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Interval-integration underlies amplitude modulation band-suppression selectivity in the anuran midbrain

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Abstract We examined the mechanisms that underlie 'band-suppression' amplitude modulation selectivity in the auditory midbrain of anurans. Band-suppression neurons respond well to low (5–10 Hz) and high (> 70 Hz) rates of sinusoidal amplitude modulation, but poorly, if at all, to intermediate rates. The effectiveness of slow rates of sinusoidal amplitude modulation is due to the long duration of individual 'pulses'; short-duration pulses (< 10 ms) failed to elicit spikes when presented at 5–10 pulses s^{-1}. Each unit responded only after a threshold number of pulses (median = 3, range = 2–5) were delivered at an optimal rate. The salient stimulus feature was the number of consecutive interpulse intervals that were within a cell-specific tolerance. This interval-integrating process could be reset by a single long interval, even if preceded by a suprathreshold number of intervals. These findings indicate that band-suppression units are a subset of interval-integrating neurons. Band-suppression neurons differed from band-pass interval-integrating cells in having lower interval-number thresholds and broader interval tolerance. We suggest that these properties increase the probability of a postsynaptic spike, given a particular temporal pattern of afferent action potentials in response to long-duration pulses, i.e., predispose them to respond to slow rates of amplitude modulation. Modeling evidence is provided that supports this conclusion.

Keywords AM tuning · Band-reject · Inferior colliculus · Temporal coding · Torus semicircularis

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Abbreviations *AM* amplitude modulation · *PRR* pulse repetition rate · *SAM* sinusoidal amplitude modulation

Introduction

Amplitude modulation (AM) is an important temporal feature of acoustic communication signals in animals ranging from insects to man (Falls 1963; Huber and Thorson 1985; Gerhardt 1988; Olive et al. 1993). In many species of anurans, the manner in which signal amplitude is modulated over time is the primary distinguishing feature between various intraspecific call types (Gerhardt 1988). Recognition of particular calls depends, therefore, on the capacity of the auditory system to differentiate between distinct patterns of signal AM.

The mechanisms that underlie auditory temporal processing are only beginning to be understood. In contrast to spectral information, which is coded in the differential activation of peripheral frequency filters (Capranica 1976), AM is coded in the fluctuations of the discharge rate of auditory-nerve fibers over time (Capranica and Moffat 1975; Rose and Capranica 1983). This raises the fundamental question of how this 'periodicity code' is read in the central nervous system. Rose and Capranica (1983, 1984) showed that, in the anuran auditory system, there is a transformation from a periodicity coding of sinusoidal AM in the peripheral auditory system to a temporal filter representation in the midbrain torus semicircularis (homologous to the inferior colliculus in mammals; Wilczynski and Capranica 1984). Four classes of temporally selective neurons were described: low-pass, high-pass, band-pass, and band-suppression. Band-pass neurons respond best over a narrow range of AM rates, and constitute the largest class of AM-selective units; using AM tones as stimuli, 56% of the units recorded were band-pass (Alder and Rose 2000). The AM tuning of these cells is species specific and generally related to the AM rates, i.e., pulse repetition rates (PRR), seen in the calls of each species (Rose and Capranica 1984; Rose 1986). More enigmatic, however, are the band-suppression neurons. These cells respond reliably at high and low (5–15 Hz) AM rates but weakly, if at all, to mid-range AM rates. This temporal selectivity is level tolerant, and typically enhanced at higher stimulus intensities. Although relatively rare (6–8% of all units recorded), band-suppression neurons have been found in all species of anurans that have been extensively investigated. In addition to anurans, band-suppression neurons have also been found in birds (Albert et al. 1989). Nevertheless, the functional role of these cells has remained somewhat of a mystery. It is particularly puzzling that band-suppression units have been found in anurans that do not use slow AM rates in their calls. Here we show that band-suppression cells are mechanistically and functionally a subset of 'interval-integrating' neurons (Edwards et al. 2002). The latter are AM band-pass cells that, in most cases, respond selectively to fast rates of AM, and respond only after a threshold number of specific interpulse intervals have occurred. Band-suppression neurons require few (median = 2) intervals to respond and generally have a relatively broad interval tolerance. It appears that this lack of temporal stringency underlies the tendency of these integration neurons to respond to low AM rates.

In *Hyla regilla*, the Pacific tree frog, band-suppression neurons, like band-pass interval-integrating cells, appear to function as detectors of the temporal features of the advertisement calls.

Materials and methods

Surgery and animal preparation

Northern leopard frogs (*Rana pipiens pipiens*) and Pacific tree frogs (*H. regilla*) were anesthetized by immersion in 3% urethane. Following the loss of all reflexes, the animals were wrapped in moist gauze to facilitate cutaneous respiration. After topical application of a local anesthetic (Lidocaine HCl), a small opening was made through the dorsal surface of the skull to expose the optic tectum. The hole was then sealed with a cap made from Gelfoam (Upjohn) and tissue adhesive (Vetbond, 3 M), after which the animals were allowed to recover overnight from the anesthesia. They were then immobilized by intramuscular injection of *d*-tubocurarine chloride (6 μg g^{-1} body weight), wrapped in moist gauze and placed on a platform in a soundproof room (Industrial Acoustics). The frog's body temperature was maintained at 17–18°C.

Recording procedure

Extracellular recordings were made from single neurons in the torus semicircularis of 12 *R. pipiens* and 5 *H. regilla* using glass micropipettes. Threshold was defined as the sound-pressure level necessary to evoke at least one spike during 75% of the presentations of repetitive sinusoidal amplitude modulation (SAM) bursts, at an AM rate that is determined audio-visually to produce the greatest response. Although band-suppression neurons generally responded to pure tones, provided they were of sufficient duration, many integration neurons did not. The frequency tuning characteristics of these neurons, therefore, could not be determined by conventional methods. Instead, the carrier frequency in the modulation was varied, holding the rate of AM at the optimal value, until the maximal response was obtained.

Stimulus generation and delivery

Acoustic stimuli were generated using Tucker Davis Technologies (TDT) System II hardware and custom software on a Pentium II computer. Amplitude modulated stimuli were generated by multiplying a white noise or pure tone carrier with a modulating waveform, which contained a d.c. offset equal to one-half its peak-to-peak amplitude. Tones and noise were created using a TDT AP2 card. The sampling rate for these carriers and all modulating waveforms was 25 kHz.

Stimuli consisted of pulses of natural shape and were generated by multiplying the carrier signal by a modulating envelope that was a mathematical representation of the natural pulse envelope. Based upon analysis of field-recorded calls, a single pulse envelope was generated using the following equations:

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

where $\tau 1$ [$\tau 1 = 0.47$(pulse duration)] and $\tau 2$ defined the relative rising and falling phases of the envelope and k was a constant ($k = 4$). The pulse envelope was then repeated to produce the modulating waveform. For the constant duty cycle stimulus regimen (Alder and Rose 2000), pulse duration varied with AM rate such that it equaled the interpulse interval; because stimulus duration remained constant, pulse number increased with AM rate. For the variable duty cycle stimulus regimen, pulse duration was held at a value approximately equal to the interpulse interval at the highest PRR tested. As the pulse repetition rate of the stimulus increased, pulses moved closer together, thereby increasing the pulse duty cycle and decreasing total stimulus duration. Since pulse shape, duration and number did not vary with pulse repetition rate, total energy remained constant.

While searching for auditory units, a sinusoidally amplitude modulated acoustic stimulus was delivered. Stimuli were amplified and presented free field in an audiometric room. The speaker (Bose) was situated 0.5 m from the frog, contralateral to the recording site. For frequencies greater than 500 Hz, reflections in the booth were attenuated by at least 30 dB relative to the stimulus. Stimuli were therefore 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, a rate that is sufficient for producing a consistent response across stimulus repetitions. Sound level was varied using a programmable attenuator. Upon encountering a single unit that was excited by any of these search stimuli, threshold was determined and tests of the neuron's temporal selectivity were performed at approximately 10 dB above this threshold value. Recording sites were labeled with biocytin iontophoresis.

Analysis

Neurophysiological data were analyzed off-line using SPIKE-2 software and the 1401 data acquisition interface from Cambridge Electronic Design, Cambridge, UK. The degree of synchronous firing during a particular modulation phase is quantified by calculating the coefficient of synchronization:

$$r = \frac{1}{N}\left[\left(\sum_{i=1}^{n} R_i \cos\frac{2\pi i}{n}\right)^2 + \left(\sum_{i=1}^{n} R_i \sin\frac{2\pi i}{n}\right)^2\right]^{\frac{1}{2}}$$

where n is the number of histogram bins, R_i represents the number of spikes in bin i, and N is the total number of spikes in the histogram. Its value ranges from zero to unity: as the histogram becomes more peaked, the coefficient of synchronization approaches unity. Significance of the vector strength (dependent on the number of spikes in the histogram) was computed using the Rayleigh test.

Results

Role of pulse duration versus rate

Single-unit extracellular recordings were made from 23 band-suppression neurons. Band-suppression neurons differed markedly in their responses to low rates of AM. Some neurons showed pronounced band-suppressive properties, such that their response level at low AM rates was equal to or greater than that at high-rates (Fig. 1A, B). Other cells were weakly band-suppressive (Fig. 1C, D). Interestingly, band-suppression neurons failed to respond (or responded very weakly) when pulses of short duration (ca. 10 ms) were repeated at slow rates (Fig. 1E–H); the number of pulses was held constant across pulse repetition rates to keep stimulus energy constant.

Interval-integrating properties

Band-suppression neurons responded at high AM or PRR rates, provided that a sufficient number of consecutive optimal intervals (median = 2, range 1–5) were presented (e.g., Fig. 2A, B). This neuron did not respond when only one optimal interval was presented (i.e., two pulses), but responded on nine of ten presentations of a stimulus that had two optimal intervals (Fig. 2B). Eight of 22 band-suppression neurons responded when only one correct interval was presented. No responses occurred when only one pulse ($<$ ca. 10 ms) was presented. Those neurons that did respond to one correct interval still showed interval-integration properties; their normalized response (probability of a spike/number of pulses) increased as pulses were added (Fig. 3).

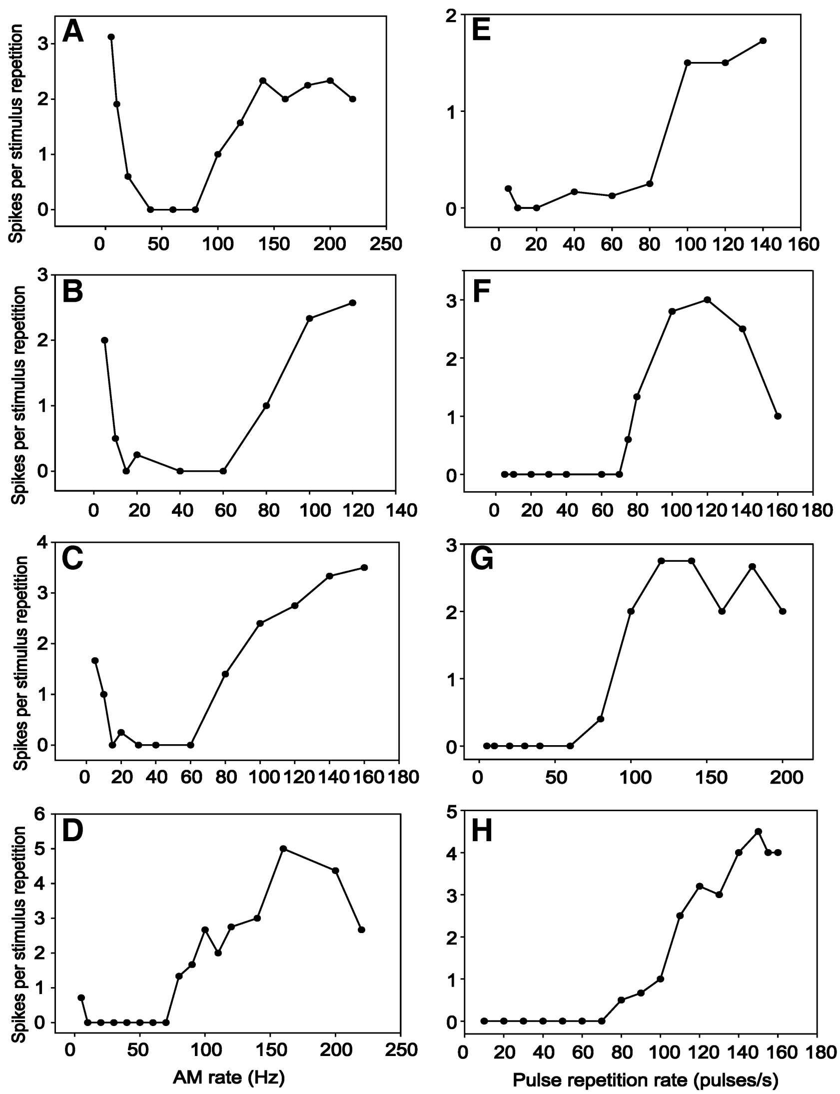

Fig. 1 Response level versus rate of amplitude modulation (AM) (**A**–**D**) or pulse repetition rate (**E**–**H**) for four band-suppression neurons. A 'natural' pattern of AM was employed (see Materials and methods), and pulse duration varied with AM rate. When only pulse repetition rate was varied (**E**–**H**), pulse duration was held constant (7, 6, 5, and 5 ms in **E**–**H**); pulses had natural shape. Thresholds for these four neurons were 49, 52, 52, and 58 dB and carrier frequencies were 400, 300, 1500, and 600 Hz, respectively. The responses represent the average of 4–10 repetitions of the stimulus

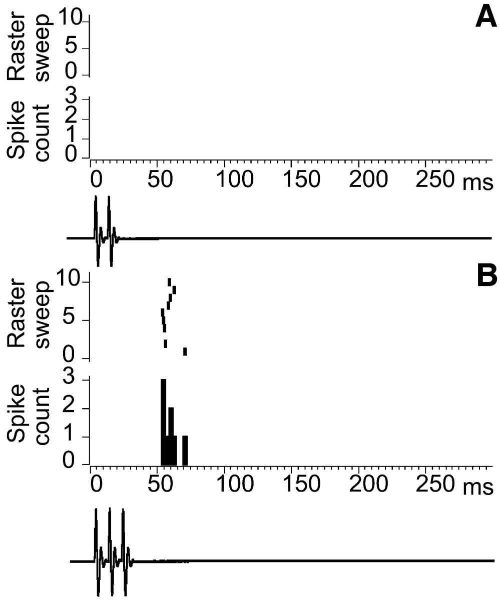

Fig. 2 Histograms (bin size = 3 ms) and raster plots of the responses of a band-suppression neuron to **A** two and **B** three pulses, respectively. The PRR (100 Hz) was the optimal high rate for this particular neuron; the carrier frequency was 300 Hz

The integration process in band-suppression units could be reset when a long interval was inserted into a series of optimal intervals (Fig. 4A–D). This neuron required three optimal intervals (four pulses) in order to respond, and the interval-integrating process was completely reset when a 30-ms interval was inserted between two sets of three pulses (Fig. 4C). When four optimal intervals were presented before the long interval, the reset time was actually reduced slightly, i.e., a 25-ms interval eliminated response to the second series of pulses; note that the responses shown in Fig. 4D were elicited by the first set of pulses (compare response

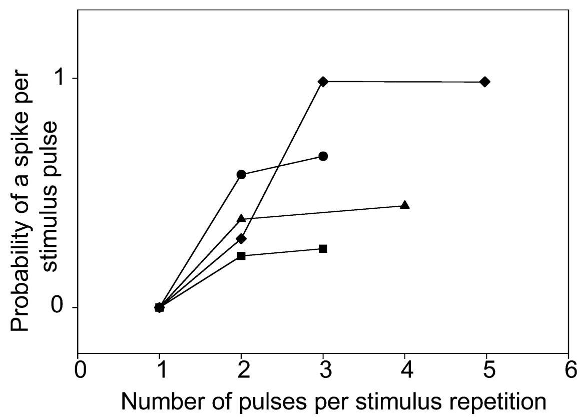

Fig. 3 The mean response per stimulus pulse versus number of pulses in the stimulus for four band-suppression cells. These neurons required only one correct interval to respond. The best PRR at the best carrier frequency was used for each neuron: 80 Hz AM with 600-Hz carrier (*diamonds*); 50 Hz AM with 500-Hz carrier (*circles*); 100 Hz AM with 400-Hz carrier (*triangles*); 70 Hz AM with 300-Hz carrier (*squares*)

latencies of Fig. 4B and Fig. 4D). A 25-ms interval that was inserted between two sets of three pulses still elicited a small response (data not shown).

Temporal distribution of responses to AM stimuli

Across band-suppression neurons, responses at their best rate of AM varied from highly to moderately phasic (Fig. 5A–C). In one case, inter-spike intervals were well matched to the stimulus inter-pulse interval (Fig. 5E). In all other cases, however, there was no match between the predominant inter-spike interval and the inter-pulse interval (e.g., Fig. 5D, F).

Although all but one neuron failed to represent high AM rates in their interspike intervals, temporal encoding of AM rate might still be achieved by the synchronization of spikes to a particular phase of the modulation cycle. At their best rates of AM (maximum response), however, only 2 out of 18 neurons showed significant response synchronization, (median vector strength = 0.114; range = 0.03–0.55) and the two units that did show significant synchronization had relatively low best rates (50 and 60 Hz).

Factors contributing to band-suppression AM selectivity

To gain insight into the factors that determine whether an integration unit will respond at low rates, i.e., whether it is an AM band-suppression type, we compared a cell's interval-integration, AM-tuning, and band-suppression properties (Fig. 6). The magnitude of band-suppression was inversely related to the integration time (interval-number threshold×duration of the optimal interval) of the cell and directly related to how broadly it was tuned at high AM rates ($R^2 = 0.47$, multiple nonlinear regression); a significant portion of the variance in band-suppression magnitude could be accounted for by these two variables ($F_{4,38} = 8.38$, $P < 0.001$); tuning breadth was calculated by dividing the response at half an octave above the optimal rate by the response at the optimal rate. Band-suppression units are clustered in the quadrant that is characterized by short integration times and broad tuning at the high rates. Although band-suppression cells typically had short interval-integration times, the converse was not necessarily true; units that had short integration times, but were sharply tuned to PRR, did not show band-suppression properties. Units that were broadly tuned at high PRRs, but had long interval-integration times, also were not band-suppression types.

Discussion

Based on their response levels to sinusoidal AM stimuli, auditory neurons in the midbrain of anurans have been classified as all-pass, low-pass, high-pass, band-pass or

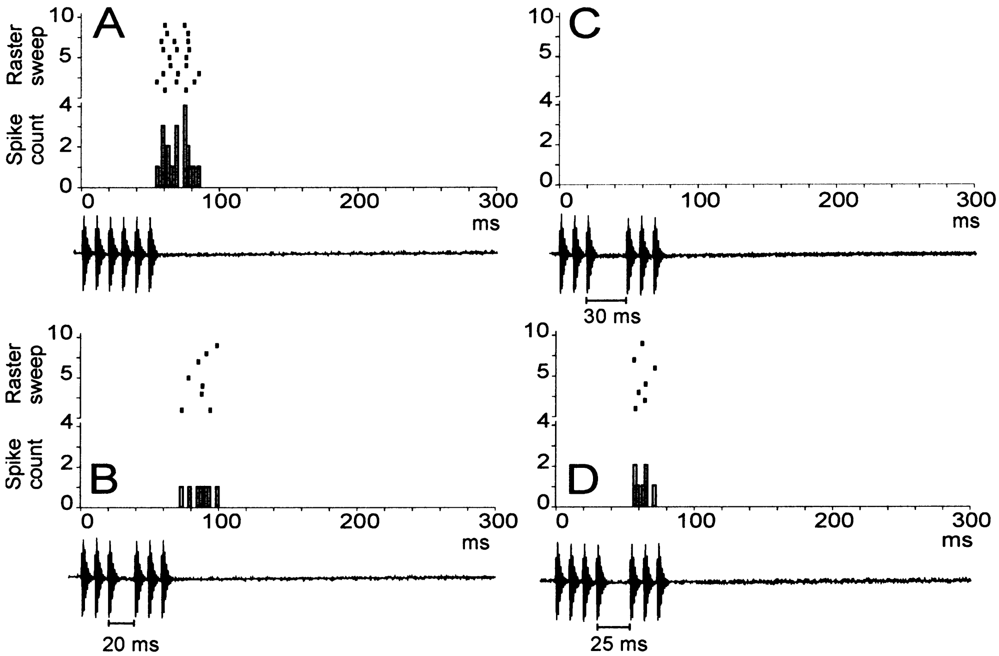

Fig. 4 Raster plots and histograms of the responses of a band-suppression neuron to stimuli (carrier = 800 Hz) consisting of five optimal (10 ms) interpulse intervals (**A**), two sets of two optimal interpulse intervals (three pulses) separated by an interval of 20 ms (**B**) or 30 ms (**C**). **D** Response of the same band-suppression neuron to a series of three optimal intervals followed by two optimal intervals; the two sets were separated by an interval of 25 ms. Three consecutive optimal intervals elicited responses, but the following set of two intervals was ineffective when the long interval was at least 25 ms

band-suppression. It has been unclear whether these different temporal filtering functions are produced by separate or similar mechanisms. We examined the hypothesis that band-suppression neurons, like some band-pass cells, derive their temporal selectivity from an interval-integrating process (Alder and Rose 1998; Edwards et al. 2002). Our results support this hypothesis; band suppression cells, like band-pass neurons that are tuned to high AM rates, responded to short-duration pulses only if a threshold number of consecutive 'correct' interpulse intervals were presented. Consequently, these neurons responded in a high-pass or band-pass manner when PRR was varied and pulse duration was kept constant ($<$ca. 10 ms); band-suppression response characteristics were only observed when pulse duration was varied with AM rate.

Why do band-suppression units respond to low AM rates?

The answer to this question appears to reside in how the interval-integrating properties of band-suppression neurons differ from those of band-pass cells. Relative to AM band-pass cells, band-suppression neurons had low interval-number thresholds and broad tuning at the high AM or PR rates. The latter characteristic indicates that these cells have a relatively large interval tolerance (range of interval values that are effective for a particular neuron). To understand why an integration unit might respond to low SAM rates, first assume that it receives input from an afferent that responds throughout much of each stimulus modulation cycle, i.e., each stimulus pulse, at low rates of SAM (e.g., 5 Hz, Fig. 7A). Next, assume that some of the intervals between successive spikes, and therefore inputs, fall within the interval tolerance limits (assumed to be 5–12 ms) of the interval-integrating cell. Also assume that this integration neuron responds after only two consecutive acceptable intervals have occurred. This condition will be met at low and high AM rates, but not at intermediate rates (50 Hz, Fig. 7A); at intermediate SAM rates, individual pulses elicit fewer afferent spikes. At high AM rates, acceptable interspike intervals occur in the afferent neuron because discharges are phase-locked to the periodicity of the sound pulses (90 Hz, Fig. 7A). Spikes will be elicited in the postsynaptic cell, therefore, when the SAM rate is low or high, i.e., the cell will be a band-suppression type. Further, when only the afferent spikes that occurred during the first 100 ms of response to each presentation of fast PRR stimuli ($>$70 Hz) are considered, the spike-rate versus AM rate function is similar to that shown for band-suppression neurons (compare circles in Fig. 7B and Fig. 1C). Increasing the interval-number threshold (squares in Fig. 7B) or reducing the interval tolerance (diamonds in Fig. 7B) gave rise to a more high-pass function.

Presently it is not known whether the integration process occurs pre- or postsynaptically. In the case of a postsynaptic origin, the model would require that the cell be driven primarily from a single afferent or that multiple afferents have synchronous activity. However, if the integration process occurs presynaptically (e.g., presynaptic facilitation), there would be no requirement for synchronous activity in a multiple input scenario.

Band-suppression neurons that had relatively high interval-number thresholds (i.e., 4–5) also were broadly tuned at high PRRs. We assume that an integration unit's interval tolerance is proportional to the broadness of tuning at high rates; a narrow interval toler-

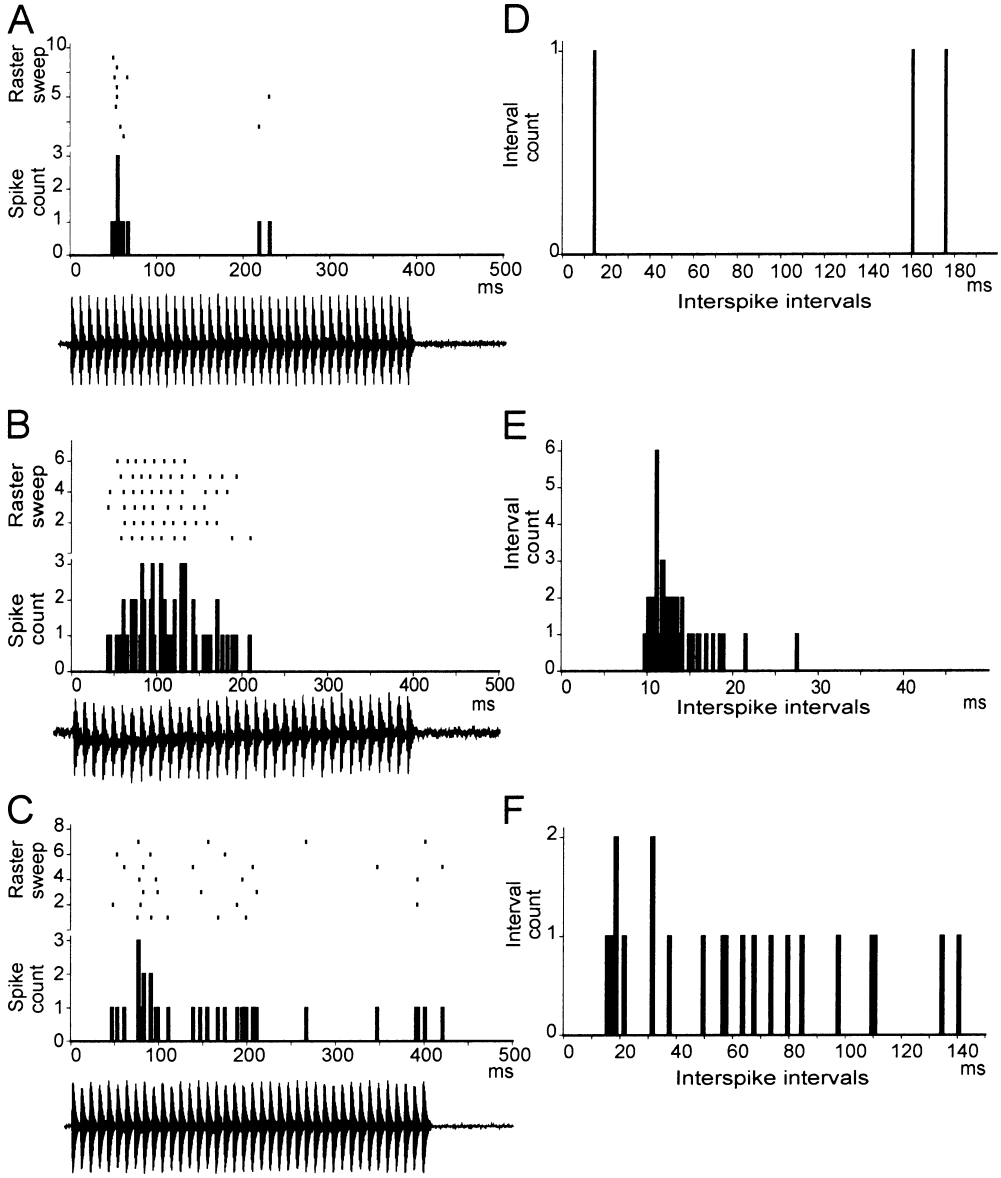

Fig. 5 Raster plots and histograms of the responses of a very phasic unit (**A**), a phasic burster (**B**), and a more tonic unit (**C**). The AM rates were optimal for each neuron: 100 Hz in **A**, 90 Hz in **B**, and 100 Hz in **C** with carrier frequencies of 600 Hz, 600 Hz, and 1500 Hz respectively. **D**–**F** Interspike intervals (ISIs) in the responses of the neurons in **A**–**C**

ance results in sharp tuning at high PRRs. Because these neurons had a broad interval tolerance (Fig. 6), the probability of receiving 4–5 successive acceptable inter-spike intervals at 5–10 Hz SAM was rather good. Conversely, in neurons that have a very narrow interval tolerance, the integration process should be frequently reset by inappropriate inter-spike intervals. Accordingly, cells that had interval-number thresholds of 4–5 and were tightly tuned did not respond to slow rates of SAM, i.e., were not band-suppression types.

Interval-integration and temporal filtering

A question that has been unanswered since the discovery of interval-counting neurons is why many of these cells require six or more consecutive specific intervals in order to respond. What is the advantage of this stringency? A possible answer to this question is that neural temporal selectivity increases with larger interval-number thresholds and narrower interval tolerance. In support of this idea, neurons that have interval-number thresholds of 1 or 2, and broad interval tolerance, respond to single pulses, provided they are of sufficient duration. Consequently, integration units of this type could be erroneously activated by sounds in the frog's environment other than its fast PRR call. Perhaps this mechanism prevents such errors from occurring. Also, cells with larger interval-number thresholds are better able to reject PRRs below their best rate, i.e., have sharper temporal tuning. The requirement for a high number of successive optimal intervals, therefore, makes these neurons much more stringent filters that will be less likely to fire in response to anything but a particular conspecific call.

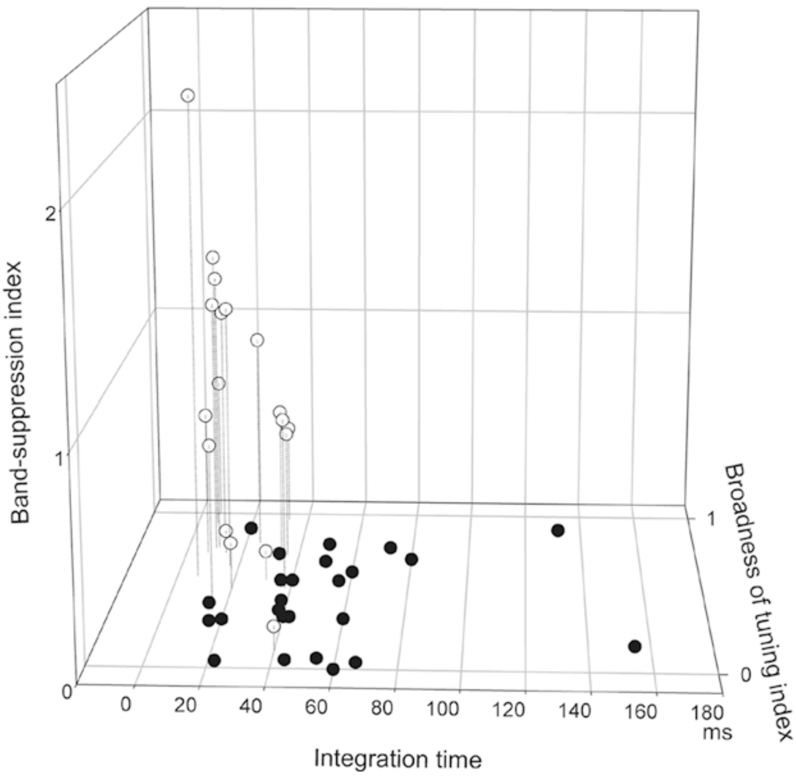

Fig. 6 Degree of band-suppression versus integration time and AM tuning. Data represent neurons that did (*open symbols*) or did not (*closed symbols*) respond to low AM rates. The latter units were AM band-pass. Integration time = interval number threshold×the optimal interval duration. The *Y*-axis represents how broadly tuned a unit was at high AM rates, which was calculated by dividing the response at half an octave above the optimal rate by the response at the optimal rate using the unit's response to natural AM; units that were very broadly tuned at high rates have a value close to 1. The band-suppressive index, a measure of the relative strength of response at low versus high rates, was calculated by dividing the response at the best low rate by the response at the best high rate; integration units that were not band-suppression types had a value of zero

The role of band-suppression neurons in behavior

Because band-suppression neurons respond well to fast PRRs, such as that of the advertisement calls of *H. regilla*, the question arises as to whether these neurons play a role in the process of advertisement call recognition. 'Cross-accommodation' (Brenowitz and Rose 1994; Rose and Brenowitz 1997) studies of Pacific tree frogs showed that stimuli consisting of alternating advertisement and encounter interpulse intervals produced small, but significant, elevations of aggressive thresholds to advertisement calls (Rose and Brenowitz 2002). Because many band-suppression neurons respond after just one to two intervals, it seems likely that they might account for these small threshold elevations. Most interval-integrating neurons have interval-number thresholds of 6 or more, and, therefore, do not respond to this stimulus; thus, it is not surprising that only small thresholds elevations are induced. These behavioral data suggest that band-suppression neurons contribute to recognition of advertisement calls.

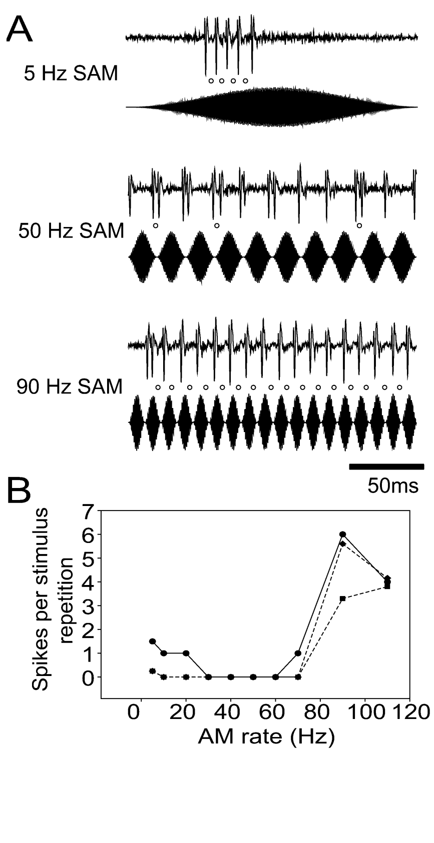

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Fig. 7A, B Model of a band-suppression neuron. **A** Responses of a unit to 5, 50 and 90 Hz sinusoidal amplitude modulation. The hi-pass selectivity of this cell for sinusoidal amplitude modulation (SAM) is similar to that of afferents from the dorsal lateral nucleus. This assumption is strengthened by the fact that this unit was able to phase-lock to AM rates up to 200 Hz, which is atypical for neurons in the torus. ISIs that were within an interval-tolerance window of 5–12 ms are denoted by *open circles*. **B** Spike output of the model versus rate of SAM. Each occurrence of two consecutive ISIs that fell within the tolerance window was assumed to generate a spike in the interval-integrating neuron. At the high rates (e.g., above 70 Hz) only the first 100 ms of the stimulus was analyzed, to reflect the phasic response properties of band-suppression neurons, e.g., Fig. 4. For an interval-tolerance window of 5–12 ms, the model exhibited band-suppression properties (*circles*). A requirement of four consecutive intervals of 5–12 ms (*squares*) or a requirement of two consecutive intervals of 8–12 ms (*diamonds*) almost completely abolished responses to low rates

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