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One-tone suppression in the cochlear nerve of the gerbil

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One-tone rate suppression has been reported several times for auditory nerve fibers of mammalian and non-mammalian vertebrates. Because its properties are very similar to those of two-tone rate suppression, the possibility exists that one-tone rate suppression is the result of an interaction within the inner ear of the suppressing tonal stimulus and some ongoing extraneous acoustic stimulus. For this reason, reports of one-tone rate suppression often elicit suspicions that the investigators were not sufficiently careful in controlling leaks in their acoustic barriers or in the electrical pathways to their acoustic drivers. Recent reports of one-tone rate suppression in pigeon basilar-papillar fibers and goldfish saccular fibers were accompanied by descriptions of measures taken to avoid such leaks. In this paper, we describe one-tone rate suppression in a mammal, the Mongolian gerbil; and we demonstrate that the background spike activity being suppressed is not driven by either external sounds coming from outside the acoustic isolation test chamber or by non-stimulus electrical inputs to the acoustic driver. The suppressed background spike activity evidently arises from sources within the animal. These sources may be non-acoustic, associated with spontaneous pre- or post-synaptic ion-channel activity; or they may be acoustic sources – internal sound or vibration generators.

One-tone suppression; Gerbil; Two-tone suppression

Introduction

In spite of the publication of several papers describing one-tone rate suppression of background spike activity of auditory nerve fibers, doubt remains as to whether it differs from two-tone rate suppression. * In the first publication of recordings from individual cochlear nerve fibers, Tasaki (1954) reported that background activity of auditory nerve fibers of the guinea pig were never suppressed, and this constituted one of the major differences between primary and higher neurons of the auditory system. On the other hand, Kat-suki et al., (1962) reported that suppression of back-

ground firing was observed in some primary auditory units of the monkey. This suppression was found in response to tones having frequencies higher than the characteristic frequency (CF) of the neuron, but never at the lower frequency range. Their Methods and Results section leave the reader uncertain whether they observed one-tone suppression or not. For example, their Fig. 2 and its written description appear to illustrate one-tone suppression, with description of only one tone being presented at any given moment. But their Methods section mentions that, when necessary, two or more tones were combined.

Rupert et al., (1963) reported one-tone suppression in primary afferent fibers from both the awake and the anesthetized cat. A variety of response types was noted. They reported two types of reduction of spontaneous discharges of auditory nerve units: Some which are suppressed promptly, and others which are suppressed many seconds after tone onset.

That same year, Frishkopf and Goldstein reported two separate populations of auditory nerve units in the bullfrog. The simple units showed only excitatory responses, but the complex units showed suppression as well. Because the suppression they described required simultaneous presentation of two tones, it was undoubtedly what is now termed two-tone suppression. To illustrate the confusion inherent in early literature on this topic, an abstract of an Acoustical Society presentation by this group (Goldstein et al., 1962) described one class of neurons as being suppressible,

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* Because this paper is concerned with rate suppression, not synchrony suppression, suppression will mean rate suppression throughout the remainder of the text. Background spike activity can be phase-locked to low-frequency sinusoidal stimuli with amplitudes that are too low to change mean spike rate. This phase locking is seen as a sinusoidal modulation of the probability of spike production, with enhanced spike production during half of the modulation cycle and suppressed spike production during the other half (Rose et al., 1967). In this paper, suppression will mean causing a reduction in mean spike rate (averaged over the complete stimulus cycle and over many cycles) rather than causing a reduction of spike rate during one half of the stimulus cycle. By this use of suppression we do not intend to imply that the immediate causes of reduction are different in the two cases.

without mentioning whether one or two tones were used to obtain this effect. Frishkopf (1964) also reported that, in the little brown bat, evoked primary activity in some of the auditory units could be suppressed by the presentation of a tone having a frequency either below or above the excitatory range of the unit.

Nomoto et al., (1964) then published a paper which was described as an extension of their earlier Katsuki et al. (1962) study. They continued to use primates, but the paradigm they used was significantly different than in the 1962 study: A low level continuous tone at the characteristic frequency (CTCF) was used to tonically excite a neuron, while a tone burst at a different frequency was used to phasically suppress the firing of this axon. Suppression areas were found to flank both the low and the high frequency slopes of the unit tuning curve. Because this suppressive effect persisted when the contralateral auditory nerve was cut, when the monkey was under the influence of strychnine, and because it had a latency of less than 2 ms, it was considered to be peripheral in origin. Two-tone suppression of this sort was described subsequently in a number of studies, typically using this CTCF paradigm (e.g., Kiang et al., 1965; Sachs and Kiang, 1967; Sachs, 1969; Arthur, Pfeiffer and Suga, 1971).

Two-tone suppression has certain qualities which led to its being more extensively investigated than one-tone suppression. These include:

Reliability

Although earlier reports (e.g., Nomoto et al., 1964; Frishkopf and Goldstein, 1963) did not find two-tone suppression in all neurons, Sachs and Kiang (1968) reported this characteristic to be present in every one of the more than 300 fibers they examined in the cat. More recent studies have described two-tone suppression as being a normal property of auditory afferent neurons (e.g., Arthur et al., 1971; Abbas and Sachs, 1976; Schmiedt and Zwislocki, 1980). By contrast, one-tone suppression is generally observed only in a subpopulation of auditory afferents (e.g., Gross and Anderson, 1976; Schmiedt and Zwislocki, 1980; Henry and Lewis, 1989).

Relationship to the frequency threshold curve (FTC)

The often reproduced illustration of the high and low frequency two-tone suppression regions flanking the FTC provides an easily remembered and communicated image of two-tone suppression (e.g., Sachs and Kiang, 1967; Arthur et al., 1972). One-tone suppression has not been represented so elegantly.

Relationship to other cochlear events

Two-tone suppression (or an effect which appears to be similar to two-tone suppression) has been described

in the mechanical movements of the basilar membrane (Rhode and Robles, 1974; Rhode, 1977), in the receptor potentials of cochlear hair cells (Sellick and Russell, 1979), and flanking the tuning curve of the compound action potential (Harris, 1979).

Relationship to psychophysics

When psychophysical tuning curves (PTCs) are obtained with a probe stimulus and a forward masker, an unmasking technique can reveal regions flanking the PTC which have the properties of two-tone suppression (Houtgast, 1973; Shannon, 1976). The ubiquity of two-tone suppression has been so great that earlier reports of one-tone suppression have been reinterpreted as being two-tone suppression (e.g., Arthur et al., 1971, described the Rupert et al. (1963) study as being an example of two-tone suppression).

Nonetheless, several reports of one-tone suppression have appeared in the literature since 1964; one of these reports involved a mammalian subject. Schmiedt and Zwislocki (1980) reported that one-tone suppression of background activity occurs in some gerbil cochlear nerve fibers, and that it is most commonly observed when fibers with best excitatory frequencies (BEFs) of from 4 to 12 kHz were stimulated with tones at frequencies of 1.2 to 1.5 times that of the BEF. In spite of this paper, there seems to be a common perception, stated in the literature, that mammalian cochlear fibers do not exhibit one-tone suppression (e.g., Manley, 1978; Hill et al., 1989b; Dolan et al., 1990).

Gross and Anderson (1976) provided clear examples of one-tone suppression in auditory nerve axons of the pigeon. They observed peristimulus time histograms (PSTHs) whose shapes for individual fibers varied conspicuously with frequency and intensity. Some of these PSTHs showed suppression to below the background rate of the neuron. Suppression of background activity during stimulation did not occur frequently in this experiment, and was suggested to be the property of a few special fibers of unknown function. Nor did all units displaying one-tone suppression show the same pattern of suppression of background activity during the tonal presentation. One-tone suppression sometimes was observed over a limited range of stimulus intensities, with stimuli below and above this range producing an excitatory response. Some units showed one-tone suppression to only the initial portion of the tone burst, where others showed one-tone suppression for the entire duration of the 250 ms stimulus. Although it was observed most frequently in response to tones at amplitudes and frequencies outside the area bounded by the FTC (response area), sometimes it was found to occur within the response area and even at the BEF of the unit.

In starling auditory-nerve fibers, Manley et al., (1985)

described one-tone suppression of background activity, followed by an 'off' response when the suppressing tone ended. Some fibers also showed on-off responses, even at BEF.

Temchin, in a series of papers published in Russian during the early 1980s (referenced in Temchin, 1988), described one-tone suppression in the auditory nerve of the pigeon. In a more recent paper, Temchin (1988) observed a difference in the firing patterns of auditory nerve fibers which had either random background or quasiperiodic background activity. One-tone suppression was seen only in fibers belonging to the latter group, for tones at frequencies well below BEF in some units, well above BEF in others, and both in still others. One-tone suppression was found at the high frequency end of the FTC in 93% of the neurons showing a quasiperiodic background firing pattern. Suppression of the firing level to below the background rate during the stimulus presentation was often accompanied by onset and offset responses. In some units, the one-tone suppression regions flanked the FTC in a manner very similar to those often shown for two-tone suppression (see his Figs. 7 and 8). Because the nature of the background activity was not affected by cutting the columella or by inserting cotton plugs into the external ear canal, however, Temchin concluded that it was not driven by extraneous sound.

Hill and colleagues also reported finding one-tone suppression in a subpopulation of the auditory-nerve fibers of the pigeon. This occurred with ambient acoustic noise (100 Hz to 20 kHz) less than 10 dB (SPL). The one-tone suppression regions bordered the low and/or the high sides of the CF of some neurons. Off responses were sometimes observed at the end of one-tone suppression (Hill, Mo and Stange, 1989a). Subsequently they observed that all fibers excited by broadband noise could be suppressed by tones having frequencies and amplitudes outside the response area (Hill et al., 1989b). In all cases, suppressive tones reduced the firing rate to a level below that produced by the noise alone; in some cases, it reduced the firing rate to below the background level. The authors proposed that the reduction of firing rate of the tone-noise combination was the same as that seen with the tone alone. Finally, Hill and colleagues (1989) suggested that suppression was accomplished by means of hyperpolarization of the axon membrane, resulting from the dc receptor current.

One-tone suppression also has been observed in the saccular nerve of the goldfish (Fay, 1986, 1990). This effect occurred most often in response to stimuli outside the neuron's response area on the high-frequency side, and was often associated with on- and off-responses. For most fibers, the suppressed background spike rate was not affected by opening the door to the acoustic chamber; nor was it affected by changing the

level of attenuation in the path between the stimulus power amplifier and the acoustic driver, or by turning off the respirator water flow. Because some goldfish saccular axons are driven by both vestibular (tilt) and acoustic stimuli, Fay stated that he could not rule out the possibility that the background activity was driven by the former.

If one ignores the results of Katsuki et al. (1962), Rupert et al. (1963), and Schmiedt and Zwislocki (1980), or if one considers them to be examples of two-tone suppression, one-tone suppression might be taken to be an effect that occurs only in nonmammalian vertebrates. The literature promotes this conclusion, with several persons stating that the mammal does not express one-tone suppression (e.g., Manley, 1978; Hill et al., 1989b; Dolan et al., 1990).

Occasionally, in studies of onset and offset responses of cochlear axons in the gerbil (Lewis and Henry, 1988, 1990; Henry and Lewis, 1989), we encountered axons in which a single tone produced suppression of ongoing activity. When evidence of this suppression appeared, incidentally, in our public presentation or publication of the data, it was met with consternation among some of our colleagues. In spite of the fact that we described our double-walled acoustic barrier, with internal ambient noise level (1 to 20 kHz) estimated (by extrapolation) to be less than -10 dB SPL, uncertainty among members of the auditory community about the existence of one-tone suppression in mammals led to concern over whether or not the suppressed background activity was a consequence of extraneous stimuli (e.g., Patuzzi, 1989). Reviewing the literature, we realize that the same concern applies to many reported incidents of one-tone suppression, in non-mammals as well as mammals. The present experiments were designed to eliminate two potential sources of extraneous stimuli - sound leaks through the acoustic barriers surrounding the animal subject, and sound produced by inadvertent electrical input (e.g., amplifier noise) to the acoustic driver. Such experiments have not been reported to date for one-tone suppression in mammals.

Methods

The gerbil preparation used in these experiments has been described previously (Lewis and Henry, 1989). The animals were pretranquilized with chlorprothixene (5 mg/kg, i.m.) and anesthetized with ketamine (40 mg/kg, i.p.). The auditory nerve was exposed in the otic capsule immediately lateral to the internal auditory meatus, by means of the technique described by Chamberlain (1977). Animals were placed in a lab-built acoustic barrier system: a 0.7 m by 0.8 m by 1.0 m box constructed of 2.0 cm thick plywood, with tightly glued

joints and a gasket sealed door of the same material, all lined with 7 cm thick Sonex acoustic foam. The box rested on a vibration-isolation table comprising three second order mechanical filter stages constructed from lightly inflated wheelbarrow inner tubes and approximately 700 kg of bricks. This entire structure resided within a shielded 2.35 m × 2.4 m × 2.4 m Industrial Acoustics Corporation (IAC) Model 403A Acoustic Room lined with 10 cm thick Sonex acoustic foam. The mean attenuation provided by this system for airborne sound in the frequency range of 300 to 20,000 Hz was 66 dB. This was determined with a calibrated 1" free field B and K microphone and an external noise source. Both the wooden box and the acoustic room were electrically shielded.

Acoustic waveforms were generated digitally, with 12 bit resolution. Analog translations of the waveforms exhibited harmonic distortion less than -50 dB, and signal-to-noise ratio greater than 80 dB for 200 Hz bandwidth. Analog signals were delivered through an input attenuator (Hewlett Packard 350D, 110 dB range, 600 ohm output impedance) to a Proton D450 amplifier, the output of which was passed through a lab built output attenuator with 40 dB range and 1/16 ohm output impedance. The signal from the output attenuator was fed directly to an Etymotic ER-2 driver, which was coupled (via an ER-10 coupling system, with plastic coupling tube 15 mm long and 3.8 mm inside diameter) to the bony portion of the external auditory canal (the pinna and fleshy material adjacent to the ear canal entrance having been removed). Incorporated into the coupling system was an ER-10 microphone (monitoring the sound at end of the coupling tube farthest from the ear), and the (1 mm outside diameter) probe tube of an ER-7 microphone (monitoring the sound at the entrance to the ear canal). A Hewlett Packard 3561A Signal Analyzer was used to analyze the outputs of the microphones. Intracellular, single unit recordings were made with glass micropipettes filled with 3 M NaCl and having impedances ranging from 40 to 150 M Ω . The second electrode was placed in the neck tissue adjacent to the opened bulla on the ventral and dorsal surface of the gerbil's body. Units were identified as primary afferents by virtue of their being within 500 μ m of the surface of the nerve (less than the distance through the internal auditory meatus), their primary-type responses at BEF, and response latencies less than 1.5 ms. Units with substantial spike rates in the absence of intentionally-applied stimuli were selected.

To test for the possibility that unintentional, externally-applied stimuli were responsible for some of this ongoing activity, we disconnected the digital signal source from the input attenuator and monitored the spike rate under the following conditions: (1) door to outer acoustic barrier (IAC 403A) closed, output atten-

uator set at 0 dB; (2) door to outer barrier open, output attenuator set at 0 dB; (3) door to outer barrier closed, output attenuator set at -40 dB. Periodic tone bursts (300 ms period, 30 ms duration, 1 ms linear rise and fall times) of various frequencies and intensities were applied. The acoustic stimuli (output of ER 2), the spike responses, the stimulus trigger, and voice descriptions of experimental conditions were recorded on a tape cassette (by means of a TASCAM 234). Spike responses were analyzed off-line by means of peristimulus-time histograms.

Results

In most units that we studied, under evidently constant conditions, the ongoing activity exhibited a mean spike rate that varied slightly, but conspicuously from one 30-s sample period to another. This made it difficult to eliminate definitively the possibility of correlation of the ongoing activity with the setting of the output attenuator or the state of the outer door. In the absence of deliberately applied stimuli (i.e., with the signal source disconnected from the input attenuator), however, the shape of the spike-interval histogram and the mean spike rate of the ongoing activity typically were not obviously correlated with those conditions: the mean spike rate, for example, seemed as likely to decrease as to increase when the outer door was opened or the output attenuation was reduced by 40 dB. In a few units the ongoing activity was sufficiently stationary to provide unambiguous evidence that it was not driven by chamber leaks or extraneous electrical excitation of the acoustic driver (ER2). Fig. 1 shows mean spike rates over a series of consecutive 30-s samples from such a unit.

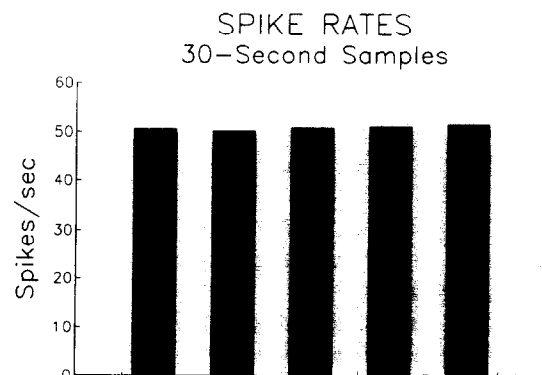


Fig. 1. Mean background spike rates taken over successive 30-s periods (left to right). DC denotes periods during which the IAC acoustic room's door was closed; DO denotes the period during which it was open. NA denotes periods during which Attenuator II was set at 0 dB; A denotes the period during which it was set at -40 dB.

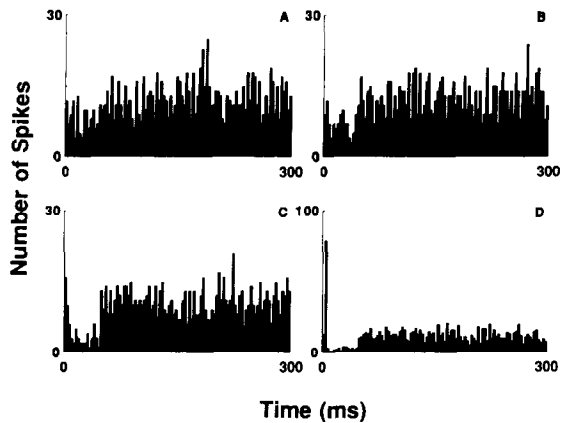


Fig. 2. Peristimulus-time histograms taken for tone bursts at 10.5 kHz, for the unit with 7-kHz BEF. In each case the sample time was 25 s. (A) Stimulus amplitude = 60 dB SPL; total spike count = 1205. (B) Stimulus amplitude = 65 dB SPL; total spike count = 1204; (C) Stimulus amplitude = 70 dB SPL; total spike count = 991; (D) Stimulus amplitude = 82 dB SPL; total spike count = 1172 (note that the maximum value on the vertical scale is 30 for A-C and 100 for D).

This unit had a best excitatory frequency (BEF) of approximately 7 kHz. In studying the unit, we used 70-dB (SPL) tone bursts at frequencies ranging from 2.5 kHz to 10.5 kHz, and stimuli of various intensities at 7 kHz and a few, selected higher frequencies. The unit exhibited primary-type response patterns to 70-dB tone bursts at frequencies from 3 kHz to 9 kHz. At 9.5 kHz, it exhibited a conspicuous onset response, but no obvious response to the remainder of the tone burst. When the stimulus intensity was increased to 80 dB at 9.5 kHz, the PSTH showed a conspicuous increase in tendency for spike synchrony at onset, but still no obvious response to the remainder of the tone burst. At 10 kHz and 80 dB SPL, however, the onset response was followed by reduction of the spike rate to below the background rate.

We examined responses to tone bursts at 10.5 kHz at various intensity levels ranging from 60 to 90 dB SPL. Weak suppression was evident at 60 dB SPL, and

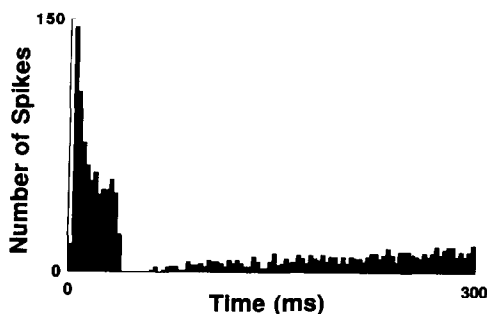


Fig. 3. Peristimulus-time histogram for a tone burst at 7 kHz (approximate BEF) and 70 dB SPL for the unit of Fig. 2. Sample time = 30 s; total spike count = 1634.

suppression became stronger as the intensity was increased. Onset response was absent for 10.5 kHz stimuli at 60, 65 and 70 dB SPL, but was conspicuously present at 82 and 90 dB SPL (see Fig. 2). For stimuli at approximate BEF, 7 kHz, (Fig. 3), we observed primary-type responses from 35 to 90 dB SPL (the highest intensity used). At 30 dB the unit showed increased spike rate during the tone burst, but no adaptation. At 25 dB the unit showed no conspicuous response to the tone burst.

Discussion

Evidently, the unit that was the principal subject of this paper is an example of the class reported by Schmiedt and Zwislocki (1980), exhibiting suppression of ongoing activity by single tones at frequencies greater than approximately 1/2 octave above BEF. With respect to the qualitative nature of its onset responses and its suppressibility of ongoing activity, this unit is typical of a small but substantial subset (approximately 20%) of the several hundred primary units we have studied in the gerbil. With respect to the stability of its ongoing activity (under constant conditions), the unit was unusual. It was this property that allowed us to obtain strong evidence that the ongoing activity of the unit was not a consequence of sound leaking through our acoustic barrier or through our stimulus delivery system. This apparently leaves two possibilities as sources for the background activity that was suppressed: (1) those internal to the cochlea or to the VIIIth-nerve axon (e.g., thermal motion of the micromechanical structures, spontaneous ion-channel activity in the axon, and the sources of spontaneous otoacoustic emissions), or (2) acoustic sources outside the cochlea but internal to the animal subject – such as respiratory, cardiovascular, or gastro-intestinal activities.

The frequency range (beginning approximately 1/2 octave above BEF) over which we have observed one-tone suppression is consistent with that observed for two-tone suppression by moderate to high-intensity stimuli in the gerbil (Schmiedt, 1982). A major inconsistency is the fact that we have not seen one-tone suppression of this sort at frequencies below BEF (and we often have searched carefully for it in units exhibiting one-tone suppression above BEF).

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