Ambiguities in Sound-Duration Selectivity by Neurons in the Inferior Colliculus of the Bat *Molossus molossus* From Cuba

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**INTRODUCTION**

For several species of bats, it has been found that most auditory neurons respond best to frequencies and sound pressure levels (SPL) that closely match their own species-specific echolocation calls (Casseday and Covey 1992; Jen and Suthers 1982; Pollak and Bodenhamer 1981; Pollak et al. 1978; Schuller and Pollak 1979). More recently, it has been demonstrated that neurons in the inferior colliculus (IC) and auditory cortex of bats selectively respond to sound duration, one of the simplest temporal features (Casseday et al. 1994; Ehrlich et al. 1997; Fuzessery 1994; Fuzessery and Hall 1999; Galazyuk and Feng 1997; Pinheiro et al. 1991). Because the observed neuronal duration selectivity in each of the three species of bats studied so far approximates the durations of their own echolocation calls, it is suggested that the filter mechanism that produces duration tuning could supplement the filters for sound frequency and intensity (Ehrlich et al. 1997; Fuzessery and Hall 1999; Galazyuk and Feng 1997).

Two different models could explain duration selectivity: coincidence (Casseday et al. 1994; Ehrlich et al. 1997) and anti-coincidence mechanisms (Fuzessery and Hall 1999). Biologically the same components are involved in both of them: a short-latency inhibitory input that persists for the duration of the stimulus, a delayed excitation triggered at stimulus onset, and an excitatory rebound from inhibition. In the coincidence model, the response appears only when the rebound from the inhibitory component coincides and summates with the delayed excitation, and this model could effectively explain short- and band-pass duration selectivity. The second model differs from the first one in that the early inhibition does not contribute to excitation (the 3rd component is not present). At short stimulus durations, inhibition (1st component) is over before the arrival of the excitatory input (2nd component), and the neuron responds maximally. Because increases in stimulus duration reduce or abolish the response due to the coincidence of inhibitory and excitatory events, this model provides a simple mechanism for creating short-pass duration selectivity. Most, if not all duration-selective neurons studied in the IC and auditory cortex of bats could derive their selectivity through one of these models, which are not mutually exclusive (Casseday et al. 1994, 2000; Ehrlich et al. 1997; Faure et al. 2003; Fuzessery and Hall 1999; Galazyuk and Feng 1997; Zhou and Jen 2001).

The existence of duration-tuned neurons would allow bats to identify by duration, at least partially, their own echolocation calls. However, other acoustic parameters relevant for echolocation need to be processed in parallel and therefore could affect duration selectivity. Such effects have been shown for repetition rate and FM (Fuzessery 1994; Jen and Zhou 1999; Pinheiro et al. 1991), but not in a systematic way for SPL of the stimulus. Only recently, changes produced in duration selectivity by varying the SPL were described for a population of neurons in the IC of *Eptesicus fuscus* (Faure et al. 2003; Zhou and Jen 2001) and the house mouse (Brand et al. 2000) as well as previously observed in the auditory cortex of *Myotis lucifugus* (Galazyuk and Feng 1997). Those results strongly indicate that the consistency of duration selectivity needs to be proven by varying other acoustic parameters to come to conclusions on the significance of duration-selective neurons in a species’ behavior. The SPL of echoes, for example, can vary considerably in relation with the distance to a reflecting surface, whereas their duration will remain constant. Echoes coming back from an insect at a distance of 3 m will be > 60 dB attenuated at the bat’s ears (Lawrence and Simmons 1982; 30-kHz call frequency). That is why SPL is one of the most...
important parameters to be tested to assess the consistency in duration selectivity.

Duration-selective neurons have been found in the IC or the cortex of bats (Ehrlich et al. 1997; Fuzessery and Hall 1999; Galazky and Feng 1997), frogs (Hall and Feng 1986; Narins and Capranica 1980; Penna et al. 2001; Potter 1965), cats (He et al. 1997), mouse (Brand et al. 2000), and chinchillas (Chen 1998). However, most of the results concerning the physiological basis and properties of this process have been described in bats.

The three species of bats studied to date—E. fuscus (Casseday et al. 1994; Faure et al. 2003; Pinheiro et al. 1991), M. lucifugus (Galazky and Feng 1997), and Antrozous pallidus (Fuzessery and Hall 1999)—all belong to the family Vespertilionidae. It is known that molossid bats show a more complex echolocation behavior than that observed in vespertilionid bats, i.e., search calls alternating in frequency, approach calls of longer durations and higher frequencies than search calls, and different designs of calls emitted in the surroundings of the colonies (Kössl et al. 1999; Simmons et al. 1979). This complexity could have physiological correlates at the level of the IC. The aim of this study was to determine whether the population of duration-selective neurons in the IC of a bat from the family Molossidae, Molossus molossus, selectively responds to species-specific calls durations. We also evaluated the effects of stimulus intensity on duration selectivity over a wide range of intensities to study the consistency of duration selectivity. The results are discussed in relation to the possible mechanisms underlying duration coding and the echolocation behavior of this bat species.

METHODS

Animals

The study was conducted on the IC of 13 female bats, M. molossus tropidorrhynchos (Gray 1839) (Molossidae, Chiroptera). The animals were captured at the entrance to one of their colonies located in a building in the city of Havana and kept in captivity in a room with temperature, humidity, and photoperiod conditions similar to those of the bat’s natural environment. The animal use in this study was authorized by the Centre for the Inspection and Control of the Environment, Ministry of Science, Technology, and Environment, Cuba.

Surgical procedures

Bats were prepared for surgery by anesthetizing them with sodium pentobarbital (0.05 mg/g body wt) via a subcutaneous injection in the neck. A longitudinal midline incision was made through the skin overlaying the skull, and the underlying temporal musculature was reflected from the incision along the midline. Wound surfaces were treated with a lidocaine solution applied topically. A custom-made metal rod was then glued to the skull using dental cement. We let the animals rest for 24 h before electrophysiological recordings. After recovery, during the experiment, the awake bats were placed in a body holder. Using skull and brain-surface landmarks (the skull in this bat is semitransparent), a small hole (1 mm diam) was made over the IC with a scalpel blade. The hole was covered with saline solution during the experiments, and care was taken to prevent desiccation. A microelectrode (see following text) was then inserted through the hole in the skull. The experiments were conducted inside a soundproofed room (temperature: 27–32°C) for <6 h. After a recording session, the exposed skull was covered with sterile bone wax, and the animal was returned to its individual cage. Bats could be studied for several consecutive days. All experiments were in accordance with the Declaration of Helsinki (Experimental animal approval: Regierung von Oberbayern: AZ 211-2531-37/98)

Acoustic stimulation and recording

Acoustic stimuli were delivered from a MicroTech Gefell 1-in microphone capsule used as a loudspeaker and placed ~2 cm away from the bat’s ear. The speaker response was flat (±5 dB) in the frequency range from 20 to 80 kHz, and intensity of the presented pure tone stimuli was on-line corrected in accordance with calibration frequency response curves of the speaker. Stimuli were controlled by custom software written in ASYST (Keithley Instruments). The stimuli used were pure tones for most neurons. Broadband noise bursts were used in five cases in which the neurons only responded to noise. For most measurements, stimuli were presented monaurally at the contralateral ear. Once an auditory neuron was isolated, an automatic routine calculated its threshold frequency tuning curve and measured the best frequency (BF) and BF threshold. The tone stimuli (rise/fall time: 0.5 ms, repetition period: 300 ms) were adjusted to the neuron’s best frequency, and the intensity was changed in steps of 10 dB between threshold and 100 dB SPL (0 dB SPL = 20 μPa). At each intensity tested, the duration of the stimulus was changed, usually between 1 and 30 ms, at steps of 1 ms. Extracellular single-unit recordings were made from the animals with glass micropipettes (6–24 MΩ) filled with 3 M KCl. By injecting HRP at the recording sites, we verified that the neurons under study were located at the central nucleus of the IC. The spike activity was monitored audiovisually; band-pass filtered (200 Hz to 3 kHz), and discriminated by amplitude. Temporal resolution to discriminate single spikes was 0.001 ms, which correspond to a sampling rate of 1 GHz. From the spike times, peristimulus time histograms (PSThs, 1-ms bin width) were constructed. The response latency was taken as the time needed to reach the 25% of maximal spike activity in the peristimulus time histogram.

Classification of filter characteristics

For classification of duration selectivity (i.e., short-, band-, and long-pass), we used the criteria proposed by Fuzessery and Hall (1999). The response of a neuron was classified as duration-selective if the spike count reached a maximum at a certain stimulus duration (best duration), and dropped to <50% of the maximum response at three consecutive longer and/or shorter durations. Band-pass selectivity was defined as a response in which the spike count dropped to <50% of peak value at three consecutive shorter and longer durations. Short-pass responses were defined as those that dropped to <50% of peak value at three consecutive longer duration. In addition, those responses maintain the number of spikes >50% of the maximum number when the stimulus duration was shortened (down to minimally 0.5 ms) below best duration. Because of the temporal resolution of 1-ms step for testing duration tuning, there is a limitation in the classification of short-pass responses because some of them could become a band-pass response if the stimuli were shortened beyond the 0.5-ms minimum limit. However, this limitation would apply only to two neurons in this study because the short-pass responses remain >50% of peak value at the shortest duration tested, and a move to the band-pass group would require three consecutive shorter duration which produce responses <50% of maximum activity.

In long-pass responses, the spike count either increased with duration to a maximum plateau value at longer durations or continued to increase over the range of durations tested. Long-pass responses were defined as those that required ≥5 ms of stimulus duration to reach 25% of maximum activity and the spike count of which did not decrease with longer durations. The 5-ms minimum duration criterion was used to emphasize the point that the magnitudes of long-
short-pass duration responses will be changing dramatically in opposite directions over a narrow range of durations. At a duration of ≤3 ms, the majority of short-pass duration responses will be near 100% maximum value, while long-pass duration responses will be at only 0–25% maximum value.

Because the duration-filter characteristic of a neuron could change with the intensity of the stimuli, something that indeed happened frequently along this study, a filter type will characterize the response of a neuron at a particular intensity. Thus one neuron could contribute to more than one filter group if it showed different filter characteristics at different intensities.

Three different procedures were used as experimental controls to ensure that the variations observed in duration-filter characteristics were caused by variations in intensity. 1) Whenever we detected changes in spike rate or firing pattern, we repeated the stimulation protocol to make sure that the neuron’s duration selectivity characteristics were stable over time. 2) Instead of varying the stimulus duration for a fixed sound level we varied the SPLs for a fixed duration to confirm the observed intensity-dependent changes in duration selectivity. 3) During all experiments, higher and lower intensity values were alternated, to rule out adaptation effects. The duration selectivity of only two neurons changed during the course of the experiment. The data of these two neurons were not included in this study.

RESULTS

Duration selectivity and basic response properties

Duration selectivity was studied in 61 IC neurons that responded to pure tones and in 5 neurons that responded exclusively to broadband noise. Of the 61 neurons studied, 43 (70%) showed at least one form of duration selectivity at one or more stimulus intensities. The remaining 18 (30%) were not affected by sound duration, including one of the five neurons that responded to broadband noise (Fig. 1).

Sixty percent of IC neurons, whether or not they were duration selective, had no spontaneous activity. In those that did have spontaneous activity, it was low, <5 spikes/s.

All of the neurons that were not selective for stimulus duration at any intensity had onset and sustained responses (Fig. 1). We defined as sustained responses those that contained more than three spikes for stimuli >10 ms, distributed

Fig. 1. A and B: total number of spikes (●) and the latency of the 1st stimulus-induced spike (○) as a function of stimulus duration for 2 nonselective neurons. The frequency and sound pressure level of the stimuli are given in the top right. C and D: spike histograms from 30 responses to 3 stimulus durations. The time bin was 1 ms. □, position and duration of the stimuli, and the value (in ms) is given. The left neuron [with a minimum threshold (MT) of 33 dB SPL] has a phasic response, whereas the right one (MT = 3 dB SPL) shows a phasic-tonic response. Both are onset responses. The presented data correspond A with C and B with D.
along the entire length of the stimulus or >70% of its length. In the onset responses, the first spikes of the response had a constant temporal relation to the beginning of the sound stimulus and therefore were triggered by the beginning of the stimulus.

Duration-selective neurons had either transient onset or off-set responses or both. We defined as transient responses those containing <3 spikes regardless of the duration of the stimuli, limited to <50% of the length of the stimuli >10 ms. In offset responses, the first spikes of the response varied as a function of stimulus duration and therefore were triggered by the end of the stimulus. In the cases in which offset responses were found for selective neurons, they were always transient, so we will refer to them simply as offset responses. Onset responses in duration-selective neurons were mainly transient except for long-pass neurons in which sustained responses were described.

Filter characteristics

Among the duration-selective neurons, we found three different types of filter characteristics, long-, band-, and short-pass.

Long-pass responses were found in neurons that made up 33% (14/43) of the neurons in our sample, including one that was sensitive to broadband noise (Fig. 2). In some neurons with long-pass responses, shorter durations elicited no response at all (Fig. 2, B and D). The discharge patterns of long-pass responses were sustained (Fig. 2, A and C) or offset (Fig. 2, B and D). Several long-pass neurons with offset responses, including the one shown in Fig. 2, B–D, had spike-count functions that continuously increased for durations between 9 and 39 ms. These findings support the idea that duration-selective neurons do not act as energy detectors, even in long-pass neurons that intuitively show the simplest case of duration filtering: the longer the duration, the higher the energy.

FIG. 2. A and B: total number of spikes (●) and latency of the 1st stimulus-induced spike (○) as a function of stimulus duration for 2 long-pass neurons. - - - , the stimulus offset. C and D: spike histograms of 30 responses to 4 stimulus durations. The left neuron (MT = 12 dB SPL) shows a tonic response, whereas the right one (MT = 43 dB SPL) has a phasic offset response. The latency values of the onset neuron cross the line that represents the stimulus offset (A), whereas in the offset neuron the latency curve runs parallel to this line. The same conventions as in Fig. 1 are used. A corresponds with C and B with D.
content, and consequently the larger the response (Ehrlich et al. 1997).

Short-pass responses were found in only 16% (7/43) of the neurons in our sample, including one that responded only to broadband noise (Fig. 3). Neurons with short-pass responses fired transiently to stimulus offset, (3/7 neurons; Fig. 3, A and D), onset (3/7 neurons; Fig. 3, B and E), or both (1 neuron; Fig. 3, C and F). In the neuron with both onset and offset responses, both components showed short-pass duration selectivity.

Band-pass duration selectivity was present in 81% (35/43) of the neurons in our sample (Fig. 4). Band-pass neurons responded transiently at either the offset of the stimulus (12/34; Fig. 4, A and D) or the onset (22/34; Fig. 4, B and E). In the case of one neuron in Fig. 4C, the onset response (Fig. 4C, —) was nonselective to stimulus duration while the offset response (Fig. 4C, - - -) was band-pass. Thus this neuron coded the duration of the stimulus in the offset component only.

**FIG. 3.** A–C: total number of spikes (●) and latency of the 1st stimulus-induced spike (○) as a function of stimulus duration for 3 short-pass neurons. ---, the stimulus offset. **Neuron A** (MT = 26 dB SPL) responds only to broadband noise and shows an offset response with its latency fixed to the stimulus offset. **Neuron B** (MT = 13 dB SPL) shows an onset response with its latency curve crossing the line of stimulus offset. **Neuron C** (MT = 23 dB SPL) shows a response with 2 components of different latencies: an onset component of shorter latency, and an offset component of longer latency. **D–F**: spike histograms of 30 responses to 5 stimulus durations. The same conventions are used as in Fig. 1. Correspondence: A with D, B with E, and C with F.
In the response of neurons that behaved as band- or short-pass filters for stimulus duration, often a second peak in their spike count functions was visible (Fig. 5). The second peak, however, was always confined to the range of stimulus durations between 10 and 16 ms. Thirty percent of the duration-selective neurons showed two distinct best durations at least at one of the intensities tested. In those two-peaked responses, the number of spikes elicited at each of the peaked durations is >200% of the number of spikes elicited at durations consecutively shorter and longer than that of the peak. Both onset (Fig. 5, A and C) and offset (Fig. 5, B and D) responses could have two peak durations.

**Duration selectivity and stimulus intensity**

The influence of stimulus intensity on duration selectivity was examined in 44 neurons. Of the 44 neurons in which two or more intensities were tested, 36 (82%) showed duration selectivity at some of the intensities presented. In Table 1, the neurons are arranged according to the number of used stimulus

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**FIG. 4.** A–C: total number of spikes (●) and latency of the 1st stimulus-induced spike (○) as a function of stimulus duration for 3 band-pass neurons. - - -, the stimulus offset. A (MT = 33 dB SPL) represents an onset response and B (MT = 12 dB SPL) an offset response. C (MT = 17 dB SPL) shows the onset response (—) and the offset response (- - -) for the same neuron. The onset component is not selective for the stimulus duration, whereas the offset component shows a band-pass response. D–F: spike histograms of 30 responses to 5 stimulus durations. The same conventions are used as in Fig. 1. Correspondence: A with D, B with E, and C with F.
levels to show that the probability of finding duration selectivity is correlated with the range of intensities tested.

In 9 of the 36 neurons showing duration selectivity, varying the stimulus intensity did not affect the type of selectivity (Table 1, Fig. 6A). For example, in three of the eight neurons tested with seven intensities, covering a range of 80 dB, the type of filter characteristic remained unchanged across sound level. In some neurons, however, although the filter characteristic type was not affected by sound level, the best duration changed dramatically (Fig. 6B). In the neuron shown in Fig. 6B, an increment of just 10 dB caused the spike count at 11 ms to change from peak count to minimum count.

In the majority of neurons, changes in SPL produced dramatic changes in the type of filter characteristic. For example, in the neuron shown in Fig. 6C, the nonselective response at 50 dB SPL changed to a short-pass response at 60 dB SPL and

### Table 1. Effect of stimulus intensity on duration selectivity in neurons from the IC of M. molossus

<table>
<thead>
<tr>
<th>No. of Neurons</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nonduration selective</td>
<td>10</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>Duration selective</td>
<td>7</td>
<td>6 (5)</td>
<td>4 (2)</td>
<td>3 (1)</td>
<td>7 (6)</td>
<td>3 (3)</td>
<td>8 (5)</td>
<td>4 (4)</td>
<td>1 (1)</td>
<td>43 (28)</td>
</tr>
</tbody>
</table>

Number of neurons refers to those with changes in selectivity. The numbers in the column heads indicate the quantity of sound pressure level (SPL) tested. A neuron is classified as duration selective if its response shows certain type of duration selectivity with at least one of the intensities tested. The numbers inside the parenthesis indicate how many neurons change the type of duration selectivity with SPL variations. IC, inferior colliculus.
again to a nonselective response at 70 dB SPL. The neuron in Fig. 6D acted as a high-pass filter at 8 dB SPL, changed to a nonselective response at 18 dB SPL, and finally to a band-pass filter at 28 dB SPL. In the example displayed in Fig. 7, an additional response component at short durations appeared at sound pressure levels ≥85 dB SPL. This change in discharge pattern changed the neuron’s filter characteristic from long-pass (1st component) to band-pass (2nd component, best duration: 3.5 ms) and later to short-pass (2nd component, best duration: 2.5 ms).

Because we found that duration selectivity varied with stimulus intensity, we used three different intensity ranges to quantify best durations in the population of neurons studied. Low intensities were defined as 10–30 dB SPL, medium intensities as 40–60 dB SPL, and high intensities as 70–90 dB SPL. The distribution and range of best durations was approximately the same for all groups (Fig. 8A). In each group, all best durations are <20 ms except one different neuron in each of the three categories. The maximum number of neurons was at a best duration of 2 ms for all intensities tested. Figure 8B plots best duration as a function of BF. We included the best duration values obtained at each intensity tested in a single neuron. Therefore for the same BF, one neuron can be represented in this figure with more than one best duration. It should be noted that the widest range of best durations (from 1 to 25 ms) is found in the frequency range between 30 and 40 kHz.

DISCUSSION

Mechanisms underlying duration selectivity

It is well known that a large proportion of auditory neurons above the lower brain stem respond transiently regardless of the duration of the acoustic stimuli (e.g., Galazyuk and Feng 1997; Jen and Schlegel 1982), so there are few sustained responses to provide information about stimulus duration. On the other hand, neurons selective to narrow ranges of durations are common in the auditory midbrain and the primary auditory cortex (Brand et al. 2000; Casseday et al. 1994; Chen 1998; Erlich et al. 1997; Faure et al. 2003; Fuzessery and Hall 1999; Hall and Feng 1986; He et al. 1997; Ma and Suga 2001; Narins and Capranica 1980; Penna et al. 2001; Pinheiro et al. 1991). Two different physiological mechanisms have been proposed to explain how duration selectivity arises in the IC of bats: coincidence and anti-coincidence (Casseday et al. 1994; Erlich et al. 1997; Fuzessery and Hall 1999). It has been shown that these same mechanisms can explain duration selectivity in other animal groups such as cats and mice (Brand et al. 2000; He et al. 1997).

The coincidence model requires offset excitation or rebound from inhibition in duration-selective neurons. Support for this model comes from the fact that >50% of duration-selective neurons in the IC of E. fuscus (Erlich et al. 1997) and 42% of neurons that responding best to short durations in the IC of A. pallidus (Fuzessery and Hall 1999) are clearly offset responders. In the population of duration-tuned cells studied in the IC of M. molossus, a similar proportion of offset neurons was found. Thirty-nine percent of the short- and band-pass neurons in Molossus were clearly offset responders and thus consistent with the coincidence model (Figs. 3, A and C, and 4, A and C). The coincidence model predicts that the broader the range of latencies in a population of neurons, the broader should be the range of best durations. Latencies measured in neurons of the IC of E. fuscus were between 2 and 30 ms (Haplea et al. 1994), whereas the best durations of duration-selective neurons were between 1 and 20 ms (Ehrlich et al. 1997). In M. molossus, the latencies of the collicular neurons ranged between 5 and 38 ms, and the best durations between 1 and 25 ms, which is comparable to the situation in E. fuscus.

In addition to an offset excitatory component, the coincidence model requires also an onset-evoked subthreshold excitatory input. In other words, the presence of off responses does not automatically implicate a coincidence mechanism; particularly if off responses occur over a wide range of durations. Thus the coincidence of the two components predicts that
maximum off responses will occur over a limited duration range. In view of the complexity of neural connectivity in the IC, there is a high probability that single neurons receive several excitatory input synapses, which are temporally segregated and strong enough to produce postsynaptic potentials that would bring the cell to threshold if they coincide with a postinhibitory rebound (Fig. 9). Thus the coincidence model would predict that the temporal shift of the rebound produced by increasing the stimulus duration could lead to a spike response at more than one stimulus duration. Two-peaked duration spike-count functions have been described only in some neurons of the IC of *E. fuscus* (Pinheiro et al. 1991), and 28% of the duration-selective neurons in the IC of *M. molossus* have two-peaked spike-count functions. Therefore we propose that the synaptic interactions underlying duration selectivity are in some cases more complex than those modeled so far in the literature. In >50% of the neurons showing two duration peaks in our study, the presence of the two peaks (Fig. 5B) could be explained by two temporally segregated excitatory inputs interacting with the postinhibitory rebound over two different duration ranges (visualized in Fig. 9). In some neurons, there appeared to be convergence between excitatory inputs involved in duration tuning and other excitatory components that were independent of stimulus duration. In the neuron shown in Fig. 4C, the onset excitatory input was strong enough to generate spike responses at every duration tested. Because some duration-tuned neurons in *E. fuscus* (Ehrlich et al. 1997) and most duration-tuned neurons in *A. pallidus*
(Fuzessery and Hall 1999) respond to sound onset, a second model, anti-coincidence, was proposed to explain duration selectivity (Fuzessery and Hall 1999). In the anti-coincidence model, excitatory input will generate spikes until duration is such that a shorter-latency sustained inhibitory input lasts long enough to coincide with the transiently excitatory response and cancel it. So, responses are triggered only if excitation and inhibition are noncoincident. This type of mechanism may produce short-pass selectivity. In *M. molossus*, we have found neurons showing responses consistent with the noncoincidence model (Figs. 3B and 4B). However, this model alone cannot account for the two-peaked spike-count functions that we found in *M. molossus* (Fig. 5A). One possible explanation for onset double-peaked duration tuning could be a noncoincidence mechanism that creates one of the peaks and that the other peak reflects a strong input from another duration-selective neuron. Thus some duration-selective neurons in the IC would project on other duration-selective IC neurons that will end up showing each selectivity. There is evidence that some IC neurons preserve the selectivity properties of their input because blocking local inhibitory synapses did not affect duration tuning in those neurons (Casseday et al. 1994; Fuzessery and Hall 1999).

**Duration selectivity and stimulus intensity**

When only one stimulus intensity was considered, ~41% (7/17) of the neurons in *Molossus* are duration selective. This percentage is roughly comparable to that described in other species [*E. fuscus*: 36% (Ehrlich et al. 1997); *A. pallidus*: 53%...
result, together with the finding that every cortical duration-selective neuron had an onset response, made the authors suggest that duration selectivity undergoes considerable transformations between the IC and the cortex. Because our data suggest that the types of transformations that occur between the IC and cortex in Myotis have already occurred at the IC in M. molossus, more studies of the vespertilionid IC would be needed before conclude about this physiological difference as an interfamily distinctive character.

Neuroethological considerations

Neuronal selectivity for stimulus duration is a mechanism that presumably operates during the processing of biologically important signals such as echolocation calls in bats. In the pallid bat, all duration tuned IC neurons had best durations below 7 ms, which coincides with the range of duration values in its echolocation calls (Fuzessery and Hall 1999). Similarly, in E. fuscus and M. lucifugus, this range was broader with best-duration values ≤20 ms corresponding to the longer call durations used by these species (Ehrlich et al. 1997; Galazyuk and Feng 1997). In M. molossus, the best-duration histograms showed peaks around the duration values that characterize the echolocation calls used by this species while searching for its prey or while entering or exiting its diurnal roost (Kössl et al. 1999). In addition, these are calls with a frequency content usually limited to the range from 30 to 40 kHz, where most duration tuned neurons were found. Neurons’ best durations coincide with duration values of M. molossus echolocation calls, even in the cases in which neurons showed two peaks in their spikes count functions. Approximately one-third of the duration-selective neurons in the IC of this species process stimulus durations between 8 and 14 ms, a range that corresponds to the calls emitted when searching for prey. Another 40% of IC neurons in M. molossus process durations between 2 and 5 ms, a range of durations that includes the three types of calls that are emitted when the animals leave or return to their roost and those calls emitted during the final buzz of their hunting behavior (Kössl et al. 1999). These percentages remain constant along the three groups of intensities analyzed.

Duration coding appears to be a general mechanism spread throughout the animal kingdom. In species that strongly depend on acoustic information (i.e., bats and frogs), it seems to contribute to selective processing of behaviorally relevant sounds, such as those used to find food or mates (Ehrlich et al. 1997; Fuzessery and Hall 1999; Galazyuk and Feng 1997; Hall and Feng 1986; Penna et al. 2001). However, the significance of duration-selective neurons in species that rely more on visual information is not as clear (Brand et al. 2000; He et al. 1997).

The observed intensity-dependent changes in duration tuning point to the possibility that different subpopulations of duration-selective neurons in the IC of M. molossus are responsible for different tasks concerning sound identification based on sound duration. Thus the subpopulation of neurons in which the duration-filter characteristics remain unchanged across sound level (25% in this study) could be in charge of tracking the bat’s own sounds both while dealing with emitted calls or returning echoes. Another subpopulation of neurons show pronounced changes in their duration-filter characteristics with slight changes in sound intensity. These neurons may respond
preferentially to specific combinations of duration and intensity of a sound signal such as the duration of the echolocation calls and the echo intensity that corresponds to a limited bat-target distance. If this is the case, this subpopulation of neurons will help in addressing the estimation of the distance to the target in parallel to delay-sensitive neurons (Covey and Casseday 1999; Saitoh and Suga 1995).

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