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Sensitivity of neurons in the dorsal medullary nucleus of the grassfrog to spectral and temporal characteristics of sound

Ivo H.M. van Stokkum

Dept. of Medical Physics and Biophysics, University of Nijmegen, Nijmegen, The Netherlands

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The responses of 58 dorsal medullary nucleus units to a set of spectrally and temporally structured stimuli were investigated. Responses to tonepips and noise indicated monomodal spectral sensitivities, with diverse response patterns. Phase-locking was strong for frequencies from 0.1 to 0.2 kHz, and in one unit extended up to 0.6 kHz. To clicks, amplitude modulated tonebursts and natural and artificial versions of the mating call various responses were found. Most low-frequency units fired tonically. They showed a non-selective or low-pass rate response to increasing modulation frequency, and a low-pass synchronization behavior to the envelope. A group of mid-frequency units fired phasically and exhibited a band-pass rate characteristic of amplitude modulated tonebursts. Frequently this was combined with a low-pass rate characteristic of click trains. These units hardly responded to the time-reversed mating call, but fired in a time-locked fashion to the pulses of the original mating call, up to a signal-to-noise ratio of 0 dB. This suggests that aspects of pulse envelope and interpulse interval are coded in the dorsal medullary nucleus.

Amplitude modulation; Anuran; Click; Dorsal medullary nucleus; Mating call detection

Introduction

The dorsal medullary nucleus is the first auditory relay nucleus. High frequency fibers from the basilar papilla terminate in the dorsomedial part of the DMN, whereas mid- and low-frequency fibers from the amphibian papilla terminate ventrolaterally (Lewis et al., 1980; Fuzessery and Feng, 1981). According to Frishkopf and Capranica (1966), Feng and Capranica (1976), Bibikov and Kalinkina (1982) and Fuzessery and Feng (1983) all DMN units show monomodal tuning curves. Feng and Capranica (1976) found that half of the DMN units received input from both ears. Only low-frequency units show two-tone suppression (Fuzessery and Feng, 1983). Synchronization to sinusoidal waveforms was found by Bibikov and Kalinkina (1982). Nearly all fibers exhibited good phase-locking from 0.1 to 0.2 kHz. In addition some units showed phase-locking up to 0.8-1.0 kHz.

The natural calls of the grassfrog (Rana temporaria L.) have a relatively simple spectral and a distinctive temporal structure. An example of its mating call is shown in Fig. 1. It consists of a train of practically identical pulses with a slowly changing interpulse interval and a more rapidly changing pulse amplitude. In the past, studies of the single-unit representation of temporal characteristics of sound have concentrated on the torus semicircularis, the largest auditory midbrain nucleus. Thus, most studies conducted in the grassfrog and other anurans focused on rate coding. Bibikov (1980) found that the optimal pulse duration at a constant pulse repetition rate of 27/s was 6-12 ms. Varying the AM frequency of tones or noise Bibikov and Gorodetskaya (1981), Rose and

Correspondence to: I.H.M. van Stokkum, Department of Medical Physics and Biophysics, University of Nijmegen, Geert Grooteplein Noord 21, 6525 EZ Nijmegen, The Netherlands.

Abbreviations: AM, amplitude modulation: BF, best frequency; BP, band-pass; CoSTID, coherent spectro-temporal intensity density; DMN, dorsal medullary nucleus; HP, highpass; LP, low-pass; LT, latency; MF, modulation frequency; NS, non-selective; PESE, pre-event stimulus ensemble; PRR, pulse repetition rate; SNR, signal-to-noise ratio; SON, superior olivary nucleus; SPL, sound pressure level; TS, torus semicircularis; TTS, two-tone suppression.

Capranica (1985) and Epping and Eggermont (1986b) reported a diversity of responses, which they classified as low-pass, band-pass, high-pass, bimodal or band-suppression and non-selective. Using pulse or click trains with different pulse repetition rates Walkowiak (1984) and Epping and Eggermont (1986a) reported a similar diversity. There are a few accounts of temporal selectivity in the medulla. Fuzessery and Feng (1983) found temporal LP units in both the DMN and SON. These units responded consecutively to pulse trains up to PRRs of 280 Hz. In the same nuclei Schneider-Lowitz, cited in Walkowiak (1984), found weakly BP units as well. Using continuous amplitude modulated tones Gorodetskaya and Bibikov (1985) observed an enhancement of small amplitude changes in the SON for modulation frequencies of 70 to 150 Hz. Finally in the auditory nerve Rose and Capranica (1985) found that the firing rate of eighth nerve fibers was largely independent of the rate of AM. Strong synchronization to the envelope of pulses and of AM sound is reported in the eighth nerve (Frishkopf and Goldstein, 1963; Rose and Capranica, 1985) and in the medulla (Fuzessery and Feng, 1983). In the midbrain the synchronization to the envelope has declined appreciably, although a small number of units shows the same synchronization capability as in the medulla and auditory nerve (Rose and Capranica, 1985; Epping and Eggermont, 1986b). Generally speaking synchronization to the envelope is declining with higher pulse repetition rates or AM frequencies. Ascending from auditory nerve to midbrain synchronization capability decreases, whereas rate coding becomes more prominent.

In this report the first results are presented of an investigation into the coding of spectral and temporal features of sound in the DMN. A broad set of stimuli, which has also been used by Epping and Eggermont (1985a, 1986a,b) and Eggermont and Epping (1986), is presented. From their studies in the TS it appeared that a simple characterization with a few stimuli usually was impossible. Spectral sensitivities as determined with tonepips and noise are presented. Responses of DMN units with similar spectral sensitivity to temporally structured stimuli are compared. As an illustration the response of one unit to all stimuli is presented in detail.

Materials and Methods

Animal preparation and recording procedure

Adult grassfrogs (R. temporaria L.) from Ireland were anesthetized with a 0.05% solution of MS-222. After a hole was drilled into the parietal and exoccipital bones above the brain stem, the animal was allowed to recover overnight. The next day it was immobilized with an intralymphatic injection of buscopan (0.12 mg/g bodyweight). A local anesthetic, 4% xylocaine, was applied to the wound margins. The cartilage over the medulla was removed, thereby exposing the choroid plexus. This dense network of blood vessels covers the dorsomedial side of the alar plates and the fourth ventricle. The animal was placed in a sound attenuated room (IAC type 1202A) onto a damped vibration-isolated frame. Temperature was maintained around 15°C and the skin was kept moist to aid cutaneous respiration. The animal's condition was monitored with help of ECG recording (Epping and Eggermont, 1985a) and by examination of the blood flow in the choroid plexus. A successful preparation was usually kept intact for two days.

The position of the DMN was determined from anatomical studies of Opdam et al. (1976). Ultrafine or tapered tungsten microelectrodes (Micro Probe Inc.), coated with parvlene-c, having a 5-25 μ m exposed tip and a 1 kHz impedance of 1-5 $M\Omega$ were used for extracellular recording. Using hydraulic microdrives one or two electrodes were lowered just medial to the large blood vessel (vena spinalis posterior) overlying the alar plate longitudinally. Great tissue lag was noticed due to indention of the choroid plexus. After piercing the choroid plexus and penetrating the dorsomedial part of the alar plate abundant auditory activity was usually found, from which sometimes single units could be isolated. Occasionally separable few-unit recordings from one electrode were obtained, with the help of a spike separation procedure (Eggermont et al., 1983). Waveform features and spike epochs were stored on a PDP 11/34 with a resolution of 40 µs, and analyzed off-line with a PDP 11/44.

Acoustic stimulus presentation

The acoustic stimuli were generated by a pro-

grammable stimulus generator, as described by Epping and Eggermont (1985a). The stimuli were presented to the animal by two electrodynamic microphones (Sennheiser MD211N) coupled to the tympanic membrane using a closed sound system. The SPL was measured in situ with a half inch condenser microphone (Brüel and Kjaer 4143) connected to the coupler (Hermes et al., 1981). The frequency response of the system was flat within 5 dB for frequencies between 100 and 3000 Hz, a sufficient range for studying the auditory system of the grassfrog (Brzoska et al., 1977). The amplitude characteristics of the left and right coupler were equal within 2 dB for the range of interest. The stimuli were usually presented ipsilaterally with respect to the recording site, at SPLs of 70 to 100 dB peak. These SPLs are sufficient to evoke behavioral responses (Walkowiak and Brzoska, 1982; Brzoska, 1984).

The following stimulus ensembles have been used.

(1) Tonepips To study spectral sensitivity tonepips of 46 ms, modulated with a gamma envelope, were presented once per second. The carrier frequency was chosen pseudorandomly from 45 logarithmically equidistant values between 0.1 and 5 kHz. The envelope had a rise and fall time of, respectively, 9 ms (20%) and 37 ms (80%). Examples of two gammatones are shown in Fig. 2. For a more extensive description of this stimulus see Epping and Eggermont (1985a). To study TTS a second tonepip at BF, attenuated 0, 10 or 20 dB with respect to the tonepip stimulus, was presented simultaneously.

(2) Noise Pseudorandom Gaussian white noise with a cut-off frequency of 5 kHz generated by a Hewlett Packard HOI3722A noise generator was used to study spectral sensitivity and phase-locking (Epping and Eggermont, 1985a). A -3 dB per octave LP filter with a cut-off frequency of 100 Hz converted this white noise to pink noise.

(3) Periodic click trains Trains of 10 equidistantly spaced clicks, with onset intervals of 3 s. The intervals between clicks were varied pseudorandomly between 128 and 4 ms, corresponding with logarithmically equidistant PRRs of 7.8 to 250/s.

The duration of the condensation click was 0.7 ms, and its amplitude spectrum was flat within 5 dB for the range of interest (Epping and Eggermont, 1986a).

(4) Sinusoidally amplitude modulated tonebursts Tonebursts of 500 ms duration with 100 ms rise and fall times were presented every 3 s. BF was chosen as carrier. The modulation depth was 16 dB, corresponding with 84%. The MFs were the same as the PRRs of the periodic click trains. In addition an unmodulated toneburst was presented (Epping and Eggermont, 1986b).

(5) Random clicks Stimulus ensemble consisting of 0.7 ms clicks with an average rate of 16/s. The interclick intervals are drawn independently from a negative exponential distribution with a minimum interval of 1 ms. The interval distribution corresponds to a Poisson process with a dead-time of 1 ms (Epping and Eggermont, 1986a).

(6) Variations on the mating call The mating call of Fig. 1, which was recorded at 16°C, was taken as starting point for spectral and temporal variations. The basic sequence consisted of 10 s silence, followed by three original mating calls. After this the envelope of the original mating call served as amplitude modulator for carrier frequencies of 201, 557, 1067 and 1542 Hz. Then the interpulse intervals of the original mating call were multiplied by 0.5, 1, 2 and 4, corresponding with PRRs of 72, 36, 18 and 9 Hz. Finally the original mating call was presented again followed by its time-reversed version. Intervals between the calls were about 2.5 s. To this sequence of mating calls and variations an increasing noise background was added. The noise was either white or pink, see 2. The peak ratios between vocalizations and noise were consecutively ∞ , 6, 0 and -6 dB. After the sequence with the highest noise level a 50 s silence was added (Eggermont and Epping, 1986).

(7) Pulse waveform variations To study the effect of pulse waveform a sequence consisting of a click, a pulse from the mating call, tonepips, gammatones, and if appropriate also their time-reversed versions, was used. The tonepips had 1 ms rise and fall times and durations of 5, 10, 20 and



Fig. 1. Example of grassfrog mating call. (a) Oscillogram showing the pulsatile structure on different time scales. (b) Sonogram representing a spectro-temporal image of the mating call, on the same time scale as the upper oscillogram. The inset shows the spectral content of the call averaged over time. From Eggermont and Epping (1986).

50 ms. The gammatones had rise and fall times of, respectively, 20% and 80% of 10, 20 and 50 ms. BF was chosen as carrier for the tonepips and gammatones. Onset interval was 1 s.

(8) Search stimulus Consisting of variations on the mating call, tonepips and 500 ms pink noise bursts.

For adequate data collection all stimuli were repeated, respectively, 4, 32, 10, 10, 3, 5 and 20 times immediately after each other. The responses are presented as reordered event displays (Epping and Eggermont, 1985b, 1986a,b; Eggermont and Epping, 1986), except in the case of 2 and 5. Thereby the actual response is reordered systematically according to a stimulus parameter.

Period histograms were made of the responses to the pulse trains and AM tonebursts. From these the synchronization index, defined as the vector strength (Goldberg and Brown, 1969), was derived. Responses to the noise stimulus were analyzed by crosscorrelating the response with a functional of the stimulus. First order crosscorrelation resulted in the averaged pre-event stimulus, or Revcor function (De Boer and Kuyper, 1968). A second order functional, the CoSTID, represents the energy distribution of a signal in the time-frequency plane (Johannesma et al., 1981). A CoSTID of the Revcor function, and an average CoSTID of the PESE were calculated, and normalized for the frequency spectrum of the noise (Hermes et al., 1981).

Results

Experiments were performed throughout the year, except for the winter, on 16 male and female grassfrogs. From 79 recordings in 12 frogs, 58 were designated as single unit on the ground of spike waveform constancy. These 58 single units were analyzed further. The units could be recorded from 3 min to 3 h. In the other frogs either only synchronized multi-unit activity or no activity at all was found. At the end of some electrode tracks the fading auditory activity was replaced by spontaneous activity, most probably from ventral medullary nucleus units. Twenty-six of the 58 units were spontaneously active, 5 of them had a spontaneous activity of more than 2/s.

Tonepips

Forty-eight units were tested with the tonepip ensemble. Of the five that did not respond, four responded only to clicks. In Fig. 2a and b responses of two units are shown. The responses to the four presentations of each tonepip are superimposed. Both units responded tonically, the unit in Fig. 2b showing a chopping response pattern. In Fig. 5e a phasic response is visible. From the reordered event display a best excitatory frequency was estimated, respectively, 130, 1100 and 630 Hz in Figs. 2a, b and 5e. In the case of phasic responses the frequency corresponding with the shortest latency was chosen as BF. Twelve units responded phasically to the tonepips, and 10 of



Fig. 2. Spectral sensitivities of units 297,0,1 (a,c) and 284,0,2 (b,d) as determined with gammatones and noise. (a) Unit 297,0,1. Reordered event display of response to tonepip stimulus, 34 events. Underneath gammatone with carrier frequency of 131 Hz on the above time scale. (b) Unit 284,0,2. Reordered event display of response to tonepip stimulus, 507 events. Underneath gammatone with carrier frequency of 1111 Hz. (c) Unit 297,0,1. Reverse correlation function of 129 events during 335 s of pink noise stimulus. (d) Unit 284,0,2. Average PESE-CoSTID of 1570 events during 84 s of white noise stimulus. All stimuli were presented ipsilaterally at intensities of 90 dB peak SPL.

the 31 tonically responding units showed a chopping response pattern. The latencies were between 6 and 15 ms for 36 of the 43 units. Three of the longer latency units were excited contralaterally. One of these three had a BF of 0.7 kHz for ipsilateral and a BF of 1.2 kHz for contralateral stimulation. A histogram of the response properties of 43 units is shown in Fig. 3. In the remainder of this article units with a BF below 0.4 kHz are called low-frequency units. Mid-frequency units have BFs between 0.4 and 1.0 kHz, and units with BF greater than 1.0 kHz are designated high-frequency units. All seven of the lowfrequency units tested with a two-tone stimulus



Fig. 3. Histogram of best frequencies of 43 units as determined with tonepip stimulus. Units with chopper characteristic are indicated by the sparsely stippled areas and phasically responding units by the closely stippled areas. Intensity of tonepips 90 dB peak SPL, except for 3 units. All units, except for 3, stimulated ipsilaterally.

showed TTS by mid-frequency tones to various extents. None of the four mid- and high-frequency units tested showed TTS.

Noise

The noise stimulus was presented to 21 units, mostly at 90 dB peak SPL. In addition, 25 units were exposed to noise in combination with other sounds. Of these 46 units nine did not respond to noise at all, of which only one was low-frequency sensitive. Twenty of the 21 units showed existence of a stimulus-response relation with the noise, as determined with the help of a crosscoincidence histogram (Aertsen et al., 1979). Nine of the 12 low-frequency units showed a reverse crosscorrelation function, an example is shown in Fig. 2c. The CoSTID of this Revcor function showed a peak from 100 to 200 Hz. The only Revcor function of a mid-frequency unit is shown in Fig. 4a. The CoSTID of this Revcor function (Fig. 4b) showed a peak from 360 to 660 Hz. These 10 units thus exhibited phase-locking to parts of the noise, in one unit extending up to 660 Hz. The CoSTID of the Revcor function qualitatively agreed with the average PESE-CoSTID shown in Fig. 4c. Quantitatively however they disagreed, Fig. 4b has been scaled to one-tenth of the extrema of Fig. 4c. The 10 units without a Revcor function all showed a



Fig. 4. Spectral sensitivity of unit 307,0,2 as determined with pink noise at an intensity of 50 dB peak SPL. (a) Average PESE, or Revcor function, 1642 events in 116 s. (b) CoSTID of average PESE, scaled to one-tenth of the extrema of (c). (c) Average CoSTID of PESE.

PESE-CoSTID, an example is shown in Fig. 2d. The broad maximum at 10 ms before a spike from 0.9 to 1.6 kHz indicates the high-frequency sensitivity of the unit. All spectral sensitivities de-



Fig. 5. Response of unit 297,0,6 to the stimulus set. From left to right in panels a and b: a reordered event display; the accessory iso-intensity rate histogram; and the synchronization index histogram. (a) Periodic click trains. 1154 events, 1600 clicks. (b) AM tonebursts, 630 Hz carrier frequency, 70 events. (c) Random clicks. Time-dependent crosscorrelation diagram of clicks with spikes, underneath the accessory crosscoincidence histogram. 3251 events, 11755 clicks. (d) Variations on the mating call. Event display reordered according to noise level. x indicates the mating call shown in Fig. 1; 1, m, i and h are variations of carrier frequency: 201, 557, 1067 and 1542 Hz, 0.5, 1, 2 and 4 are variations of interpulse interval; r is the time-reversed mating call. A pink noise was added, signal-to-noise ratios are shown on the left. 1504 events. (e) Spectral sensitivity as determined with 46 ms gammatones, reordered event display, 13 events. (f) Pulse waveform variations. From left to right: click (c); pulse from mating call (x); time-reversed pulse from mating call (r); tonepips of 5, 10, 20 and 50 ms; gammatones (Γ) of 10, 20 and 50 ms, alternated by time-reversed gammatones (r). Underneath the accessory histogram. Carrier frequency 630 Hz, 196 events, 260 pulses. All stimuli were presented ipsilaterally, at intensities of 80 (e,f), 90 (b,d) and 100 (a,c) dB peak SPL.

termined with noise were monomodal. Four units with spontaneous activities from 1 to 14/s showed post-activation suppression with tonepips as well as with noise.

Unit 297,0,6

An example of the response of a mid-frequency unit to the stimulus set is shown in Fig. 5. The unit is practically not spontaneously active. It responds with one spike to tonepips with carrier frequencies between 500 and 800 Hz (Fig. 5e). At an intensity of 80 dB peak SPL the LT is 10 ms. The LT as determined with the periodic click trains (Fig. 5a) at 100 dB peak SPL is 7 ms. In Fig. 5a one spike to each click is seen for PRRs up to 50 Hz. For higher PRRs its response to the later clicks disappears, ending with one spike after the onset of click trains with a PRR of 250 Hz. The iso-intensity rate histogram on the right of the reordered event display shows a temporal LP response with a cut-off PRR of 79 Hz. The cut-off PRR is defined as the PRR where the response is half the maximum. The synchronization index histogram on the right also shows a temporal LP characteristic, with a cut-off PRR greater than 200 Hz. For a PRR of 250 Hz the synchronization index is not properly defined because the unit responds only with a single spike at the stimulus onset. The response to AM tonebursts with a carrier frequency of 630 Hz is shown in Fig. 5b. The first spike appears at 57 ms after onset, the last spike at 104 ms. Thus all spikes are elicited during the rise time of the AM tonebursts. Moreover the unit is only sensitive to MFs between 50 and 125 Hz, with a maximum at 79 Hz. The synchronization index is nearly one. The random clicks with an average rate of 16/s evoke a nonstationary response. This is visible in the time-dependent crosscorrelation diagram (Van Stokkum et al., 1986) in Fig. 5c. Vertically at $\tau = 0$ ms, an event display of the stimulus may be envisioned. Each stimulus event functions as a trigger for the spikes, and all spikes within 50 ms are plotted horizontally. The crosscoincidence histogram that results after integration over time t is shown underneath. The unit's response declines within 10 s to a level of 1 spike/s. Then the response slowly grows again, ending with 8 spikes/s. LT changes in the diagram from 10 to 9 ms. A suppression is seen after the activation around 10 ms. There are no spikes from 12 to 20 ms after a click, regardless of the clicks in between.

After these rather artificial stimuli the response to variations on the mating call is presented in Fig. 5d. In the upper part (∞) , where no noise is added, the unit responds with a time-locked spike to nearly every pulse of the original mating call (x), the mid-frequency carrier variation and the 1, 2, 4 times interpulse interval variations. The responses to the 1067 Hz carrier variation and to the 0.5 times interpulse interval variation are about half as much. There is hardly any response to the time-reversed mating call (r). The noise evokes no spikes, which is visible in the first 10 s of the 6, 0 and -6 parts. The first noise presentation, which is represented in the first lines of the 6, 0 and -6parts, shows a greatly decreased response to the mating call, the mid-frequency carrier variation and the 1, 2 and 4 times interpulse interval variations. The other four stimulus presentations, as can be seen in the next four lines, show a greater response. The noise masks the responses to the 1067 Hz carrier variation and the 0.5 times interpulse interval variation. The persisting responses are 60% and 15% at a SNR of, respectively, 6 and 0 dB. Finally in Fig. 5f the response to pulse waveform variations is shown. The carrier frequency is 630 Hz, the click is at 100 dB peak SPL, the other pulses are at 80 dB peak SPL. The unit responds with one spike to the click (c), the pulse from the mating call (x), the tonepips and the 10 and 20 ms gammatones. A smaller response is seen to the 50 ms gammatone, to the 10 ms time-reversed gammatone, and to the time-reversed mating call pulse (first r). At a 10 dB higher intensity the unit only failed to respond to the 20 and 50 ms time-reversed gammatones. These responses of unit 297,0,6 will be interpreted in the discussion.

Temporal sensitivity

The responses of 39 units to the temporally structured stimuli are summarized in Table I. With the random clicks three main response patterns are found. A preference for interclick intervals corresponding to BF, called tuning, is found in three low-frequency units. Four units show only activation, whereas eight units show activation

TABLE I SUMMARY OF RESPONSES TO TEMPORALLY STRUCTURED STIMULI

Dotted lines indicate correlations. Further explanation in text. Special abbreviations: act, activation; act-sup, activation followed by suppression; tuning, preference for interclick interval corresponding to BF. Rate response types: BPa, weakly band-pass; BPb, pronounced band-pass. $r \approx x$, response to normal and time-reversed waveform approximately equal; $r \ll x$, response to time-reversed waveform much smaller; r, x not, no response to normal or time-reversed waveform. P, phasic; T, tonic.

| Spectral sensitivity | Random clicks | Click trains | AM tone bursts | Mating call variations | Pulse variations | |
|----------------------|------------------|-----------------|-------------------|---------------------------|---------------------|--|
| Low | 3 tuning | 2 tuning | 5 NS | 4 r ≈ x | 8 T, r ≈ x | |
| | 1 act | 2 LP | 2 LP | 3 r,x not | | |
| | | 1 NS | 2 BPa | | | |
| | | | 1 complex | | | |
| (400 Hz) | | | | | | |
| Mid | 4 act-sup | | 4 BPb | | | |
| | 1 act | 2 NS | 1 LP | 3 r ≈ x | 2 T, r ≈ x | |
| | | 1 HP | 1 NS | | | |
| | | 1 BPa | 1 BPa | | | |
| (1000 Hz) | | | | | | |
| High | 2 act | 3 LP | 2 BPa | 4 r,x not | $3 T, r \approx x$ | |
| | 1 act-sup | 1 BPb | 1 BPb | 2 r ≈ x | 1 P, $r \ll x$ | |
| | - | 1 NS | 1 NS | | $1 P, r \approx x$ | |
| No | 3 act-sup | | | 3 r,x not | | |
| Units | 15 | 20 | 21 | 26 | 17 | |



followed by suppression, e.g. Fig. 5c. The range of suppression lasts from 6 to 60 ms. This activation-suppression response is combined with a LP rate response to click trains, e.g. Fig. 5a. LTs to clicks are all between 5 and 12 ms. Time-locking to the clicks is usually strong, resulting in NS or LP synchronization characteristics.

In Fig. 6a the response of a low-frequency unit (BF 160 Hz) to AM tonebursts with a carrier frequency of 200 Hz is shown. The firing rate is highest for the unmodulated toneburst, and practically independent of MF. This is termed a NS rate response. The synchronization index histogram shows a LP characteristic, with a cut-off MF of 62.5 Hz. The peak at a MF of 200 Hz results from phase-locking to the 200 Hz carrier, producing a modulation depth of 100%. Five of the 10 lowfrequency units showed a NS rate response. A pronounced BP rate response is shown by four of

Fig. 6. Responses to AM tonebursts, see legend Fig. 5. (a) Unit 297,1,0, carrier frequency 200 Hz, 2397 events, 80 dB peak SPL. (b) Unit 281,1,0, carrier frequency 800 Hz, 442 events, 90 dB peak SPL.

the seven mid-frequency units, e.g. Figs. 5b and 6b. The response of the unit in Fig. 6b to AM tonebursts with a carrier frequency of 800 Hz is again best for the rising parts. In contrast to Fig. 5b the response persists, albeit weaker. This unit responds best to MFs from 79 to 156 Hz. The synchronization to the modulator is weak, as is seen in the synchronization index histogram on the right, probably due to the later part of the response. Seven of the 10 mid-frequency units respond in a time-locked fashion to the pulses of the original mating call, and show hardly any response to the time-reversed mating call. Three of these seven also show a smaller response to the 0.5 times interpulse interval variation, and all seven units respond to the calls against a noise background up to at least 0 dB, e.g. Fig. 5d. One mid-frequency unit responds to the normal and to the time-reversed mating call at an intensity of 90 dB peak SPL, but much stronger to the normal mating call at 70 dB peak SPL. The low- (4) and high- (2) frequency units which respond to the mating call also respond to its time-reversed version. With the pulse waveform variations the tonically responding units respond to time-reversed and normal waveforms, whereas three of the four phasically responding units do not respond to the time-reversed pulse waveforms, e.g. Fig. 5f.

Discussion

Recordings

The preparation was moderately successful. In the preparations where no single units could be isolated the vena spinalis posterior was nearer to the middle. This probably hindered the penetration of the DMN. In one preparation the alar plates and the fourth ventricle could be seen through the choroid plexus. The entrances of electrode-tracks where auditory activity was found were in accordance with the topological maps of Opdam et al. (1976).

The general results are in agreement with the literature. LTs of 5 to 12 ms to clicks, and mostly of 6 to 15 ms to tonepips, monomodal spectral sensitivities, TTS of low-frequency units by mid-frequency tones and phasic-on responses are also reported by Fuzessery and Feng (1983). The usually ipsilateral stimulus presentation introduced a

sampling bias, in view of the contralateral excitatory and ipsilateral inhibitory inputs found by Feng and Capranica (1976).

Spectral sensitivity

The distribution of BFs in Fig. 3 is comparable with Fig. 7 in Epping and Eggermont (1985a) for the TS. But in the present study no units with a BF higher than 1.4 kHz were encountered. BF mismatches like the one found in this study were also reported by Epping and Eggermont (1985b) in the TS. Care must be taken with the interpretation of the temporal response patterns to gammatones, because these tones are short and decay fast. There appear to be correlations between BFs of 0.6 to 0.8 kHz and a phasic response pattern, and between BFs of 0.8 to 1.0 kHz and a chopping response pattern. The spectral sensitivities as determined with noise agree with those determined with tonepips, e.g. Fig. 2. But the spectral sensitivity as determined with tonepips was always broader than the one determined with noise, e.g. Fig. 2b and d. Phase-locking as determined with noise extends up to 660 Hz, at a temperature of 13°C. But the quantitative difference between the CoSTID of the average PESE (Fig. 4b) and the average PESE-CoSTID (Fig. 4c) indicates that the phase-locking is only weak. Epping and Eggermont (1985a) found phase-locking up to about 250 Hz in the TS. They remarked that the upper frequency limit for phase-locking seems to be positively correlated with the temperature. Bibikov and Kalinkina (1982) reported some DMN units showing phase-locking up to 1 kHz but unfortunately did not mention the temperature. In the eight nerve phase-locking is also found up to 1 kHz (Hillery and Narins, 1987).

Unit 297,0,6

An attempt will be made to synthesize the responses of unit 297,0,6 to the different stimuli, shown in Fig. 5. In response to clicks the unit shows a LP rate response, Fig. 5a. This can be explained by the post-activation suppression pattern seen in Fig. 5c. A click first activates the unit, resulting in a spike after 7 ms in Fig. 5a. But after the spike the response is suppressed for at least 8 ms. This can be due to adaptation of the input supplying units. An absolute refractory time of 8

ms is less probable, interspike intervals as short as 2.5 ms are found in DMN units. A third possibility is inhibition. Adaptation might also explain the long-term non-stationarity seen in Fig. 5c. This is qualitatively comparable to the adaptation pattern of Fig. 3c in Zelick and Narins (1985). Unit 297,0,6 responds phasically to tonepips with carrier frequencies of 0.5 to 0.8 kHz (Fig. 5e). Megela and Capranica (1981) reported a group of rapidly adapting mid-frequency auditory nerve fibers, exhibiting little or no spontaneous activity. Perhaps such fibers provide input to the unit. LT of 10 ms to tonepips is longer than the 7 ms LT to clicks due to the lower intensity and longer rise time of the tonepip. The BP rate response during the onset of AM tonebursts (Fig. 5b) is qualitatively comparable with the whole nerve action potential (AP) modulation detection function in Fig. 3 of Hillery (1984). The AP reflects the synchronous activity of groups of eighth nerve fibers. A rapid intensity change as provided by a click or tonepip with short rise time provides a cue for time-locking of eighth nerve fibers. It thus seems that unit 297,0,6 needs synchronous inputs. The LP part of the BP rate response is probably again due to adaptation, as in Fig. 5a. It is noteworthy that the modulator of MFs around 79 Hz bears a great resemblance to the envelope of a pulse from the mating call (Fig. 1a). The lack of response to the AM tonebursts after 100 ms might again be due to adaptation. The smaller response to timereversed pulse waveforms in Fig. 5f is probably due to the long rise times, as with the low MFs in Fig. 5b. Finally the response to the variations on the mating call, Fig. 5d. The time-locked response to each pulse of the normal mating call can be understood from the spectral sensitivity of Fig. 5e together with the envelope sensitivity of Fig. 5b. The weak response to the 1067 Hz carrier variation was not expected from Fig. 5e. But at a 10 dB higher intensity the spectral sensitivity was found to extend from 380 to 1200 Hz. The weaker response to the 0.5 times interpulse interval variation, corresponding with a 72 Hz PRR, can be understood from Fig. 5a, where the response is seen to adapt for PRRs higher than 50 Hz. There is no response to the noise, probably because it does not synchronize the inputs. The weak responses are masked at the first noise level, whereas the responses to calls with a mid-frequency carrier persist. The non-stationarities of Fig. 5c and d may be related, they both show slow recovery. In spite of the 50 s silence after the highest noise level the unit's properties regarding the masking by the noise change. Summarizing, unit 297,0,6 responds with one time-locked spike to clicks and pulses with mid-frequency carriers and short rise times, after that the unit's activity is suppressed for 8 ms. Convergent input by fast-adapting midfrequency sensitive auditory nerve fibers might explain its sensitivity.

Temporal sensitivity

A variety of responses to temporally structured stimuli is shown in Table I. On the one hand, this is remarkable in view of the absence of cellular subdivisions in the DMN (Opdam et al., 1976; Feng, 1986). On the other hand, a variety of adaptation patterns is already found in the auditory nerve (Megela and Capranica, 1981). The main findings in the DMN are the activation followed by suppression and the discrimination between short and long rise times. The first provides a temporal LP filter with cut-off PRRs as low as 40 Hz, the second selects for pulse envelopes with short rise times. In contrast to the studies in the TS (Walkowiak, 1984; Epping and Eggermont, 1986a.b) no BP units with best MFs or best PRRs under 50 Hz have been found. The BP rate characteristics found in the DMN with AM tonebursts seem to be more related to the pulse envelope than to the interpulse interval, e.g. Fig. 5b and d.

A further investigation into the coding of temporal features of sound against a noise background is in progress.

Behavioral relevance

Walkowiak and Brzoska (1982) reported an evoked calling response to mating calls. Male grassfrogs stimulated with mating calls at intensities of 66–95 dB peak SPL increased their calling rates with 100 to 400%, relative to the spontaneous rate of mating calls. The mating call envelope with a carrier frequency of 400 Hz was equally effective. An interpulse interval variation of 2 times the normal interpulse interval was not much less effective, whereas a 0.5 times interval variation was considerably less effective. A group of mid-frequency units in the DMN reported here have similar characteristics, e.g. Fig. 5d. These units are suitable building blocks for the identification of mating calls, even against a noise background. Inspection of the responses of 207 auditory midbrain units to the variations on the mating call stimulus (Eggermont and Epping, 1986) showed no such clear discrimination of normal and time-reversed mating call. Both calls seemed to be about equally effective, with some units responding better to one of them. In view of the hypothesized identification function of the TS it is remarkable that this discrimination is no longer present on the single-unit level.

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