Chinese Journal of Physiology 49(1): 46-55, 2006

Duration Selectivity of Bat Inferior Collicular Neurons Improves with Increasing Pulse Repetition Rate

Xiaoming Zhou*, and Philip H. -S. Jen

Division of Biological Sciences
and Interdisciplinary Neuroscience Program
University of Missouri-Columbia
Missouri 65211, USA

Abstract

Insectivorous big brown bats, *Eptesicus fuscus*, progressively increase the pulse repetition rate (PRR) throughout the course of hunting. While increasing PRR conceivably facilitates bats to extract information about the targets, it also inevitably affects sensitivity of their auditory neurons to pulse parameters. The present study examined the effect of increasing PRR on duration selectivity of this bat's inferior collicular (IC) neurons by comparing their impulse-duration functions determined at different PRRs. Impulse-duration functions plotted with the number of impulses in response to single pulses against pulse duration at different PRRs were described as short-pass, band-pass, long-pass, and all-pass. Short- or long-pass neurons discharged maximally to a range of short or long pulse durations. Band-pass neurons discharged maximally to one pulse duration. These three types of IC neurons were called duration tuned neurons. All-pass neurons were not duration tuned because they did not discharge maximally to any pulse duration. Increasing PRR improved duration selectivity of IC neurons by (1) increasing the number of duration tuned neurons; (2) decreasing the critical duration concomitant with increasing slope of the impulse-duration function; and (3) decreasing the 50% duration range of the impulse-duration function. This improved duration selectivity with PRR may potentially facilitate prey capture by bats.

Key Words: bat; critical duration; inferior colliculus; duration selectivity; pulse repetition rate

Introduction

Sound duration is an important feature that contributes to the distinct spectral and temporal attributes of individual biological sounds. To understand how auditory neurons may encode sound duration, many studies have examined the duration selectivity of auditory neurons in bats (3, 4, 8, 10-12, 18, 20, 25, 33), cats (16), chinchillas (5), frogs (14), and mice (2, 32). These studies showed that auditory neurons behave as short-, band-, long-, or all-pass filter to pulse duration based on their impulse-duration functions (i.e. duration tuning curves). Possible neural mechanisms underlying the formation of duration tuning properties include [1] an early sustained inhibitory input and a delayed transient excitatory input that coincide with an offset depolarization due to rebound from inhibition or offset excitation (3, 4, 8, 10); [2] an earlier arrival of excitation and coincidence of inhibition and excitation at longer durations (11); [3] a consequence of a long recovery cycle (12); and [4] a prolonged inhibition after excitation (18).

Because insectivorous bats, such as the big brown bats, *Eptesicus fuscus*, progressively increase the pulse repetition rate (PRR) as they search, approach and finally intercept the target (15), sensitiv-

Corresponding author: Dr. Philip H.-S. Jen, Division of Biological Sciences and Interdisciplinary Neuroscience Program, University of Missouri-Columbia, Missouri 65211, USA. Tel: 573-882-7479, Fax: 573-884-5020, E-mail: jenp@missouri.edu
*Present address: College of Life Science, East China Normal University, Shanghai, 200062, P.R. China
Received: April 8, 2005; Revised: June 9, 2005; Accepted: June 20, 2005.

ity of their auditory neurons to pulse parameters would be inevitably affected by PRR. For example, previous studies in the midbrain inferior colliculus (IC), which is an obligatory relay station in the central auditory pathway receiving excitatory and inhibitory inputs from all lower auditory nuclei [4], have shown that increasing PRR improves selectivity of IC neurons to frequency, intensity, and direction of sound pulses (13, 21, 25, 31, 35). Increasing PRR also elevates the minimum threshold (MT) and lengthens the response latency of IC neurons (6, 17) as well as shortens the best delay of auditory cortical neurons (23, 29); similar to other studies in rats (1), gerbils (9), and cats (24).

An earlier study conducted in our laboratory reported that increasing PRR of single pulses changed impulse-duration function of one third of IC neurons of *Eptesicus fuscus* from one type to another (25). However, how did the PRR affect the duration selectivity of IC neurons was not determined. Another study examined duration selectivity of IC neurons using temporally patterned pulse trains with different inter-pulse intervals (20). This study plotted the impulse-duration function of IC neurons using the total number of impulses discharged to pulse trains of different pulse durations. This study reported that the slope of impulse-duration functions of IC neurons became sharper with increasing PRR of pulse trains such that duration selectivity of IC neurons increased. However, the total number of impulses in response to a pulse train reflects the neuron's integrated response to co-variation in the number of pulses and inter-pulse gap with PRR of pulse trains. For this reason, this study examined the effect of temporally patterned pulse trains on duration selectivity of IC neurons in terms of interaction among pulse duration, PRR, and inter-pulse gap. It is therefore conceivable that the improvement of duration selectivity of IC neurons with PRR might be due to shortening of inter-pulse gap with increasing PRR.

In the present study, we examined the effect of PRR on duration selectivity of IC neurons by specifically examining the duration selectivity of IC neurons to single pulses within the pulse trains of different PRRs. We report here that increasing PRR increases the number of duration tuned IC neurons and improves their duration selectivity.

Materials and Methods

Seven big brown bats, *Eptesicus fuscus* (18-24 g body weight, b.w.), were used for this study. As in previous studies (20), the flat head of a 1.8 cm nail was glued onto the exposed skull of each Nembutal-anesthetized (45-50 mg/kg b.w.) bat with acrylic glue and dental cement one or two days before the recording session. Exposed tissue was treated with an antibiotic (Neosporin) to prevent inflammation. During recording, the bat was administered the neuroleptanalgesic, Innovar-Vet (Fentanyl 0.08 mg/kg b.w., Droperidol 4 mg/kg b.w.), and placed inside a bat holder (made of wire mesh) which was suspended in an elastic sling inside a double-wall soundproof room (temperature: 28°C-30°C). The ceiling and inside walls of the room were covered with 3-inch convoluted polyurethane foam to reduce echoes. After fixing the bat's head with a set screw (28), small holes were made in the skull above the IC for insertion of 3 M KCl glass pipette electrodes (impedance: 5-10 MΩ). Additional doses of Innovar-Vet were administered during later phases of recording when necessary. A local anesthetic (Lidocaine) was applied to the open wound area. The recording depth was read from the scale of a microdrive (David-Kopf). A common indifferent electrode (silver wire) was placed at the nearby temporal muscles. These procedures were conducted in compliance with NIH publication No. 85-23, "Principles of Laboratory Animal Care" and with the approval of the Institutional Animal Care and Use Committee (#1438) of the University of Missouri-Columbia, MO, USA.

For sound generation, continuous sine waves from an oscillator (KH model 1200) were formed into 4 ms tone pulses (0.5 ms rise-decay times) at 2 pulses per second (pps) by a homemade tone burst generator (electronic switch) driven by a stimulator (Grass S88). The tone pulses were then amplified after passing through a decade attenuator (HP 350D) before they were fed to a small condenser loudspeaker (AKG model CK 50, 1.5 cm diameter, 1.2 g). The loudspeaker was placed 23 cm away from the bat and 30° contralateral to the recording site. Calibration of the loudspeaker was performed with a 1/4 inch microphone (B & K 4135) placed at the position where the bat's head would be during recording.

Upon isolation of an IC neuron, its best frequency (BF) was determined by changing the frequency and intensity of sound pulses. The MT at the BF was defined as the intensity at which the probability of responding to BF sounds was 50%. The effect of PRR on the neuron's duration selectivity was studied using three 300 ms pulse trains delivered 2 trains/s. The inter-pulse interval within each pulse train was set at 100, 33.3, and 11.1 ms to produce a PRR of 10, 30, and 90 pulses per second (pps). These three PRRs are comparable to the PRRs occurring during the search, approach, and terminal phases of hunting by the big brown bats (15). Sound pulses were delivered at the BF and 10 dB above the MT of each neuron. Pulse durations of 1, 2, 4, 6, 8, 10, and 20 ms were used for this study. However, when tested at 90 pps, the 20 ms pulse was not used because of overlap

between pulses. Rise-decay times were 0.5 ms but they were 0.25 ms for 1 ms pulse duration.

To avoid the potential effect of presentation order of pulse trains on duration selectivity of IC neurons, the three pulse trains were randomly presented. For example, duration selectivity of one neuron was studied with pulse trains of 10, 30, and then 90 pps, while duration selectivity of another neuron was studied with pulse trains of 90, 10, and then 30 pps.

Recorded action potentials were amplified, band-pass filtered (Krohn-Hite 3500), and fed through a window discriminator (WPI 121) before being sent to an oscilloscope (Tektronix 5111) and an audio monitor (Grass AM6). They were then sent to a computer (Gateway 2000, 486) for acquisition of peri-stimulus-time (PST) histograms (bin width: 500 μs, sampling period: 300 ms) to 32 train presentations.

The effect of PRR on duration selectivity of IC neurons was studied by comparing the impulse-duration functions of each IC neuron plotted at three PRRs. For convenience, a neuron's impulse-duration function was plotted with the number of impulses in response to the first pulse of each pulse train against pulse duration. Duration selectivity of IC neurons was then studied by comparing the type, width, and slope of impulse-duration functions obtained at three PRRs using repeated measures one-way ANOVA at $P < 0.05$.

Results

The Type, Critical Duration (CD), and Slope of Impulse-Duration Functions of IC Neurons

Duration tuning selectivity of 42 IC neurons recorded at depths of 115-1870 μm was studied at three PRRs. The BFs, response latencies, and MTs of these neurons were between 14.2-80.1 kHz (43.7±6.0 kHz), 4.5-16.0 ms (10.7±2.6 ms), and 0-53 dB SPL (30±13 dB SPL). Consonant with our previous studies (25, 26), the BF of these neurons progressively increased with recording depth indicating that they were tonotopically organized along the dorsoventral axis of the central nucleus of the IC. These neurons discharged fewer than five impulses in response to BF pulses. Pulse duration or PRR did not affect this discharge pattern.

The discharge patterns of two representative IC neurons in response to different durations of single pulses at three PRRs are shown in Fig. 1. The number of impulses of both neurons varied with pulse duration at each PRR. One neuron always discharged maximally to 1 ms pulse duration regardless of PRR (Fig. 1A). Conversely, another neuron discharged maximally to different pulse durations at different PRRs (Fig. 1B at 4, 8, and 10 ms). As described in the

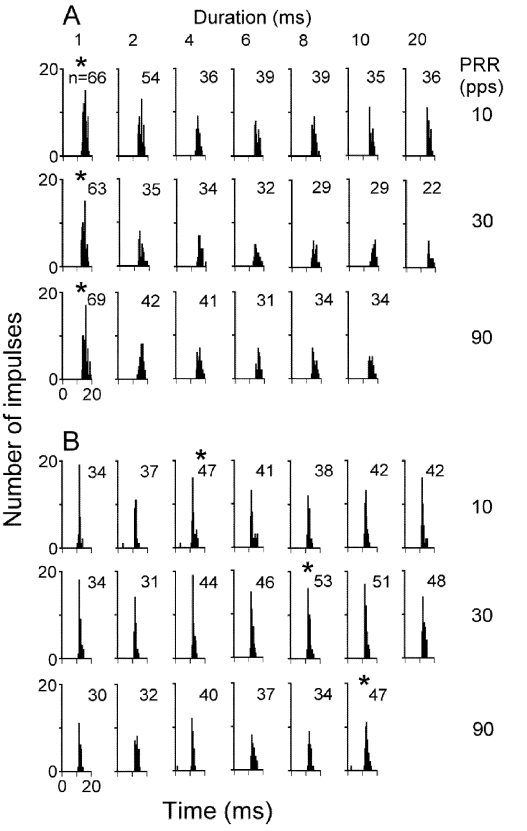

Fig. 1. Peri-stimulus-time (PST) histograms showing discharge patterns of 2 neurons in the inferior colliculus (IC) of the big brown bat, *Eptesicus fuscus*, in response to best frequency pulses delivered at different pulse repetition rates (PRR in pps, right) and pulse durations (ms, top). Note that PRRs and pulse durations affect the number of impulses but not the discharge pattern of these neurons. The pulse duration to which a neuron discharged maximally is denoted with a star (see text for details).

Materials and Methods, we plotted a neuron's impulse-duration function using the number of impulses discharged to different pulse durations.

Using 50% difference between the maximal and minimal responses as a criterion adopted in previous studies (18, 20, 33), impulse-duration functions of all IC neurons plotted at three PRRs can be described as the following four types. [1] Short-pass: the maximal number of impulses obtained at a short duration was 50% greater than the minimal number of impulses obtained at a long duration (Fig. 2A); [2] Band-pass: the maximal number of impulses at the most preferred pulse duration was at least 50% greater than the number of impulses at two minimal responses obtained at long and short durations respectively (Fig. 2B); [3] Long-pass: the maximal number of impulses obtained at a long duration was 50% greater than that obtained at a short duration (Fig. 2C); and [4] All-pass: the number of impulses discharged at all dura-

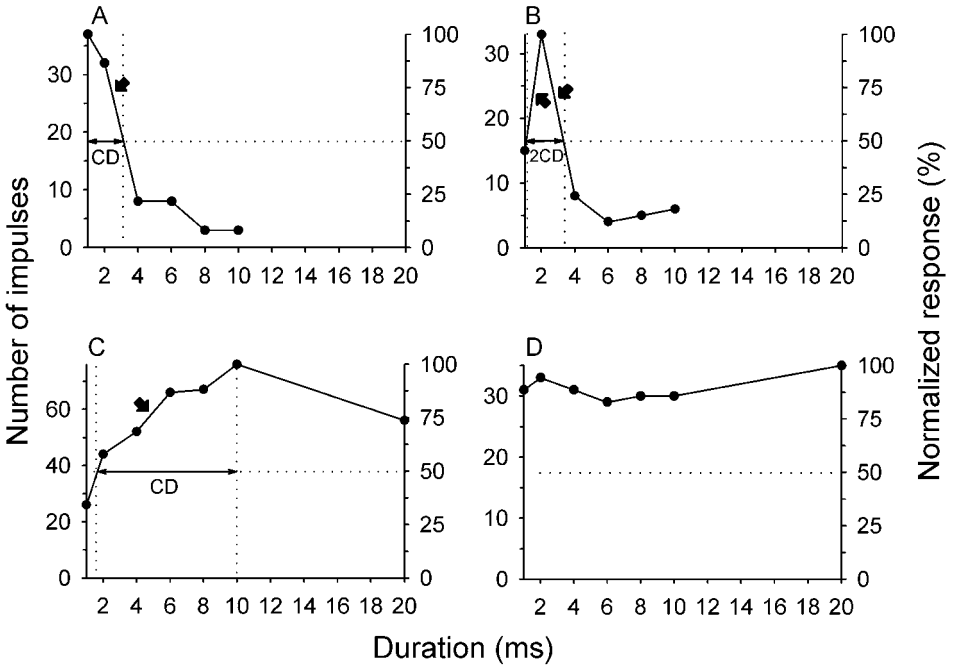

Fig. 2. Impulse-duration functions of 4 IC neurons plotted with the number of impulses against the pulse duration. Left and right ordinates represent the number of impulses per 32 pulse presentations and normalized response. The abscissa represents pulse duration (ms). Impulse-duration functions of these 4 neurons are short-pass (A), band-pass (B), long-pass (C), and all-pass (D). The critical duration (CD) is shown by a double arrow line and bordered by vertical dotted lines for neurons A, B, C. For short- and long-pass impulse-duration functions, CD is the duration difference between a neuron's maximal response and 50% response (A, C). For the band-pass impulse-duration function, CD is half of the duration difference between a neuron's two points of 50% of the maximal response (e.g. half of the double arrow line in B). The all-pass impulse-duration function (D) does not have a CD. Each horizontal dashed line indicates the 50% maximal response. Single head arrows indicate the slope of impulse-duration function.

tions never differed by more than 50% (Fig. 2D). In this study, the duration of maximal response in the short-, band- and long-pass impulse-duration functions is defined as the best duration (BD)(e.g. 1 ms in Fig. 2A, 2 ms in Fig. 2B and 10 ms in Fig. 2C). Other durations that evoked responses from IC neurons are defined as non-BDs.

As in our previous studies (18, 20, 33), we quantified the duration tuning properties of IC neurons by calculating the CD of impulse-duration functions (Fig. 2). For short- and long-pass impulse-duration functions, the CD is the duration difference between a neuron's maximal response and 50% of maximal response (Fig. 2A,C). For band-pass impulse-duration functions, the CD is half of the duration difference between a neuron's two points of 50% of the maximal response (Fig. 2B). Because the CD is an indication of the width of an impulse-duration function, a small CD represents high duration selectivity. An all-pass impulse-duration function does not have a CD because the number of impulses never varies by more than 50% at any pulse duration (Fig. 2D).

We also quantified the duration tuning properties of these neurons by calculating the slope of impulse-duration functions. For short- and long-pass neurons, the slope was calculated for the portion of impulse-duration function that shows 50% difference from the maximum (Fig. 2A,C, arrow). That is, the slope was calculated by dividing 50% by the CD and expressed as %/ms. For band-pass neurons, the slope is half of the sum of the slopes calculated for both limbs of the impulse-duration function (Fig. 2B, arrows). The slope is an indication of a neuron's sensitivity to duration change. Thus a large (sharp) slope represents a high sensitivity to duration change.

The Effect of PRR on Impulse-Duration Functions of IC Neurons

PRR did not affect the impulse-duration function of 25 (60%) neurons but changed those of the remaining 17 (40%) neurons from one type to another. For convenience, these two groups of IC neurons are called PRR-independent duration tuned neurons and PRR-dependent duration tuned neurons.

Figure 3 shows the impulse-duration functions of 4 PRR-independent duration tuned neurons determined at three PRRs. These 4 neurons had short-pass

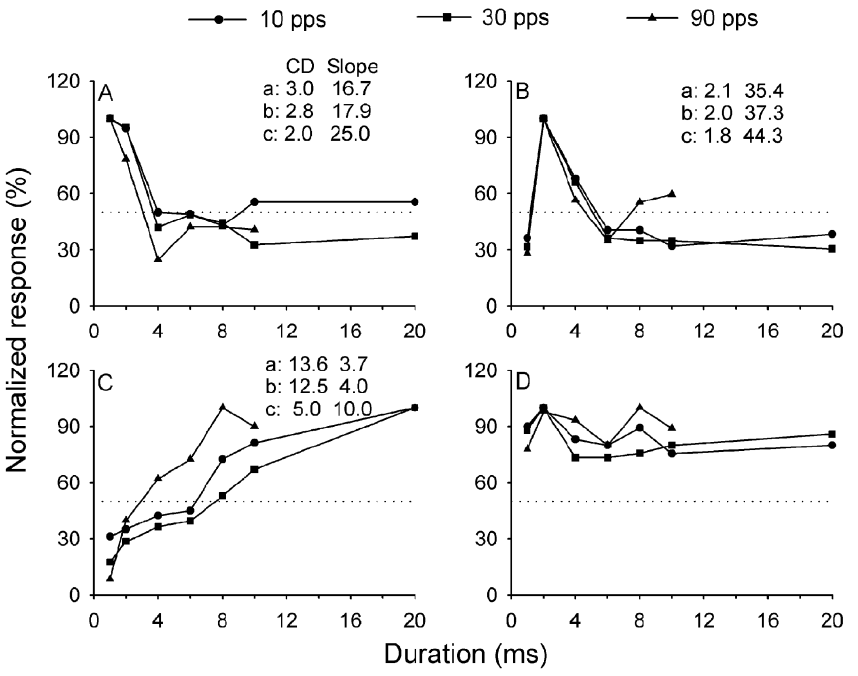

Fig. 3. Impulse-duration functions of 4 PRR-independent IC neurons determined at different PRRs. Note that increasing PRR systematically decreases the CD and increases the slope of these impulse-duration functions but does not affect their duration tuning properties. Each horizontal dashed line indicates the 50% maximal response.

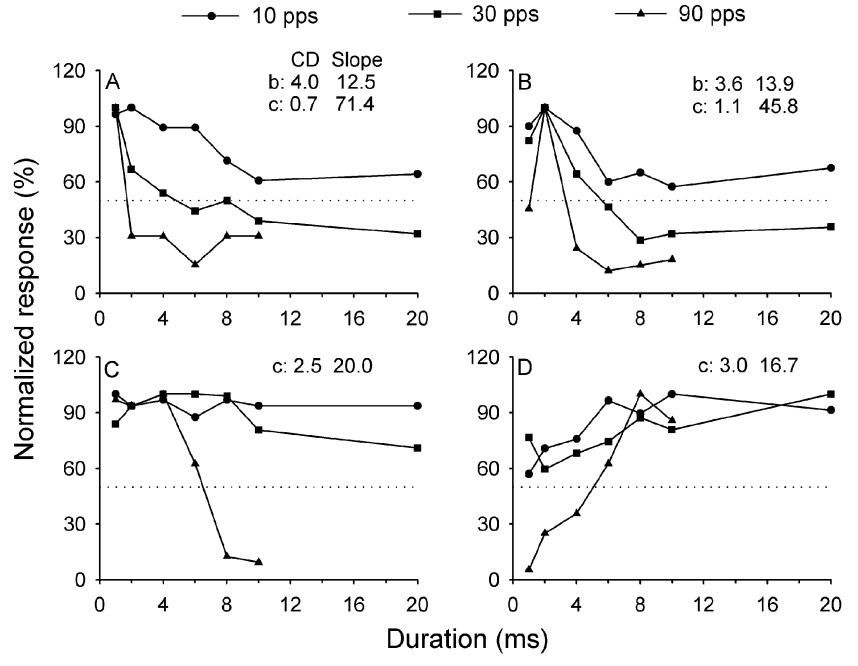

Fig. 4. Impulse-duration functions of 4 PRR-dependent IC neurons determined at different PRRs. Note that increasing PRR systematically decreases the CD and increases the slope of these impulse-duration functions but also changes their duration tuning properties.

(Fig. 3A), band-pass (Fig. 3B), long-pass (Fig. 3C), or all-pass (Fig. 3D) impulse-duration functions obtained at all three PRRs. The CD of these functions progressively decreased and the slope decreased with increasing PRR.

PRR did not affect the impulse-duration functions of PRR-dependent duration tuned IC neurons in any predictable way. As shown in Fig. 4, one neuron

Table 1. Distribution of impulse-duration functions of 42 IC neurons determined at three PRRs.

PRR (pps)	Impulse-duration function			
	Short-pass	Band-pass	Long-pass	All-pass
PRR-independent (n = 25)				
10, 30, 90	4 (16%)	1 (4%)	8 (32%)	12 (48%)
PRR-dependent (n=17)				
10	3 (18%)	0 (0%)	2 (12%)	12 (70%)
30	6 (35%)	2 (12%)	1 (6%)	8 (47%)
90	4 (23%)	2 (12%)	10 (59%)	1 (6%)

n: number of neurons.

Table 2. The range and average critical duration (CD) and slope of impulse-duration functions of 42 IC neurons determined at three PRRs.

Type of neurons	ANOVA	CD (ms) or slope (%/ms) at PRR (pps)			
		10	30	90	p
PRR-independent (n = 25)					
CD	range	2.1-19.0	2.0-18.2	1.2-6.5	
	m±sd (n)	11.2±6.4(13)(a)	7.1±5.0(13)(b)	3.2±1.5(13)(c)	0.0006
Slope	range	2.6-35.4	2.7-37.3	6.7-44.3	
	m±sd (n)	8.4±9.3(13)(d)	11.9±9.6(13)(e)	21.0±12.0(13)(f)	0.0111
PRR-dependent (n = 17)					
CD	range	2.0-16.3	1.1-16.5	0.7-8.2	
	m±sd (n)	10.5±7.5(5)(g)	4.9±4.6(9)(h)	3.0±2.3(16)(i)	0.0065
Slope	range	3.1-25.0	3.0-47.0	6.1-71.4	
	m±sd (n)	10.9±10.8(5)(j)	18.5±12.0(9)(k)	33.1±20.9(16)(l)	0.0300

Repeated measures one-way ANOVA (p=0.0300-0.0006) shows that all average CDs are significantly different regardless of dependence of duration tuning characteristics on PRR. A post test with the Student-Newman-Keuls Multiple Comparison test shows significant differences between (a) and (b) ($P < 0.05$); (a) and (c) ($P < 0.001$); (b) and (c) ($P < 0.05$); (d) and (f) ($P < 0.05$); (e) and (f) ($P < 0.05$); (g) and (h) ($P < 0.05$); (g) and (i) ($P < 0.01$); (j) and (l) ($P < 0.05$). *P*: significance level. n: number of neurons.

had an all-pass impulse-duration function when plotted at 10 pps but had short-pass duration function when plotted at 30 or 90 pps (Fig. 4A, circles *vs.* squares *vs.* triangles). Another neuron had an all-pass impulse-duration function that changed to short-pass and then to band-pass with increasing PRR (Fig. 4B circles *vs.* square *vs.* triangles). The impulse-duration functions of other 2 neurons changed from all-pass to short-pass or long-pass with increasing PRR (Fig. 4C,D).

Table 1 summarizes the distribution of impulse-duration functions of all 42 IC neurons determined at different PRRs. About half (12, 48%) of 25 PRR-independent duration tuned neurons had all-pass impulse-duration functions. One third (8, 32%) had long-pass impulse-duration functions. Most (4, 16%) of the remaining neurons had short-pass impulse-duration functions. Most (12, 70%) of 17 PRR-dependent duration tuned neurons had all-pass impulse-duration functions when determined at 10 pps. However, all but one were duration tuned neurons (short-pass: 4, 23%, band-pass: 2, 12%, and long-pass: 10, 59%) when determined at 90 pps.

Table 2 shows the average CD and slope of impulse-duration functions of the two groups of neurons determined at three PRRs. It is clear that the CD of both groups of neurons significantly decreased and the slope increased with increasing PRR (Repeated measures one-way ANOVA, $P < 0.05$).

The Effect of PRR on 50% Duration Range of IC Neurons

As shown in Fig. 2, the CD of each short- or long-pass impulse-duration function or the 2CD of band-pass impulse-duration function corresponds to a dura-

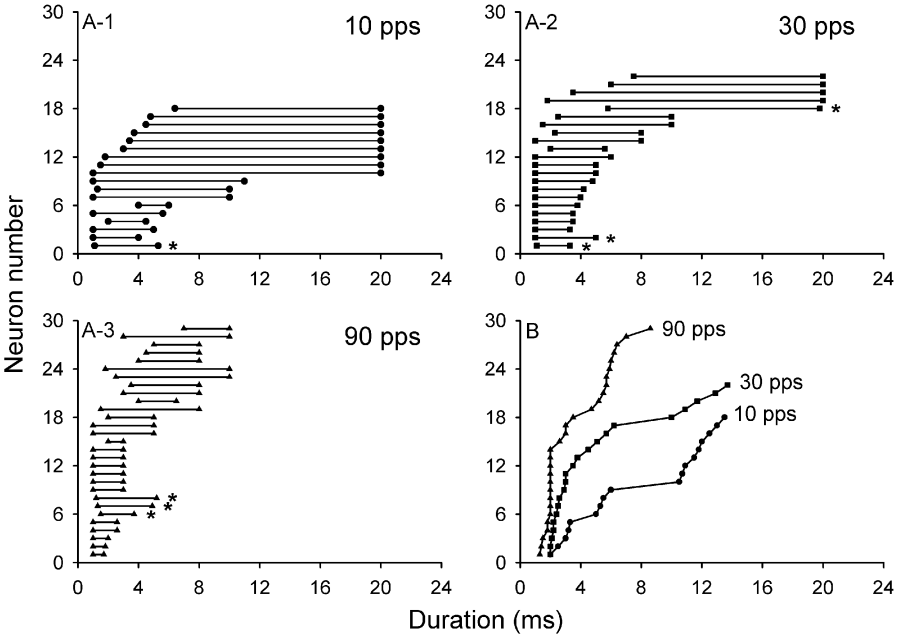

Fig. 5. Distribution of 50% duration range of IC neurons determined at PRR of 10 (A-1), 30 (A-2), and 90 pps (A-3). The duration ranges denoted with stars indicated data obtained from band-pass neurons. B: The center duration curves of IC neurons determined at 10, 30 and 90 pps. These curves are drawn by connecting the center points of 50% duration range of all IC neurons shown in A-1, A-2, and A-3. Note that the center duration curve progressively shifts left-ward with increasing PRR (see text for details).

tion range within which a neuron's discharge varied by 50%. To further quantify the effect of PRR on duration selectivity of IC neurons, we compared this 50% duration range of IC neurons determined at three PRRs.

As shown in Fig. 5A-1, the 50% duration range was longer than 12 ms in half (9/18, 50%) of IC neurons when determined at 10 pps. However, the 50% duration range was longer than 12 ms in only about one-fifth (4/22, 18%) of IC neurons when determined at 30 pps (Fig. 5A-2). The 50% duration range of all neurons was shorter than 12 ms when determined at 90 pps (Fig. 5A-3). To highlight the variation of 50% duration range of IC neurons with PRR, we connected the center point of each 50% duration range (referred to as the center duration) of all IC neurons to produce a center duration curve. As shown in Fig. 5B, the center duration curve of IC neurons progressively shifted left-ward with increasing PRR. That is, the center duration of IC neurons progressively shortened with increasing PRR.

Figure 6 shows the percent distribution of the center duration of all IC neurons determined at three PRRs. When determined at 10 pps, the center duration of 50% of IC neurons was longer than 10 ms; 22% between 5 and 10 ms; and another 22% between 2 and 5 ms. When determined at 30 pps, the center duration of 56% of IC neurons was between 2 and 5 ms; 23% longer than 10 ms; and 14% between 5 and 10 ms. The center duration of 51% of IC neurons was between 1 and 2 ms; 31% between 5 and 10 ms; and 17% between 2 and 5 ms when determined at 90 pps. A statistical analysis showed that the average center duration of these IC neurons significantly shortened with increasing PRR (Table 3, Repeated measure one-way ANOVA, $P < 0.0005$).

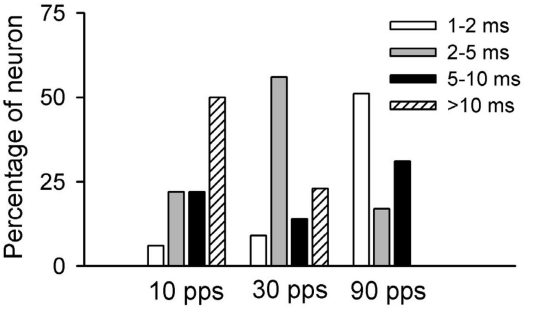

Fig. 6. Percent distribution of center duration of IC neurons determined at three PRRs. Note that the center duration of most IC neurons progressively decreases from > 10 ms to 2-5 ms and eventually to 1-2 ms with increasing PRR (see text for details).

Discussion

Duration Selectivity and PRR

In this study, we plotted the impulse-duration

Table 3. The range and average center duration of IC neurons determined at three PRRs.

PRR (pps)	10	30	90	ANOVA p
range	2.0-13.2	2.0-13.7	1.3-8.6	
m±sd (n)	7.9±4.2 (18)(a)	5.2±3.9 (22)(b)	3.6±2.1 (29)(c)	0.0003

Repeated measures one-way ANOVA shows that all average center duration are significantly different ($P = 0.0003$). A post test with the Student-Newman-Keuls Multiple Comparison test shows significant differences between (a) and (b) ($P < 0.05$); (a) and (c) ($P < 0.001$). *P*: significance level. n: number of neurons.

functions of IC neurons using the number of impulses discharged to single pulses of pulse trains of different pulse durations at three PRRs (Fig. 1). Since each function shows the variation in the number of impulses of a neuron with pulse duration at each PRR, the effect of PRR on a neuron's duration selectivity can be examined by comparing the properties of impulse-duration functions plotted at different PRRs (Figs. 3, 4).

We showed that band-pass, short-pass, or long-pass duration tuned neurons discharged maximally to a specific duration or a range of duration (Fig. 2). Whereas the PRR did not affect the impulse-duration function of PRR-independent duration tuned neurons, the PRR changed the impulse-duration functions of PRR-dependent duration tuned neurons from one type to another (Figs. 3, 4). We found that increasing PRR improved duration selectivity of IC neurons by [1] changing all-pass impulse-duration functions of PRR-dependent duration tuned neurons into short-, long-, or band-pass (Table 1); [2] decreasing the CD with concomitant increasing slope of impulse-duration functions (Figs. 3, 4; Table 2); and [3] decreasing the 50% duration range and the center duration (Figs. 5,6; Table 3).

What might be the possible mechanism underlying the PRR-independent and PRR-dependent duration tuned IC neurons? Why duration selectivity of IC neurons improves with PRR such that the CD of impulse-duration functions of IC neurons progressively decreased with concomitantly increasing slope?

Because the IC receives both excitatory and inhibitory inputs from many lower auditory neurons [4], inhibition and excitation inputs would vary among individual IC neurons depending upon their neural inputs. Furthermore, the strength of inhibition relative to excitation would also vary with PRR. For example, previous studies showed that high repetitive stimulation may produce temporal facilitation or depression of excitatory and inhibitory synaptic potentials depending on the rate of neurotransmitter release (30, 36). Therefore, the strength of inhibition relative to excitation on the postsynaptic neurons is determined by the time course of release of inhibitory and excitatory transmitters.

Previous studies have shown that GABAergic neural inhibition shapes the duration selectivity of IC neurons (3, 4, 8, 10, 18). It is conceivable that variation of GABAergic inhibition with PRR may be the underlying mechanism for the improvement of duration selectivity of IC neurons. For example, when the release of GABA is facilitated at a faster rate or depressed at a slower rate than the release of excitatory transmitter at high PRRs, postsynaptic inhibition would become greater than excitation. This increasing GABAergic inhibition with PRR would improve the duration selectivity of IC neurons. This is evident by two recent studies showing that the strength of GABAergic inhibition is greater at high than at low PRRs (19, 35). This increasing GABAergic inhibition contributes to increasing directional selectivity of IC neurons at high PRRs (35).

A previous study has shown that increasing GABAergic inhibition with PRR decreases the responses of IC neurons at a greater degree to non-BDs than to the BD sound stimulation such that impulse-duration functions of IC neurons becomes progressively narrow (19). However, increasing strength of GABAergic inhibition with PRR might have a slow time course in PRR-independent duration tuned IC neurons such that increased GABAergic inhibition would only sharpen the impulse-duration functions with decreased CD and increased slope of the function (Fig. 3). Conversely, increasing strength of GABAergic inhibition with PRR might have a fast time course in PRR-dependent duration tuned IC neurons such that the strong GABAergic inhibition at high PRR would sharpen and change the impulse-duration functions from one type to another (Fig. 4).

Comparison with the Previous Study

As described earlier, we previously examined the duration selectivity of IC neurons by plotting impulse-duration functions of IC neurons using the total number of impulses discharged to pulse trains of different PRRs (20). We reported that 75% of IC neurons studied were PRR-dependent duration tuned and most had short-pass impulse-duration functions at 90 pps. In the present study, we observed that only

40% of IC neurons were PRR-dependent duration tuned and most had long-pass impulse-duration functions at 90 pps (Table 1). These different observations are due to the fact that IC neurons often only respond to the first or initial few pulses of temporally patterned pulse trains at high PRRs (7, 21, 20, 24). As such, a neuron's total number of impulses discharged to a pulse train would drop sharply at high PRRs. For this reason, most neurons that only responded to first or initial few pulses of pulse trains at high PRRs would have short-pass impulse-duration functions (20).

Our earlier study examined the effect of temporally patterned pulse trains on duration selectivity of IC neurons in terms of the interaction among pulse durations, PRR, and inter-pulse gap. For this reason, increasing duration selectivity of IC neurons with PRR might be due to shortening of inter-pulse gaps. In the present study, we examined the effect of PRR on duration selectivity of bat IC neurons by comparing the duration tuning properties of IC neurons to a selected pulse within the pulse trains of different PRRs. We showed that duration selectivity improves with PRR by increasing the number of duration tuned IC neurons and increasing sensitivity to duration change (Figs. 3-6; Tables 2, 3).

Behavioral Relevance to Detection of Echo Duration

Because *Eptesicus fuscus* progressively increase the pulse repetition rate (PRR) as they search, approach and finally intercept the target (15), sensitivity of their auditory neurons to pulse parameters would be inevitably affected by PRR. For example, we have recently shown that an increase in sound intensity decreases duration selectivity of one third of IC neurons studied (33). Conversely, shortening of sound duration changes the rate-intensity functions and improves intensity selectivity of more than half of the neurons studied (34).

In the present study, we showed that increasing PRR increases the number of duration tuned neurons and improves duration selectivity sensitivity of IC neurons (Figs. 3-6; Tables 1-3). Because *Eptesicus fuscus* shorten pulse duration during the final phase of hunting with high pulse emission rate (15), the increased duration sensitivity to short pulse duration at high PRR would conceivably facilitate detection of short echo duration.

Acknowledgements

We thank two anonymous reviewers for commenting on an earlier version of this manuscript. This work is supported by a research grant from the National Science Foundation of USA (NSF IBN 9604238) and the matching grants from the College of Arts and Sciences of the University of Missouri-Columbia, USA and the College of Life Sciences of the East China Normal University, Shanghai, PRC.

References

1. Backoff, P.M.and Caspary, D.M. Age-related changes in auditory brainstem responses in Fischer 344 rats: effects of rate and intensity. *Hear. Res*. 73: 163-172, 1994.
2. Brand, A., Urban, R. and Grothe, B. Duration tuning in the mouse auditory midbrain. *J. Neurophysiol*. 84: 1790-1799, 2000.
3. Casseday, J.H., Ehrlich, D. and Covey, E. Neural tuning for sound duration: role of inhibitory mechanisms in the inferior colliculus. *Science* 264: 847-850, 1994.
4. Casseday, J.H., Ehrlich, D. and Covey, E. Neural measurement of sound duration: control by excitatory-inhibitory interactions in the inferior colliculus. *J. Neurophysiol*. 84: 1475-1487, 2000.
5. Chen, G.D. Effects of stimulus duration on responses of neurons in the chinchilla inferior colliculus. *Hear. Res.* 122: 142-150, 1998.
6. Chen, Q.C. and Jen, P.H.S. PRR increases the minimum threshold and latency of auditory neurons. *Brain Res*. 654: 155-158, 1994.
7. Condon, C.J., White, K.R. and Feng, A.S. Processing of amplitude-modulated signals that mimic echoes from fluttering targets in the inferior colliculus of the little brown bat, Myotis lucifugus. *J. Neurophysiol*. 71: 768-784, 1994.
8. Covey, E., Kauer, J.A. and Casseday, J.H. Whole-cell patch clamp recording reveals subthreshold sound-evoked postsynaptic currents in the inferior colliculus of awake bats. *J. Neurosci*. 16: 3009-3018, 1996.
9. Donaldson, G.S. and Rubel, E.W. Effects of stimulus repetition rate on ABR threshold, amplitude and latency in neonatal and adult Mongolian gerbils. *Electroencephalogr. Clin. Neurophysiol*. 77: 458-470, 1990.
10. Ehrlich, D., Casseday, J.H. and Covey, E. Neural tuning to sound duration in the inferior colliculus of the big brown bat, *Eptesicus fuscus*. *J. Neurophysiol.* 77: 2360-2372, 1997.
11. Fuzessery, Z.M. and Hall, J.C. Sound duration selectivity in the pallid bat inferior colliculus. *Hear. Res*. 137: 137-154, 1999.
12. Galazyuk, A.V. and Feng, A.S. Encoding of sound duration by neurons in the auditory cortex of the little brown bat. *Myotis lucifugus*, *J. Comp. Physiol. [A]* 180: 301-311, 1997.
13. Galazyuk, A.V., Llano, D. and Feng, A.S. Temporal dynamics of acoustic stimuli enhance amplitude tuning of inferior colliculus neurons. J. Neurophysiol. 83: 128-138, 2000.
14. Gooler, D.M. and Feng, A.S. Temporal coding in the frog auditory midbrain: the influence of duration and rise-fall time on the processing of complex amplitude-modulated stimuli. *J. Neurophysiol*. 67: 1-22, 1992.
15. Griffin, D.R. Listening in the Dark. New Haven, CT: Yale Univ. Press, 1958 (Reprinted by Comstock Pub. Asso. Cornell Univ. Press 1986).
16. He, J., Hashikawa, T., Ojima, H. and Kinouchi, Y. Temporal integration and duration tuning in the dorsal zone of cat auditory cortex. *J. Neurosci*. 17: 2615-2625, 1997.
17. Jen, P.H.S. and Chen, Q.C. The effect of PRR, pulse intensity, and bicuculline on the minimum threshold and latency of bat inferior colliculus neurons. *J. Comp. Physiol. [A]* 182: 455-465, 1998.
18. Jen, P.H.S. and Feng, R.B. Bicuculline application affects discharge pattern and pulse-duration tuning properties of bat inferior collicular neurons. *J. Comp. Physiol. [A]* 184: 185-194, 1999.
19. Jen, P.H.S. and Wu, C.H. The role of GABAergic inhibition in shaping the response size and duration selectivity of bat inferior collicular neurons to sound pulses in rapid sequences. *Hear. Res.* 202: 222-234, 2005.
20. Jen, P.H.S. and Zhou, X.M. Temporally patterned pulse trains affect duration sensitivity of bat inferior collicular neurons. *J. Comp.*

Physiol. [A] 185: 471-478, 1999.
21. Jen, P.H.S., Zhou, X.M. and Wu, C.H. Temporally patterned sound pulse trains affect intensity and frequency sensitivity of inferior collicular neurons of the big brown bat, *Eptesicus fuscus*. *J. Comp. Physiol. [A]* 187: 605-616, 2001.
22. Jen, P.H.S., Wu, C.H., Ruan, R.H. and Zhou, X.M. GABAergic inhibition contributes to pulse repetition rate-dependent frequency selectivity in the inferior colliculus of the big brown bat, *Eptesicus fuscus*. *Brain Res.* 948: 159-164, 2002.
23. O'Neil, W.E. and Suga, N. Encoding of target range information and its representation in the auditory cortex of the mustache bat. *J. Neurosci.* 2: 17-31, 1982.
24. Phillips, D.P., Hall, S.E. and Hollett, J.L. Repetition rate and signal level effects on neuronal responses to brief tone pulses in cat auditory cortex. *J. Acoust. Soc. Am.* 85: 2537-2549, 1989.
25. Pinheiro, A.D., Wu, M. and Jen, P.H.S. Encoding repetition rate and duration in the inferior colliculus of the big brown bat, *Eptesicus fuscus*. *J. Comp. Physiol. [A]* 169: 69-85, 1991.
26. Poon, P.W.F., Sun, X.D., Kamada, T. and Jen, P.H.S. Frequency and space representation in the inferior colliculus of the FM bat, *Eptesicus fuscus. Exp. Brain Res.* 79: 83-91, 1990.
27. Smalling, J.M., Galazyuk, A.V. and Feng, A.S. Stimulation rate influences frequency tuning properties of inferior colliculus neurons in the little brown bat, *Myotis lucifugus*, *Neuroreport* 12: 3539-3542, 2001.
28. Suga, N. and Schlegel, P. Neural attenuation of responses to emitted sounds in echolocating rats, *Science* 177: 82-84, 1972.
29. Wong, D., Maekawa, M. and Tanaka, H. The effect of pulse repetition rate on the delay sensitivity of neurons in the auditory cortex of the FM bat, *Myotis lucifugus. J. Comp. Physiol. [A]* 170: 393-402, 1992.
30. Wu, L.G. and Betz, W.J. Kinetics of synaptic depression and vesicle recycling after tetanic stimulation of frog motor nerve terminals. *Biophys. J.* 74: 3003-3009, 1998.
31. Wu, M. and Jen, P.H.S. Temporally patterned pulse trains affect directional sensitivity of inferior colliculus neurons of the big brown bat, *Eptesicus fuscus*. *J. Comp. Physiol. [A]* 179: 385-393, 1996.
32. Xia, Y.F., Qi, Z.H. and Shen, J.X. Neural representation of sound duration in the inferior colliculus of the mouse. *Acta. Otolaryngol.* 120: 638-643, 2000.
33. Zhou, X.M. and Jen, P.H.S. The effect of sound intensity on duration-tuning properties of bat inferior collicular neurons. *J. Comp. Physiol. [A]* 187: 63-73, 2001.
34. Zhou, X.M. and Jen, P.H.S. The effect of sound duration on rate-intensity functions of inferior collicular neurons of the big brown bat, *Eptesicus fuscus*. *Hear. Res.* 166: 124-135, 2002.
35. Zhou, X.M. and Jen, P.H.S. The role of GABAergic inhibition in shaping directional selectivity of bat inferior collicular neurons determined with temporally patterned pulse trains. *J. Comp. Physiol. [A]* 188: 815-826, 2002.
36. Zucker, R.S. Short-term synaptic plasticity. *Annu. Rev. Neurosci.* 12: 13-31, 1989.