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ON–OFF units in the mustached bat inferior colliculus are selective for transients resembling "acoustic glint" from fluttering insect targets

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Summary. Of 311 single units studied in the central nucleus of the inferior colliculus (ICC) in 18 mustached bats *(Pteronotus parnelli)*, a small but significant population (13%) of cells with on-off discharge patterns to tone bursts at best frequency (BF) was found in the dorsoposterior division. In contrast to units with the same BF's but other discharge patterns, the majority of ON–OFF units were unresponsive to sinusoidally amplitude-modulated tone bursts (SAM). To define the contribution of linear and nonlinear components to the responses of ICC neurons to amplitude modulation, we tested some of these neurons with a long, seamlessly repeating pseudorandom sequence of ternary amplitude-modulated tones at BF. Wiener-like kernels were subsequently derived from cross-correlation of spikes with acoustic events in the sequence. These kernels provided estimates of neural impulse responses that proved unusual in SAM-unresponsive ON–OFF units. First, their estimated impulse response had no linear component. Second, the predicted second-order impulse responses to both increments and decrements in stimulus intensity were long (about 20 ms) and nearly identical in shape: triphasic, with the positive phase bounded by leading and trailing negative periods. The similar shape of responses to increments and decrements in these neurons suggests a full-wave rectifier. The triphasic, initially negative second-order prediction of the impulse response accounted for an unusual result in experiments measuring the recovery cycle of ON–OFF units using a pair of identical stimulus pulses separated by various time delays. This recovery cycle can be related to their response to amplitude modulation. As the delay between two brief, near-threshold BF tone bursts decreased, the response to the first tone diminished, rather than to the second. The second-order prediction of this experiment derived from impulse responses obtained with pseudorandom noise suggests that, at short interpulse intervals, the initial negative phase of the response to the later stimulus cancels the positive phase of the response to the first. Such cancellation at short interpulse intervals may help explain why the majority of ON–OFF units are unresponsive to SAM. The unusual properties of these ON–OFF units make them ideally suited to respond selectively to infrequent acoustic transients superimposed on an ongoing background of modulation. Such patterns are commonly encountered by mustached bats foraging in cluttered habitats for small, fluttering insects, which generate "acoustic glints" upon a background of modulated echoes from the surroundings (Schnitzler et al. 1983; Henson et al. 1987).

Key words: Amplitude modulation – Inferior colliculus – Pseudorandom noise – Pattern recognition – Mustached bat

Introduction

One of the major unsolved problems of audition concerns the recognition of acoustic patterns in the presence of competing sounds. Insectivorous echolocating bats are an especially good model for the study of this problem, because they must detect and process the echoes of small, rapidly flying prey that are often embedded within competing echoes from nearby objects. To hunt flying insects in and around dense foliage, some species have evolved a distinctive biosonar signal characterized by a long-duration constant-frequency (CF) component, preceded and followed by rising and falling frequency-modulations (FM). Current thought suggests that the long CF component evolved to differentiate stationary objects

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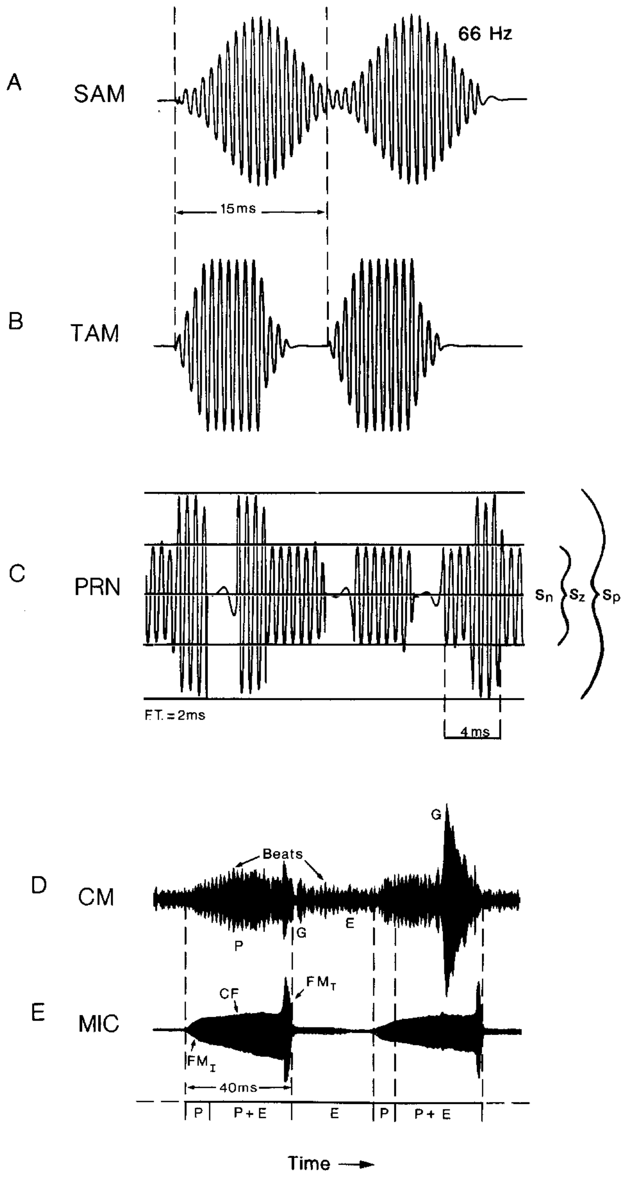

Fig. 1A–E. Waveforms of SAM (**A**, 66 Hz), two-pulse TAM (**B**) and PRN (**C**) stimuli compared with cochlear microphonic (**D**, CM) and microphone-recorded echo patterns (**E**, MIC) recorded from a mustached bat echolocating a flying insect in a cluttered habitat (the latter adapted with permission from Henson et al. 1987; Copyright 1987 by the National Geographic Society). For clarity, the carrier frequencies of the stimuli shown in **A–C** are much below the actual frequencies of the stimuli used in the experiments (hence the artifactual distortion seen in the "s_n" phase of the PRN stimulus). The two-pulse TAM stimulus in **B** is of the type used for measuring unit "recovery cycles". Such stimuli are also models for SAM stimuli, but allow independent control of the rise-time, duration and repetition rate of the modulated waveforms. For the PRN stimulus (**C**), s_p s_z, *and* s_n refer to the three amplitudes of the ternary sequence. The segment shown here is merely a short period of the entire PRN sequence. *F.T.* is the frame time. In the radiotelemetry recordings at the bottom (**D, E**), prominent acoustic glints ("G") are missed by the microphone ("MIC"), but are clearly visible in the highly-tuned cochlear microphonic ("CM"), riding on a background of ongoing beat modulation patterns ("Beats") caused by Doppler-shifts between echoes from multiple sources and overlap of the emitted pulse ("P") and target echo ("P + E"). Note how the amplitude of the first glint is about the same as the acoustic clutter, while the second is larger due to its occurrence during the P + E overlap. Labels show CF and initial ("FM_I") and terminal ("FM_T") frequency-modulated components of the emitted pulse. Prominence of FM_T is an artifact caused by the directional nature of the sonar pulse and the location of the recording microphone on the head of the bat. Also note the large difference in time scales between the three stimulus classes and the recordings in **D, E**

from fluttering prey by acting as a carrier for amplitude and frequency modulations in the echo produced by movement of the target's wings (Griffin 1958; Pye 1967; Schnitzler 1970; Simmons et al. 1979; Schnitzler et al. 1983; Ostwald et al. 1988). The ears of these so-called "long CF/FM" bats are extraordinarily sharply tuned, perhaps to facilitate the analysis of such minute modulations. In the mustached bat, *Pteronotus parnelli,* the ears are tuned to a frequency approximately 400–500 Hz above the "resting" frequency of the dominant second harmonic CF component of the biosonar signal (Kössl and Vater 1985; Pollak et al. 1972; Suga et al. 1975; Suga and Jen 1977). Because the movement of a flying bat causes Doppler-shifts in the echo frequency, these bats adjust the frequency of the emitted biosonar signal to keep the echo centered at a "reference" frequency, which lies between the resting frequency and the tuned frequency of the Organ of Corti. This behavior is called "Doppler-shift compensation" (Schnitzler 1968, 1970). A very narrow band around the reference frequency is enormously over-represented in the auditory system; between one-third to one-half of the neurons at a given level are tuned within it (Suga et al. 1975; Suga and Jen 1976; Suga and Jen 1977; Suga and Manabe 1982; Pollak and Bodenhamer 1981; O'Neill 1985; O'Neill et al. 1989). By analogy to the representation of central visual space in the visual system, this over-representation has been called an "acoustic fovea" (Schuller and Pollak 1979).

Behavioral studies have suggested that long CF/FM bats, including the mustached bat and some horseshoe bats (family Rhinolophidae), will attack only fluttering targets (Goldman and Henson 1977; Schnitzler and Flieger 1983; Link et al. 1986). Recordings of the echoes of flying insects have shown the presence of ongoing modulations punctuated by prominent amplitude transients, dubbed acoustic "glints". These transients are caused by reflections from the insect's wings at one or two points during the stroke when they are perpendicular to the incident sound waves (Schnitzler et al. 1983; Schuller 1984). However, Henson et al. (1987) have shown that wing-generated glints reaching the bat's ears are embedded in an echo background amplitude-modulated by many other spurious factors. These include beats caused by acoustical interference between the outgoing sonar signal and returning echoes, and between echoes from both the target and the surroundings Doppler-shifted to different degrees (see Fig. 1D and E). Only the wing-beat glints uniquely identify the flying insect target.

Acoustic transients are prominent in the vocalizations of many animals, and are often important cues in communication sounds, including speech. As part of an extensive study of the encoding of amplitude modulations by neurons in the inferior colliculus of the mustached bat, we have discovered a class of "foveal" ON–OFF neurons that seem to have "clutter rejection" properties that allow them to respond selectively to transients. These units may be responsible for carrying wing-beat information unique to the insect target. In this report we describe the unusual features of these units. More extensive analyses of the modulation responses of other types of units in the inferior colliculus can be found in Lesser (1988).

Methods

Jamaican mustached bats *(Pteronotus p. parnelli)* were surgically prepared for recording as described in detail elsewhere (O'Neill 1985). All data were obtained from awake bats restrained in a form-fitting foam block, and placed inside an echo-attenuated, double-walled, sound-proofed booth (IAC). Recording sessions lasted 5–7 h. Water was provided roughly every hour. By clamping a small nail previously glued to the skull during surgery under anaesthesia, the animal's head was painlessly immobilized facing a 3.75 cm-diameter electrostatic loudspeaker (Polaroid) located 49 cm away. Glass micropipette recording electrodes (10–15 MΩ @ 22 Hz) were introduced through small holes made in the skull above the inferior colliculus (ICC). A sharpened tungsten wire surgically implanted in the skull and contacting the dural surface over the cerebral cortex served as an indifferent electrode. Single units were isolated in the dorsoposterior and anterolateral divisions of the central nucleus.

Search stimuli consisted of sinusoids (Wavetek 111) trapezoidally shaped by a programmable electronic switch (Wilsonics BSIT) into 30 ms-long tone bursts with linear rise-fall times of 0.5 ms, at an interstimulus interval of 200 ms. Unit best frequencies (BF) and minimum thresholds (MT) were first determined in response to these stimuli. The units were then tested with various forms of amplitude modulation. Using a four-quadrant, linear multiplier (Analog Devices AD534J), sinusoidally amplitude-modulated tone bursts (SAM; 80% modulation depth) were produced by multiplying 30 ms BF tone-bursts by a second sinusoid phase-locked to the tone-burst envelope. SAM was presented at selected modulation frequencies between 16 (i.e., one half cycle of modulation) and 800 Hz (24 cycles). Peristimulus time (PST) and period histograms were computed from 100 presentations of each stimulus condition. Modulation transfer functions (MTF's) were computed by dividing the spike count elicited with SAM by the spike count elicited by a pure-tone at the same average intensity level. Unless otherwise stated, spikes were counted during two time windows: a 5- or 10-ms "prestimulus" period just prior to stimulus onset, to obtain an estimate of spontaneous activity; and either a 45 or 95 ms "post-stimulus" period beginning at stimulus onset. The spike count elicited by the stimulus was obtained by subtracting the prestimulus count (multiplied by the appropriate value to equal the poststimulus period) from the poststimulus count. Further discussion of other techniques for quantification of SAM data can be found in Lesser (1988).

Trapezoidally amplitude-modulated (TAM) stimuli modeling the SAM (Fig. 1B) were used to test unit responsiveness independently to stimulus rise-time, duration, and repetition rate (interstimulus interval). These were generated by a programmable electronic switch under computer control (DEC Micro-11/23+). "Two-pulse" TAM experiments, in which the interstimulus interval between two otherwise identical tone-bursts was systematically changed, are basically equivalent to the "recovery cycle" experiments of previous studies (Grinnell 1963; Suga 1964; Friend et al. 1966; Suga and Schlegel 1973; Pollak et al. 1977).

In later recordings, we multiplied the amplitude of continuous best-frequency pure-tones by the waveform of a pseudorandom-noise sequence (PRN; Fig. 1C), similar to the method pioneered by Møller (1983; Møller and Rees 1986). The modulation pattern consisted of a single sequence of pseudorandomly-assigned amplitude events drawn from values of a ternary "M-sequence" (modulo-3, with a length of $3^9 - 1 = 19{,}682$ events). At regular time intervals, or "frames", the sound level could assume one of three discrete amplitudes: 0, 1, and 2 times (+6 dB) the mean amplitude of the carrier (i.e., 100% modulation). Level transitions within the sequence were abrupt, causing some spreading of energy in the stimulus spectrum, but the mean sound levels used in these experiments were no more than 20 dB (typically 10 dB) above single-unit minimum thresholds, where spectral analysis showed the energy spread to be far below threshold. Each amplitude level occurred with equal probability, and the sequence had an exactly counter-balanced combination of single stimuli and pairs of stimuli (equal numbers of increments and decrements, etc.). Typical frame times in these experiments were 2, 4 or 8 ms, chosen to be near or somewhat below the neuron's integration time. The sequence was repeated seamlessly, without intervening silent periods, until a sufficient number of spikes was recorded to calculate the average response, called a "kernel", to these single and paired impulsive events. To maximize the signal-to-noise ratio, we recorded long enough to gather a number of spikes greater than an experimentally-determined value of about 8000 divided by the frame time.

Impulsive events are used here because it is well known that, in a linear system, the impulse response is a compact and complete representation of the system's behavior. Through superposition, the impulse response can be used to predict the response to other stimuli whose time-course can be approximated by a sequence of impulses. This same technique can be applied to a nonlinear system by considering the nonlinear interaction that occurs when the responses to two stimuli occurring closely in time fail to add linearly. Simultaneous stimuli, the limiting case of two-pulse interactions, test the neuron's "intensive" linearity. Separated stimuli test its temporal linearity.

In this study we have used second-order Wiener-like kernels to predict neuronal responses along a three-valued intensity domain, i.e., to an incremental or "positive" pulse (k_p; see Fig. 5), and to a decremental or "negative" pulse (k_n), both measured from an intermediate mean sound level ("z"). (For a discussion of the interpretation and calculation of Wiener kernels, see Marmarelis and Marmarelis (1978) and Schetzen (1980).) The full second-order nonlinear Wiener-like kernel (h_2) for both simultaneous (therefore, single) sound pulses ($h_2(1)$ in Fig. 5), or separated sound pulses ($h_2(\tau, \Delta\tau)$, where $\Delta\tau$ is the time separation), represents the nonlinear correction that must be added to the linear prediction of the single impulse response (h_1 in Fig. 5) to represent more accurately a neuron's measured response.

To calculate these kernels, we cross-correlate the neural responses with the stimulus sequence by time-locking an average response measure (i.e., a PST histogram) to the individual positive and negative stimulus phases, for both single- and time-separated pairs of stimuli. These raw, time-locked responses can be combined easily to generate either the standard Wiener kernels, such as h_1 and h_2; or the direct estimates for increments and decrements, k_p and k_n. For details of the calculation, see Appendix of Emerson et al. (1987).

It should be noted that the reliability of the the cross-correlation procedure is critically dependent on synchronization between the timebases for presenting stimuli and for recording spike arrival times. To avoid drift, we linked one crystal oscillator to two programmable clocks (DEC KWV–11C, Data Translation DT2769), one of which controlled the high-speed D/A board (Data Translation DT2771) that generated the waveform of the PRN sequence to be multiplied with the sinusoidal carrier, while the other registered spike arrival times with 10-microsecond precision.

Results

Using 30-ms tone bursts at BF near minimum threshold, we obtained PST histograms from 311 single units re-

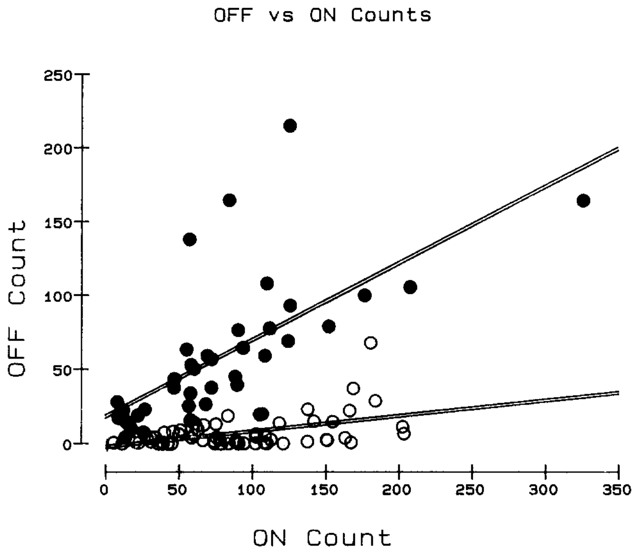

Fig. 2. Spike counts to BF tone bursts taken in two time windows differentiate ON units (open circles) from ON–OFF units (filled circles; the same symbols are used in Figs. 3 and 6). "ON" counts (abcissa) were taken between 5 ms and 24.5 ms after the onset of a 30 ms tone burst. "OFF" counts (ordinate) were taken between 25 and 44.5 ms post-onset. (Note that these windows were offset by 5 ms to ignore the response latency, which was never less than 5 ms, including a 1.5 ms transmission time delay from the loudspeaker). Most values of on and off counts were averaged from two samples of 100 stimulus presentations each, taken as controls before and after a series of SAM stimuli at selected modulation rates, as illustrated in Fig. 4. The lines were fitted by least squares analysis to each unit class, as an aid to differentiating the two. The scattergram shows that ON–OFF units respond about equally to both stimulus onset and offset, while ON units only discharge at the onset

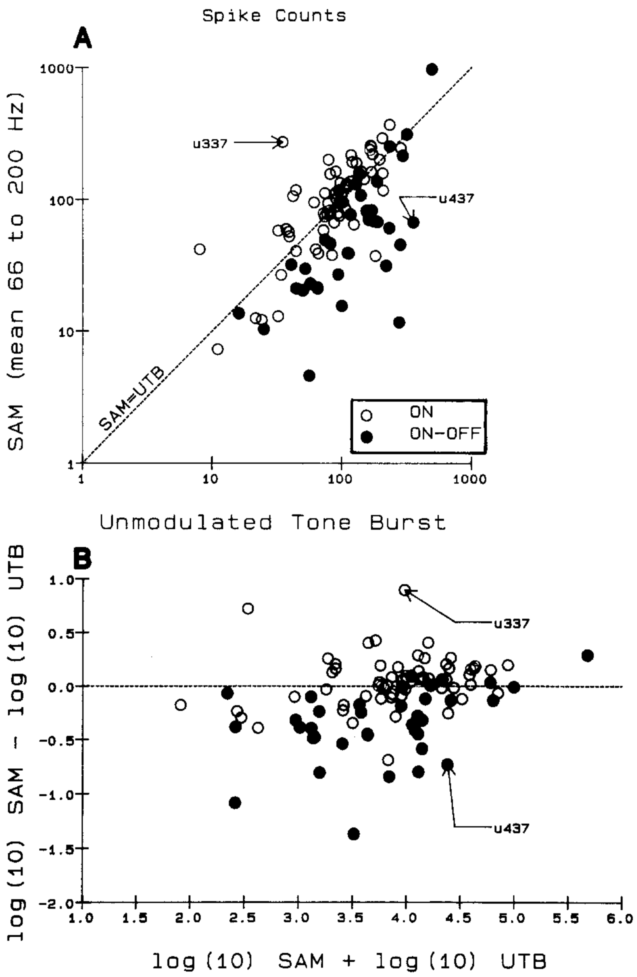

Fig. 3A, B. Spike counts to SAM vs. unmodulated tone-burst controls in ON and ON–OFF units (symbols as in Fig. 2). "SAM" counts (ordinate) were averaged for modulation frequencies of 66, 100, 133, and 200 Hz, deliberately avoiding the extreme low and high frequency modulations which elicited poor responses in most units. At each frequency, counts were made for 100 presentations of 30-ms SAM tones at BF, between 0 and 100 ms *re* stimulus onset. "Unmodulated Tone Burst" counts (abcissa) are averages from the same time window in response to two unmodulated tone burst controls, one taken before and the other after stimulation with SAM at the above frequencies. **A** Bivariate scattergram showing that responses to SAM in ON units are usually equal to, or better than, control, while ON–OFF units are generally suppressed by SAM (the diagonal line indicates equal counts to both stimulus conditions). Since this fact is obscured by a strong, but irrelevant, positive correlation between the magnitudes of response to modulated and unmodulated stimuli, the data are replotted in **B** in the form of a sum-difference plot (Tukey 1977): the difference between the values for each unit are plotted against the sum. The effect is basically a rotation around the diagonal in **A**, resulting in a clearer view of the relationship of interest, namely, the deviations of each unit from equality of the two values (i.e., the diagonal in **A**). Values above the dashed line indicate enhanced response to SAM vs control, while those below indicate suppression by SAM. Most ON–OFF units are suppressed by SAM

corded in 18 mustached bats. The temporal discharge patterns were classified as ON (111 units), ON-sustained (57), ON–OFF (34), primary-like (31), Flat (30), Chopper (17), OFF (18), and ON-late (13), based on traditional criteria (Pfeiffer 1966). To compare quantitatively the responses of units to tone-burst onset (on response) and offset (off response), we used two counting windows, one between 10 and 29.5 ms, and the other between 30 and 49.5 ms. Figure 2 shows the on and off counts for the two qualitatively-defined unit classes of interest in this paper, ON and ON–OFF units. With few exceptions the scattergram distinguishes the two groups rather clearly. The regression lines fitted to the data indicate that, on average, ON–OFF units have a ratio of on and off counts of about 2:1, while the ratio for ON units is about 10:1.

On-off discharge patterns *at unit threshold* occured only in certain RF (or "filter") units. RF units are tuned within ± 500 Hz of the bat's reference frequency, comprise about 1/3 of all units in the ICC, and form an anatomically distinct dorsoposterior division (DPD; Zook et al. 1985). BF's of ON–OFF units in our sample averaged 61.90 ± 0.51 kHz (S.D.), quite close to the average resting frequency of our bat population (61.87 ± 0.54 kHz). Q–10dB values ranged from 23 to 315.

In response to SAM, most units tested showed either low-pass, high-pass, band-pass or band-reject modulation transfer functions (Lesser 1988). Most ON units were more responsive to low- and mid-frequency SAM than to unmodulated tone bursts (UTB), and showed phase-locked discharges to the modulation envelope, increased spike count, or both. Most ON–OFF units, however, were suppressed by SAM. This tendency can be

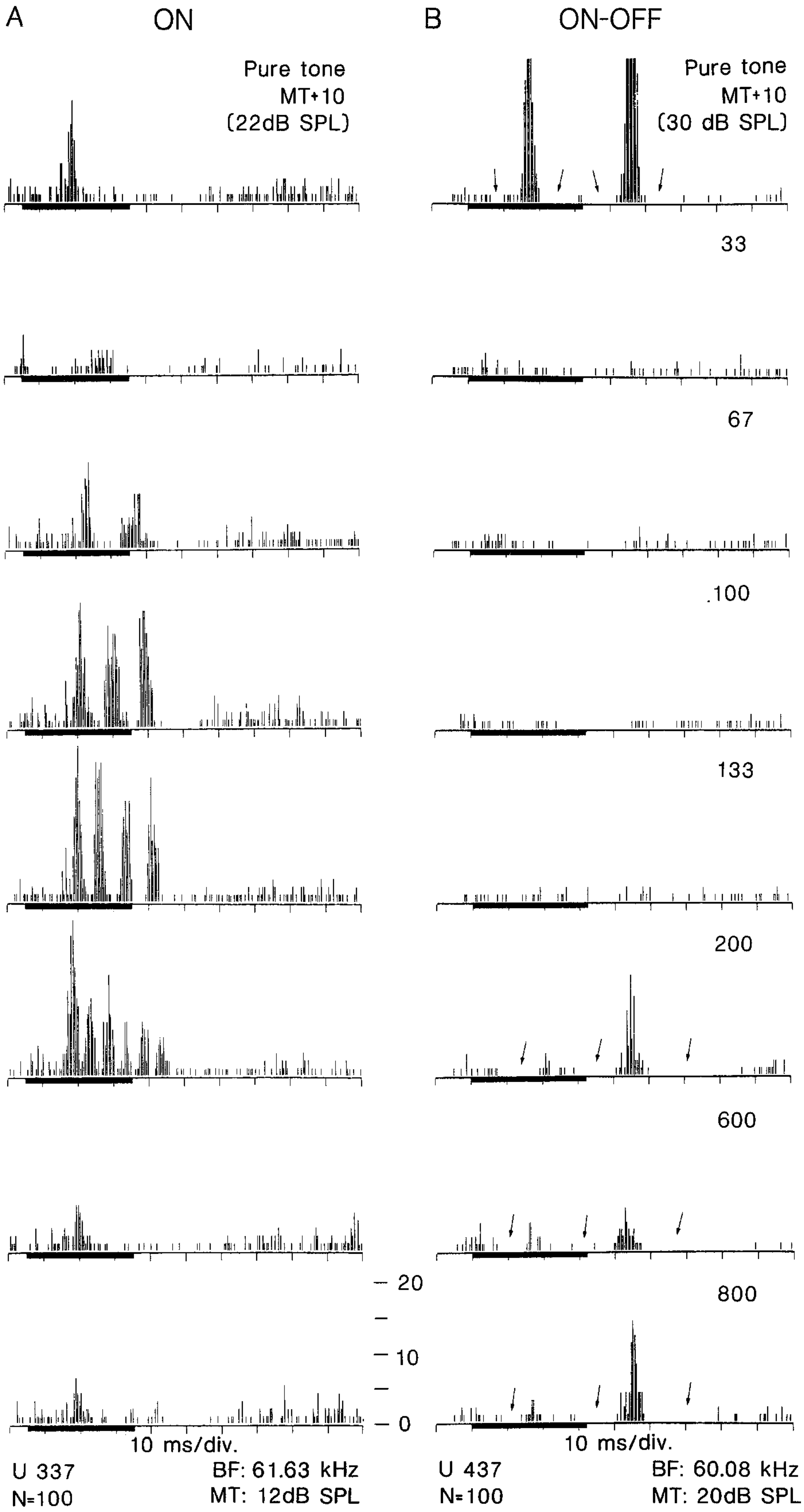

Fig. 4A, B. Peristimulus-time histograms (PST's) of the responses of an ON (U 337 in **A**) and an ON–OFF unit (U 437 in **B**) to SAM. Average stimulus amplitudes were 22 dB SPL (**A**), and 30 dB SPL (**B**), i.e., 10 dB above each unit's threshold at BF (shown at the bottom). PST's are paired according to the frequency (in Hz) of the SAM stimulus, shown on the right side in **B**. The topmost pair show the responses to unmodulated tone bursts. The ON unit shows strong, stimulus-locked responses to the envelope of the SAM between 67 and 200 Hz. The ON–OFF unit, however, failed to respond to SAM below 200 Hz, and responded to higher frequency SAM mainly with an off-response. For all PST's shown, vertical scale between two lower panels indicates number of spikes. *Arrows* indicate apparent negative periods in PST's of the ON–OFF unit, further revealed in Wiener-like predictions of Fig. 5 and 7C, D. Stimulus duration is indicated by the *black bar* beneath the time axis in each PST seen in Fig. 3a, which plots the spike count to SAM (averaged for SAM frequencies of 66, 100, 133 and 200 Hz) against that for UTB (note that this measure of SAM response ignores synchronization). Figure 3b replots the data as the difference between the spike counts to SAM and UTB against their sum, which better depicts the deviations of the spike counts from equality. The majority of ON units fall on or above the dashed lines in Fig. 3a and b, indicating that their response to SAM was equal or better than their response to unmodulated tones, while 30 out of 37 ON–OFF units fall below the line, indicating suppression. Figure 4 compares PST histograms obtained from two extreme cases, an ON unit (A, U337) which was strongly enhanced by SAM, and an ON–OFF unit (B, U437) which was strongly suppressed. The ON unit showed strong discharge synchronization to the SAM envelope, with a best response at 133 Hz. The ON–OFF unit was totally suppressed below modulation frequencies of 200 Hz, and showed only off-discharges above that. Note that with SAM there is a periodic modulation (arrows in Fig. 4B) of background discharges in the ON–OFF unit, especially above 200 Hz, which is not synchronized to the modulation envelope. This hints at underlying suppressive events, a point to which we shall return below.

Stimulation with pseudorandom modulation gave very different results in these two unit classes as well. In all, 90 ICC units were tested with PRN. Figure 5 shows the single-pulse predictions and Wiener-like kernels of the same ON–OFF unit (U437) shown in Fig. 4 superimposed on the responses of a typical ON unit (U438). Displayed on a common time base are the second-order estimates of impulse responses to increments (k_p) and decrements (k_n) in intensity, as well as linear estimates of the impulse response of the unit (h_1), and the intensive nonlinearity, or second-order diagonal ($h_2(1)$). (For a detailed explanation of these measures, see Methods and Emerson et al. 1987.)

For all ON–OFF units tested with PRN, the magnitude, and especially, the phase of the impulse response to brief increments in intensity were nearly identical to that for decrements ($k_p \cong k_n$). Therefore, the linear component is close to zero ($h_1 = (k_p - k_n)/2$) and their predicted impulse responses are purely nonlinear ($h_2(1) = (k_p + k_n)/2$). All of the PRN-tested ON–OFF units also showed differences from ON units in the time course of their impulse responses. Unit 438 (the ON unit in Fig. 5) had a biphasic h_1 suggestive of a band-pass modulation transfer function. The ON–OFF unit (U437), on the other hand, had no discernable h_1, and a markedly triphasic $h_2(1)$ (as well as a triphasic k_p and k_n). Therefore, this cell responded strongly to either an increment or decrement, but the positive phase in each case was *preceded* by a negative phase. The lack of a linear component and identical nonlinear impulse responses to increments and decrements are defining features of a full-wave rectifier.

Although the on-off property of the response to a 30-ms tone burst (e.g., Fig. 4B) might seem attributable to a transient temporal response, in fact such a response to inverse phases of the stimulus depends also on some sort of *intensive* nonlinearity. Furthermore, by using brief stimuli, such as those in Fig. 5, we have found that all PRN-tested ON–OFF units exhibited a full-wave rectifying intensive nonlinearity.

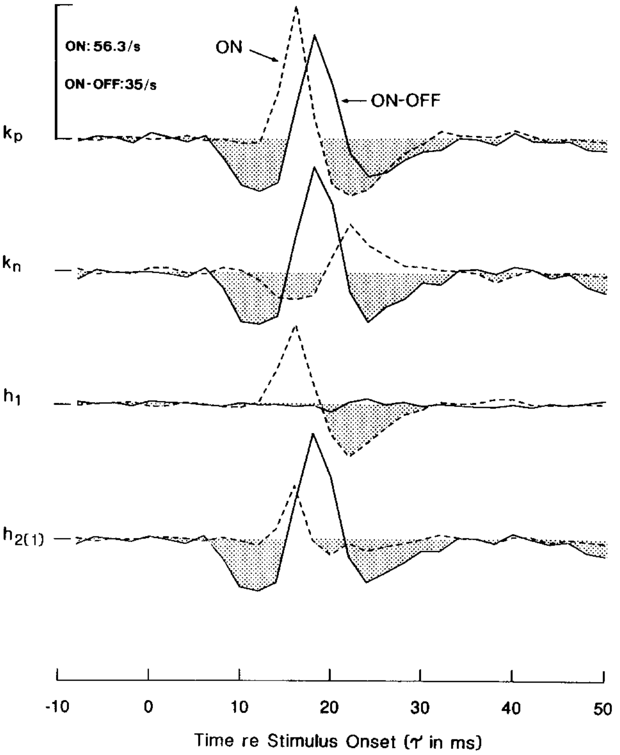

Fig. 5. Wiener predictions (k's) and kernels (h's) to single-pulse presentations for an ON unit (U438, broken line) and an ON–OFF unit (U437, solid line), the latter being the same unit shown in Fig. 4B. The estimated second-order Wiener impulse responses to amplitude increments (k_p) and decrements (k_n) are shown above the estimated linear kernel impulse response (h_1), and the intensive non-linearity, or second-order diagonal kernel ($h_2(1)$). Time (τ) is shown with respect to the onset of brief (2 ms) stimuli. h_1 is calculated by averaging k_p and the inverse of k_n. $h_2(1)$ is simply the estimate of the nonlinear intensive correction necessary because of rectifying and other nonlinearities in neurons (see Methods and Emerson et al. 1987 for details). Values of the curves above the baseline (unshaded) show positive, and those below (shaded) show negative responses with respect to background activity. The ON-unit response to increments shows positive followed by negative phases, and to decrements, negative followed by mild positive phases. It has both linear (h_1) and nonlinear ($h_2(1)$) impulse-response components. In contrast, the ON–OFF unit responds similarly to increments or decrements, i.e., with initial negative, followed by positive, and then negative phases ("Mexican hat" response). Since k_p and k_n are about equal, the ON–OFF unit has no linear component in its impulse response. Firing probability calibrations (vertical bars) are expressed in spikes/s, as calculated for a 2-ms pulse binned at 2 ms

ON units have h_1's that are either monophasic (i.e., low-pass) or, as in the case of U438, biphasic (band-pass). The incremental impulse responses (k_p's) have a positive phase first, and decremental impulse responses (k_n's) have a negative phase first. This means that in response to tone onset (i.e., an intensity increment), there will be an initial excitation followed rapidly by inhibition, resulting in a phasic-on spike pattern. In response to tone offset (i.e., a decrement), they show ("post-excitatory") inhibition followed by excitation (often called "rebound excitation"). Although the linear component is strong, there is also a significant nonlinearity in many ON units, as shown by the presence of the h_2 component in this example. This nonlinear component has recently been associated with the firing threshold in visual neurons (Emerson et al. 1989).

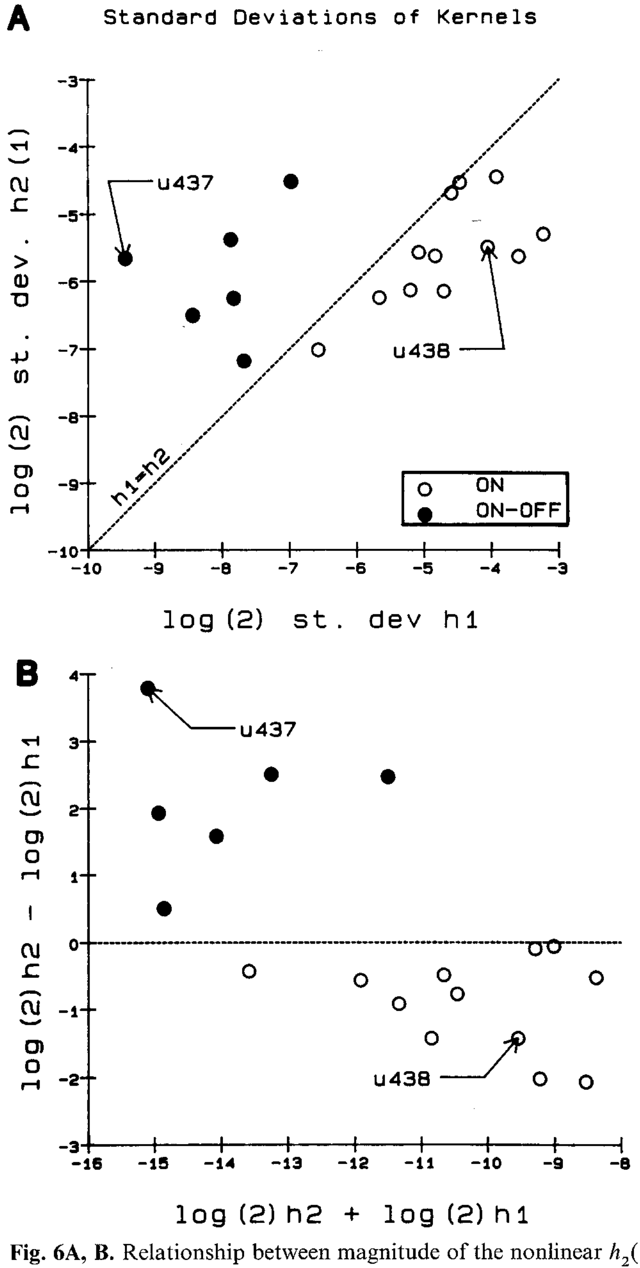

Fig. 6A, B. Relationship between magnitude of the nonlinear $h_2(1)$ and linear h_1 estimates of the impulse response in ON and ON–OFF units. "Magnitude" refers to the standard deviation of the kernel measured in a time window between 0 and 40 ms re stimulus onset, which is roughly equivalent to the rms amplitude of the waveform over that period. **A** Is a scattergram of the values for each unit, **B** is the sum-difference transformation of **A**. ON–OFF units are very clearly distinguished here by their much larger $h_2(1)$ component compared to h_1, whereas ON units are more equally balanced between linear and nonlinear contributions to their impulse responses. The dashed line indicates equality of the h_1 and $h_2(1)$ kernels. The values for units 437 (ON–OFF) and 438 (ON), shown in Figs. 4, 5, and 7, are indicated

Because of the similarity between k_p and h_1 in ON units, it makes sense to use the terms we normally use for linear responses, "excitation" and "inhibition". On the other hand, full-wave rectifying ON–OFF cells like unit 437 have such weak linear response predictions (because of small h_1's) that their responses are primarily nonlinear, and might deserve the terms "facilitation" and "suppression". However, to reserve those terms for temporal second-order interactions (h_2) that depend on two stimuli, we use the adjectives "positive" and "negative" to refer to phases of responses in ON–OFF units that depend on full-wave rectification in single-pulse responses.

ON–OFF units can be distinguished quantitatively from ON units on the basis of the shapes of their linear and non-linear impulse response estimates. This is shown in Fig. 6, which plots the standard deviation of h_1 against h_2 (standard deviation, an approximation of the root-mean-square amplitude of the kernels, was calculated for a time window of 40 ms beginning at stimulus onset). These graphs emphasize two important points. First, ON–OFF units are very non-linear, as evidenced by their much smaller values of h_1 compared to ON units. Second, without exception, ON–OFF units consistently fall above, and ON units below, the diagonal which indicates equality of h_1 and h_2.

The results from TAM experiments (to be reported elsewhere) showed that the best modulation frequency for ON units was determined by preferences for a particular rise-time or pulse duration (i.e., duty cycle). ON–OFF units nearly always showed preferences for tone bursts with very fast rise-fall times, consistent with the results from the above-described experiments demonstrating decreased responses to low-frequency (i.e., slow rise-time) SAM. However, two-pulse TAM experiments produced an unexpected result in the responses of ON–OFF units. In these "recovery cycle" experiments, two pulses of identical duration are presented at various interpulse intervals, and the effect of the first pulse (typically) on the response to the second is measured. In the example shown in Fig. 7A, as the interpulse interval decreased between two brief BF pulses (duration 4 ms, rise-fall time 0.5 ms), the response of an ON unit to the second pulse decreased (akin to forward masking). However, in the same type of experiment (Fig. 7B) the response of an ON–OFF unit to the second pulse remained relatively constant, while the response to the *first* pulse decreased (akin to backward masking)!

To explore the nature of this unusual interaction, we simulated the two-pulse recovery cycle experiment for both types of units (Fig. 7, C and D) using a pair of their respective second-order impulse responses, including the purely intensive nonlinearity ($h_2(1)$), plus any possible temporal interactions afforded by the full second-order Wiener kernel (h_2). For the ON unit prediction (Fig. 7C), the response magnitude of the *second* pulse decreases at delays shorter than about 12 ms, where the trailing negative phase of the impulse response to the first pulse begins to cancel the leading positive phase of the second pulse. For the ON–OFF unit, the apparently non-causal decrease in the response to the *first* pulse found in the

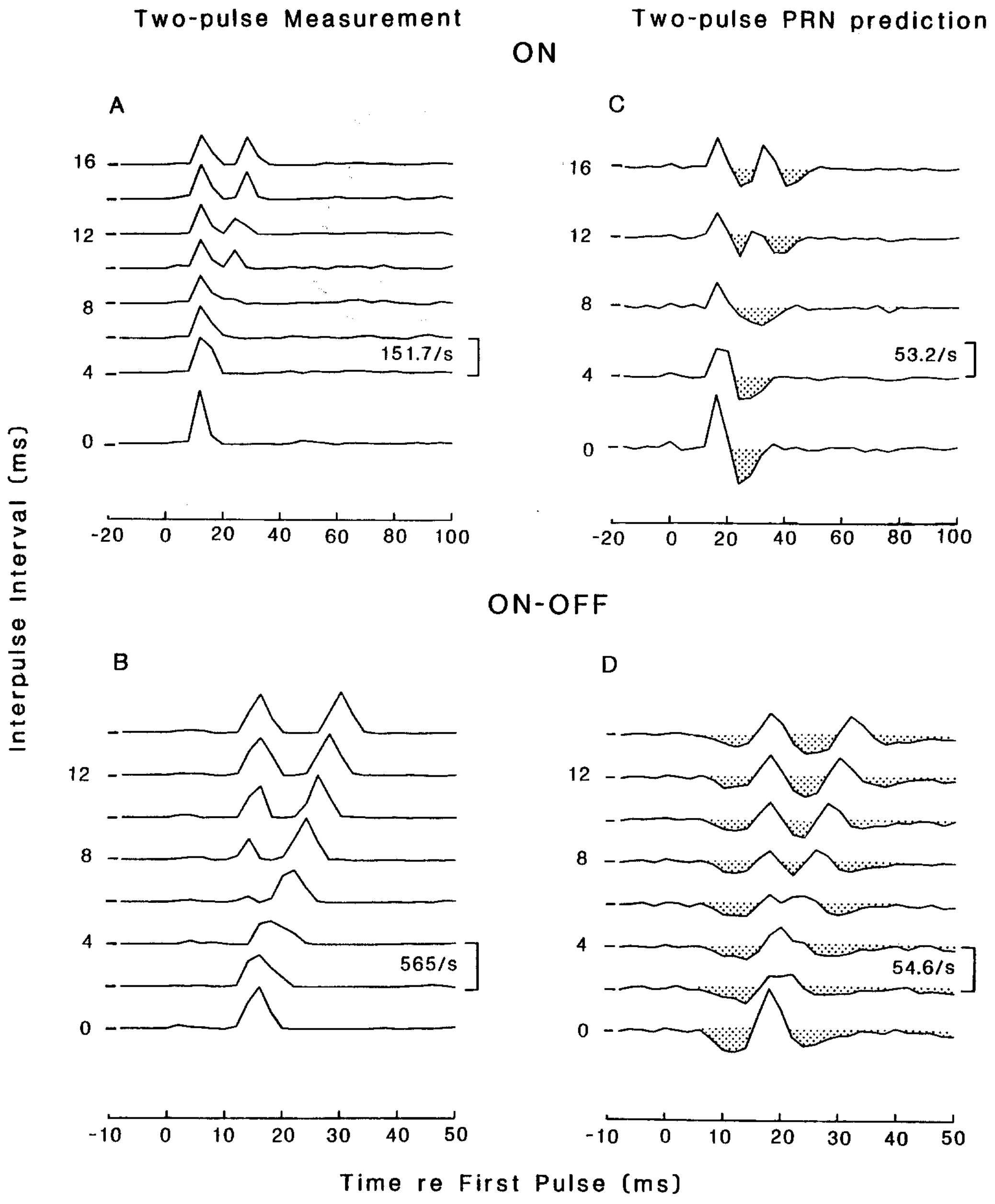

Fig. 7 A–D. Measured and PRN-predicted two-pulse recovery cycle experiments in an ON unit (U438, **A, C**) compared with an ON–OFF unit (U437, **B, D**). For the empirically-measured two-pulse experiments (**A, B**), the interpulse interval (IPI) between two identical tone bursts was varied in steps between 0 and 16 ms (**A**), or 0 and 14 ms (**B**). Tone burst duration was 4 ms in **A** and 2 ms in **B**, and intensity was 10 dB above each unit's threshold at BF. The plots represent the envelopes of the PST histograms of responses to the pulse pairs. In the measured experiments shown on the left for each unit, the "zero" interpulse interval was actually just a single tone burst whose amplitude was increased by 6 dB. The accuracy of a predicted response is enhanced by including the second-order diagonal, or intensive non-linearity of the impulse response ($h_2(1)$), shown in the second-order prediction at the corresponding location of **C, D**. The two-pulse predictions shown in **C, D** are derived from computer simulations of the same experiments as in **A, B**, using linear predictions (h_1), plus the second-order impulse responses ($h_2(1)$, plus the full $h_2(\tau)$ for temporal interactions) obtained with the PRN stimulus. In the ON unit, the measured two-pulse experiment shows that the response to the *second* pulse diminishes as the IPI decreases, while in the ON–OFF unit, the response to the *first* pulse diminishes. The PRN-predicted experiments show the same trends, but allow one to view the combinations of the positive (unshaded) and negative (shaded) phases of the responses to each stimulus pulse. The lack of negative responses in the two-pulse measurements (**A, B**) is caused by low spontaneous activity levels in these neurons. Otherwise, the second-order interactions in **C, D** accurately predict the two-pulse recovery cycle experimental results. The higher peak response rates of measured over predicted tests (see firing rate calibrations) indicate that the lower duty cycle of the conventional pulse-pair (repetition rate 5/s) adapts the neurons (i.e., lowers their gain) less than the continuous PRN stimulus. Although the absolute firing rate differs, the time-course of each predicted response matches that of the measured response. (Open spaces in **A, C** correspond to unavailable interpulse intervals at some odd intervals)

experimental results (Fig. 7B) is attributable mainly to the "Mexican hat" shape of its impulse responses to increments and decrements (Fig. 5). As can be seen in Fig. 7D, when the two pulses are brought together, the leading negative phase in the response to the second pulse tends to cancel the positive phase in the response to the first pulse. The inter-pulse interval for which cancellation of the response to the first pulse initially occurs in the PRN prediction (Fig. 7D) is the same interval (8 or 10 ms) where a decrease in the first pulse in the measured two-pulse recovery cycle experiments was observed (Fig. 7B).

For neither type of cell are any negative phases visible in the conventional, experimentally-measured two-pulse responses shown in Fig. 7A and B, because the background firing rates in the absence of PRN were too low to see a decrease. In the ON–OFF unit, the predicted response to the second pulse is only slightly depressed, because the trailing negative phase is lower in amplitude than the leading negative phase.

The initial, strong negative phase in the impulse response differentiates the responses of the ON–OFF unit from the ON unit in these examples. The two negative components in the triphasic second-order interactions, whose combined strength exceeds that of the positive component, may help account for the poor responses of ON–OFF units to SAM. This is because strong amplitude modulation with PRN or SAM activates a net-negative influence (note low firing rates in Figs. 7C and D).

In summary, ON–OFF units are unusual not only for the presence of a strong off response, but also for showing suppression to sinusoidally amplitude modulated stimuli. They are also distinguished by having similar responses to increments and decrements, and long-duration, triphasic, non-linear impulse responses with strong negative components, which may account for their lack of response to SAM. In addition, these units apparently only reside within DPD, where all neurons are very sharply tuned near the bat's individual reference frequency around 60–63 kHz.

Discussion

We have described a population of ON–OFF units in the mustached bat ICC that is distinguished from the much more common ON units by at least three characteristics. First and most obviously, this class is identifiable by its unique on-off discharge pattern (see Figs. 2 and 4B). Although other unit types can show responses to both onsets and offsets, only ON–OFF units maintain this discharge pattern at all frequencies and sound levels within the response area. Second, the majority of ON–OFF units are unresponsive to, or suppressed by, sinusoidal amplitude modulation (Figs. 3 and 4B). And finally, ON–OFF units show full wave rectification, a nonlinearity evident in the estimates of impulse responses to increments and decrements in sound level of pseudorandomly modulated sinusoidal carriers. These properties suggest that ON–OFF units may have an unique ability to respond to acoustic transients in noisy backgrounds, perhaps subserving the detection of fluttering insect targets in cluttered habitats.

ON–OFF units and the detection of acoustic glints

A bat encounters formidable problems trying to extract the echo of a flying insect embedded in acoustic clutter from other reflecting objects. Fortunately, there are unique cues to be found in the echo from a fluttering target. When continuous pure tones that roughly approximate the sonar signals of long CF/FM bats are directed at flying insects, the echoes contain prominent acoustic transients, or glints (Schnitzler et al. 1983; Schuller 1984). Glints are also prominent in cochlear microphonic potentials recorded from actively hunting mustached bats (Henson et al. 1987). These glints often, but not always, stand out clearly from a background of ongoing, less intense amplitude modulations (Fig. 1D). These ongoing modulations are caused not only by the movement of the insect's wings, but also by beats produced by Doppler-effect frequency differences between the insect echo and the bat's overlapping sonar pulse, and interactions between target and habitat echoes.

Many neurons at the midbrain level, such as the ON units briefly described here, are capable of encoding many of these modulations in their firing pattern, their overall magnitude of discharge, or both (Schuller 1984; Rees and Møller 1983; Lesser 1988). Most of these units show low-pass or band-pass "tuning" to the frequency of amplitude modulation, with high-frequency cut-offs around 100–200 Hz. Thus any beat modulation with a frequency higher than about 100–200 Hz will not be encoded in the discharge pattern of the majority of cells in the sharply-tuned, "filter" unit population (or, for that matter, cells tuned to other harmonics of the sonar signal)[1]. However, differences between the pulse and echo frequency below 100 Hz could occur during pursuit when the velocities of the bat and target are relatively similar, resulting in beats well within these units' pass-band. Consequently, at their best frequency for pure-tone stimuli, such units are not able to distinguish wing-generated acoustic glints from Doppler-generated modulations of the type recorded in the above-mentioned studies. Thus acoustic clutter, especially in the form of low-frequency beat modulations, could interfere with the detection of target glints by these units.

In contrast with ON units (and neurons with other conventional discharge patterns), many ON–OFF units have properties that might allow them to respond selectively to glints. Because most ON–OFF units are unresponsive to sinusoidal amplitude modulations, they would probably not respond strongly to ongoing low-level modulations like beats caused by small differences

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[1] This is not to say, however, that there is no effect at all from high frequencies of modulation, since in many cases they can be shown to reduce the responses of units below that of an unmodulated tone burst.

between the frequency of the echo and the emitted pulse. In our experiments, responses to tone bursts could be elicited in ON–OFF units only by the fast (0.5 ms) on- and off-transients of an otherwise unmodulated envelope, or by SAM at very high modulation rates (600–800 Hz), where the stimulus envelope approaches the shape of an unmodulated tone burst (e.g., Fig. 4B). Most ON–OFF units are full-wave rectifiers, meaning that either incremental or decremental transients are effective stimuli for this class of cells. Furthermore, regardless of the shape of the amplitude modulating input, such a cell, even if highly suppressed, would carry a signal whose mean (D.C.) level is proportional to the RMS (root mean square) level of the modulation (akin to the indication on an A.C. voltmeter). This signal could be used to set the gain of the cell itself, so that only inputs substantially above the RMS level would produce a meaningful discharge. This mechanism might permit a selective response to rarely-occurring transients independent of the level of ongoing background sounds.

Such differences in modulation power level may account for differences among two-pulse, PRN, and SAM experimental results. Note, for example, that the firing rates of PRN predictions in Fig. 7 fall far below measured firing rates (see figure legend). The lack of ON–OFF unit responses to SAM suggests that the gain of these neurons under SAM may be adapted to an extent similar to that in our PRN experiments. Explicit modeling of responses to SAM stimuli is needed to determine whether the strong negative second-order effects measured here are adequate to explain the SAM results, or whether higher-order nonlinear effects would have to be considered. Apparently, the recovery time of the gain increase is longer than the 170 ms period between SAM tone bursts, because the SAM on-response remains small in repeated presentations of such stimuli (e.g., Fig. 4B).

ON–OFF responses: occurrence, underlying mechanism

In long CF/FM bats, on-off responses of various types have been found at every recorded level of the auditory system. In the periphery, such response patterns occur in neurons of the cochlear nucleus, and possibly even in auditory nerve fibers, in both the mustached bat (Suga et al. 1975), and the horseshoe bat, *Rhinolophus ferrumequinum* (Suga et al. 1976; Neuweiler and Vater 1977). Centrally, on-off response patterns have been described in the IC of horseshoe bats (Pollak and Schuller 1981) and mustached bats (Pollak and Bodenhamer 1981; O'Neill 1985). Ostwald (1984) has also reported that up to 24% of all units recorded in the auditory cortex of the horseshoe bat show some form of on-off discharge pattern, depending on the stimulus frequency and intensity. The association of this discharge pattern with full-wave rectification has not been tested, except for the present study in the IC.

Unlike most other mammals, at frequencies near 61 kHz the cochlear microphonic (as well as the N_1 potential) of the mustached bat produces unusual on- and off-transients due to mechanical resonances in the ear (Suga et al. 1975). The on-response to an abrupt-onset pure tone pulse is typically tuned a few thousand Hz above the bat's resting frequency, while the off-response is only a few hundred Hz above, i.e., approximately at the bat's reference frequency. Recordings from peripheral auditory neurons corroborate these observations, the units often showing sustained or transient off-discharges. When a unit showed on- and off-discharges, the off-response was always tuned close to the best frequency of the cochlear microphonic off-response (around 61 kHz), regardless of the BF for the on-response. Thus the tuning of the off-response is attributable to the mechanical resonance frequency of the Organ of Corti, while that of the on-response is determined by the precise location along the basilar membrane from which the central neuron is receiving excitatory input. These results suggest a frequency-dependent gain change, or some other form of nonlinearity. Recent evidence from Kössl and Vater (1985) showed that the best frequency of the cochlear microphonic is normally equal to the best frequency of the spontaneous otoacoustic emission in the mustached bat. Consequently, the tuning of the off-response in single units should be indicative of the resonance frequency of the Organ of Corti.

In their pioneering study of neural responses in mustached bat ICC, Pollak and Bodenhamer (1981) did not report the occurrence of ON–OFF units, as we define them. Nevertheless, they showed that on-off discharge patterns could be elicited in *any* sharply-tuned filter unit, using stimuli lower than BF and higher than minimum threshold by 20 dB or more. Although we also noted on-off patterns in other unit types at off-BF stimulus frequencies, our, and by analogy Ostwald's (1984), discovery of units with on-off patterns even at threshold (i.e., ON–OFF units) shows that such discharge patterns can also be found at the best frequencies of some neurons. Since the experiments of Suga et al. (1975) and Kössl and Vater (1985) suggest that off-responses of mustached bat neurons are apparently tuned to the ear's resonance frequency, it seems reasonable to hypothesize that the *on-response* of *all* ON–OFF units will also be tuned very close to the resonance frequency, the cells thereby showing an on-off pattern even at minimum threshold.

ON–OFF units would therefore constitute that part of the filter unit population whose BF's fell very near the ear's resonance frequency. Cells with other discharge patterns at their best frequencies would have on-responses tuned near, but not precisely at, the bat's resonance frequency, and consequently only show an on, but not an off or on-off, pattern at BF. However, the above-mentioned studies suggest that for echoes compensated to the ear's resonance frequency, the discharge pattern of all unit types should be on-off. The question remains as to whether they would also show full-wave rectification at this frequency, and also not respond to SAM stimuli, like most of the ON–OFF units we examined. If most neurons in the bat's acoustic fovea did not respond to SAM-like modulations of echoes with carrier frequencies near the ear's resonance frequency, then this might represent a clutter rejection mechanism for the entire system. This hypothesis is the subject of current investigation.[2]

An as yet unresolved issue that poses a problem for this clutter-rejection hypothesis is whether mustached bats compensate the Doppler-shift of the insect they are pursuing. Trappe and Schnitzler (1982) have shown that horseshoe bats do not compensate the insect target, but only their own flight speed with respect to the surroundings. No similar experiment has been performed yet with mustached bats, but some indirect, positive evidence for compensation of the insect target comes from the observation that mustached bats not only compensate Doppler-effect frequency shifts, but also regulate echo amplitude by adjustments of the intensity of their pulses (Kobler et al. 1985). Amplitude compensation reduces the effect of distance on the amplitude of the echo, thus allowing amplitude to convey information mainly about the size (subtended angle) of the target of interest. Such a percept is more likely to be important for the insect target than for background clutter. In any case, for the mustached bat more behavioral data are needed to determine which echoes it compensates.

In conclusion, by combining linear and nonlinear systems analytic approaches, we have been able to differentiate a class of cells in the mustached bat IC with distinctive full-wave rectification properties. The predominantly-negative, triphasic, Wiener-like kernels of these cells help to explain their lack of response to periodic amplitude modulations in the frequency range associated with wing-beat rates in insect prey. However, they seem to retain the ability to respond to transients in the form of acoustic glints. Thus, full-wave rectifying, strongly-negative, triphasic responses may act as a mechanism for clutter-rejection, improving the detection and recognition of targets by CF/FM bats. It remains for us to investigate whether the 60 kHz-tuned neurons that have other pure-tone discharge patterns at BF also show full-wave rectification when stimulated at off-BF frequencies and at higher mean amplitudes that produce on-off responses.

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[2] Unfortunately, in the present study we did not obtain recordings from sufficient numbers of ON–OFF units in any one animal to determine if all were tuned to the same best frequency. Nor could we investigate correlations between the best frequencies of ON–OFF units and the bat's resting or reference frequency, because we did not record the bat's vocalizations, or measure the tuning of it's midbrain evoked potential off-response, both of which are indirect estimates of the ear's resonance frequency.

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