneous activity. Note that the recovery process is very gradual since a change of 30 dB brings about only a 60% recovery in spontaneous activity.

In the case of the second unit, at 56 dB SPL the total number of discharges was 60 for 178 msec of post-stimulus time which was the same for the control series — the ratio is 1.0. However, it will be noted that the discharge rate is still less immediately after the termination of the stimulus and the recovery process is fairly regular. Raising the intensity of the tone reduced the spontaneous activity to 23 and the ratio is reduced to about 0.3. The greatest suppression occurs at the beginning of the recovery period but the discharge rate shows little recovery. At 76 dB SPL there was a total of 5 discharges and the ratio is reduced to about 0.1. In this case the intensity difference needed to produce a change from a ratio of 1.0 to 0.3 is only 5 dB. The data presented for the third unit in many ways is similar to that presented for the second unit but suppression starts at a lower intensity level and develops more gradually.

Suppression of the post-stimulus spontaneous activity is related to the duration

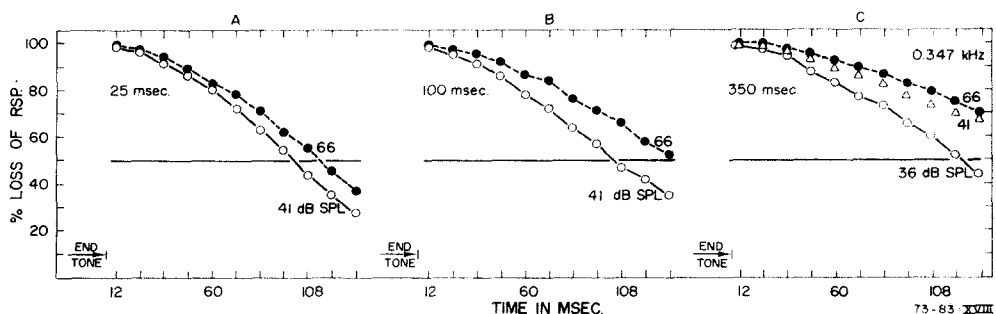


Fig. 4. Post-stimulus recovery for 3 different lengths of tone for the same neuron. The stimulus frequency in all cases is 0.347 kHz. The length of tone increases from 25 msec to 350 msec. The percentage loss is based on the total number of neural responses for 132 msec of spontaneous activity to the cumulative number of responses for 12 msec periods of post-stimulus time.

of the tone, as can be seen in Fig. 4. For this analysis the total number of responses was determined for 132 msec of spontaneous activity after a given duration of tone. In addition cumulative sums of responses were obtained for successive 12 msec periods after the termination of the tone. The per cent loss was determined from the cumulative sums.

In Fig. 4A, the data were obtained for a 'on-off' time of 5 msec and the duration of the tone was 25 msec. At 41 dB SPL the rate of spontaneous activity recovered by 50% approximately at 96 msec after the termination of the tone. Raising the intensity of the tone 25 dB prolongs the recovery time to approximately 114 msec.

The tone was then increased 4 times longer to 100 msec. The rate of spontaneous activity recovered by 50% about 106 msec after the termination of the tone. When the tone was increased by 25 dB the 50% recovery point was reached about 138 msec after the termination of the tone (Fig. 4B).

The tone was then increased to 350 msec. In this case the tone was reduced to 36 dB and it reached the 50% point of recovery about 122 msec after the termination of the tone. The rate of spontaneous activity for a 5 and 10 dB increase in intensity did not reach the 50% recovery point during the period of measurement (Fig. 4C).

In this case both intensity and duration were important variables. Recovery is faster to lower intensities, and increased duration of the stimulus also prolongs suppression of the neural activity after the termination of the tone. A series of experiments was also carried out to evaluate the importance of 'rise-fall' times. No significant changes could be found in the recovery process that could be attributed to the length of the 'rise-fall' times.

DISCUSSION

The data presented by Sachs *et al.*¹⁷, established that the responses recorded from single first order units in the auditory system of the pigeon — class Aves — are similar to those recorded from the cat — class Mammalia — in spite of the marked anatomical differences in the sensory epithelium of these two animals^{12,14,19,20}. The data obtained from the single units in this study support their findings. There are, however, several observations which serve to supplement those of Sachs *et al.*¹⁷. It should be noted that the combined number of units sampled in the two studies represents only a very small percentage of the total number of first order neurons. Some differences in the two studies can be attributed to the small sample of units studied and some of the observations were made possible in the present study by the longer recording times available from extracellular recordings.

The pattern of discharge at the BF and for most of the frequencies within the response area of a unit was consistent for the majority of the units encountered. At low and intermediate intensities the rate of discharge tended to be uniform throughout the period of stimulation (250 msec). At higher intensities the highest rate of discharge occurred after the onset of stimulation and with time there was a reduction in rate to a steady state. In one case there was a terminal increase in rate of discharge.

The relationship between discharge rate and intensity within the intensity range used was monotonic.

The units that responded solely to sweep frequencies demonstrate that this response characteristic, which has been noted at higher centers, need not necessarily be the product of synaptic interaction at the higher centers but can have a peripheral origin as well^{4,22,23}. Only two such units were identified, therefore this type of unit probably does not represent a large proportion of the units within the eighth nerve.

Suppression of unit activity during stimulation has been demonstrated in these experiments in several ways for frequencies within the response area of a unit. The rate of discharge of one unit decreased with increase in stimulus strength. Units of a similar response pattern have been identified at higher centers¹³. Again, the appearance of this type of response pattern at the periphery would preclude it as being solely a central nervous system synaptic event. The one unit which responded in this way did so at its BF.

The responses of unit 73-83:XV, Fig. 2B at 0.165 and 1.413 kHz, demonstrate another instance of suppression during stimulation. At the BF the response was greatest after the onset of the tone and rate was later reduced to a steady state. At the two extreme frequencies the pattern of discharge was quite different. The unit discharged at the onset of the tone at lower intensities and at the onset and termination of the tone at higher intensities. During the interim period the rate of discharge was probably the same as the spontaneous discharge of the unit. (An estimate of the level of spontaneous discharge can be obtained by noting the response in the first time interval at the lowest intensity at the BF.)

Finally, another example of suppression can be seen in the data from unit 73-40:V at 0.5 kHz at 51 and 56 dB SPL and at 3.98 kHz (Fig. 2A) and again in unit 73-83:XVIII at 0.180 kHz (Fig. 1B). The stimulus was not excitatory; rather, the stimulus suppressed the rate of spontaneous activity. Note that in all but one case suppression develops during the period of stimulation. The ratio is initially about 1.0 and then is reduced with time, followed in some cases by recovery while in other cases the ratios remain below 1.0 throughout the period of stimulation. Suppression was associated in two of these cases with tones outside of the response curve of the unit but in the third case at low intensities the stimulus is suppressive while at the highest intensity the tone is excitatory.

Suppression of the spontaneous activity after the termination of the tone was found for every unit studied. It was found whether the rate of spontaneous activity was very low or high. The general finding is that when the threshold for suppression is reached, the rate of response is reduced and at times maintains this reduced rate for at least 100 msec. When the intensity of the tone is raised the usual finding is that suppression is greatest immediately after the termination of the tone and there follows a gradual return to pre-stimulation level, although again the reduction in rate is still significantly below the pre-stimulus level for as long as 168 msec which in these experiments was the usual length of the post-stimulus period analyzed. The 'on-off' times of the stimulus were not important but the length of the stimulus was an important variable.

Suppression of spontaneous activity during and after the termination of the tone has been investigated in mammals during stimulation and after stimulation. There have been discrepancies among the results of the experiments^{1,2,5-11,15,16,18,21}. The results of the present experiments would suggest that part of the problem lies in sampling. Suppression of spontaneous activity during stimulation did not occur frequently in the data of this experiment, therefore, it may be the response characteristic of a few special fibers whose function is not known. Even among the data presented it is obvious that it is not a simple process triggered by a uniform stimulus since the time course and recovery process is not uniform. It is also important to note that the stimulus for suppression sometimes lies at the BF or within the response curve but in some cases the triggering frequencies were beyond the low frequency end or above the high frequency end of the response curve. The intensity of the tone was also an important ingredient in the triggering process since often small changes in intensity could change a tone from suppressive to excitation.

Suppression after the termination of stimulation differs from suppression during stimulation since it is always present, given sufficient intensity, after the termination of the stimulus. The degree of suppression depends both on intensity and the length of the preceding tone. The time course for the development and recovery from suppression during stimulation and after the termination of the tone differ sufficiently to suggest that two different processes are involved.

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