Discharge patterns of single units in the lateral superior olive of decerebrate cats

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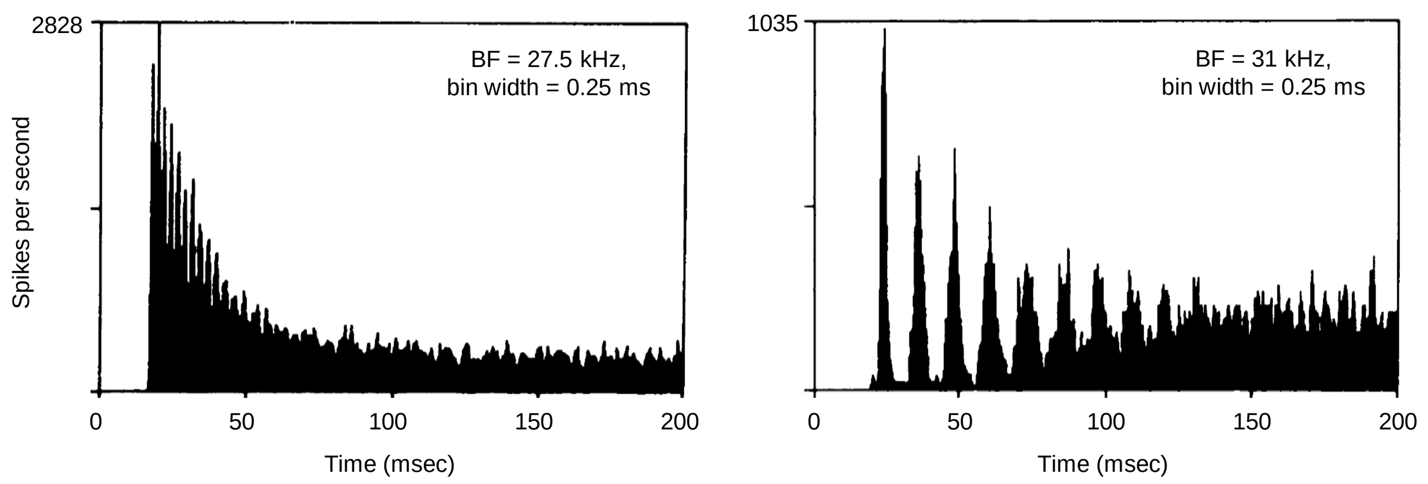
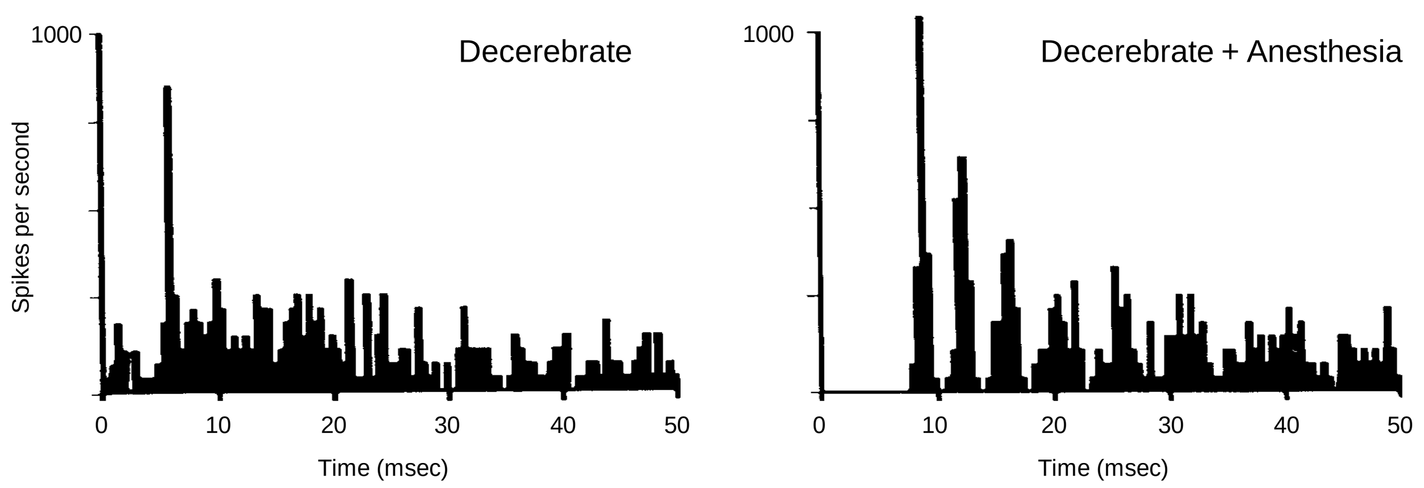
1 Most units in the LSO have been found to exhibit chopper-type discharge patterns in response to tone bursts …



Peri-stimulus time (PST) histograms for two LSO units recorded in anesthetized cat are shown above. The unit to the left shows a narrow chopper response; that is, it fires spikes that are time-locked to the onset of the tonal stimulus and the inter-spike interval is short (on the order of 2 ms). The unit to the right shows a wide chopper response (with an inter-spike interval on the order of 10 ms). Most units in the LSO of anesthetized cat (around 80%) show some variety of chopper-type discharge pattern (Tsuchitani 1982, 1988).

… however, most LSO data have been acquired in anesthetized preparations and there is evidence that anesthesia augments regularity of discharge.



In two experiments, the last LSO unit studied by Brownell et al. (1970) in a decerebrate cat preparation was re-examined after an anesthetic dose of sodium pentobarbital was administered. In both cases, the unit's discharge pattern changed from primary-like (above left) to chopper type (above right). Chopper responses with interpeak intervals greater than 2 ms were not observed in LSO units collected in unanesthetized decerebrate preparations. Unit BF, 11 kHz, bin width = 0.5 ms

2 The goal of our study was to test whether LSO units produce chopper type discharge patterns in the unanesthetized, decerebrate cat.

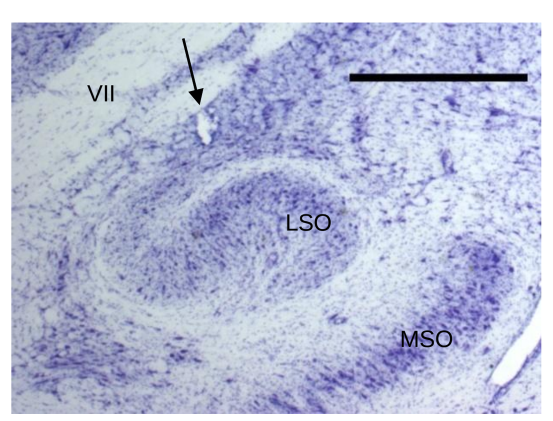
Data were acquired from decerebrate cats. The floor of the fourth ventricle was visualized by opening the skull about the nuccal ridge and aspirating the underlying cerebellum. Electrodes were placed on the brainstem, and advanced dorsoventrally. LSO units were identified based upon location (verified via tract tracing techniques, right) and physiological responses.

Acoustic stimuli were delivered via electrostatic speakers that were coupled to hollow ear bars. At the start of each experiment, the frequency response of each system was measured with a probe tube microphone that was inserted into the ear bar near the tympanic membrane. The magnitude spectra of all stimuli were corrected to compensate for non-flat calibrations.

Test stimuli were 200 ms duration, gated on and off with 10 ms rise/fall times, and presented once per second. Signals were created by playing the waveforms through a 16-bit D/A converter at a sampling rate of 100 kHz.

Unit activity was recorded with platinum-iridium metal electrodes. The signal from this electrode was amplified (x10000-30000) and filtered (0.1-6 kHz); template matching software (Alpha-Omega) was used to isolate individual action potentials from background noise.

PST histograms were computed from responses to 100 or more presentations of best frequency (BF) tones at 20 dB above the unit's threshold. Results are based on data from 32 LSO units.



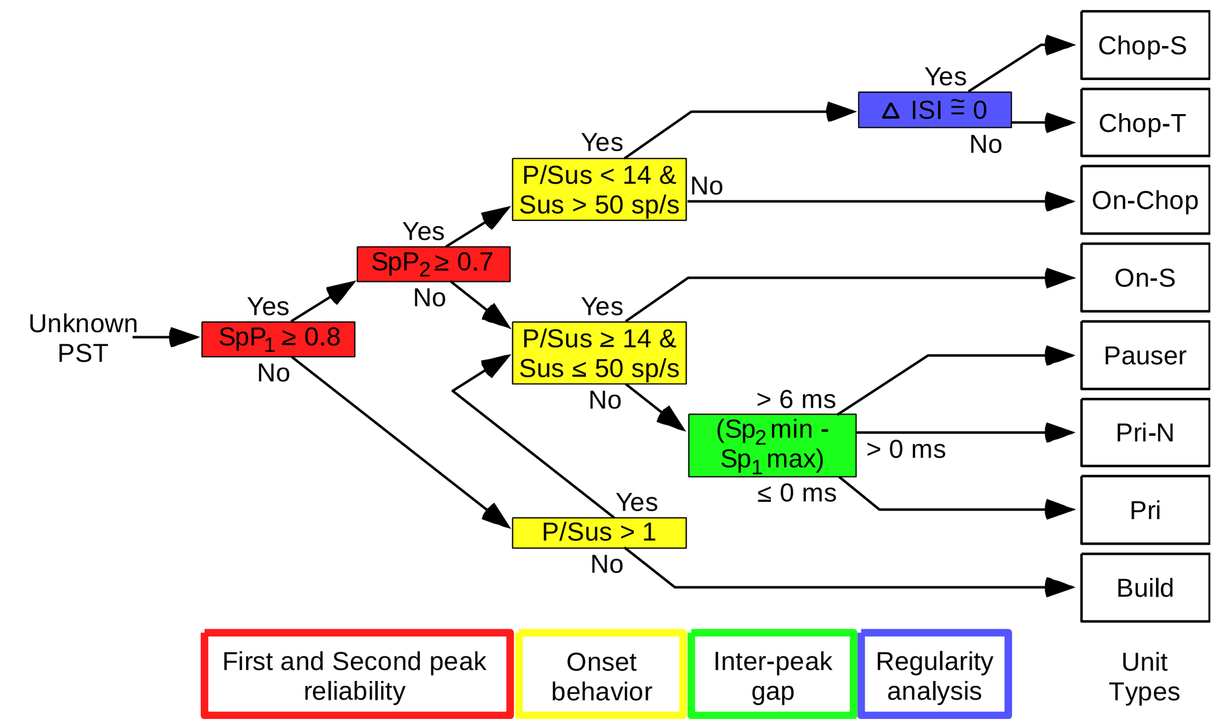
Frontal section of the left LSO (exp 07-03-13). The arrow indicates the path of the electrode and points to a lesion just dorsal to the LSO. Scale bar=1mm. VII, facial nerve. MSO, medial superior olive

3 The discharge patterns of LSO units were classified objectively based upon a decision tree; the responses can be grouped in three major types including chopper, onset and primary-like.

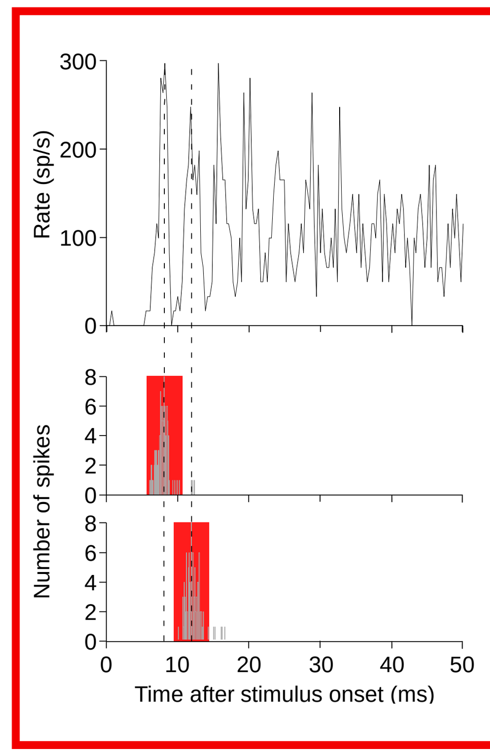
The decision tree shown to the right was adapted from similar trees developed for use in the cochlear nucleus (CN; Blackburn and Sachs 1989; Young et al. 1988). Specific threshold values were altered from those used in the CN in order to properly label a number of exemplar units (e.g., the units shown in panel 7).

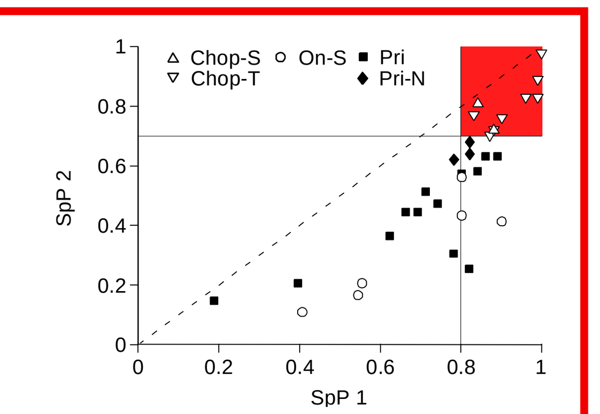
All units exhibited sustained discharges to BF-tonal stimulation. Most units had BFs greater than 3 kHz; no units exhibited substantial phase-locking.

Illustrations of each test, including the spikes per peak (SpP) test, peak to sustained rate (P/Sus) ratio, first to second inter-peak gap (Sp2min-Sp1max) and regularity analysis (ΔISI), along with population results, are color coded and shown in panels 4-6.



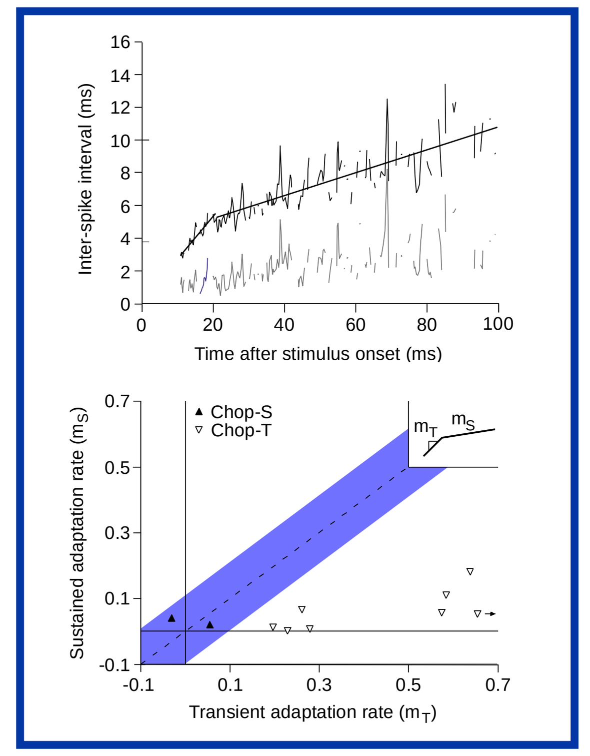
4 Chopper units give at least two well-timed spikes after stimulus onset, and can be sub-classified based on their regularity as a function of time.



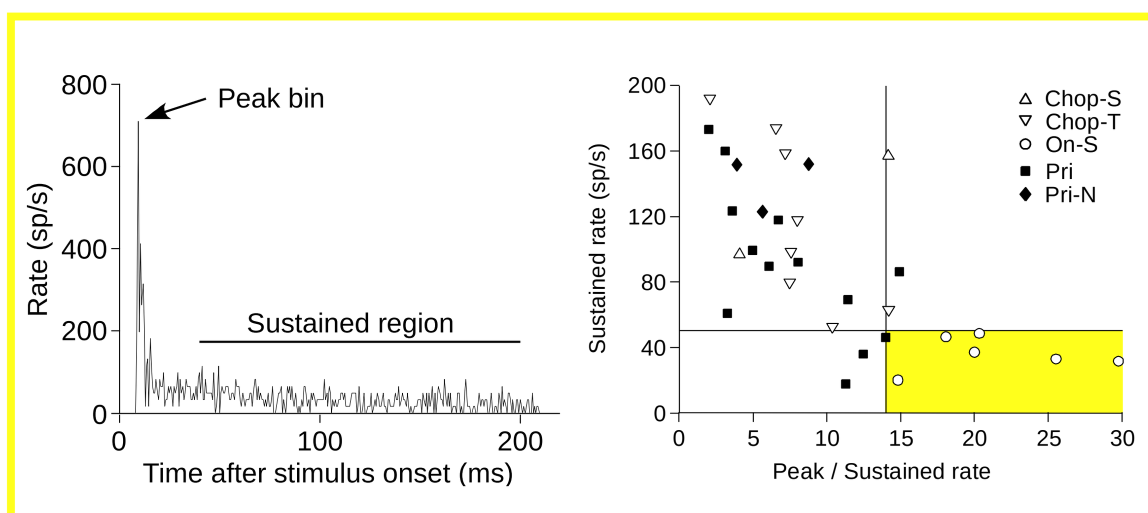


Choppers are identified using the spikes per peak (SpP) test (left). From first and second spike latency histograms, the probability of a spike occurring each trial within a 5 ms window (red lines) centered on the mode (dashed lines) is calculated. Choppers have 1st and 2nd SpP values above 0.8 and 0.7, respectively (red field above).

Choppers are sub-classified based on mean inter-spike regularity as a function of time (right). Lines are fit to the mean intervals over the first 10 ms and next ~80 ms of the response. If the two slopes are equal (blue field), then the unit is called a chopper-sustained (Chop-S) unit, otherwise it is a chopper-transient (Chop-T) unit.

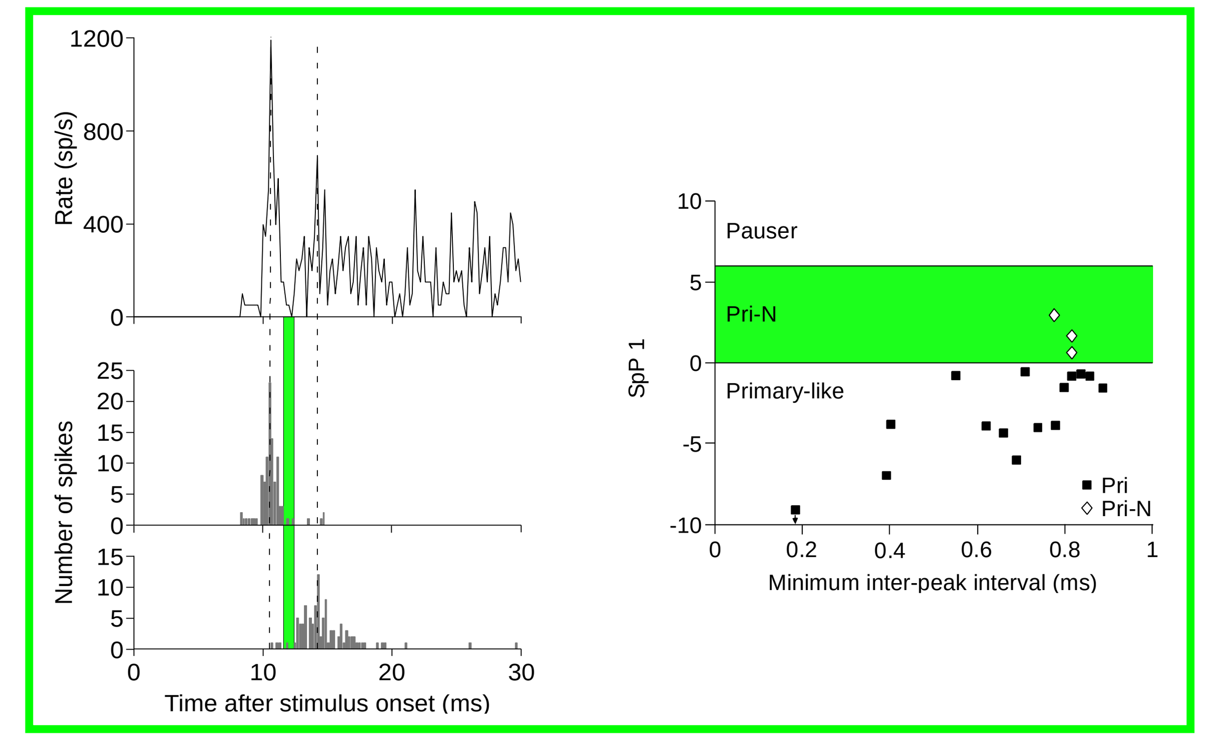


5 Onset units may have a well or poorly timed first peak, but all exhibit a high peak to sustained rate ratio and a low sustained rate.



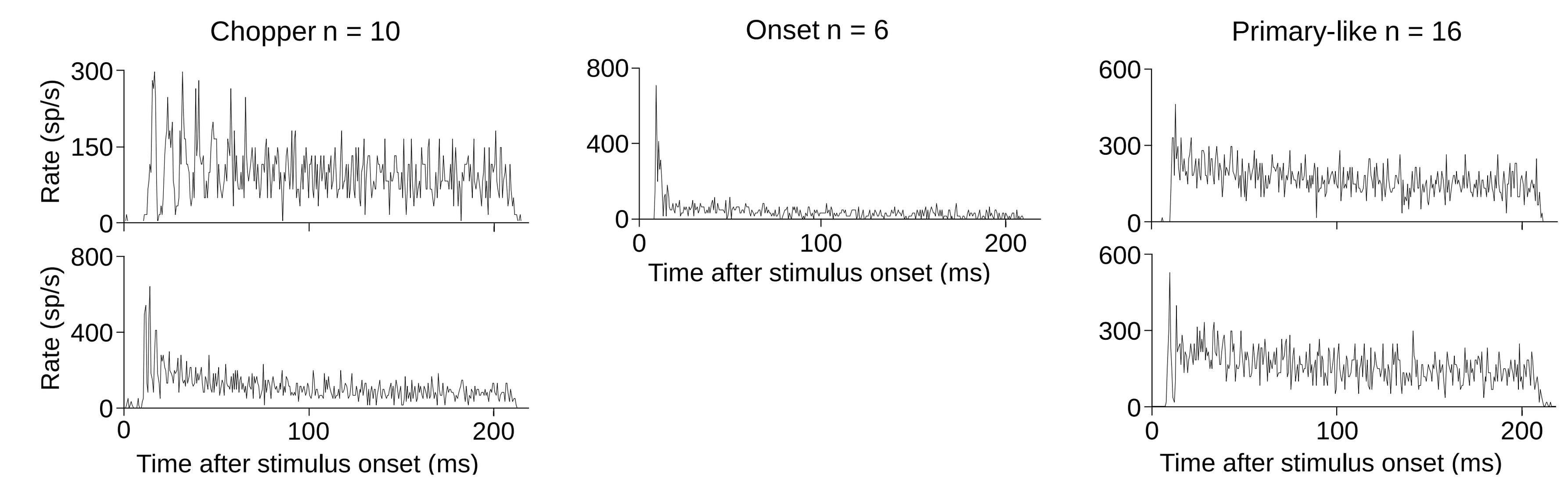
Onset units are distinguished from other PST types based primarily on the combination of a high peak rate and a low sustained rate. Here, the peak to sustained rate ratio (left) was computed by dividing the peak rate in the first spike latency histogram by the average rate over the sustained region of the response (the last 80% of the stimulus duration). The plot to the right shows sustained rate plotted against peak/sustained ratio for each unit in our population. The data appear to form a continuum: onset units were defined to have a peak/sustained ratio greater than 14 and a sustained rate less than 50 spikes/s (yellow field).

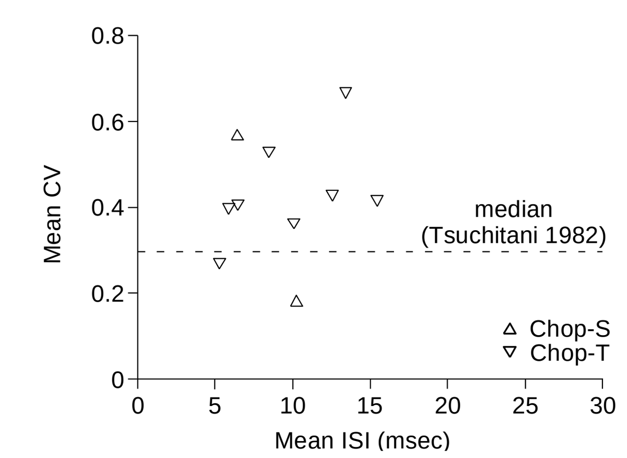
6 Primary-like units have discharge patterns that resemble strongly those of auditory nerve fibers; these units may or may not exhibit a gap (notch) between the first and second spike latency histograms.



Primary-like units have either a well or poorly timed first peak, and either a peak/sustained ratio less than 14 or a sustained rate greater than 50 spikes/s. For the purposes of identifying primary-like with notch units, primary-like PSTs are evaluated for the presence of a gap separating the first and second spike latency histograms (left). Here, the inter-peak gap is defined as the time between the end of the 1st peak and start of the 2nd peak (green band). Each unit's inter-peak gap is plotted against its spikes per first peak (SpP1) value in the plot on the right. Note that only units with a well-timed first peak exhibit positive gaps (green field); these units are sub-classified as primary-like with notch (Pri-N).

7 Chopper responses account for only one third of LSO responses.





Of 32 units included in the current analyses, 10 (31 %) were identified as choppers, 16 (50 %) as primary, and 6 (19 %) as onsets. 80 % (8/10) of choppers were classified as transient, indicating a dramatic change in spike timing following the first 10 ms of the response. 81 % (13/16) of primary type units were classified as primary-like. All units included in the current study displayed a sustained response. 9 (28 %) units displayed very low sustained rates (< 50 sp/s), and 6 of these exhibited strong onset responses, thus are classified Onset-sustained.

The chopper responses we have identified are not as precise as those identified . Coefficient of variation (CV), is calculated by dividing the mean inter-spike interval by the standard deviation, and is a good measure of the regularity of the response. As shown to the left, the median CV for our units is approximately 0.4, which is significantly higher than the median Tsuchitani (1982) found in anesthetized cat.

8 Summary and Conclusions

We have demonstrated that units in the LSO of decerebrate cat fire with chopper discharge patterns only approximately 1/3 of the time. A much greater proportion of units (~50 %) fire with primary-like discharge patterns, which resemble the patterns seen in the inputs to LSO cells much more closely. Additionally, the chopper responses we do identify are of a lower quality, displaying lower regularity, than LSO units recorded in the anesthetized cat. Some of the currently identified choppers may have been incorrectly identified due to our relatively liberal classification criteria, but this would only act to increase the already low number of chopper responses identified.

As the test results (panel 4) attest, responses generally do not separate cleanly, instead revealing the continuous nature of LSO units. This similarity of response properties matches the known homogeneity of LSO neuronal structures. Therefore, we believe that the continuous nature of these responses is indicative of small changes in the location and strength of excitatory and inhibitory input terminals on LSO cells, thus varying degrees of dendritic filtering. Anatomically, excitatory inputs form terminals on distal dendrites, while inhibitory inputs terminate proximally, thus providing the mechanism for such filtering (for review, see Cant 1991).

This anatomical organization may also explain the dramatic effects of anesthesia on discharge patterns. Modeling of cochlear nucleus stellate cells has shown that varying the location of [distal] excitatory synapses, and the strength of [proximal] inhibitory synapses can cause discharge patterns to switch between sustained chopper, transient chopper and primary-like with notch (Banks & Sachs 1991). Thus, the difference in responses under anesthesia may be explained by a decrease of inhibitory effect on LSO units.

Overall, these results are consistent with, and extend, those reported for decerebrate cat by Brownell et al. (1979).

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