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Temporal Pattern Recognition Based on Instantaneous Spike Rate Coding in a Simple Auditory System

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Nabatiyan, A., J.F.A. Poulet, G. G. de Polavieja, and B. Hedwig.
Temporal pattern recognition based on instantaneous spike rate coding in a simple auditory system. *J Neurophysiol* 90: 2484–2493, 2003; 10.1152/jn.00259.2003. Auditory pattern recognition by the CNS is a fundamental process in acoustic communication. Because crickets communicate with stereotyped patterns of constant frequency syllables, they are established models to investigate the neuronal mechanisms of auditory pattern recognition. Here we provide evidence that for the neural processing of amplitude-modulated sounds, the instantaneous spike rate rather than the time-averaged neural activity is the appropriate coding principle by comparing both coding parameters in a thoracic interneuron (Omega neuron ON1) of the cricket (*Gryllus bimaculatus*) auditory system. When stimulated with different temporal sound patterns, the analysis of the instantaneous spike rate demonstrates that the neuron acts as a low-pass filter for syllable patterns. The instantaneous spike rate is low at high syllable rates, but prominent peaks in the instantaneous spike rate are generated as the syllable rate resembles that of the species-specific pattern. The occurrence and repetition rate of these peaks in the neuronal discharge are sufficient to explain temporal filtering in the cricket auditory pathway as they closely match the tuning of phonotactic behavior to different sound patterns. Thus temporal filtering or "pattern recognition" occurs at an early stage in the auditory pathway.

INTRODUCTION

The processing of temporal patterns of amplitude-modulated sound by the CNS is fundamental to acoustic communication (Pollack 2000, 2001). Neurophysiological studies on temporal processing in auditory pathways are generally based on the evaluation of spike times or average neuronal spike rates [e.g., Eggermont 2001; Langner and Schreiner 1988 (cat); Kuwada and Batra 1999 (rabbit); Grothe et al. 1997, 2001 (bat); Condon et al. 1991; Penna et al. 1997; Rose and Capranica 1985; (frog); Rheinlaender et al. 1976; Wohlers and Huber 1982 (cricket), Surlykke et al. 1988 (moth)]. An analysis of spike rates averaged over long time periods neglects the dynamics of the instantaneous neuronal spike rate as a coding principle for neuronal signal processing. The instantaneous spike rate, however, is crucial for temporal summation of postsynaptic potentials, and its importance is becoming more evident (Koch 1999). Moths evade bat cries when the afferent spike rate reaches ~500 Hz (Roeder 1964). Afferent axons in the auditory system of the grasshopper (Machens et al. 2003), neurons in the electro-sensory pathway of weakly electric fish (Wessel et al. 1996) and neurons in the primary visual cortex (Reich et al. 2000) encode information using high instantaneous spike rates of ≥200 Hz. Here we take advantage of the simple behavior and auditory system of crickets and consider the instantaneous spike rate of auditory interneurons as a coding principle underlying pattern recognition in the auditory pathway.

As part of their mating behavior, male crickets produce loud calling songs and the females phonotactically walk or fly toward the singing males. Female phonotaxis is tuned to the temporal pattern of the species-specific song (Doherty 1985a; Pollack and Hoy 1979; Popov and Shuvalov 1977; Stout et al. 1983; Thorson et al. 1982). Behavioral results have led Thorson et al. (1982) to formulate a "30-Hz hypothesis", claiming that the 30-Hz syllable repetition rate is both sufficient and necessary for the release of phonotactic behavior in *Gryllus campestris*. However, because variations in chirp rate, syllable rate, and syllable number modify the attractiveness of the sound pattern in *G. bimaculatus* and *Acheta domesticus,* a more complex multicomponent analysis underlying pattern recognition has been suggested (Doherty 1985b; Stout and McGhee 1988; Stout et al. 1983).

The auditory pathway of crickets is well described (Ball et al. 1989; Michelsen 1998; Pollack 1998; Schildberger et al. 1989). From the cricket ears in the front tibiae, ~60 primary afferents project into the prothoracic ganglion. The afferent input activates several different types of local, ascending, descending, and T-shaped auditory interneurons (Atkins and Pollack 1987; Popov and Markovich 1982; Popov et al. 1978; Wohlers and Huber 1978, 1982). Besides some evidence for low-level temporal filtering (Pollack 1986; Stabel et al. 1989; Wiese and Eilts 1985), it is assumed that these prothoracic interneurons are not involved in temporal filtering of the auditory pattern (Huber 1983; Schildberger et al.1989; Wohlers and Huber 1982). The ascending interneurons are thought to copy the temporal structure of auditory stimuli and then forward this information to the brain. In the brain, serial processing by interneurons with low- and high-pass filter properties is thought to drive local brain neurons tuned to the species-specific sound pattern (Schildberger 1984; Schildberger et al. 1989). The conclusion that thoracic neurons just copy the

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sound pattern was based on evaluating the overall number of spikes elicited by different chirp patterns (Wohlers and Huber 1982). In our experiments, we challenged the preceding conclusion by analyzing the instantaneous spike rates of the local Omega neurons (ON1) (Casaday and Hoy 1977; Popov et al. 1978; Wohlers and Huber 1978) as the relevant coding principle for sound processing and conspecific pattern recognition.

METHODS

Specimen source

Female *G. bimaculatus* were taken from the departmental colony at a minimum age of 7 days after final moulting. The colony was fed with dried dog food and water and kept at 24°C with a LD 12:12.

Dissection and recordings

Prior to dissection the animals were cooled for a maximum of 30 min at 4°C. The crickets were then fixed ventral side up on Plasticine. The hind and middle legs were tethered with metal clamps and the front legs stabilized in an upright position; care was taken not to obstruct the tympana. Experiments were performed at a temperature of 21–23°C.

For extracellular recording of the summed auditory afferent activity, the cuticle of the distal femur was opened. The dorsal branch of the leg nerve (Nocke 1972) was positioned on a pair of 125-μm silver wires and insulated with petroleum jelly. Signals were amplified and band-pass filtered (100–3,000 Hz).

Intracellular recordings were obtained from the prothoracic ganglion. The ventral connective membranes and the cuticular structures between the head and the mesothoracic sternites were removed. The prothoracic ganglion was positioned on a 0.5-mm-diam platform and stabilized by a minute ring pressing gently on its ventral surface. Intracellular recordings with micro capillaries of 80–120 MΩ resistance were obtained from an ON1 in its axonal or dendritic branches. Generally the axonal recordings were found to be more stable and less sensitive to hyperpolarizing current injections. The neurons were identified by iontophoretic staining with Lucifer yellow but could always easily be recognized by their typical response patterns (Wiese and Eilts 1985). After the experiments the ganglia were dissected, fixed in 4% para-formaldehyde, dehydrated in ethanol, and cleared in methyl-salicylate and finally the staining was checked under an epifluorescence microscope.

Sound stimulation

Sound patterns with a carrier frequency of 4.8 kHz were used that were identical to the patterns of previous phonotactic experiments (Thorson et al. 1982). Chirps were 250 ms in duration and were repeated at 500-ms intervals. Different chirp patterns had a different syllable period (SP), which increased in steps of 8 ms from 10 to 98 ms and had a 50% duty cycle (Fig. 1*A*). Thus at SP42, the syllable period was 42 ms and the syllable duration (SD) and silent period were 21 ms. All syllables had a rising and falling ramp of 2 ms. Sound was presented from two speakers housed in a 17-cm brass tube, the opening of which was positioned 20 mm away from the posterior tympanum of an ear. Intensity was calibrated to 75 dB SPL (RMS, sound pressure level relative to 20 μPa) at the position of the cricket ear with a Bruel&Kjaer microphone (Type 4191) and measuring amplifier (Type 2610). Twelve chirp patterns each with a different SP were consecutively presented for 5 s, and the whole paradigm with all 12 patterns was repeated in a continuous loop for ≥600 s. In some experiments, sound pulses of 250-ms duration were used instead of chirps. All acoustic stimuli were computer generated at a sampling rate of 22.05 kHz using Cool Edit 2000 and were presented using standard audio boards.
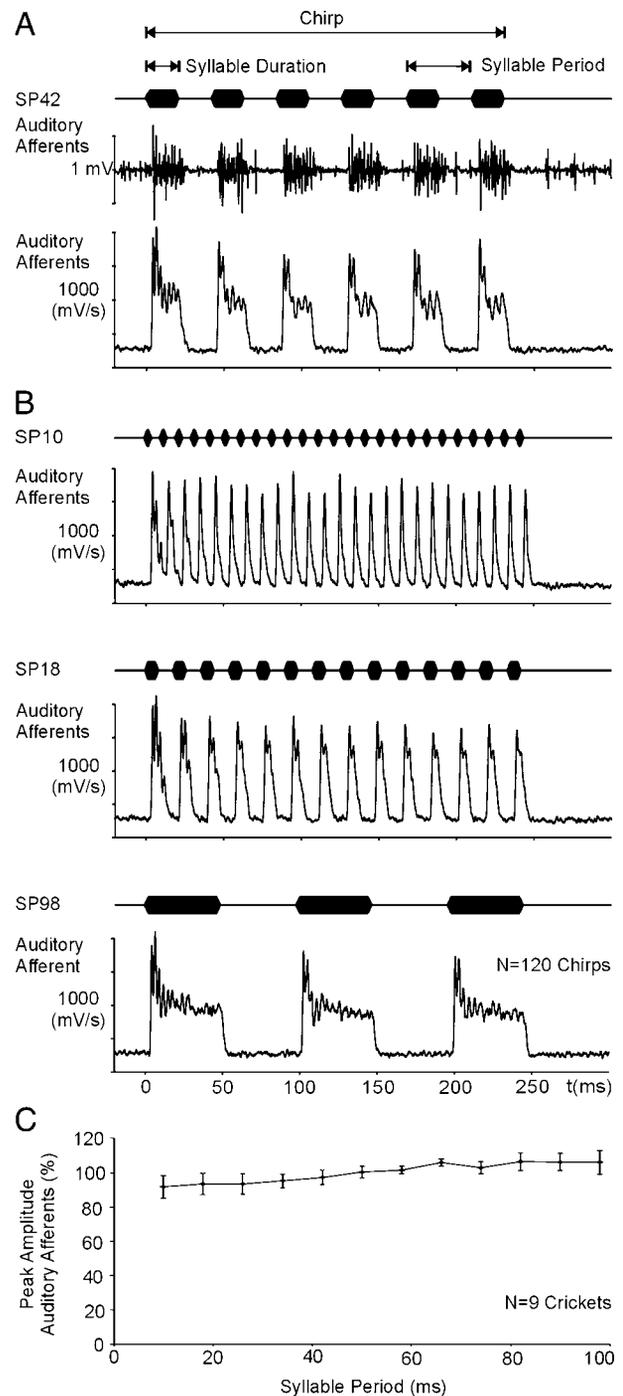

FIG. 1. Summed response of the auditory afferents to sound stimuli of different syllable periods (SP). *A*: response of the afferents (*middle*) when stimulated with the species-specific SP of 42 ms (*top*) and averaged response after the absolute voltage change of the summed nerve recording ($\Sigma|dV|/dt$) was calculated (*bottom*). *B*: sound stimuli (*top*) and averaged afferent response (*bottom*) to SP10, SP18, and SP98. *C*: peak response of the auditory afferents to stimulation with different syllable periods. Data pooled from 9 crickets and peak responses normalized to the mean (100%). All averages based on 120 chirps.

Data recording and analysis

Neuron recordings and sound patterns were sampled on-line to the hard disk of a PC using a National Instruments AD board (PC-MIO-16E-4) controlled by custom-made software written in LabView 5.01. Amplitude resolution was 12 bit, corresponding to increments 0.03

mV for the intracellular recording. The sampling rate was set to 10 kHz per channel. Data analysis was done off-line using the software NEUROLAB (Hedwig and Knepper 1992). As a measure of the auditory afferent response, the absolute voltage change of the summed nerve recording ($\Sigma|dV|/dt$) was calculated within a time window of 1 ms, which was continuously sliding in steps of 100 μs along the recording (Meyer and Hedwig 1995). This algorithm is not sensitive to DC offsets of the recording and takes into account the full amplitude of spikes even when they cross the baseline. The instantaneous spike rate, given by the number of spikes in a time interval divided by the length of the interval when this interval is small, can be calculated either fixing the time bin length and counting the number of spikes in these bins or fixing the number of spikes per bin and then using variable bin lengths. Both procedures give analogous results when the time bin lengths are comparable. We use the second method with a single spike per bin, also known as instantaneous discharge rate. The instantaneous spike rate of ON1 was calculated as the inverse of the duration of each interspike interval, e.g., if the interval was 5 ms, the instantaneous spike rate was 200 Hz. The value of 200 Hz was then assigned to that interspike interval (Hedwig and Knepper 1992; Janiszewski and Otto 1989). A Gaussian smoothing was not used to preserve the full dynamic of the instantaneous spike rate. Averages of spike rates across many trials used the beginning of chirps as the temporal reference point. Data of single experiments were exported from NEUROLAB to Excel for further pooled analysis.

RESULTS

Analysis of primary afferent activity

We first focused on the response pattern of the 60 primary auditory afferents. The synchronous activation of auditory afferents is reflected in the amplitude of extracellular recordings of the auditory nerve. When a chirp pattern similar to the species-specific calling song (SP 42 ms, SD 21 ms) was presented, the auditory afferents responded with bursts of spikes (Fig. 1*A*). These summed up to a typical extracellular multiunit recording with a phasic-tonic response. The dynamics of the response became obvious when we filtered and then averaged the afferent activity (see METHODS). The averaged response demonstrated a pronounced synchronous activity of the primary afferents triggered by the beginning of the syllables. The initial afferent response lasted for ~5–10 ms and subsequently dropped to a tonic level of ~50% of the initial peak. We systematically varied SP from 10 to 98 ms and quantitatively analyzed the afferent response pattern (Fig. 1*B*). At SP10 and SP18, the primary afferents clearly responded with phasic synchronized activity to all the individual syllables of a chirp. At SP98, the phasic-tonic response was similar to the response at SP42 with an initial peak activity triggered by the beginning of each syllable and a decline in activity to a tonic level after 5–10 ms. For nine of the crickets, we analyzed the amplitude of the peak response to the syllables of each sound pattern and pooled the results (Fig. 1*C*). The peak response showed a slight increase in peak amplitude by 10% from SP10 to SP98, although this summed activity of the auditory afferents was not tuned to any particular sound pattern. The population of afferents marked the onset of syllables, and this onset response was independent of syllable duration. This effect has a significant consequence for the coding of sound patterns. The overall duration of sound presented during the paradigms was similar for all SPs, but the number of afferent peak responses was not and corresponded to the number of syllables presented in each of the chirp patterns.

Analysis of interneuron spike activity

We studied the response properties of a prothoracic local auditory interneuron, the Omega neuron (ON1) with intracellular recordings. The ON1 neurons form mutual inhibitory connections (Selverston et al. 1985). They are involved in signal-to-noise filtering (Pollack 1988) and directional information processing (Wiese and Eilts 1985). We stimulated the ON1 neurons with the same stimulus paradigms as the auditory afferents.

When a chirp pattern with SP42 ms was presented, each syllable elicited a burst of spikes in the interneuron after a latency of ~22 ms (Fig. 2*A*).

The instantaneous spike rate (see METHODS for details of calculation) gave a stair-like function (see Fig. 6*C*) that could be averaged over many trials to reveal the dynamics of the neuronal response (Fig. 2*A, bottom*). The instantaneous spike rate of ON1 changed distinctly in response to each syllable, and peak rates of 250–300 Hz were reached at the beginning of each response. The spike rate peak then produced a shoulder-like effect (Fig. 2*A*, ▲) and rapidly declined to a background value that was determined by the last spike of a burst and the consecutive first spike of the next burst (Fig. 2*A*, *). The instantaneous spike rate of ON1 represented each syllable of the sound pattern as a distinct and rapid change in spike activity and matched the afferent input into the auditory pathway (see Fig. 1*A*).

In a similar manner, we analyzed the response of ON1 to all the other chirp patterns. At SP10 (Fig. 2*B*), the averaged instantaneous spike rate revealed just a tonic response of the neuron as the syllable pattern was not reflected in the timing or instantaneous spike rate. At SP18, the instantaneous spike rate reached 280 Hz after the first syllable. The response to each consecutive syllable then rapidly declined, and the representation of the syllables in the instantaneous spike rate progressively deteriorated (Fig. 2*C*). Near the end of the chirp, the neuron responded only with one to two spikes per syllable, and therefore its instantaneous spike rate in response to the syllables was only little higher (30 Hz) than the background caused by the syllable repetition rate. Thus at high syllable repetition rates, ON1's dynamic response is quite different to the summed afferent response (compare with Fig. 1*B*). Although the syllable pattern is clearly resolved at the summed primary afferent level, the afferent information is processed with the result that the syllable pattern is not reflected in the instantaneous spike rate of ON1. Evaluating the SP98 response (Fig. 2*D*) once again demonstrated a phasic-tonic interneuron response with a pronounced initial peak of ~300 Hz, which rapidly declined to ~140 Hz.

Evaluation of spikes/chirp versus instantaneous spike rate

In previous studies on thoracic auditory interneurons, the number of action potentials per chirp had been evaluated to analyze the coding properties of auditory interneurons but not the instantaneous spike rate (Huber 1983, Fig. 16C; Wohlers and Huber 1982, Fig. 10). From the ON1 data sets of 12 crickets, we calculated the number of spikes elicited by each of the chirp patterns as well as the maximum of the instantaneous spike rate averaged over many trials evoked by the syllables of each pattern. Both parameters were

A: SP42
ON1
ON1 (AP/s)
Chirps=100
AP=2090
40 mV

B: SP10
Omega (AP/s)
Chirps=100
AP=1214

C: SP18
Omega (AP/s)
Chirps=100
AP=1870

D: SP98
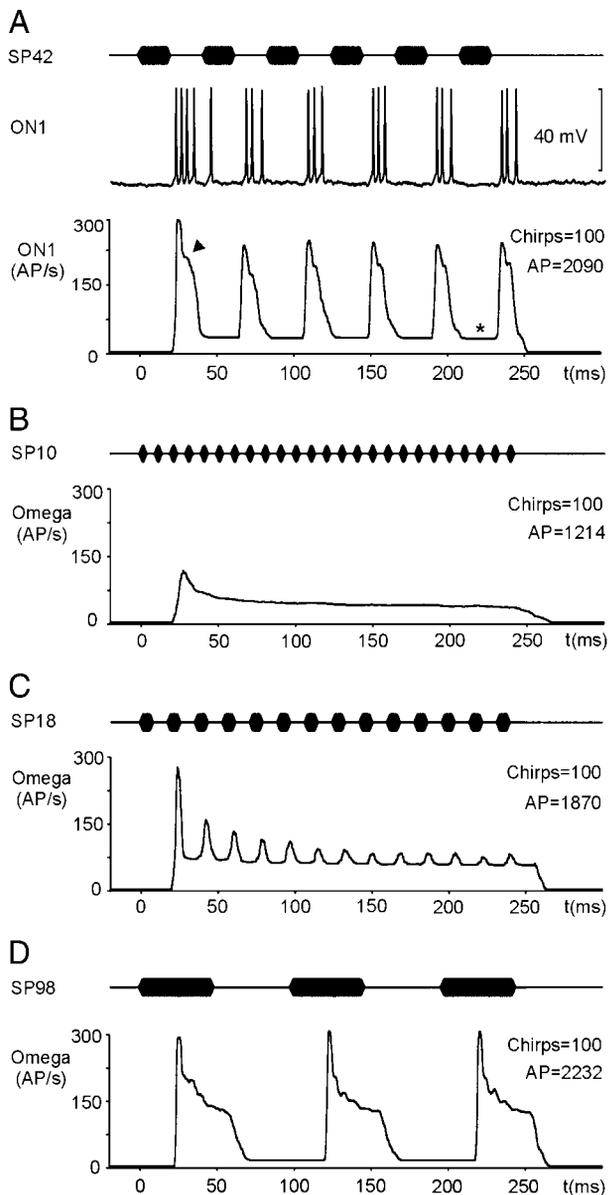Omega (AP/s)
Chirps=100
AP=2232

FIG. 2. *A*: axonal intracellular recording of Omega neuron (ON1, *middle*) when stimulated with the species-specific SP of 42 ms (*top*). Instantaneous spike rate of ON1 (*bottom*) averaged over 100 chirps. *B–D*: response of an ON1 to sound patterns with different SP. *B*: a tonic response that does not reflect the syllable pattern is indicated by the averaged instantaneous spike rate when ON1 is stimulated with SP10. *C*: presentation of SP18 yields spike rate peaks of diminishing amplitude. *D*: stimulation with SP98 demonstrates at the beginning of each response a sharp maximum in the instantaneous spike rate. All averages are based on 100 chirps.

plotted against the SP (Fig. 3). The number of spikes per chirp varied between 17 action potentials (APs)/chirp at SP10 to 23 APs/chirp at SP58. This variation can easily be explained by the stimulus design in which an integer number of syllables is fitted into 250-ms chirps. As a consequence, the overall duration of sound presented in each of the 12 chirp patterns was not identical. For example, there was 120 ms of sound for SP50 but 145 ms for SP58 although both patterns contain the same number (5) of syllables. These differences in the overall duration of the sound presented were reflected in the small variations of the number of APs/chirp (Fig. 3*A*). In spite of this, there was still no

apparent correlation between the stimulus patterns and this parameter of the neuronal response.

Plotting the maximum instantaneous spike rate against the SP patterns revealed a continuous increase in the maximum spike rate from 65 APs/s at SP10 to 240 APs/s at SP50 (Fig. 3*B*). The instantaneous spike rate of ON1 reached its maximum when the SP attained a value similar to the species-specific value of 42 ms. The maximum spike rate then stayed almost constant at 240 APs/s between SP50 and SP98. Such a response pattern with low discharge rate responses to short SPs represents a low-pass filter for syllable patterns.

Calculating neuronal tuning from instantaneous spike rate peaks

From our results we concluded that the syllables of the chirp pattern were reflected in the peaks of the instantaneous spike rate. As a consequence, the coding of the syllables in the spike rate of auditory interneurons should be sufficient to explain the tuning of cricket phonotaxis.

The relevance of instantaneous spike rate peaks has to be considered in the context of phonotactic behavior. The threshold for phonotaxis decreases with sexual maturation of the females (Sergejeva and Popov 1994) and phonotactic behavior occurs more frequently when females are male-deprived (Cade 1979). Within 1 h after copulation, the opposite happens and females become unresponsive, but phonotaxis can be restored when the abdominal connectives are cut (Loher et al. 1993). These results raise the question of whether changes in behavior correspond to changes in the activity of auditory neurons or whether they are related to threshold changes at the sensory-
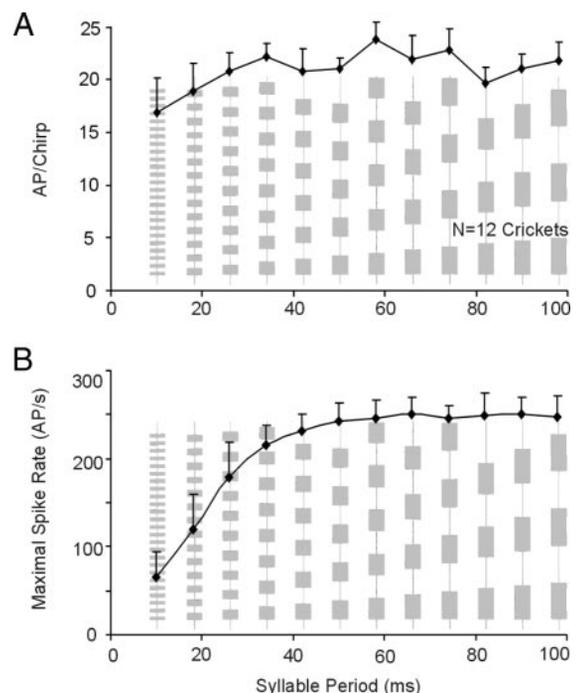

FIG. 3. *A*: number of action potentials (AP) elicited per chirp plotted against the SP. The erratic change in the curve corresponds to differences in the overall duration of the sound pattern presented at different SPs. *B*: average maximal peak spike rate of ON1 as elicited by the syllables of each of the different sound patterns. Normalized and pooled data from 12 crickets.

motor interface that drives phonotactic walking. There are contradictory reports on activity changes in auditory interneurons during sexual maturation (Loher et al. 1992; Sergejeva and Popov 1994; Stout et al. 1991). The restoration of phonotaxis after cutting the abdominal connectives may point toward a direct mechanosensory control of the motor networks by ascending abdominal activity. In any case, the auditory activity has to overcome a threshold for the release of phonotactic behavior. At present, the interaction between the activity of auditory neurons and the threshold for phonotaxis is not known, and we cannot discriminate between changes in threshold or changes in auditory activity. The authors are fully aware that therefore an analysis of what effect different thresholds have on the tuning of phonotactic behavior can only be obtained empirically. To calculate the tuning of the neuronal discharge activity, we consequently assumed several different instantaneous spike rate thresholds for the release of phonotaxis. As thresholds we used 180, 200, 212, and 225 Hz, which cover the range from 72 to 90% of the maximum ON1 response.

The calculation of the mean number of instantaneous spike rate peaks above a given threshold in a chirp can be performed directly by counting those peaks in different trials. We use an alternative method simply multiplying the probability that each syllable elicits spike rate peaks that reach a certain threshold by the number of syllables in a chirp. The probability to reach a spike rate peak above a threshold in a syllable is obtained using the variances in the instantaneous spike rate-tuning curves of ON1 (Fig. 3*B*) and approximating the distributions by Gaussians. The average number of spike rate peaks above a threshold of 200 Hz is given in Fig. 4, *B* and *C*. There are practically no syllables triggering an instantaneous spike rate of 200 Hz at SP10 and SP18 (Fig. 4*C*). There was then a steep increase in the number of syllables eliciting an instantaneous spike rate of 200 Hz, and the maximum was reached at SP34 with 6.2 discharge peaks and SP42 with 5.7 discharge peaks. The number of spike rate peaks then gradually dropped following the number of syllables constituting a chirp to about three at SP98. This result is indicative of an active band-pass filter with the maximum number of spike rate peaks reaching 200 Hz in accord with the species-specific sound pattern. In this calculation, the different syllable repetition rates were not taken into account. For instance, SP50 and SP58 both contained five syllables; however, the syllable repetition rate for SP50 was 20 Hz and for SP58 it was 17.2 Hz. The intervals between the spike rate peaks, however, might have considerable effects on temporal summation in the auditory pathway. If the number of discharge peaks reaching 200 Hz additionally was multiplied with the peak frequency, the result produced a band-pass function with a sharp rise to an optimum at SP34 and a slow gradual decrease in amplitude toward SP98 (Fig. 4*D*). Thus the tuning of this band-pass results from two principle variables: the increase in the instantaneous spike rate when SP increases from 10 to 42 ms and the decrease in the number of discharge peaks and the peak frequency elicited by each chirp pattern when SP increases from 42 to 98 ms.

The optimum curve obtained depended on the initially chosen threshold to be reached by the spike rate. In the next step we used different thresholds of 180, 200, 210, and 225

Hz and calculated the corresponding tuning curves (Fig. 5*A*). If the calculation was done for a low threshold (180 Hz), the resulting maximum was higher and shifted toward SP34. With increasing threshold the amplitude of the maximum decreased, the tuning curve became more broad and shifted to longer syllable periods. With a threshold of 225 Hz, the optimum of the tuning curve was at a SP of 50 ms. Thus our empirical choice of different thresholds resulted in a range of different neuronal tuning curves.

We then examined to what degree the calculated tuning curves fitted the observed phonotactic behavior. Data of the phonotactic performance of *G. bimaculatus* walking at 22°C (Doherty 1985a; Schildberger 1985) were used to compare the calculated tuning curves with the behavior. In these behavioral tests, syllable periods of 20–80 ms with corresponding syllable numbers had been tested. If a threshold level of 212 Hz was assumed (Fig. 5*B*), there was congruence between the calculated tuning and the performance of phonotactic walking. Both curves had an almost identical onset; both peaked at SP42 and then declined gradually toward longer SP. The close match between the calculated tuning curve based on neural instantaneous spike rates and the observed phonotactic behavior is consistent with three conclusions. First, phonotactic behavior obviously scales with the product of peak frequency *and* the number of spike rate peaks that reach a certain threshold. This means, e.g., that five syllables presented at 20 Hz are more effective than at 17.2 Hz. Second, changes in the magnitude of the phonotactic response will occur when one of these parameter changes. Third, the data indicate that phonotactic walking may be driven directly by the discharge peaks coding the syllable pattern.

Responses to tone bursts of chirp duration

Female *G. bimaculatus* not only tracked the species-specific syllable pattern, but ~40% also oriented toward tone bursts of chirp duration (Doherty 1985b; Tschuch 1977). Because these sound pulses do not contain any syllable pattern, the orientation toward them is not explained by the properties of the proposed pattern recognition system in the brain (Schildberger 1984). We therefore analyzed the instantaneous spike rate of the neuronal response to such stimuli.

ON1 responded to a 250-ms constant tone burst with a phasic-tonic depolarization (Fig. 6*A*). The instantaneous spike rate averaged over many trials showed an initial peak of 310 Hz, which then rapidly declined to a tonic level of ~155 Hz with no obvious modulation (Fig. 6*B*). If, however, an individual ON1 response was considered, the spiking of the neuron was not as regular as indicated by the average, and the variability in the neuron's instantaneous spike rate became evident (Fig. 6*C*). After the initial onset response, pairs and triplets of spikes occurred that caused transient peaks in the instantaneous spike rate that exceeded 250 Hz (Fig. 6*C* ↓). We measured the time intervals between those consecutive spike rate peaks that reached ≥212 Hz (Fig. 6*D*). The frequency distribution of the peak intervals had its maximum at 10 ms and then tailed off to about 45 ms. Longer intervals occurred only with a low probabil-
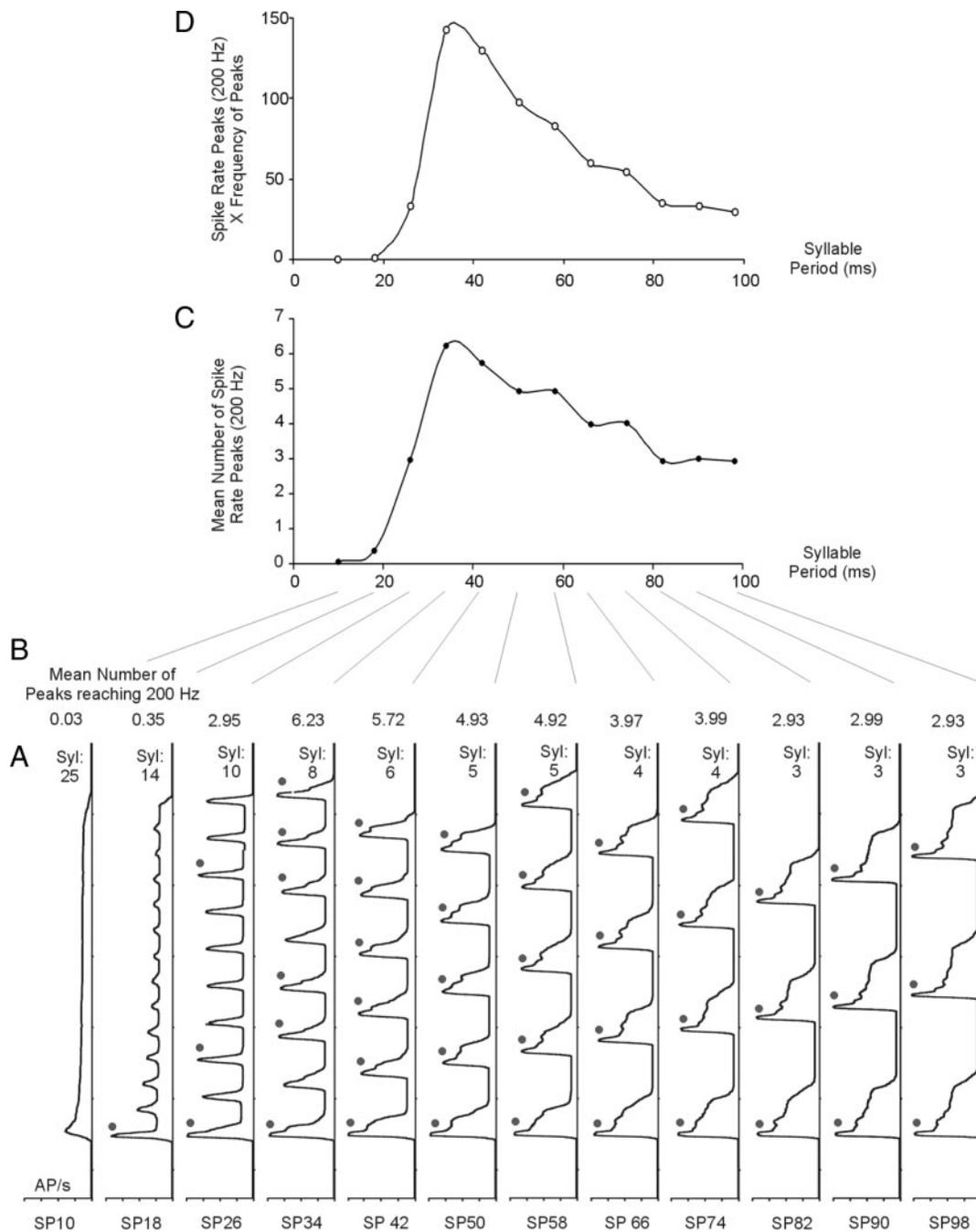
FIG. 4. Calculation of the neuronal tuning corresponding to phonotactic behavior as based on instantaneous spike rate coding. From *bottom* to *top*: *A*, the instantaneous spike rate response of an ON1 to all different SP tested. Time is indicated on the vertical axis. For all stimulus patterns, the number of syllables per chirp is indicated at the upper end of the averages. All spike rate peaks reaching 200 Hz are indicated by a dot. *B*: table with the mean number of spike rate peaks reaching 200 Hz for all crickets tested. *C*: number of spike rate peaks reaching 200 Hz plotted against the SPs. The number of spike rate peaks increased to a maximum at SP34 and then decreased in a step like manner to 3 at SP98 closely following the number of syllables per chirp. *D*: the number of spike rate peaks as given in *C* is multiplied by the frequency of the spike rate peaks and a band-pass tuning curve similar to the tuning of phonotactic behavior is obtained.

ity. The mean value for the spacing of the discharge peaks was 24.4 ms (SD 15.3 ms), which corresponds to a syllable period of 48.8 ms. The mean value was different if different thresholds for the discharge rates were considered. As a consequence, however, even during tone bursts of chirp duration, there was variation in the neuronal discharge activity that led to a statistical pattern of high discharge peaks that was very close to the maximum of *G. bimaculatus* phonotactic tuning curve (compare with Fig. 5*B*) and may therefore be sufficient to release and drive phonotactic behavior.

DISCUSSION

The simple patterns of cricket songs offer the opportunity to understand the neural principles underlying auditory pattern recognition. Here we present evidence that auditory
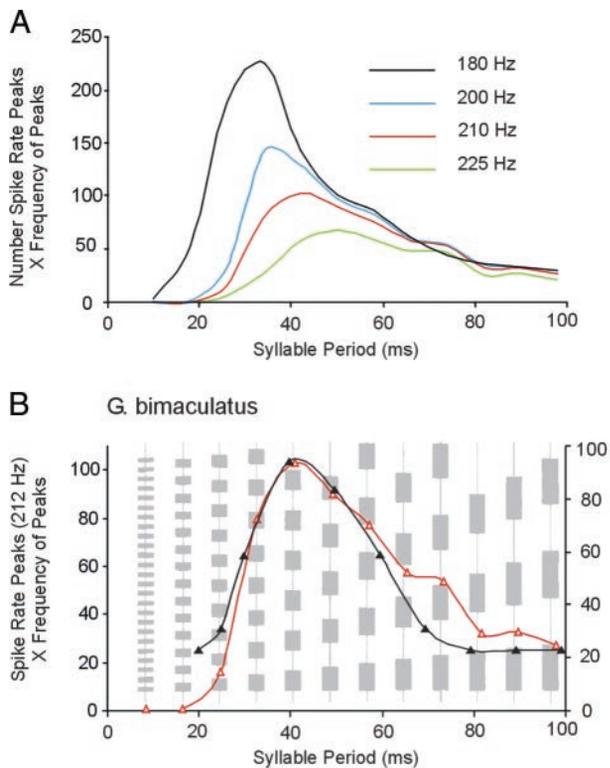
FIG. 5. Comparison of calculated tuning curves with the tuning of phonotactic behavior. *A*: calculated neural tuning curves for thresholds of 180 Hz (black), 200 Hz (blue), 210 Hz (red), and 225 Hz (green). With increasing threshold, the peak of the tuning curve drops and shifts to longer syllable periods. *B*: tuning of phonotaxis in crickets walking at 22°C (black line, closed symbols) and calculated neural tuning for discharge peaks of 212 Hz (red line, open symbols). Data for *G. bimaculatus* phonotaxis are redrawn from Doherty (1985a, Fig. 9).

afferents act as syllable-onset detectors and that the dynamics of a low-order auditory interneuron discharge activity is sufficient to explain the temporal tuning of cricket phonotaxis without the need for a higher order framework for recognition.

Afferent activity

The synchronous activity encountered in the summed recordings of the auditory afferents demonstrates that high and low syllable repetition rates are equally coded. In agreement with Esch et al. (1980), there seems to be no afferent tuning to syllable period. However, final conclusions about temporal filtering at the afferent level will have to be based on an analysis of the instantaneous spike rate of single afferents. In contrast to previous data describing tonic afferent activity (Esch et al. 1980), the summed afferent activity showed a strong phasic-tonic onset-response and marked the beginning of a syllable with a peak of synchronous activity. We conclude that the auditory afferents act as syllable-onset detectors. Interestingly, the duration of the syllables is not relevant for phonotaxis. Cricket phonotaxis can be released by syllables of only 2-ms duration and by duty cycles of 90% if presented at an optimum syllable rate (Thorson et al. 1982). Taken together, the behavioral experiments and the afferent data strongly indicate that the crucial and important coding of syllables occurs at their onset and that any further extension of sound pulses is not relevant for phonotaxis.

Instantaneous spike rates versus time-averaged spike rates

Our analysis of the number of spikes per chirp does not reveal a preferential response of the auditory ON1 neuron to any syllable pattern. Based on similar results, Wohlers and Huber (1982) concluded that thoracic neurons do not act as temporal filters for pattern recognition but merely relay any sound pattern up to the brain (Huber 1983). However, an analysis of neuronal activity by the number of spikes per chirp neglects the temporal dynamics of the neuronal response. Temporal filtering in the auditory pathway, however, must emerge from the *continuous* flow of afferent information in time. For the evaluation of this information by postsynaptic neurons, a temporal reference like the stimulus onset is not available. Surprisingly, we have noted that coding by instantaneous spike rate has been almost completely neglected in studies that analyze the activity patterns of vertebrate and invertebrate central auditory interneurons, although it is fundamental to temporal summation of postsynaptic potentials. Generally PST histograms with bins smaller than the interspike interval were derived from the overall neuronal response [e.g., Eggermont 2001; Langner and Schreiner 1988 (cat); Kuwada and Batra
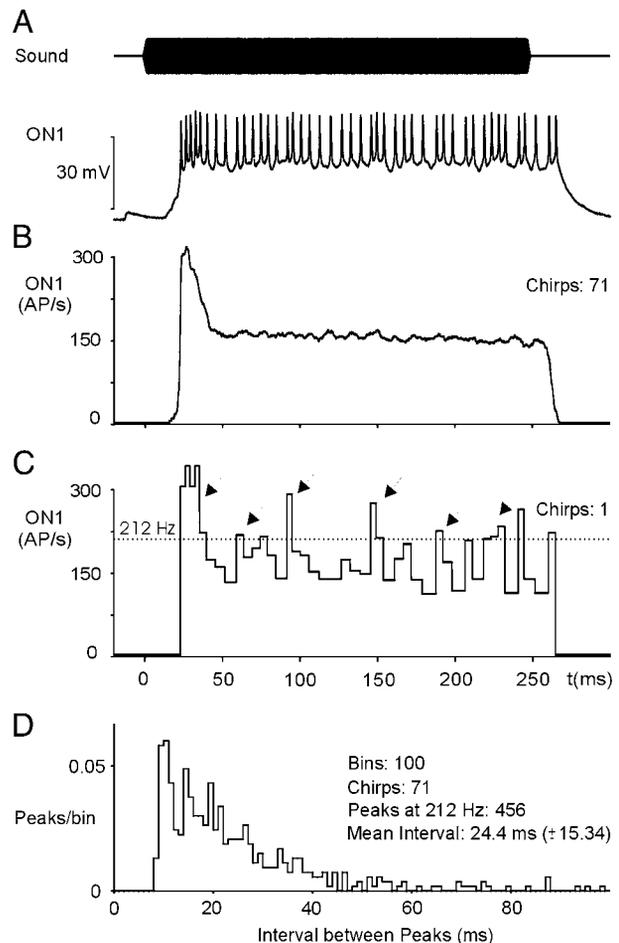

FIG. 6. Responses of ON1 to tone bursts of chirp duration. *A*: sound pulse (*top*) and dendritic ON1 recording (*bottom*). *B*: the instantaneous spike rate of ON1 averaged over 71 chirps indicates a constant response of the neuron after the initial peak response. *C*: instantaneous spike rate of ON1 in response to a single tone burst of 250 ms. · · ·, a spike rate of 212 Hz.; ↓, spike rate peaks that reach 212 Hz. *D*: frequency distribution of the intervals between spike rate peaks reaching 212 Hz. The mean interval is 24.4 ms corresponding to an SP48.8, which is close to the optimum of phonotactic tuning (see Fig. 5*B*).

1999 (rabbit); Grothe et al. 1997, 2001 (bat); Condon et al. 1991; Penna et al. 1997; Rose and Capranica 1985 (frog); Rheinlaender et al. 1976 (cricket); Surlykke et al. 1988 (moth)]. The importance of instantaneous spike rate coding, however, was demonstrated for acoustic startle responses in moths (Roeder 1964) as well as in *Teleogryllus* (Nolen and Hoy 1984), and its importance becomes evident in other sensory systems where information is encoded with high instantaneous spike rates (Reich et al. 2000; Wessel et al. 1996; see also Koch 1999).

When a quantitative analysis of instantaneous spike rates is applied to the activity patterns of ON1, filter properties become evident that are not detected by an analysis of time-averaged spike activity. These thoracic interneurons do not code high syllable repetition rates in their activity but reach a maximum spike rate at the species-specific syllable rate. Their spike rate demonstrates that a low-pass filter process has occurred at the very first stage of auditory information processing. The nature of this filter process is not yet clear, but it may relate to the gradual inhibition of ON1 that is triggered by its own suprathreshold activity (Pollack 1988; Sobel and Tank 1994).

Calculating phonotactic tuning from instantaneous spike rate peaks

The onset of syllables caused maximum activity in the auditory afferents and a peak response in the instantaneous spike rate of the ON1 interneuron. Because only the syllable onset is crucial for phonotactic behavior, these spike rate peaks must represent the syllable pattern at the neuronal level. We therefore propose that this onset activity is the neuronal representation of sound patterns that is crucial for phonotaxis.

Present data do not allow for discrimination between changes in the performance of phonotactic behavior due to changes in the threshold for phonotaxis and those due to changes of the activity level in the auditory pathway. Therefore empirical evaluations were made based on an analysis of arbitrary thresholds for the release of phonotaxis in relation to behavioral phonotactic data obtained from published literature. Considering the tuning curve of the instantaneous spike rate (Fig. 3*B*) and testing different thresholds for the processing of sound pulses allowed us to calculate how many syllables of a sound pattern are actually represented as spike rate peaks in the neural activity (Fig. 4*C*). The resulting curves are similar to phonotactic tuning but represent a rather broad band-pass filter. The increasing rising phase of the tuning curves depends on the increase in the instantaneous spike rate and the descending phase is simply a result of the decrease in the overall number of syllables presented in each chirp pattern. However, if additionally temporal summation at the postsynaptic site is considered and the frequency of the peaks is also taken into account, the number of spike rate peaks multiplied by discharge peak repetition rate reveals a tuning curve for the neuronal response that very closely matches the tuning of phonotactic behavior (Fig. 5*B*). The close correlation between the calculated tuning curves and phonotaxis indicates that phonotactic walking depends on both the number of syllables per chirp *and* the syllable repetition rate. This algorithm for temporal filtering takes into account the instantaneous spike rate and postsynaptic temporal summation and consequently can explain behavioral results that are not accounted for by previous assumptions or

models of cricket temporal filtering. The algorithm uses instantaneous spike rates averaged over many trials. However, in the cricket the phonotactic decision process must be organized by a continuous processing of afferent information. Therefore experiments to test the algorithm with real-time spike rate data are currently being performed.

Shifts in the tuning of phonotactic walking

There is very little information about the intensity dependence of the tuning of the pattern recognition process. Thorson et al. (1982) tested *G. campestris* at 80 dB SPL and assumed that the temporal tuning may not be different at lower sound intensities. Doolan and Pollack (1985) speculate that tuning may shift with sound intensity. At low intensity, the tuning may be broad, and it may get more specific with higher sound intensity. Our data may provide an experimental basis for this assumption. If a relative low threshold for the release of phonotaxis is considered, the calculated tuning of phonotaxis peaks at short SP (Fig. 5). However, the number of discharge peaks that drive phonotaxis is high and covers a wide range of SPs. With higher thresholds, the tuning shifts to longer SPs, but the overall number of discharge peaks is low and the tuning curves become rather flat. Based on these calculations we expect a threshold dependent shift in phonotactic tuning. Interestingly, *G. bimaculatus* phonotaxis shifts with temperature from preferences of long syllable periods (about SP50–SP60) at 15°C to shorter syllable periods (about SP30–SP40) at 30°C (Doherty 1985a).

Comparison with 30-Hz hypothesis and trade-off phenomena

Thorson et al. (1982) claimed a syllable modulation at 30 Hz as the sufficient and necessary parameter of a song to trigger phonotaxis in *G. campestris*. In our calculation of the neural tuning curves, the syllable rate is an important factor but is not the exclusive one. The 30-Hz hypothesis cannot explain the trade-off experiments by Doherty (1985b) in *G. bimaculatus* and the findings on *Acheta domesticus* (Stout and McGhee 1988; Stout et al. 1983) that indicate that the animals also evaluate chirp rate, syllable rate, and the number of syllables. The attractiveness of a song is shifted when any of these parameters is varied. However, because the tuning of phonotactic behavior as described by Doherty (1985a) matches the product of number of spike rate peaks *times* frequency of spike rate peaks, phonotaxis should depend on both the number of syllables presented *and* the syllable repetition rate. A change in one of these parameters should lead to a change in phonotactic performance. Therefore the assumption of a multifactor analysis by the cricket (Doherty 1985b; Stout et al. 1983) and the simplified 30-Hz hypothesis (Thorson et al. 1982) both do not fully describe the mechanism of phonotactic tuning. Different combinations of syllable number *and* syllable rate provide sound patterns of different attractiveness. However, changes in one parameter may be compensated by the other parameter.

Phonotactic response to tone burst of chirp duration

Instantaneous spike rate coding also explains the attractiveness to tone burst of chirp duration (Doherty 1985b; Popov and Shuvalov 1977; Tschuch 1977) for phonotactic behavior in *G. bimaculatus* that cannot be explained by previous hypotheses

or by the recognition process proposed to occur in the brain (Schildberger 1984). An analysis of individual ON1 responses demonstrated a considerable variability in its instantaneous spike rate during these constant pulses. Although a regular pattern of spike rate peaks is missing, the intervals of the peaks cover the natural range of effective syllables and may therefore be effective to drive phonotaxis. These patterns may not be ideal to release phonotactic walking, but it should be emphasized that in walking females the neural representation of the sound pattern is considerably distorted by central inputs and mechanical noise (Schildberger et al. 1988). Nonetheless these distorted neuronal activity patterns are sufficient to drive phonotactic behavior.

Temporal pattern recognition in the cricket auditory pathway

A processing of auditory information in the brain of *G. bimaculatus* by low-, high-, and band-pass neurons has been proposed as a basis for the recognition process underlying phonotaxis (Schildberger 1984). However, from that data, it cannot be concluded that the filter process is actually due to the integrative properties of these band-pass brain neurons. The filter process may occur at the thoracic level in the auditory pathway and may just be reflected in the activity patterns of the brain neurons. Any postsynaptic neuron in the auditory pathway that is excited by a discharge activity like the one encountered in the Omega neuron will automatically exhibit band-pass properties when stimulated with the range of syllable patterns.

So what kind of recognition process may underlie the cricket's behavior? Our data argue that temporal pattern recognition in the cricket could be based on two stages. First, the generation of instantaneous spike rate peaks as described here for the Omega neuron. Second, an instance that postsynaptically counts this spike rate peaks and activates phonotactic behavior accordingly.

The location of the second stage process is an open question. A simple implementation of this two-stage process could be realized at the thoracic sensory-motor level. Low-level auditory information processing has been used to design a robot performing auditory steering similar to crickets (Webb and Scutt 2000). The robot uses a direct excitatory connection of the artificial auditory neurons to the motor network. The tuning of robot phonotaxis closely resembled the phonotactic tuning of crickets and emerged without a high level pattern recognition process. ON1 is a central neuron of the cricket auditory pathway. Although it may not be necessary for pattern recognition as demonstrated by hyperpolarization of its spike activity in phonotactically walking *G. bimaculatus* (Schildberger and Hörner 1988) and by cell killing experiments in *A. domesticus* (Atkins et al. 1984), its spike activity indicates the kind of neural information that is available for temporal processing in the cricket auditory pathway (see also discussion by Pollack 1986). Although we cannot claim that the Omega neuron is part of the pattern recognition network, our data on ON1 demonstrate that neuronal processing based on instantaneous spike rate coding is sufficient to explain the tuning of phonotactic behavior in *G. bimaculatus*. This coding principle may also crucially contribute to temporal processing in other invertebrate and vertebrate auditory systems.

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