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Pulse Rise Time But Not Duty Cycle Affects the Temporal Selectivity of Neurons in the Anuran Midbrain That Prefer Slow AM Rates

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Edwards, Christofer J., Todd B. Alder, and Gary J. Rose. Pulse rise time but not duty cycle affects the temporal selectivity of neurons in the anuran midbrain that prefer slow AM rates. *J Neurophysiol* 93: 1336–1341, 2005; doi:10.1152/jn.00797.2004. Recovery-type auditory neurons in the anuran inferior colliculus (IC) respond with band-pass or low-pass selectivity for sinusoidal AM. These cells respond to each modulation cycle at slow AM rates and respond only at the onset of fast AM or pulse repetition rate (PRR) stimuli, failing to recover from the effects of early pulses. This selectivity is not altered by changes in pulse duty cycle. The recovery process is governed therefore by the interpulse interval and not the dimension of the gap between sound pulses. Most of these neurons preferred fast rise times, which is characteristic of the sound pulses in the calls of *Hyla regilla* and *Rana pipiens*, the two species selected for this study.

INTRODUCTION

The temporal structure of acoustic signals is important in the communication of many animals, including humans (Emlen 1972; Ghazanfar et al. 2001; Kay 1982; Langner 1992; Liegeois-Chauvel et al. 1999; Loftus-Hills and Littlejohn 1971; Remez et al. 1981). Therefore it is of considerable interest to identify how temporal information is represented and processed in the auditory system.

Anurans are well suited for investigating these questions. Acoustic communication is important in their reproductive biology, enabling females to identify and choose between conspecific males (Gerhardt 1982, 2001; Wells 1977), and subserving aggressive interactions between males (Awbrey 1978; Brenowitz and Rose 1994; Wagner 1992; Whitney 1980). Also, many anurans are able to discriminate between call types that differ only in temporal structure (Diekamp and Gerhardt 1995; Gerhardt 1988; Rose et al. 1988; Ryan 1983).

AM is one important temporal feature of the communication signals of anurans, as well as other animals (Rose 1986). In many anuran species, including the two used in this study, different call types contain the same component carrier frequencies, i.e., are spectrally nearly identical, but differ markedly in how signal amplitude is modulated over time (Gerhardt 1982, 1988). In several cases, it has been shown that anurans are able to discriminate between call types that differ virtually exclusively in AM rate, i.e., pulse repetition rate (Brenowitz and Rose 1994; Gerhardt 1982, 1988; Loftus-Hills and Littlejohn 1971; Rose and Brenowitz 1997; Straughan 1975). Given this specialization, the anuran auditory system provides an excellent opportunity to study how AM rate is represented and processed.

Neurophysiological studies have shown that there is a transformation in the representation of AM in the anuran auditory system. For sinusoidal AM with a noise carrier, auditory nerve fibers code AM rates up to ≥ 150 Hz in their periodicity of discharges (Dunia and Narins 1989; Rose and Capranica 1985); their mean spike rate is largely constant over this range. The mean firing rate of most midbrain neurons, however, depends on AM rate; low-pass, high-pass, band-pass, and band-suppression classes have been recognized (Diekamp and Gerhardt 1995; Rose and Capranica 1985; Walkowiak 1988). This physiological diversity simplifies to largely two classes, however, based on responses to stimuli wherein only the rate of repetition of pulses is varied, i.e., pulse duration and shape are held constant (Alder and Rose 2000). One group of neurons responds with short latency to individual sound pulses. These cells respond strongly and in a "phase-locked" fashion when pulses are repeated at slow rates. Their response levels decline, however, at higher pulse repetition rates (PRRs). Similar selectivity has been seen for units in the inferior colliculus of mammals (for reviews, see Frisina 2001; Langner 1992). Neurons in the second group, which are selective for fast PRRs, respond with longer latencies, and their spikes are not locked to any particular phase of the interpulse interval. These cells do not respond to slow PRRs, and in many cases, are strongly band-pass.

The mechanisms that underlie the temporal selectivities of toral neurons are incompletely understood; however, recent work suggests that integration and "recovery" processes play important roles (Alder and Rose 1998, 2000). Integration properties underlie the strong selectively of the long-latency neurons to fast AM (or pulse repetition) rates (Alder and Rose 1998; Edwards and Rose 2003; Edwards et al. 2002). These cells respond only after several "correct" interpulse intervals have occurred. Short-latency neurons, however, respond to individual, short-duration sound pulses. Their decline in response at fast PRRs (and AM rates) cannot be due, therefore, primarily to sensitivity to pulse duration (Alder and Rose 2000). Instead, recovery processes seem to underlie this selectivity. It appears that a minimum amount of time is required for the system to "recover" from the effects of the preceding pulse (Alder and Rose 2000); because of this property, we will also refer to these cells as "recovery-type" units. It is presently unclear whether the recovery process occurs in the interval from shortly after the start of one pulse to the beginning of the next pulse or just during the "silent" (subthreshold) period between pulses. To discriminate between these possibilities, we recorded the responses of single toral units to AM stimuli of different duty cycles (ratio of pulse duration to interpulse interval). The latter hypothesis would be supported if band-pass neurons are tuned to faster

AM rates for stimuli of shorter duty cycle. A second objective of this study was to further investigate why many short-latency units are strongly band-pass for sinusoidal AM, instead of simply being low-pass. The decline in response of these cells at slow AM rates stems in part from their phasic response properties; the response per stimulus pulse is largely independent of pulse duration, and because there are fewer modulation cycles (pulses) in each stimulus at very low AM rates (rates below the optimal rate for the cell), fewer spikes are elicited. A role of rise time sensitivity, however, is also likely. Toral neurons generally respond best for fast rise times (Gooler and Feng 1992). Because stimulus amplitude rises more slowly at slower AM rates, weaker responses are expected. Accordingly, in some cases, responses to slow rates of sinusoidal AM are weaker than those to square-wave AM, thereby showing an influence of pulse rise time on AM selectivity. While rise time sensitivity cannot account for AM band-pass selectivity per se (Alder and Rose 2000; Gooler and Feng 1992), it seems to contribute to the weak, phasic responses at low rates of sinusoidal amplitude modulation (SAM) and therefore the sharpness of AM tuning. The second objective of this study was to further investigate the rise time sensitivity of short-latency type neurons in the torus semicircularis and relate this property to their AM band-pass selectivity. In these experiments, we chose the optimal pulse repetition rate for the cell and varied the rise/fall properties of the pulses. As in recent studies, all recordings were performed in *Rana pipiens* and *Hyla regilla*.

METHODS

Stimulus generation

Acoustic stimulus sets were constructed using Tucker Davis Technologies (TDT) System II hardware and custom made software on a Pentium II computer (Alder and Rose 2000). Carriers used in stimulus generation were created using a TDT AP2 card. The sampling rate for these carriers and all modulating waveforms was 25 kHz.

SAM stimulus was generated by multiplying a white noise or pure tone carrier with a sinusoidal modulating waveform, which contained a DC offset equal to one-half its peak-to-peak amplitude. Stimulus duration was held constant at 400 ms. As a result, with increasing AM rate, stimulus "pulse" number increased, pulse duration decreased, and pulse rise time became faster (shorter).

In another stimulus set (natural AM), pulses had a natural shape that was generated by multiplying a pure tone carrier with a modulating envelope that is a mathematical representation of the natural pulse envelope. Based on analysis of field-recorded calls, a single pulse envelope was generated using the following equations

$$V = k[e^{-t/\tau 1} - e^{-t/\tau 2}]$$

$$\tau 2 = (\tau 1)/2$$

where $\tau 1$ and $\tau 2$ define the relative rising and falling phases of the envelope. The pulse envelope was repeatedly copied to produce the modulating envelope. This stimulus was presented at a constant duty cycle (ratio of pulse to interpulse interval) throughout the range of presented pulse repetition rates (PRRs). As with sinusoidal AM, total stimulus energy (within 0.1 dB) was maintained with changes in rate. Modulation duty cycles of 1.0, 0.5, and 0.25 were used for neurophysiological experiments.

Rise/fall time stimuli were generated by multiplying a triangular modulating waveform with a pure tone carrier. The rise and fall times were inversely proportional to each other: as rise time increased, fall time decreased. This relationship was used to maintain constant pulse energy. Therefore while duration remains constant, the distribution of

energy is moved away from the pulse onset as rise time is increased. One to 10 pulses were generally used, presented at the rate to which the cell was most responsive. Various pulse durations were used to obtain a maximum response from the neuron and ensure that rise times were long enough to observe a change in the firing pattern.

Stimulus presentation

Stimuli were amplified (Symetrix A-220) and presented free field in an Industrial Acoustics audiometric room (87 × 87 × 78 in high) via a Bose speaker situated 0.5 m from the frog, contralateral to the recording site. Reflections in the booth have been minimized by covering the walls and ceiling with acoustic foam (absorption coefficients from 250 to 4,000 Hz: 0.60–0.97). The corner directly opposite the speaker is covered with fiberglass insulation (3.5-in Owens Corning R-11, absorption coefficients from 250 to 4,000 Hz: 0.85–0.98) covered with cotton cloth. Echoes are attenuated by $\geq$30 dB relative to the stimulus for frequencies >500 Hz. Correspondingly, stimuli were presented at levels not exceeding 30 dB above each unit's threshold. A microphone (ACO Pacific, with Cetec Ivie IE-2P preamp) situated above the frog was used to measure stimulus levels via a sound level meter (Cetec Ivie IE-30A). Stimuli were presented once every 2.5 s, unless repetitions subsequent to the first consistently produced an attenuated response, in which case the rate was decreased. A Wavetek 19 function generator was used to time presentation rates, and sound level was varied using a TDT PA-4 programmable attenuator. Stimuli were presented at various root mean square (RMS) amplitudes across each neuron's dynamic range to test the intensity dependence of temporal tuning. Modulation rates presented to the animal varied from 5 to 200 Hz. Sinusoidal AM was used as the search stimulus; carrier rates were systematically varied from 300 to 2,200 Hz while modulation frequency was varied from 20 to 100 Hz.

Neurophysiology

Microelectrodes were constructed from alumina silicate glass (1.0 mm OD, 0.75 mm ID) on a Brown-Flaming puller. Tips were ~2 μm in diameter and were back filled with either biocytin (Sigma) or biotinylated dextran (10,000 MW, lysine fixable; Molecular Probes) in 2 M NaCl. Shanks were filled with 2 M NaCl (1–4 MΩ impedances). Electrodes were advanced remotely via a piezoelectric microdrive (Burleigh 6000) through the torus semicircularis until an isolated unit was encountered. Responses were amplified (Warner IE-210), displayed on an oscilloscope, broadcast over a loudspeaker monitor, and stored on VHS tape, along with the stimulus on a separate channel, with a PCM-video recorder (Vetter 3000). Best excitatory frequency (BEF; frequency at which the unit has its lowest threshold) and threshold were determined. Threshold is defined as the sound-pressure level necessary to evoke at least one spike during 75% of the presentations of repetitive sinusoidal AM bursts at an AM rate that is determined audio-visually to produce the greatest response. Because many toral neurons respond poorly or not at all to pure tones, the unit's BEF was determined by varying the frequency of the carrier (fc) while amplitude modulating the carrier at the optimal rate; the presence of side bands in the AM stimulus precludes using conventional methods of constructing a frequency tuning curve for these neurons. Also, because sidebands are present at fc − fm (modulation frequency) and fc + fm, changes in AM rate result in changes in the spectral structure of AM tone stimuli. Changes in activity stemming from such spectral differences can lead one to conclude erroneously that a neuron is selective for the temporal property, AM rate (Rose and Capranica 1983). Thus AM white noise was used routinely to determine whether a neuron was actually temporally selective. The limitation of white noise, however, is that energy is not present continually in any spectral band. This property leads to underestimation of the AM selectivity of the neuron at low AM rates. Therefore once the

temporal selectivity of a neuron had been established, amplitude modulated pure tone carriers were used in further tests.

Temporal tuning was measured using sinusoidal AM stimulus to facilitate comparisons with previous anuran auditory work. A unit was considered temporally selective if the number of spikes at the least preferred rate was at most 50% of that recorded at the most preferred rate (Rose and Capranica 1983, 1985). The frog was presented with a variety of stimulus sets (see above) at 10 dB above the neuron's threshold. Recording sites were marked by iontophoresing the dye from the electrode tip using positive DC.

Data collection and analysis

Spikes were discriminated (SA Instrumentation model 13-T dual window discriminator) and acquired, along with the stimulus waveform, using a 12-bit A/D converter (Cambridge Electronic Design 1401+). Spikes were counted over an analysis period from stimulus onset to offset plus 100 ms for each repetition; responses of toral neurons to these stimulus sets generally return to baseline within 100 ms of stimulus offset. Spike counts were averaged for each AM rate, duration, or rise time, and spike rates were calculated by dividing the average spike count by the stimulus duration. Spike2 software (Cambridge Electronic Design) was used for spike counting and modulation-cycle histogram generation. Response latency was also measured for each neuron; this is defined as the time from stimulus onset to the time of the initiation of the first spike.

RESULTS

Influence of pulse duty cycle

We recorded the responses of 43 recovery-type units to natural AM (see METHODS) stimuli having duty cycles of 0.5 and 1.0 (e.g., Fig. 1). The AM response functions of these neurons ranged from low-pass (Fig. 2, *A* and *B*) to band-pass (Fig. 2, *C* and *D*). These representative cases show that AM selectivity was only minimally influenced by the duty cycle (0.5 vs. 1.0) of the modulation. Across neurons, AM selectivity for these two duty-cycle conditions was compared by extrapolating the "corner rate" (AM rate where the response was the average of the maximum and minimum firing rates for that cell; Fig. 2*B*); this measure reflected the recovery properties of these neurons, i.e., their capacity to respond to fast AM rates. In

general, the corner rate was largely independent of the AM duty cycle (Fig. 3). The linear best fit to these data were $y = 0.68x + 6.1$ (dotted line; $r^2 = 0.65$; $P < 0.0001$). If the recovery time was determined principally by the gap between pulses, rather than the time between the start of consecutive pulses, one would expect the points to fall along the line representing a 2:1 relation (assuming a linear relation; dashed line). In addition, although 1.0 and 0.5 duty cycle stimuli differed in energy, response levels were not significantly different (sign test; $z = 0.21$, $P > 0.4$).

Effect of rise time on AM tuning

To determine each recovery unit's sensitivity to pulse rise time, we chose the pulse repetition rate that was optimal for that cell and varied the rise time (e.g., Fig. 4). We categorized a neuron as rise time sensitive if there was at least a twofold difference in response between the most effective and least effective rise times. Using this criteria, 17 of 27 units preferred fast rise times, 9 were rise time insensitive, and 1 unit preferred slow rise times. Figure 5 shows the response levels of these neurons to stimuli with reciprocal rise and fall times e.g., for a 10 pps (pulses per second) stimulus with 100-ms pulses, we compared the responses to rise times of 10 and 90 ms; differences in response magnitudes were unlikely to be due to spectral factors because stimuli of reciprocal rise and fall times were spectrally highly similar.

In some cases, sensitivity to pulse rise time appeared to account for differences in response functions for sinusoidal versus natural AM stimuli. Figure 6 shows the AM tuning curves of two units that showed strong preference for fast rise times. At slow AM rates these units responded better for natural than for sinusoidal AM. These differences can be attributed to the faster rise times of pulses in the natural AM stimuli. The optimal AM rate of neurons for these two conditions, however, only rarely differed (Fig. 6*A*); in the most extreme case (Fig. 6*B*), this cell only showed band-pass selectivity to natural AM. The relative effectiveness of natural versus sinusoidal AM stimuli for activating recovery-type neurons is shown in Fig. 7; each point is a comparison of a particular unit's response to natural versus sinusoidal AM at the
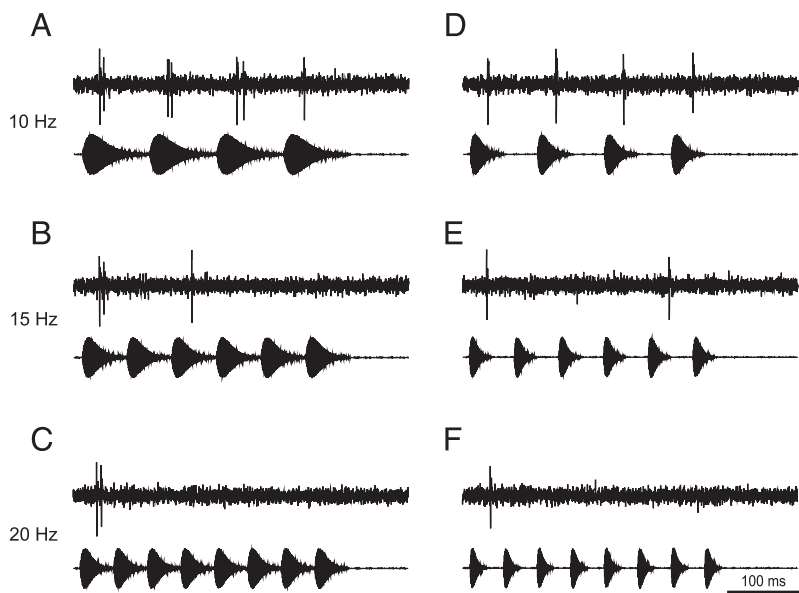

FIG. 1. Recordings of responses of a single toral unit, recorded in *Rana pipiens,* to amplitude modulated stimuli of 1.0 (*A–C*) and 0.5 (*D–F*) duty cycle. The pattern of AM is referred to as "natural" because, within each pulse, signal amplitude rises more quickly than it falls, as in the case of pulses in the natural calls of *Hyla regilla* and *R. pipiens.* The carrier frequency was 1,100 Hz, and stimulus amplitude was 60 dB SPL.
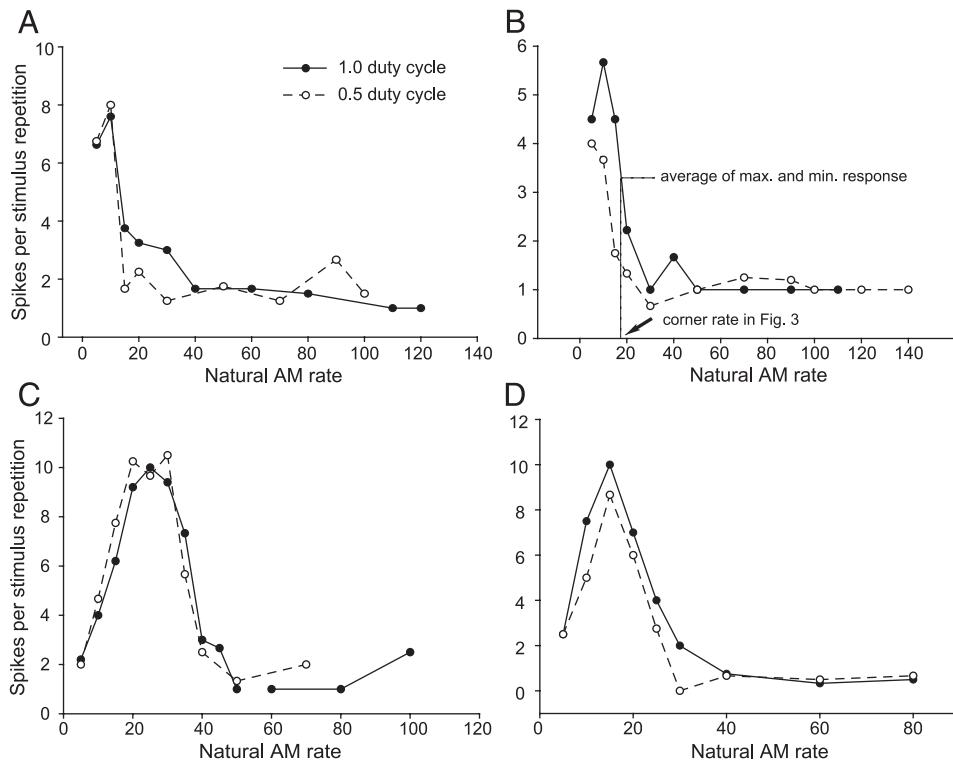
FIG. 2. Comparison of AM response functions of cells for 1.0 (●) and 0.5 duty cycle (○) stimuli. Data are from 2 units that were primarily low-pass (A and B) and 2 others that were band-pass (C and D) to natural AM stimuli. Points are the average number of spikes per repetition for 3–7 stimulus repetitions at each AM rate. The drop-down line (in B) indicates the AM corner frequency and is the AM rate at which the response is equal to the average of the response maximum and minimum values. The carrier frequencies in the AM stimuli for each unit were 800, 1,100, 700, and 700 Hz, and the thresholds for each unit were 29, 53, 39, and 53 dB SPL, respectively.

modulation rates shown. A value between 0 and 1 indicates that the unit responded better to natural AM stimuli. At low AM rates, where differences in rise time are most pronounced, most cells responded better to natural AM stimuli; the single prominent exception was the unit that preferred slow rise times (Fig. 7, ●).

between pulses. For most units recorded, the AM corner rates were similar for 0.5 and 1.0 duty cycle stimuli. This suggests that the recovery time is determined by the interpulse interval, not the gap between pulses. The latter hypothesis would have

DISCUSSION

Influences of duty cycle

One of the goals of this study was to determine if the recovery time, i.e., the amount of time required after a sound pulse for a neuron to respond similarly to the successive pulse, was determined by the interpulse interval or the silent gap
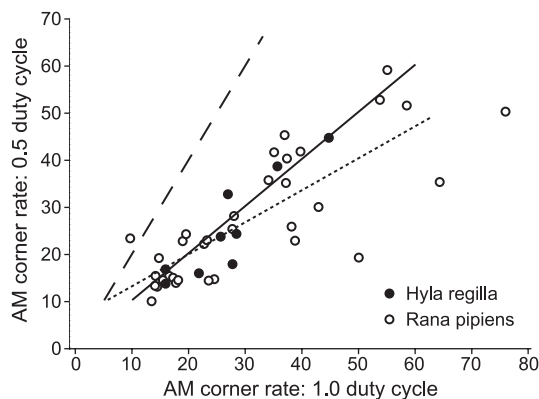

FIG. 3. Comparison of AM corner frequencies for 1.0 and 0.5 duty cycle conditions for 43 recovery units recorded from *H. regilla* (●) and *R. pipiens* (○). Corner frequency is the AM rate at which the response was equal to the average of the maximum and minimum firing rates for that cell (see Fig. 2B for a schematic that represents this calculation). Dashed line represents a 2:1 relation of this index for 0.5 vs. 1.0 duty cycle conditions, whereas the solid line represents a 1:1 relation. Dotted line represents the best linear fit for these data.
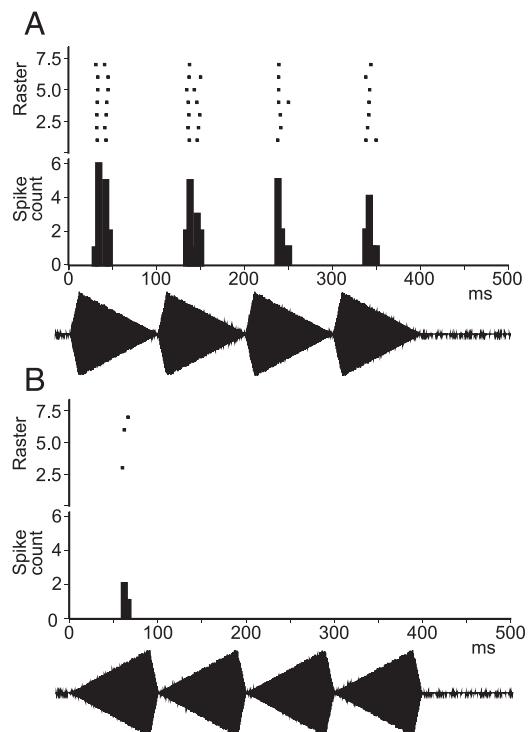

FIG. 4. Comparison of responses of a neuron to pulses with reciprocal rise/fall times. Shown above each stimulus trace are histograms (bin size = 9 ms) and raster plots of responses for pulse rise:fall times of 10:90 (A) and 90:10 ms (B). The carrier frequency was 1,100 Hz, and the threshold was 45 dB for this unit.
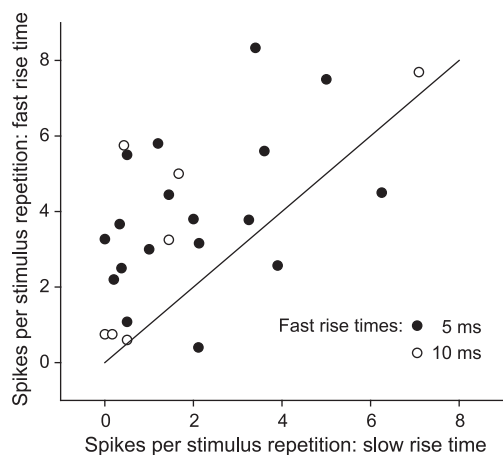
FIG. 5.   Responses of 25 neurons to fast-rise stimuli (5 ms, ●; 10 ms, ○) vs. responses to slow-rise stimuli (5- or 10-ms fall times) i.e., reciprocal rise/fall times. All neurons were tested for rise time sensitivity at their best AM rate.

FIG. 7.   Comparison of the amplitude of responses to NAM vs. sinusoidal AM. Each point is a comparison of a particular unit's responses to natural vs. SAM at the AM rates shown. The relative response amplitudes were calculated by the following formula: (R-NAM − R-SAM)/(R-NAM + R-SAM); where R-NAM and R-SAM are responses (spikes per stimulus repetition) to natural and sinusoidal AM stimuli. A value between 0 and 1 indicates that the unit responded better to the natural AM stimulus at that rate.

been supported if the corner rate was higher for 0.5 than for 1.0 duty cycle stimuli. This property is functionally relevant, because pulses in the aggressive call of *H. regilla* can range from ∼12 to ≥25 ms in duration. Pulses in this call type are repeated at ∼25 pulses/s at 17°C; therefore these neurons will respond to this call consistently amid these changes in pulse duration. Behavioral evidence also supports the hypothesis that the recovery process is governed by the interpulse interval; aggressive thresholds of male *H. regilla* were similar across stimuli that ranged from 0.25 to 1.0 duty cycle (G. J. Rose and E. A. Brenowitz, unpublished data).

These results bolster the preliminary findings by Alder and Rose (2000) that PRR-response functions were largely inde-
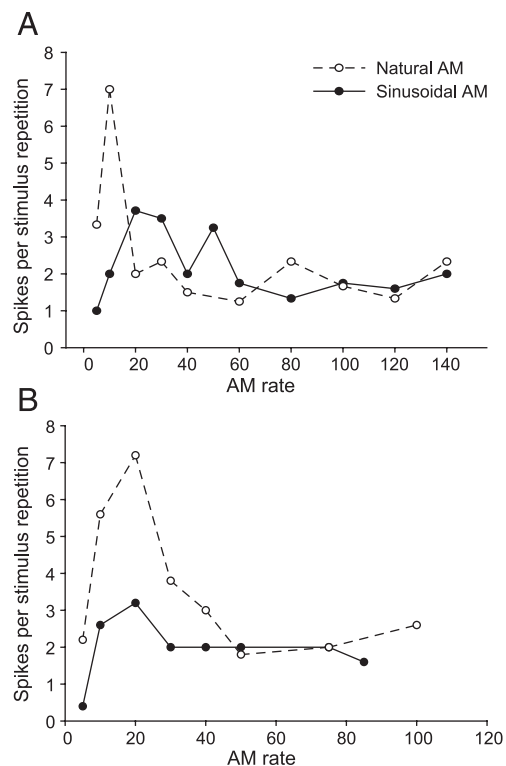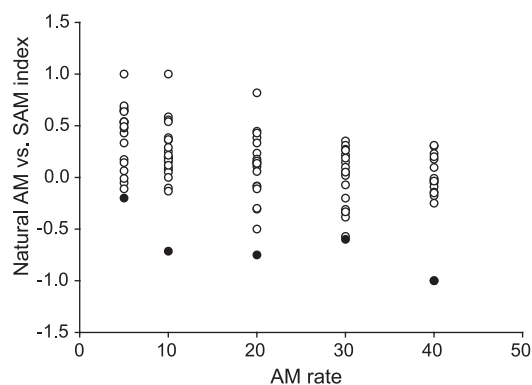

FIG. 6.   Comparison of responses of 2 units to natural AM (○) vs. sinusoidal AM (●) stimuli. Carrier frequencies and thresholds were 300 Hz and 62 dB SPL (*A*) and 1,400 Hz and 44 dB SPL (*B*).

pendent of pulse duration, which was held at a particular value while changing PRR. These earlier experiments were limited, however, in that pulse duration was not varied over an appreciable range; long pulse durations (e.g., more than ∼40 ms) resulted in pulse overlap at relatively low rates. In the present experiments, PRR (AM rate) was varied while holding pulse duty cycle constant. Consequently, very long pulse durations were present at low AM rates for the 1.0 duty cycle condition.

In the future, intracellular studies are needed to further study the mechanisms that underlie these recovery processes. From these findings, we predict that stimulus pulses at a particular AM rate will elicit an excitatory postsynaptic potential (EPSP) of a standard amplitude and time course, regardless of pulse duration. If integrative processes within the torus contribute to the recovery properties of neurons, these may also be revealed by intracellular recordings. For example, an inhibitory postsynaptic potential (IPSP) that follows the EPSP could limit the cell's ability to respond to the subsequent pulse. Presumably, the amplitude and duration of this IPSP would also be independent of the pulse duration for the reason stated above.

Influence of rise time

Our results show that most recovery-type neurons in the midbrain prefer fast rise times. This follows from the finding that most neurons in the brain stem of *R. pipiens* also prefer fast rise times (Hall and Feng 1988) and is consistent with earlier recordings from toral neurons (Gooler and Feng 1992). The rise time sensitivity we see in the midbrain is therefore most likely a consequence of the rise time sensitivity of inputs to these neurons. We encountered one unit that preferred slow rise times. Such units might be more common in anurans that produce pulses with slow rise times and use this feature for discriminating between conspecific and heterospecific calls, e.g., *Hyla versicolor*, (Diekamp and Gerhardt 1995; Gerhardt and Schul 1999). Correspondingly, across PRRs, most units in the midbrain of *H. versicolor* respond best when the conspecific pulse shape is present, relative to when pulses of fast rise time (*Hyla chrysoscelis*) are delivered. The mechanism that underlies this preference for slow rise times is unknown.

The stronger responses at low AM rates for natural AM than sinusoidal AM stimuli were consistent with their preference for

fast pulse rise times. Sensitivity to fast rise times in *R. pipiens* and *H. regilla* should therefore increase the responses of toral cells to their respective conspecific calls. In both species, calls consist of short-duration pulses (~12–25 ms) with fast rise times (~3 ms). In a few cases, AM tuning was influenced by the rise time of the stimulus pulses. At low AM rates, larger responses were elicited by natural than sinusoidal AM. This preferential enhancement of responses at low AM rates is expected because pulses in natural AM have faster rise times. In some cases, strong band-pass selectivity was observed for natural AM but not for sinusoidal AM. This appears to stem from a combination of long recovery time and strong preference for fast pulse rise time; at sinusoidal AM rates low enough to permit recovery between pulses, pulse rise time is insufficiently fast. Our investigation of rise time sensitivity and its role in AM selectivity represents an extension of that reported by Gooler and Feng (1992). In this study, we focused primarily on recovery-type neurons, whereas in the earlier study, rise time sensitivity was investigated across classes of neurons. The results of both studies are similar to those found in cat auditory cortex (Schreiner and Urbas 1986, 1988), where responses were greater to square wave AM than to SAM, especially at lower rates. This suggests that the preference for fast rise times is common feature in vertebrates.

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