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BINAURAL HEARING AND NEURAL INTERACTION

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INTRODUCTION

Binaural hearing in mammals relies on differences in spectrum (ΔS), intensity (ΔI), time (Δt) or phase ($\Delta \phi$) between the sounds processed by both ears. In birds and other lower vertebrates with small interaural distance only very minute ΔI and Δt differences are available. In cold blooded vertebrates especially, the slower pace of the central nervous system processing does not allow to resolve time differences below a few hundred microseconds (Feng and Capranica, 1976), in addition small head does not cause intensity differences sufficiently large to be detected for the frequencies below 2 kHz. In frogs and toads, as well as in reptiles or birds, there is an open connection between the tympanic membranes and mouth cavity providing the animal with a mechanism not unlike that of a combined pressure-pressuregradient microphone. At low frequencies (< 300 Hz) a single ear shows a cardioid directional sensitivity and at higher frequencies (< 1500 Hz) there is still a useful displacement difference between both ears equivalent to ΔI values of more than 2-3 dB (Aertsen et al., in preparation) that can be detected by neurons in the torus semicircularis (Feng and Capranica, 1978). The minute phase differences at both ear drums and at the sound transparent mouth cavity thus cause movement differences of the tympanic membranes large enough for reasonably accurate directional hearing: about 10-15° as the resolving power (Rheinländer et al., 1979) determined by behavioural experiments.

Neurons that are sensitive to interaural intensity differences require input from both ears. It is known that binaural units in the auditory midbrain of the grassfrog receive input from fibers with equal spectral sensitivity but with distinctly different latencies (Hermes et al., 1982). Thus minute phase differences are transformed into detectable "equivalent-intensity" differences that are processed with quite large (up to 10 msec) differences in latency.

Neurons in the torus semicircularis interact with each other, this interaction has appeared to be stimulus dependent: tone-burst or continuous noise stimulation produce a different neural correlation even after a correction procedure for stimulus lock of the spikes (Eggermont et al., in preparation). Since ipsi-, contra-, or bilateral stimulation produce a difference in neural activity for torus semicircularis units it is worthwhile to investigate this effect upon the neural correlation. *This may indicate whether processing of binaural information can be done on the single unit level or that groups of interacting neurons are involved.* In the present paper we offer preliminary results of the investigation of binaural influences on neural correlation for units in the auditory midbrain of the grassfrog (Rana temporaria L.).

METHODS

Recordings were made from the torus semicircularis in the immobilized and locally anaesthetised grassfrog (Rana temporaria L.) using metal (tungsten or stainless steel) electrodes with an exposed tip of about 10 µm and a 1 kHz impedance in the 1-3 MΩ range (For details see Hermes et al., 1981).

The multi-unit spike train was separated into single-unit spike trains on basis of spike waveform by using the matched filter approach (e.g. Abeles and Goldstein, 1977). Four orthogonal templates were used to represent each waveform but the separation was carried out using the best set of two out of these four. By using a colour code to represent spike waveform we were able to construct MU dot displays where each single unit contribution had its own colour. This procedure

facilitates the problem of finding (neural) synchrony in the firings of the different units and easily sorts out double and triple correlations which may be obscured in standard correlation analysis procedures. To give an impression part of a dot display for a four unit recording is represented; instead of colour we use symbols (Figure 1) thereby giving up resolution.

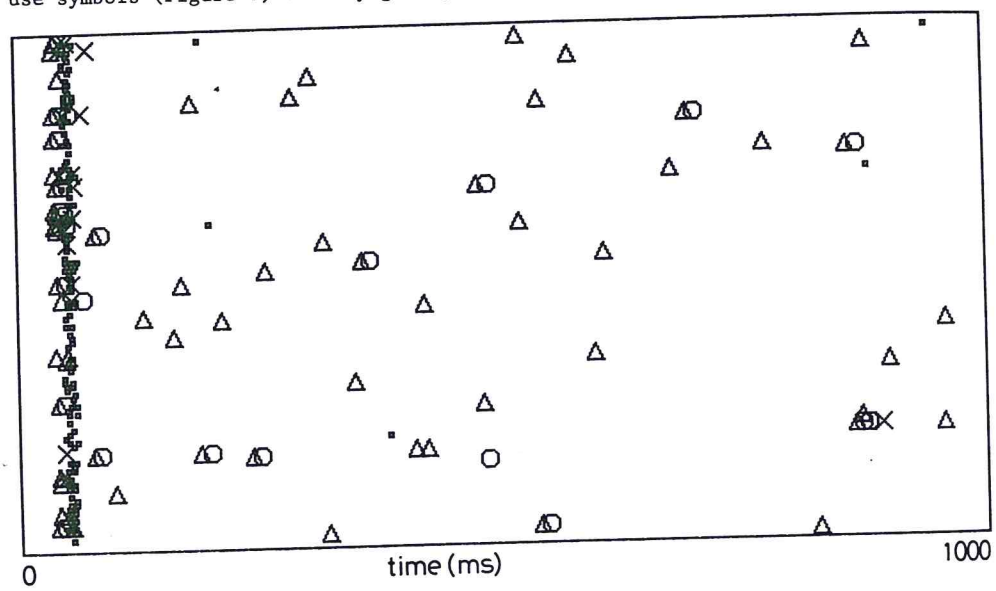

Fig. 1. Four-unit recording using single microelectrode. The responses of the separated individual units are indicated with different symbols. Stimuli consisted of 127 tonebursts randomly selected in frequency and presented once per second. One observes the onset response of all four units followed by spontaneous activity from the units indicated by Δ and 0. It is easily observed that responses of neuron 0 are likeli to be preceeded by firings of the unit indicated by Δ. A firing of the unit X is in most cases preceeded by both firings of units Δ and 0

Neural correlation under stimulus conditions contains a component due to correlation with the stimulus (Perkel et al., 1967). For the purpose of correction we present the stimulus ensemble twice (Aertsen et al., 1979) and calculate both the simultaneous and non-simultaneous cross coincidence functions between two spike trains from a multi-unit record (Eggermont et al., in preparation) (see Fig. 2).

The difference is, under the assumption of an additive effect of the stimulus on the number of spikes, a measure for the strength of the neural correlation. In case the neurons are spontaneously active a direct measure for neural interaction can be obtained.

Sound was presented using closed sound systems. Stimuli were presented ipsilateral and contralateral with respect to the recording site as well as binaural. No intensity or time differences were introduced. Three types of stimulus ensembles were used:

a. Tonal stimuli with envelope $m(t) = c(t/\beta)^{\gamma-1} \exp(-t/\beta)$; $t \geq 0$; with parameter $\gamma=3$ and duration parameter $\beta=4.35$ leading to a 48 ms duration. Frequency range was 4 octaves: 125-2000 Hz or 250-4000 Hz depending on the frequency characteristics of the neuron. Frequency values were selected in random order from 127 values equidistant on log frequency scale. Peak amplitude was kept constant. Four sequences were used leading to tonal stimulus ensemble duration of 8 min 28 s.
b. Tonal stimuli with $\gamma=3$ but $\beta=1.45$ leading to 16 ms duration. Frequency values were selected from 255 frequency values with onset intervals of 128 ms. This

sequence was repeated 9 times, resulting in a duration of 4 min 54 s. for the stimulus ensemble.

c. Noise generated by a pseudo-random binary-sequence generator. Sequence length was 1048575 steps, a sufficient number of feedback loops was provided to assure that the statistical properties of the noise, especially its second order autocorrelation function were satisfactory. Either 1.5 kHz or 5 kHz low pass noise was used with sequence duration of 34.95 s or 10.49 s. Generally 32 sequences were used.

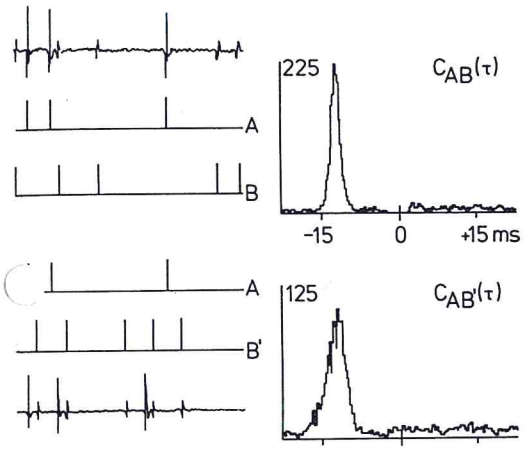

Fig. 2. Construction of simultaneous and non-simultaneous crosscoincidence histograms for a double unit recording. For the simultaneous crosscoincidence histogram $C_{AB}(\tau)$ the firings are taken from the same part of the double unit record. In case of the non-simultaneous histogram $C_{AB'}(\tau)$ one correlates the original A-train with B-spikes from a record to a repeated presentation of the stimulus sequence. The first histogram represents stimulus correlation as well as neural correlation, the second histogram only stimulus correlation

Spectro-temporal sensitivities of the single units were determined by calculating the average pre-event stimulus intensity as a function of tonepip frequency and time before the spike, and by calculating the average pre-event CoSTID $\Xi(\omega,\tau)$ which can be considered as a single Fourier transform of the second order Wiener-kernel for the noise stimulus. Further details in Hermes et al. (1981, 1982).

RESULTS

Thirty-one double-unit pairs were recorded in the auditory midbrains from eleven grassfrogs under ipsilaterally, contralaterally and binaurally presented random tone-pip sequences and continuous noise sequences. Spectro-temporal sensitivities (STS) were obtained for the separated single unit records. Two main types of STS for the double-units were observed: either there was a close resemblance with respect to the spectral properties and with only the response latencies different, or the STS's were each others complement. In 14 cases we found a close match of the STS's, while in the remaining 17 double-unit pairs the STS were largely complementary with respect to the spectral sensitivity. In most cases the STS for ipsilateral presentation was confined to the central part of the STS under contralateral stimulation. This is illustrated in Fig. 3 where for one neuron (X) out of the four-unit recording illustrated in Fig. 1 the STS are shown for both ipsi- and contralateral stimulation with the three stimulus ensembles described in the methods section. The other unit had nearly the same STS.

The spike trains for these two units obtained by two times presenting the same tonal or noise stimulus ensemble were used to compute coincidence histograms (cf. Fig. 2) for the simultaneous and non-simultaneous conditions. An example of such an analysis is shown in Figure 4 for ipsi- and contralateral stimulation. The example again represents the same two units as in Fig. 3 and the spikes of these two units are indicated in Fig. 1 using the symbols Δ and X. One observes that for the ipsilateral stimulation with 48 ms duration tonepips presented once

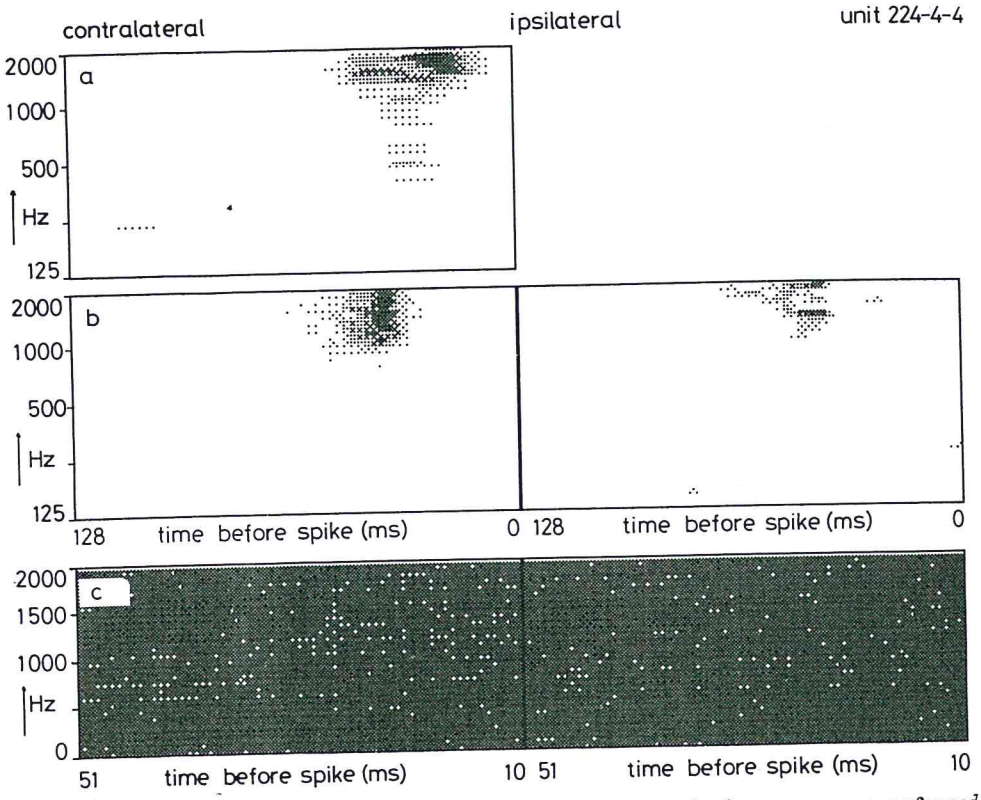

Fig. 3. Spectro-temporal sensitivities of unit 4-4 to stimulus sequences referred to as a, b and c in the methods section for both contralateral and ipsilateral presentation. Shown is the averaged pre-spike intensity in grey coding. For the tonal stimuli (a,b) the frequency scale is logarithmic, for the noise stimulus (c) linear. One observes that best frequency is between 1000 and 2000 Hz. The number of spikes are for contralateral respectively ipsilateral stimulation: a, 73-0; b, 391-45; c, 149-48

per second the coincidence histograms both are zero. This is due to the fact that unit 4-4 did not fire in that case. For the other stimulus conditions unit 4-2 generally fired more than unit 4-4. For contralateral stimulation one notes that the simultaneous and non-simultaneous coincidence histograms were the same for the long pause tonal sequence and that the difference is largest for the continuous noise stimulation. This indicates a stimulus dependent neural correlation. Comparing the ipsilateral and contralateral stimulus presentations one gets the impression that this does not so much influences the strength of the neural correlation (note the different scaling).

For the 31 double-unit pairs we observed in four cases a clear stimulus dependence and in another 4 cases some stimulus dependence. In none of these cases was an effect of stimulus presentation on the ipsilateral or contralateral side upon the strength of the neural correlation.

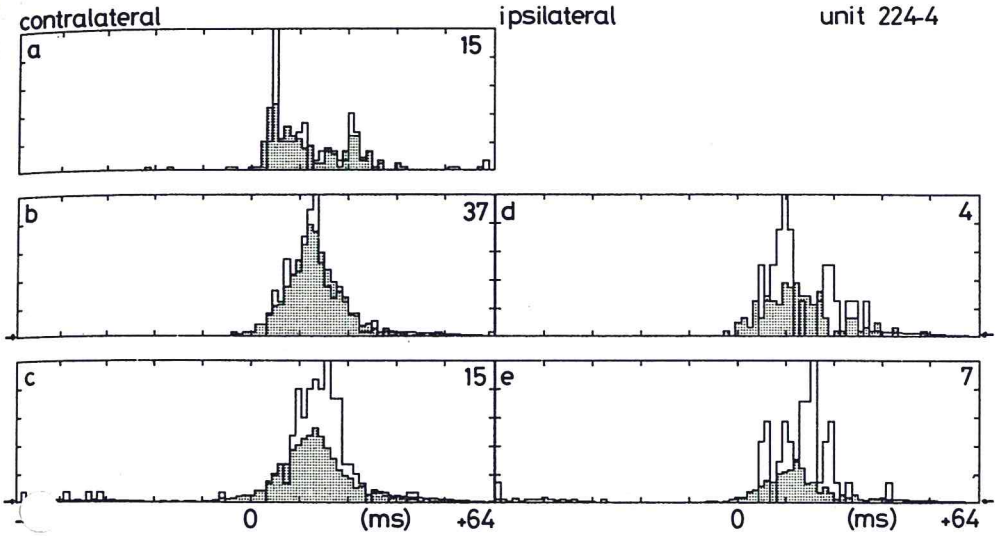

Fig. 4. Simultaneous and non-simultaneous cross coincidence histograms for units 4-2 and 4-4. In a, b and c the stimuli used were again as in Figure 3. One observes a larger difference between simultaneous and non-simultaneous cross coincidence histograms going from a to c. The numbers of spikes involved in the computation of the histograms are a: 237-73; b: 391-391; c: 516-149; d: 229-45; e: 416-48. The non-simultaneous histograms are dotted

DISCUSSION

Binaural hearing in frogs is probably based on mechanisms completely different from those attributed to mammals. First of all phase lock in the grassfrog at temperatures around 15°C is only present for best frequencies under 350 Hz as deduced from the measurement of reverse correlation functions (Hermes et al., 1981; Epping et al., in preparation). This excludes phase differences as a useful cue for directional hearing except at very low frequencies. However, in frogs in free field, small interaural phase differences are transformed by the tympanic-cavity, mouth-cavity system into quite large movement differences of the tympanic membranes. This is such that each ear acts as a pressure- pressure-gradient receiver having at low frequencies a cardioid direction characteristic. Secondly neurons in the auditory midbrain appear to be sensitive to small intensity differences between sounds applied using closed sound systems. Values of 2 dB are sufficient to change the firing rate of particular cells. Under natural conditions these differences arise only at the higher frequencies to which the frog is only marginally sensitive. When this sensitivity is combined with the peripheral pressure gradient transformer a large directional sensitivity results for the low frequencies but at the expense of an overall low sensitivity. EI cells in the auditory midbrain then are directional sensitive according to a figure-of-eight characteristic (EE cells would not show a directional preference). EI cells therefore can be seen as responding to quite large *effective* ΔI differences between both ears. The ears are most sensitive in free field around the resonance frequency of the mouth cavity, but at these frequencies (1000 - 1700 Hz) the directional sensitivity is poor. Quite a reasonable optimum combination of overall and directional sensitivity is present at the dominant frequencies found in the species own vocalisations (600 - 800 Hz), which is just below the tympanic membrane resonance.
Thirdly, on basis of evoked potential recordings from the midbrain of grassfrogs (Pettigrew et al., 1981) it is suggested that space (azimuth) is coded in the

midbrain such that rostral regions respond best to sound from the rostral aspect of the contralateral field and that caudal regions are best stimulated from tones presented in the caudal part of the contralateral field. This seems to be intermingled by a better representation of high frequencies in the rostral regions and low frequencies in the caudal regions of the midbrain (Pettigrew et al., 1981, Hermes et al., 1982).

Such spatial maps with relatively large receptive fields probably require the central reconstruction of target position on basis of the response of neural populations in order to obtain cue's for accurate source localisation. It is suggested that the synchrony within such a population of neurons plays an important role in the reliability of such a system. This synchrony will be enhanced by neural correlation. In this respect it might be of advantage that the strength of the neural correlation does not depend strongly on the site where the source is located, as is suggested by our measurements. On the other hand, our measurements suggest that neural correlation is strongly stimulus dependent, this could result in enhanced detectability in space of particular types of stimuli. The function of neural interaction would then be dominantly the enhancement of signal-to-noise ratio.

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