DURATION ECHOLOCATION, bats must track the temporal pattern of emitted calls and returning echoes. Bats exhibit a variety of echolocation signals ranging from steep, frequency-modulated (FM) signals to narrowband, quasi-constant-frequency (QCF) and constant-frequency (CF) signals with and without additional harmonics (Kalko 1995; Schnitzler and Henson 1980). The species-specific signal structure is determined mostly by ecological constraints on each species’ echolocation task. Aer- ial hawking echolocating bats, independent of the design of the echolocation calls, systematically increase pulse repetition rate and decrease call duration as they switch from the search to the final phase of prey capture (Griffin 1958; Simmons et al. 1978). The reduction in sound duration while repetition rate is increased is used to avoid an overlap of the echo with the bat’s own emitted signal. Therefore, the analysis of call and/or echo durations is vital for the success of this navigation system (Neuweiler 1990). Neurons that are selective for the duration of sound have been described in the central auditory system of several vertebrates including frogs (Narins and Capranica 1980; Potter 1965), chinchillas (Chen 1998), mice (Brand et al. 2000), rats (Pérez-González et al. 2006), and bats (Casseday et al. 1994; Feng et al. 1978; Fremouw et al. 2005; Fuzessery and Hall 1999; Galazuyk and Feng 1997; Luo et al. 2008; Mora and Kössl 2004). In all species studied so far, duration-tuned neurons have a temporal tuning preference for the durations of behaviorally relevant sounds, suggesting that the filter mechanism that produces duration tuning could supplement the auditory filters for sound frequency and intensity, to guarantee a preferred perception of the species’ important acoustic information. In the FM bats Eptesicus fuscus, Myotis lucifugus, Antrozous pallidus, and Molossus molossus the observed neuronal duration tuning approximates the duration of their own echolocation calls, mostly shorter than 10 ms (Casseday et al. 1994; Feng et al. 1978; Fremouw et al. 2005; Fuzessery and Hall 1999; Galazuyk and Feng 1997; Mora and Kössl 2004). In the horseshoe bat, Rhinolophus pusillus, neurons from the inferior colliculus (IC) are tuned to a range of duration of 10–60 ms, covering the range of pulse durations emitted during echolocation (Luo et al. 2006, 2008).

Duration tuning can be explained under a unified model based on the coincidence of onset and offset depolarizing events and onset tonic inhibitory postsynaptic potential (IPSP) (Aubie et al. 2009). For example, short-pass responses arise when the onset depolarization is suprathreshold and has a long latency (i.e., longer than the latency of the onset IPSP). In this situation the anticoincidence of postsynaptic potentials results in the neurons’ duration selectivity (Fuzessery and Hall 1999; Narins and Capranica 1980). Band pass duration tuning could be created in two different ways: 1) by anticoincidence of postsynaptic potentials, when the onset excitatory postsynaptic potential (EPSP) occurs after the onset IPSP and it produces spikes only for stimuli with high energy (i.e., stimulus is longer than certain duration) (Aubie et al. 2009), and 2) by coincidence of subthreshold events, e.g., when onset EPSP is then subthreshold and it occurs after the onset IPSP. In such a situation the offset EPSP (probably created as a rebound from tonic inhibition) is also needed. The neuron will only respond when both onset and offset subthreshold EPSPs are temporally summated (Casseday et al. 1994; Covey et al. 1996; Ehrlich et al. 1997). Anticoincidence and coincidence of postsynaptic potentials in duration-tuned neurons is supported by in vivo data. As an example, duration-selective units in the anuran midbrain exhibit sustained inhibition for the duration of tone bursts and delayed excitation (Leary et al. 2008), characteristics that are present in both the coincidence model and the anticoincidence model, and the relationship between tonic inhibition and delayed excitation causes the cell to track the offset of the stimulus (Casseday et al. 1994; Covey et al. 1996;
Ehrlich et al. 1997). Hence, behavioral decisions based on analysis of the duration of the pulses would not be expected to be complete until well after the stimulus has occurred. In the FM bats studied so far, in which echolocation calls are usually shorter than 10 ms, the latency of every duration-tuned neuron (measured at its best duration) is longer than the duration independently of the neuron’s response pattern (Casseday et al. 1994; Faure et al. 2003; Feng et al. 1978; Fremouw et al. 2005; Fuzessery and Hall 1999; Galazyuk and Feng 1997; Mora and Kössl 2004). A similar behavior was observed in the IC neurons from chinchillas, mice, and rats (Brand et al. 2000; Chen 1998; Pérez-González et al. 2006), which were tuned to longer durations (40–200 ms). In the IC of the long CF bat Rhinolophus pusillus, in response to complex stimuli (i.e., a combination of FM and CF sounds), a subset of band-pass neurons had latencies shorter than the best duration (Luo et al. 2008). However, it is not clear whether this behavior will persist if the neuronal response is assessed with pure tone stimuli.

Here we studied duration selectivity to pure tone stimuli in the IC neurons of another CF bat species, the mustached bat Pteronotus parnellii. The mustached P. parnellii emits biosonar signals with at least four harmonics, each containing a long CF component followed by a brief frequency modulation (Schnitzler and Henson 1980). Duration of calls is usually longer than 25 ms, and the CF component is ~20 ms (Macías et al. 2006; Schnitzler and Henson 1980). We studied the encoding of sound duration in IC neurons of the mustached P. parnellii by presenting pure tones. Consistent with results from other bat species, best durations were in the range of durations of the species’ echolocation calls and response latencies were always longer than best durations.

MATERIALS AND METHODS

Animals. The study was conducted on the IC of nine adult P. parnellii (4 males and 5 females). The animals were captured at the entrance of their diurnal refuge (a cave located 30 km southeast of Havana, Cuba) during their evening exodus and kept in captivity in a room with temperature, humidity, and photoperiod conditions similar to those of the bats’ natural environments. All experiments were performed in the Laboratory of Neurobiology and Biological Sensors of the Institute of Cell Biology and Neuroscience at the University of...
Frankfurt (Frankfurt, Germany). 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 pentobarbital sodium (0.05 mg/g body wt) via a subcutaneous injection in the neck. A longitudinal midline incision was made through the skin overlying 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 with dental cement. We let the animals rest for 24 h before starting the electrophysiological recordings. After recovery, during the experiment, the awake bats were placed in a body mold made of plastic foam. The head was tightly held by the rod fixed in a metal holder. With the use of skull and brain surface landmarks, a small hole (less than ~1-mm diameter) 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 below) was then inserted through the hole in the skull. The experiments were conducted inside a soundproof 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 and also with German federal regulations.

Acoustic stimulation and recording. Acoustic stimuli were delivered from a ScanSpeak Revelator R2904/7000 speaker (Avisoft Bioacoustics, Berlin, Germany) placed ~10 cm away from the bat’s ear. The speaker response was flat (± 5 dB) in the frequency range from 10 to 100 kHz, and intensity of the presented pure tone stimuli was online adjusted in accordance with the calibration frequency-response curve of the speaker. Stimuli were controlled by custom-made software. Pure tone stimuli were used. For all measurements, stimuli were presented at the contralateral ear.

Extracellular neuronal recordings were made with carbon electrodes (Carbostar 0.4–0.8 MΩ). The depth of the recording electrode was controlled and adjusted by a piezo-microstepper (PM 10–1, Maerzhaeuser). After amplification (Differential amplifier EX1, Da-}

Fig. 2. Representative examples of 2 types of long-pass neurons in the IC of the mustached bat. The same conventions as in Fig. 1 are used. A: neuron with an on-off phasic response. B: neuron with a sustained response. The same conventions as in Fig. 1 are used.

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relation to the beginning of the sound stimulus. In the offset responses, the response latency increased with the increment of the stimuli duration.

To determine whether a neuron was sensitive to sound duration, we plotted the spike count as a function of duration. We distinguished three types of duration sensitivity (short pass, band pass, and long pass) and a type of response that was not tuned to stimulus duration (all pass).

A neuron was considered to be short pass if the spike count dropped below 50% of maximum response at durations longer than best duration. In the band-pass responses the spike count dropped below 50% of maximum response at durations both longer and shorter than best duration. Long-pass neurons did not show a best duration and responded only when the duration of a best excitatory frequency stimulus exceeded some minimum duration, with little or no spiking in response to shorter-duration signals. In long-pass units, the cell’s first-spike latency and minimum duration necessary to elicit spiking do not continue to decrease as signal energy (amplitude) increases (Brand et al. 2000; Faure et al. 2003; Pérez-González et al. 2006).

RESULTS

Duration tuning and basic response properties. Duration tuning was studied in 136 neurons from the IC of *P. pannelli* that had BFs between 24 and 93 kHz depending on penetration depth (maximally 1,200 μm). Thresholds of all IC neurons ranged from −5 to 70 dB SPL, and the latencies (in response to a 10-ms pure tone presented at the unit’s BF and 10 dB above threshold) were between 3.2 and 31.7 ms (17.01 ± 7.23 ms). Sixty-three percent of IC neurons, whether or not they were duration selective, had no spontaneous activity. In those neurons with spontaneous activity (determined in a 25-ms time window prior to the stimulus presentation), it was between 3 and 6 spikes/s.

Of the 136 neurons studied, 79 (58%) showed some type of duration sensitivity. Fifty-one (37%) were not affected by sound duration (all pass). Among the all-pass neurons 15 showed phasic onset responses (15 of 37), nine neurons had on-off phasic responses, and in the remaining 27 the spike counts increased as a function of stimulus duration (Fig. 1).

Of all duration-sensitive neurons, 27% (29 of 106) showed long-pass responses (Fig. 2). Most long-pass units (24 of 29) had sustained responses, while the other five showed on-off discharge patterns. Short-pass responses were found in 15% of neurons (16 of 106) that exhibited some form of duration tuning (Fig. 3). Most short-pass neurons (9 of 16) showed a phasic onset response pattern, three units displayed an offset response, and the rest displayed a phasic on-off response. Band-pass responses were found in 32% (34 of 106) of the

![Fig. 3. Representative examples of 3 types of short-pass neurons in the IC of the mustached bat. The same conventions as in Fig. 1 are used. A: neuron with an onset response. B: neuron with an on-off phasic response. C: neuron with an offset response.](http://jn.physiology.org/)

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units (Fig. 4). Neurons with band-pass responses showed offset (9) and onset (25) discharge patterns.

The distribution and range of best durations in the population of short- and band-pass neurons studied are shown in Fig. 5A. The distribution of best durations is bimodal, with one peak at 3 ms and a second peak at 17 ms. In the IC of *P. parnelli*, eight units had best durations longer than 20 ms. Figure 5B plots best duration as a function of BF. Neurons with duration-tuned responses process mainly the frequency range of the second and third harmonics. Most duration-tuned units that had their BF in the CF2 range (59–62 kHz) responded to best durations > 9 ms (66%, 18 of 27 units). However, there is no evidence for a bias toward longer durations as there is for neurons tuned to the frequency range of the FM component of the third harmonic, where 83% (10 of 12 neurons) showed best durations longer than 9 ms.

Effect of sound level on duration tuning. Most duration-tuned neurons kept the same type of duration tuning across all SPLs tested. In six neurons, changes in SPL produced pronounced changes in the type of filter characteristics (Fig. 6), with a tendency for a decrease of best duration with increasing SPL, and these changes were accompanied by changes in discharge pattern. For example, in the neuron shown in Fig. 6A, the long-pass response at 0 dB SPL changed to a band-pass response at 10–50 dB SPL and again to a band-pass response with a shorter best duration at 60–80 dB SPL. Also, this neuron changed its response pattern from onset to offset in the level range of 50–80 dB SPL. The neuron in Fig. 6B acted as a band-pass filter at 40–50 dB SPL and changed to a short-pass response at 60–70 dB SPL and finally to an all-pass response at 80 dB SPL. This neuron showed no change in its temporal response pattern with increasing SPL. In the example displayed in Fig. 6C, the all-pass response at 40–60 dB SPL, with an onset pattern, changed to an on-off short-pass filter at 70–80 dB SPL. In the three neurons shown, the latency decreases with increase in the stimulus level.

The latency of short- and band-pass neurons remained relatively stable with increasing stimulus amplitude (Fig. 7), with exception of the six neurons that were not tolerant to changes in sound level. There was no significant difference between the mean latency at 10 dB above threshold and at higher sound levels (paired t-test, all P < 0.01). In none of the neurons studied did we observe paradoxical latency shifts in form of an increase in latency with increasing stimulus amplitude as has been described in cortical (Sullivan 1982a, 1982b) and IC (Galazyuk and Feng 2001; Galazyuk et al. 2005; Ma and Suga 2008) neurons of FM bats. In all short-pass and band-pass neurons...
tuned neurons with offset responses in the IC of *M. molossus* between 36% and 53% of all auditory neurons exhibit response patterns that can be explained by the anticoincidence model (Casseday et al. 1994; Covey et al. 2008). We did not find neurons that showed multipeaked or band-reject duration selectivity. In contrast to other studies (Luo et al. 2008), we did not find neurons that showed onset responses, most types of duration-tuned neurons exhibited on-responses for all durations tested. A possible mechanism responsible for band-pass tuning in onset neurons could be that at short stimulus durations inhibition and excitatory rebound are over before the arrival of the delayed excitatory input, which can still cause the neuron to fire. With increasing durations, the excitatory rebound coincides with the excitatory input and the neuron responds maximally. As the duration increases further, the inhibition is still ongoing while the delayed excitatory input arrives, which reduces or even eliminates the response (Luo et al. 2008). In the band-pass duration-tuned neurons of the IC of *P. parnellii* the response does not disappear when stimulus duration is increased, suggesting that the onset-evoked excitation is suprathreshold and cannot be suppressed by onset inhibition. This result is in agreement with a computational model for duration-tuned neurons (Aubie et al. 2009; Sayegh et al. 2011).

Results of intracellular recordings from a single band-pass duration-selective neuron in the IC of the anuran (Leary et al. 2008) suggested that band-pass selectivity could be attributable, in part, to the enhancement of excitation that occurred at certain stimulus durations. Short-duration stimuli did not elicit any detectable depolarization of the cell, whereas longer stimuli effectively produced excitation after a certain value of stimulus duration. At the stimulus duration that best excited the cell, spiking occurred slightly after the inhibition had reached its peak. This suggests that, although no postinhibitory rebound was observed when only inhibition was present, the peak activity occurs during the release from inhibition and the occurrence of the excitation, producing an onset band-pass response (Leary et al. 2008). This result is different from that found in intracellular recordings in the IC of *E. fuscus* (Covey et al. 1996). Whole cell recording of a typical duration-tuned cell showed that leading inhibition dominated the early part of the response and that there was an inward current associated with sound offset. These observations demonstrate the importance of the interaction of excitatory and inhibitory inputs that are temporally shifted against each other in creating tuning to simple temporal features of a stimulus (Casseday and Covey 1996).

In both models, coincidence and anticoincidence, duration tuning to longer or shorter sounds can be created by having longer or shorter latency in the onset excitatory input. According to what is found in other species with shorter durations of echolocation pulses (Casseday et al. 2000; Faure et al. 2003), in the IC of the mustached bat response latencies were always longer than corresponding best durations of duration-tuned neurons. The same has been found in nonecholocating mammals. For example, in the rat band-pass neurons responding maximally to sound durations between 25 and 160 ms showed longer latencies (Pérez-González et al. 2006). In the IC of guinea pigs the subset of onset neurons showing band-pass responses showed significantly longer latencies than onset neurons with the response latency was longer than the best duration (Fig. 8).

**DISCUSSION**

In the midbrain of the FM bats *E. fuscus*, *A. pallidus*, and *M. molossus* between 36% and 53% of all auditory neurons exhibit duration tuning, and most of them are tuned to short sound durations <10 ms (Casseday et al. 1994; Ehrlich et al. 1997; Fuzessery and Hall 1999; Mora and Kössl 2004). In the long CF bat *R. pusillus*, approximately two-thirds of all duration-tuned neurons were either short pass or band pass (Luo et al. 2008). In the IC of the mustached bat, 47% (50 of 106) were classified as short pass or band pass; these ratios are similar to those described for other bats. In contrast to other studies (Luo et al. 2008; Mora and Kössl 2004), we did not find neurons that showed multipeaked or band-reject duration selectivity.

**Mechanisms underlying duration tuning.** The coincidence mechanism requires offset excitation or rebound from inhibition in duration-tuned neurons. The high number of duration-tuned neurons with offset responses in the IC of *E. fuscus* (>50%), *A. pallidus* (42%), and *M. molossus* (39%) supports this fact. In the mustached bat IC, only 12 neurons were offset responders (3 short-pass and 9 band-pass neurons). In those neurons with offset responses, the coincidence model could easily explain duration tuning (Casseday et al. 1994; Covey et al. 1996; Ehrlich et al. 1997).

The temporal selectivity of short-pass neurons with an onset response pattern can be explained by the anticoincidence of postsynaptic potentials (Aubie et al. 2009; Fuzessery and Hall 1999). In the anticoincidence model, the onset excitatory input will generate spikes until duration is such that a shorter latency sustained inhibition input lasts long enough to coincide with the transient excitatory response and cancels it.

Similar to those described in the IC of the long CF bat *R. pusillus* (Luo et al. 2008), in which all band-pass neurons showed onset responses, most types of duration-tuned neurons exhibited on-responses for all durations tested. A possible mechanism responsible for band-pass tuning in onset neurons could be that at short stimulus duration inhibition and excitatory rebound are over before the arrival of the delayed excitatory input, which can still cause the neuron to fire. With increasing durations, the excitatory rebound coincides with the excitatory input and the neuron responds maximally. As the duration increases further, the inhibition is still ongoing while the delayed excitatory input arrives, which reduces or even eliminates the response (Luo et al. 2008). In the band-pass duration-tuned neurons of the IC of *P. parnellii* the response does not disappear when stimulus duration is increased, suggesting that the onset-evoked excitation is suprathreshold and cannot be suppressed by onset inhibition. This result is in agreement with a computational model for duration-tuned neurons (Aubie et al. 2009; Sayegh et al. 2011).

![Fig. 5. A: distribution of best durations of short-pass (open bars) and band-pass (filled bars) neurons from the IC of the mustached bat *Pteronotus parnellii*. The histogram was constructed using a bin size of 2 ms. B: best frequency of each duration tuned neuron (n = 50 units). The graphic does not include the best durations obtained with each of the intensities tested for those neurons that changed duration tuning when the sound level was changed. Open circles, short pass; filled circles, band pass.](http://jn.physiology.org/lookup/doi/10.1152/jn.01571.2010)
all-pass neurons (Wang et al. 2006). Also, in mice most of the band-pass neurons had offset responses (Brand et al. 2000). Only two studies (Luo et al. 2008; Yin et al. 2008) report duration-tuned neurons whose response latencies were shorter than best durations (*R. pusillus*: Luo et al. 2008; guinea pigs: Yin et al. 2008). In these two studies either complex acoustic stimuli (i.e., a combination of FM and CF sounds in the study by Luo et al. 2008) or narrow time analysis windows were used to assess the neuronal response. Therefore it is hard to know whether the duration selectivity of these neurons could be explained by coincidence or anticoincidence models.

Behavioral role of duration-tuned neurons in the CF bat *Pteronotus pumilus*. The behavioral role of duration tuning is still poorly understood. One hypothesis is that in bats neuronal

Fig. 6. Examples of units with variations in duration tuning properties due to intensity changes. A: the response changes from a long-pass response at 0 dB SPL to a band-pass response between 10 and 50 dB SPL and to a short-pass response with levels above 60 dB SPL. B: a band-pass response changes to short pass and to all pass with successive increases in SPL. C: an all-pass response changes to short pass when SPL is increased. Included are the dot-raster plots obtained for 2 intensities in each neuron. Insets: 1 ms of the action potential waveforms (y-axis in arbitrary units) obtained after the spike sorting. Duration response areas and dot-raster displays were calculated, in each neuron, by using the cluster with the higher number of spikes.

Fig. 7. Relation between response latency for stimulation with tones at best duration and 10 dB above threshold compared with response latency for a best duration tone at 20 (A) and 30 (B) dB above threshold in short- and band-pass neurons (*n* = 50 responses). Solid line, 1:1 line.
tuning for stimulus duration is a mechanism that operates during the processing of echolocation calls and/or echoes. This hypothesis is supported by the correlation between echolocation pulse duration and neuronal best durations, although this is not exclusive to bats, since neuronal tuning for sound duration has been found in a number of nonecholocating species (Brand et al. 2000; He et al. 1997; Leary et al. 2008; Pérez-González et al. 2006; Wang et al. 2006). Other evidence suggesting that duration tuning might be important for the processing of echolocation calls and/or echoes is the finding that duration tuning improves as the acoustic stimulus mimics the natural scenarios of the species. In E. fuscus duration selectivity improves during presentation of tone pairs at a certain delay mimicking call and echo (Wu and Jen 2006), and frequency tuning and amplitude coding of the duration-tuned neurons can improve at the best duration (Wu and Jen 2007, 2008). On the other hand, the same argument could be made for communication calls. The presentation of two stimuli could lead to phenomena such as backward and forward masking, which would shift thresholds upward, thereby appearing to sharpen any sort of tuning. Faure et al. (2003), in a two-pulse experiment in the IC of E. fuscus, showed that the relative time between best duration and nonexcitatory pulses affects the activity of the neurons, suggesting that inhibition could explain temporal masking phenomena.

In the species of FM bats studied, the range of best durations reported extends beyond the duration of the echolocation pulses and is usually shorter than 10 ms (Ehrlich et al. 1997; Fuzessery and Hall 1999; Mora and Kössl 2004). In the long CF bat R. pusillus, duration of echolocation calls ranged from 16 to 58 ms (Luo et al. 2006). In this species, Luo et al. (2008) found that most of the best durations in short- and band-pass neurons covered the range of pulse duration emitted during echolocation.

The acoustic behavior of the mustached bat during prey pursuits and capture has not been studied in detail. However, during hunting sequences a progressive shortening of the emitted pulse can be expected. In enclosed rooms, during exploration flights, the duration of echolocation signals of P. parnelli was around 22 ms (Macías et al. 2006). Overall, the range of best duration encompassed the range of duration of the echolocation calls.

Theoretically, duration-tuned neurons can also be involved in the perception of target distance (Sayegh et al. 2011). However, at present there is no evidence of duration-tuned neurons being also tuned to echo delays. It is thus difficult to assess whether duration-tuned neurons will support target ranging (at least not in the form in which delay-tuned neurons do). However, it is possible that they do help bats to keep tracking their position relative to a specific target. For example, different populations of duration-tuned neurons could be activated during different echolocation phases. Drastic changes in call duration are known to occur in all insectivorous bats. In P. parnelli the duration of the CF component is reduced from ~20 ms (search phase) to <5 ms (final buzz). We found an overrepresentation of long and short best durations in the IC of P. parnelli. This could indicate that selective activation of different subsets of duration-tuned neurons can trigger different motor behavioral programs about two possible stages: far from target (search phase) and close to target (final buzz). These two phases of echolocation demand very different behaviors, which could be triggered by the different neuronal subsets. Of course, the duration-tuned neurons constitute only one of several components of the sonar imaging process. For creating an accurate image of the surroundings the duration-tuned neurons have to operate together with other populations of neurons (i.e., the delay-tuned neurons).

The fact that the duration-tuned neurons in P. parnelli largely are level insensitive would contribute to this purpose. Such behavior emphasizes the functional role assigned to duration tuning because it indicates that the activation of a specific neuron might mark the duration of an incoming sound, without being affected by its intensity (Fremouw et al. 2005; Zhou and Jen 2001). In a very small subpopulation of collicular neurons (6 of 136), however, the intensity of the stimuli affects duration tuning. In these neurons, a change in duration tuning to shorter best duration at higher sound levels often was accompanied by a decrease in the response latency, which is different from what is found in duration-tuned neurons in low-duty cycle bats (Fremouw et al. 2005). Of course, extracellular recordings in which the spiking pattern changes during larger changes in sound pressure level could have been produced by activation of different neurons within a multunit cluster. An onset cell sensitive at low to moderate SPLs and an offset cell responding at higher SPLs could produce the observed spike pattern changes in an extracellular multunit recording. However, only spikes of large amplitude (at least 3 times the amplitude of the base noise) were fed into the spike sorting algorithm. Spikes were sorted by using a principal component analysis (PCA). In the PCA, to represent any particular data point (i.e., a spike) the principal components are scaled and added together. Because the components are or-

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**Fig. 8.** Relation between best duration and latency for the best duration in duration-tuned neurons at 10 (A) and 30 (B) dB above threshold (n = 50 responses). Solid line indicates stimulus offset.
dered in terms of how much variability they capture, adding together the first k components will describe the most variation in the data. Lewicki (1998) and Wheeler and Heetderks (1982) showed that in most cases the first three components (which is the number of components used in our spike sorting procedure) are enough for an accurate characterization of the spike waveforms. Wheeler and Heetderks (1982) also showed that PCA is more robust than other spike sorting methods such as, for example, the cluster analyses. Neurons in which the duration properties are dependent on the sound level were also found to be well represented in the IC of the FM bat M. molossus (Mora and Kössl 2004), which exhibits a high plasticity in its echolocation calls (Mora et al. 2004). It is still an open question whether and by which mechanism the ambiguous duration-tuned neurons could contribute to the perception of sounds.

AUTHOR CONTRIBUTIONS

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