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Neural Representation of the Acoustic Biotope

A Comparison of the Response of Auditory Neurons to Tonal and Natural Stimuli in the Cat

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Abstract. Cats were stimulated with tones and with natural sounds selected from the normal acoustic environment of the animal. Neural activity evoked by the natural sounds and tones was recorded in the cochlear nucleus and in the medial geniculate body. The set of biological sounds proved to be effective in influencing neural activity of single cells at both levels in the auditory system. At the level of the cochlear nucleus the response of a neuron evoked by a natural sound stimulus could be understood reasonably well on the basis of the structure of the spectrograms of the natural sounds and the unit's responses to tones. At the level of the medial geniculate body analysis with tones did not provide sufficient information to explain the responses to natural sounds. At this level the use of an ensemble of natural sound stimuli allows the investigation of neural properties, which are not seen by analysis with simple artificial stimuli. Guidelines for the construction of an ensemble of complex natural sound stimuli, based on the ecology and ethology of the animal under investigation are discussed. This stimulus ensemble is defined as the Acoustic Biotope.

1. Introduction

In the neurophysiological study of the peripheral auditory system the stimuli used are mostly pure tones or tone bursts, clicks and continuous noise or noise bursts (Evans, 1975). Natural sounds have been used seldomly, and mainly for illustrative purposes (Watanabe, 1972; Kiang and Moxon, 1974). Representation of the experimental results in terms of stimulus-response relationships has mostly been low-dimensional: one aspect of the neuronal spike trains vs. one or two parameters of the stimulus. Examples are the tuning-curves (Kiang et al., 1965), PST-histograms (Kiang et al., 1965) and reverse correlation functions (De Boer, 1968; De Boer and De Jongh, 1978). Arguments for this approach are the simplicity of these stimuli and the ease with which they are generated in a laboratory. Moreover the quasilinear behaviour of peripheral parts of the auditory system allows an explanation of neural responses to complex and behaviourally interesting sounds from the responses to simple artificial stimuli. In higher parts of the auditory system the approach with this type of stimuli is less profitable; they are less effective and information on the responses to simple stimuli may not help in understanding the responses to complex stimuli (Evans, 1974). More recently investigations with more complex sounds have been made. A problem is the choice of the complex stimuli. One may start for instance with pure tones and gradually increase the degree of complexity by introducing amplitude and frequency modulation, addition of harmonics and noise. In most cases the complexity induced is relatively simple: modulation with linear or logarithmic sweeps, ramps or sinusoidal frequency and intensity variations (see e.g. Møller, 1973, 1978; Evans, 1974). In some special cases (e.g. *FM* bats (Suga, 1972)) such signals may resemble natural stimuli, but in most cases their structure does not resemble that of natural sounds. Another way is to start from a wide ensemble of complex sounds that may play a role in the natural behaviour of the experimental animal. This approach may be based on the argument that in phylogenesis the acoustic system has adapted structurally and functionally to process the sounds which occur in the environment of the animal and which are important for behaviour (Worden and Galambos, 1972). On the other hand species vocalisations have adapted in phylogenesis and ontogenesis to the properties of the auditory system (Marler, 1961; Sebeok, 1968; Gersuni and Vartanian, 1972; Worden and Galambos, 1972; Suga, 1978). A recent collection of papers related to this

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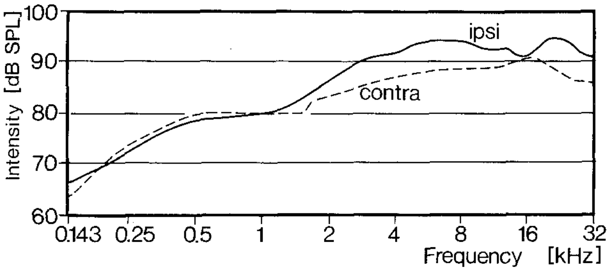

Fig. 1. The frequency response of the closed sound system. The graph is representative for all experiments and shows the sound pressure level (re 2.10^{-5} N/m^2) as a function of frequency at 0 dB attenuation. Relative sound levels in the Figures represent dB attenuation relative to this level

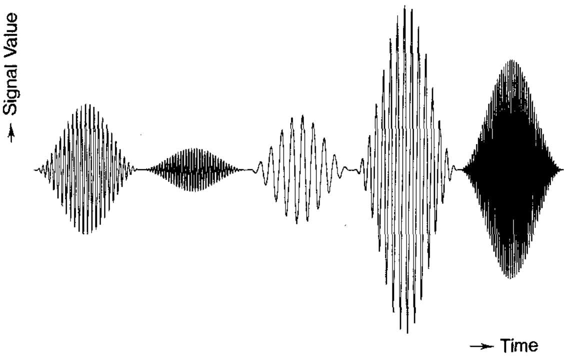

Fig. 2. A segment from a sequence of smooth tone bursts. Explanation in the text

approach is provided by the Dahlem report (Bullock, 1977).

In the present investigation a proposal is made for the construction of a wide stimulus ensemble on an ecological and ethological basis, not limited to specialised behavioural functions and neural structures (Suga, 1972) or animal vocalisations (Gersuni and Vartanian, 1972). A necessary condition for the usefulness of such a stimulus ensemble for neurophysiological investigation of single cell properties is that biological sounds influence neural activity in a significant and reproducible manner.

The methodological aspects of testing whether neuronal responses are indeed effected by a long complex ensemble of natural sounds in a reproducible way have been treated recently (Aertsen et al., 1979). It is the aim of the present paper to investigate *whether* responsiveness to natural sounds can be explained on the basis of the responsiveness to tones, *or* if some new information is gained from the use of such a wider stimulus ensemble. To this end we have compared single unit responses to natural sounds with those to tonal stimuli in a peripheral structure (cochlear nucleus: CN) as well as in a more centrally located nucleus (medial geniculate body: MGB) of the cat.

2. Methods

2.1. Preparation, Recordings and Histological Procedures

Five yound adult laboratory grown cats were used for the experiments. The methods used for the preparation of the animal, recording of single unit activity and histological control of the anatomical location of neurons were the same as have been described in detail by Van Gisbergen et al., (1975). Only a brief outline is given here.

The animals were premedicated with 0.25 mg atropine sulphate and anaesthetised with an intraperitoneal injection of Nembutal (30 mg/kg). A cannula was placed in the trachea. The head of the animal was fixed in a stereotaxic apparatus by means of a small holder screwed to the skull. A small hole was drilled in the skull over the desired brain area. Rectal temperature was kept at 37–38 °C.

Neural activity was recorded from two levels in the auditory system: the cochlear nucleus and the medial geniculate body. For experiments at the level of the cochlear nucleus the anaesthesia was maintained by additional intravenous injection of Nembutal (6 mg/kg) whenever reflexes to pinching of the skin between the toes of the hindlegs occurred. For experiments at the level of the medial geniculate body local anaesthesia of wounds was applied by infiltration with 0.5 % Marcaine before the administration of Nembutal was stopped and the animals were respirated with a mixture of 30 % O_2 and 70 % N_2O. The cats were immobilized by continuous infusion of a Flaxedil/glucose solution (0.2 % Flaxedil, 5 % glucose in Ringers solution) at a rate of 5 ml/h. The artificial respiration was adjusted for an end tidal CO_2-percentage of 3.8.

Neural activity was recorded extracellularly using glass micropipettes filled with 0.5 M sodiumacetate and 2 % Pontamine Sky Blue. Tip diameters were approximately 1 µm and impedances varied from 7 to 20 MΩ. Neural activity was amplified and action potentials were transformed to unitary pulses by means of a level discriminator for on line computer analysis. At characteristic points in an electrode track dye deposits were made for later histological identification of the recording sites. For this purpose, at the end of the experiment the animals were deeply anaesthetised and perfused with a 10 % formaline solution buffered to pH 4. Histological sections were made in a sagittal plane through the cochlear nucleus and in a frontal plane through the medial geniculate body. The sites of recording were reconstructed from the dye deposits made in each electrode track and the registration of recording depth with a micrometer.

2.2. Acoustic Stimulation

During the experiments the cat was placed in an electrically shielded acoustic chamber (IAC type 1202 A). Acoustic stimuli were applied by means of half inch condensor microphones (B&K 4134) and acoustic couplers, filled with damping material, sealed into the cat's external ear canals (Van Gisbergen et al., 1975). The sound pressure level was monitored using an identical B&K microphone. The frequency response of the system was measured in situ at the beginning of each experiment. A representative result is shown in Fig. 1.

Relative sound levels mentioned in the text refer to the sound pressure level (SPL re 2.10^{-5} N/m^2) obtained with an attenuator setting of 0 dB. Harmonics in the acoustic output of the sound generating system were at least 40 dB down. Stimulation was to both ears (I + C) unless stated otherwise (I for stimulation ipsilaterally, C for stimulation contralaterally with respect to the recording electrode).

The stimulus ensemble consisted of two classes of sound stimuli. Natural sounds (vocalisations of animals and abiotic sounds generated by wind and water) were recorded on analog tape (recorder Uher 4200, tape speed 19 cm/s, microphone Sennheiser transistor condensor microphone MKH 805). Selected sounds were repeatedly presented from a Sony TC 252 recorder in order to compile PST-histograms.

Artificial stimuli consisted of sequences of smooth tone bursts. The envelope of the bursts (squared cosine) was approximately Gaussian in order to minimize the product of the duration and bandwidth (Gabor, 1946). The frequency and peak intensity of subsequent tones were varied in a pseudorandom manner (Fig. 2). Standard parameters were: 127 frequency values (range 1 to 8 octaves) and 63 peak intensity values (range 40 dB). Both the frequency and the peak intensity values were distributed uniformly on log scale. The time intervals between the onsets of the Gaussian shaped tone bursts as well as the duration of the bursts were constant in one sequence (standard values 80 ms each).

2.3. *Analysis of Natural Sound Stimuli*

The set of natural sounds used for the present experiments consisted of 9 elements, arbitrarily chosen at this stage of the investigation. The sounds were classified into three groups: a) animal vocalisations with a low background noise level, b) animal vocalisations with a noisy background, c) noisy sounds (possessing no definite tonal structure). For a more detailed analysis spectrograms of each sound were made. The bandwidth of the sounds was limited to 10 kHz by low-pass filtering (Krohn-Hite 3343, 96 dB/oct) and the sounds were sampled by a digital computer at a rate of 20 kHz. The power spectral density as a function of time (the *dynamic power spectrum*) was calculated from these samples. The mewing sound of the tomcat (Fig. 3) may serve as an example. Figure 3-1 shows a representation equivalent to conventional sonograms (Potter, 1947). In Fig. 3-2 the same data are represented in a threedimensional way. Power as a function of frequency and time is presented as an amplitude on the time-frequency plane (Singleton and Poulter, 1967) allowing a more detailed inspection of the sound structure. The following properties of the sound become clear in this analysis: It has a tonal structure and shows many harmonics. The fundamental frequency is at about 600 Hz, the dominant frequency at 1.2 kHz (Fig. 3-3). There is only moderate modulation of frequency and amplitude. A substructure of noisy and harmonic parts is clearly discernible (compare Figs. 3-3 and 3-4).

2.4. *Analysis of the Stimulus-Response Relation*

2.4.1. Stimulation with Natural Sounds. The relation between the natural stimulus and the associated neural activity was studied by means of *peristimulus time histograms* (PSTH's): neural responses to repeated presentation of the stimulus were summated (time axis was divided in 1000 bins). The PSTH's were compared with the dynamic spectrum of the sounds, presented on the same time scale. The beginning and the end of the PSTH's are indicated by vertical bars in the spectrograms, the arrow *S* in the PSTH indicates the level of spontaneous activity, which is 0 in this case (Fig. 4-1). This representation allows simple visual comparison of the relation between spike density and power spectral density of the stimulus. Figure 4-1 illustrates this for a simple cochlear nucleus neuron.

2.4.2. Stimulation with Smooth Tone Bursts. The frequency-intensity response area in the classical sense was investigated with a sequence of smooth tone bursts, pseudorandomly varied in frequency and intensity (see Sect. 2.2).

Each action potential was represented by a dot in a cubic display: *IFT-cube.* The position of the dot was determined by three stimulus parameters:

I: The maximum *intensity* (in dB attenuation) of the tone burst during which the action potential occurred.

F: The carrier *frequency* of this tone burst (in kHz on a logarithmic scale).

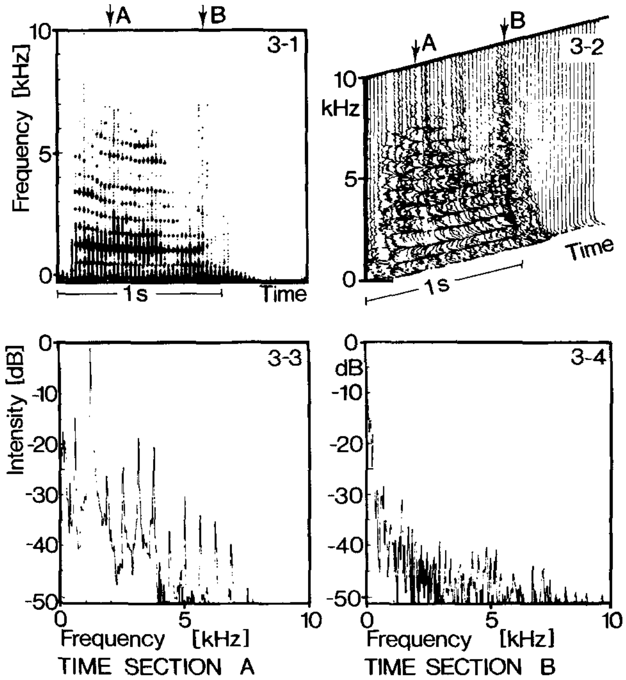

Fig. 3. The spectrogram of the mewing sound of the tomcat, illustrating the substructuring of noisy and harmonic parts of the sound. The resolution of the spectrogram is 40 Hz, 25 ms. **3-1.** The conventional representation as a sonogram (intensity resolution 10 dB). **3-2.** The same data in a threedimensional representation. **3-3.** Power spectrum of time sect. A of the sound (282–307 ms) showing the harmonic structure of this section. The dominant component is at 1.2 kHz. **3-4.** Power spectrum of another time sect. B of the sound (896–921 ms) where harmonic structure is lost. The location of sects. A and B is indicated in 3-1, 3-2

T: The *time* difference between the onset of the tone burst and the occurrence of the action potential (in ms). The length of the time axis equals the interval between onsets of tones.

For the purpose of good visualisation the IFT-cube (see Fig. 4-3) was divided into 5 intensity windows, with equal width and equidistant on the dB attenuation scale, and neural activity within each window was projected onto a FT-plane in the middle of that window. So each FT-plane represents the responses of the neuron to tone bursts of different frequencies and approximately the same peak intensity (within ±4 dB in Fig. 4-3) i.e. an isointensity scan. Projection of the data on a vertical IF-plane presents the response area of the neuron as a function of frequency and intensity (Fig. 4-2). The outer border of the cloud of dots represents the "*tuning curve*".

3. Results

The data were obtained from 5 cats. Neural activity was recorded from 6 units in the cochlear nucleus and from 19 units in the medial geniculate body. The sites of measurement were verified histologically.

3.1. *Cochlear Nucleus*

Results from the analysis of unit 93-3, located in the central region of the dorsal cochlear nucleus (nomen-

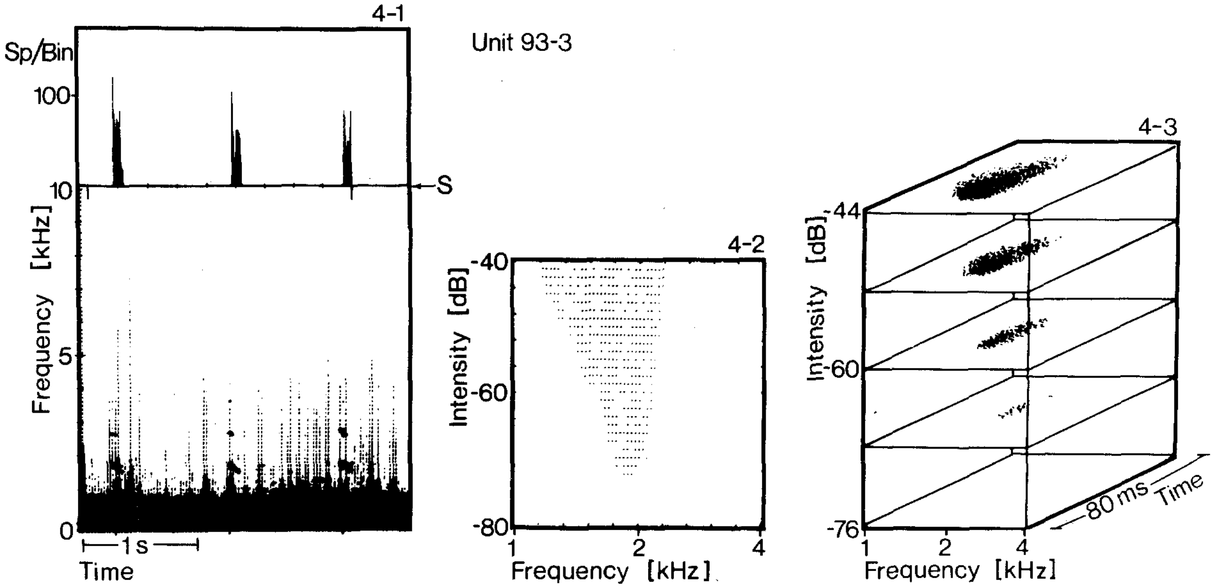

Fig. 4. Unit 93-3. Analysis of a cochlear nucleus neuron with natural and artificial stimuli. **4-1** Spike responses as a function of time (top) and power spectral density of the sound of the coot (Fulica atra) as a function of time. The sound was presented with a maximum peak intensity of −40 dB relative sound level and repeated 64 times. Presentation was to both ears. Beginning and end of the PSTH are indicated with vertical bars. Resolution is 1000 bins. The time mark corresponds to 1 s. The vertical axis represents the total number of action potentials per bin. Spontaneous activity is indicated by the arrow *S*. The resolution of the spectrogram is 40 Hz, 25 ms, 10 dB. **4-2** Neural response as a function of frequency and intensity summated over the duration of the tone bursts (80 ms). Action potentials are represented as dots. The outer border of the dotted area represents the "tuning curve" of the neuron. The characteristic frequency is approximately 2 kHz. **4-3** *IFT*-cube: neural activity as a function of tone burst maximum intensity *I*, tone burst frequency *F* and time *T* after tone burst onset. Explanation in the text

clature from Osen, 1969a, 1969b) are presented in Fig. 4. Comparison of the PSTH and the spectrogram of a vocalisation of the coot (Fulica atra) shows that stimulus evoked action potentials occur only when there is appreciable energy at frequencies above 1 kHz (Fig. 4-1). The level of spontaneous activity for unit 93-3 is zero. The sound of the coot has a harmonic structure: it consists of three "tweets", with tonal components at 1.8, 2.7 and 3.6 kHz. Apparently these tweets activate the neuron whereas the background noise in the vocalisation is confined to frequencies responses are higher at the on- and offset of each tweet. The maximum peak relative sound level at presentation time was −40 dB.

A comparison of these data with the results of tonal analysis shows that for this cochlear nucleus neuron the responses to natural sounds can be understood quite well from tone burst responses. The background noise in the vocalisation is confined to frequencies below 1 kHz; from tonal analysis it is seen that the neuron is not activated by tone bursts with frequencies below 1 kHz at intensities below −40 dB relative sound level (Figs. 4-2, 4-3). This explains why the PSTH shows no events inbetween the coot tweets. The tweets have energy up to −40 dB relative sound level at 1.8 and 2.7 kHz and the neuron is activated by tone bursts of these frequencies and intensities (Figs. 4-2, 4-3). This explains the high event density at time moments corresponding to the occurrence of the tweets.

One discrepancy between the analysis with natural sounds and the analysis with tone bursts is very obvious: the response to the coot tweets is higher at

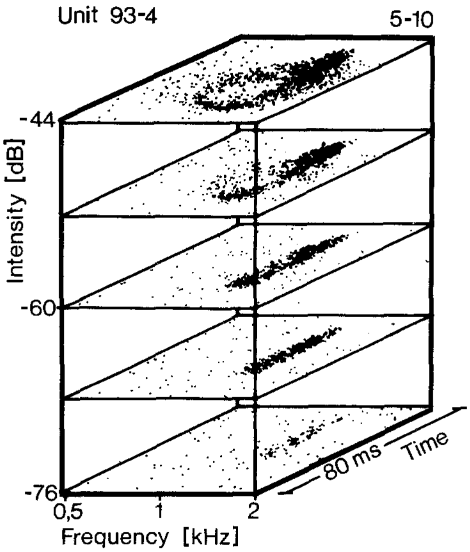

Fig. 5-10. IFT-cube: neural activity as a function of tone burst maximum intensity I, tone burst frequency F and time T after tone burst onset. Explanation in the text

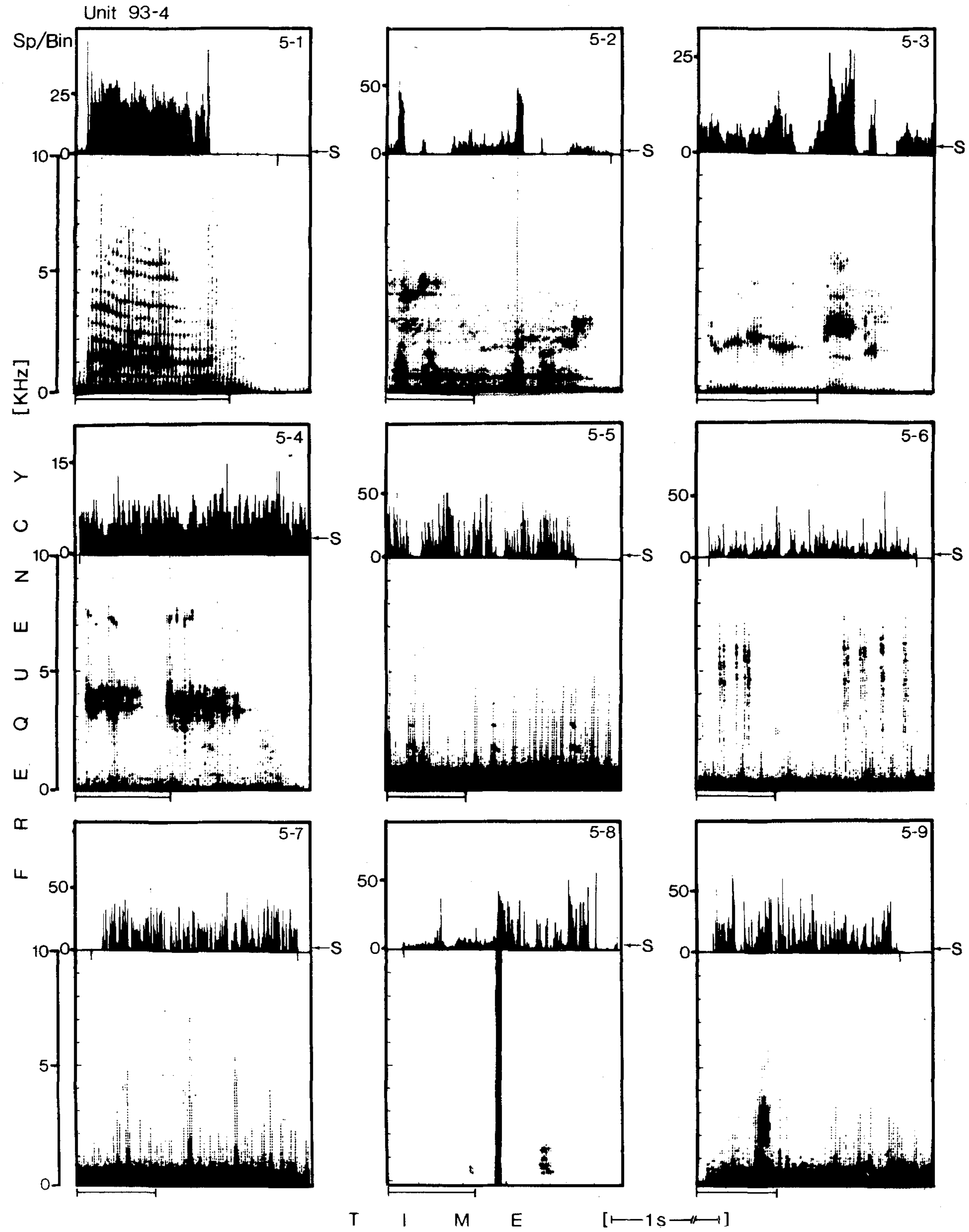

Fig. 5. Unit 93-4. Analysis of a cochlear nucleus neuron with a variety of natural sounds. The maximum peak intensity for all sounds was −40 dB relative sound level. Each sound was presented 64 times to both ears. The resolution of the PSTH's is 1000 bins. The time mark corresponds to 1 s. The vertical axis represents the total number of action potentials per bin. Spontaneous activity was 16.5 imp/s (2.7 imp/bin in the PSTH) as indicated by *S*. The resolution of all spectrograms is 40 Hz, 25 ms, 10 dB. The 9 biological sounds are: **5-1.** Mewing of tomcat (Felix catus). **5-2.** Sound of cuckoo (Cuculus canorus). The vocalisation occurs twice in the sonogram. **5-3.** Sound of blackbird (Turdus merula). **5-4.** Song of a robbin (Erithacus rubecula). **5-5.** Vocalisation of coot (Fulica atra). **5-6.** Alarm sound of wren (Troglodytes Aroglodytes). **5-7.** Wind, rustling trees, titmouses (Parus spec.). **5-8.** Barking of dog (Canis), preceeded and followed by growling. **5-9.** Wind, rustling leaves, twigs, breaking twigs

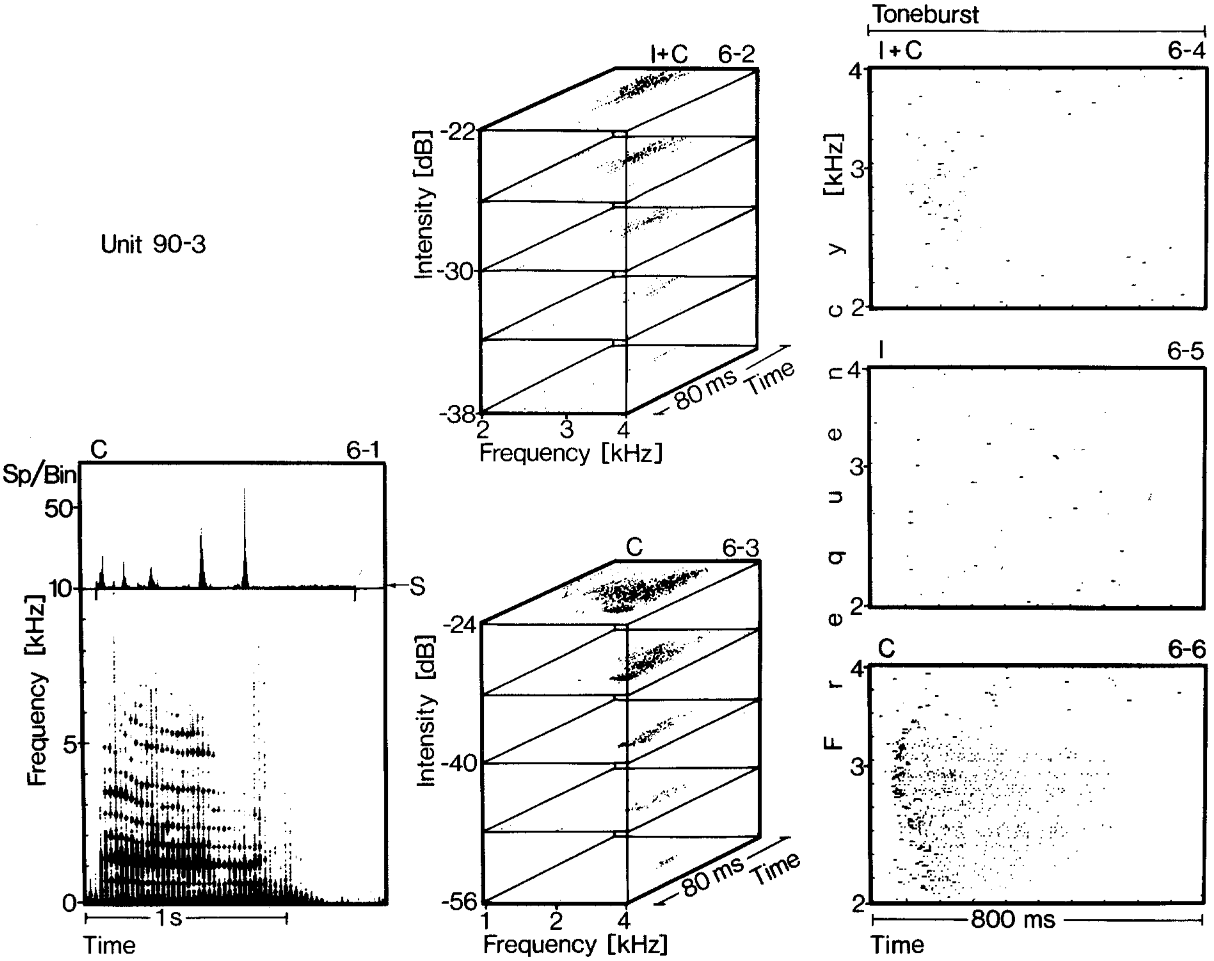

Fig. 6. Unit 90-3. Analysis of a neuron from the medial geniculate body with mewing of a tomcat and with tone bursts. The maximum peak intensity of the mewing sound was 0 dB; it was repeated 256 times. **6-1** Sonogram of mewing sound and PSTH of neural activity evoked by contralateral stimulation (*C*). Further details as in Fig. 4-1. **6-2** *IFT*-cube: neural activity as a function of tone burst maximum intensity *I*, tone burst frequency *F* and time *T* after tone burst onset. Explanation in the text. Stimulation was bilaterally (*I*+*C*). **6-3** *IFT*-cube upon contralateral stimulation (*C*). **6-4, 6-5, 6-6** Random *FT*-scans upon bilateral (*I* + *C*), ipsilateral (*I*) and contralateral (*C*) stimulation. Explanation in the text

the on- and offset (Fig. 4-1) whereas the responses to the smooth tone bursts show gradual build up and decline (Fig. 4-3). The temporal structure of the stimulus apparently plays a role here.

Figure 5 presents the experimental results for unit 93-4, which was located in the posteroventral cochlear nucleus at the border of the pyramid cell layer. The unit was tested with a variety of natural sounds.

In all cases except in 5-4 the neural activity on stimulation with a natural sound is quite different from the spontaneous activity which amounts to 16.5 impulses/s and is indicated by the arrows in the PSTH's. So for eight out of nine natural sounds a stimulus-response relation clearly exists.

The responses to tone burst stimuli show simple activation for intensities below −60 dB attenuation, at frequencies of about 1.3 kHz (Fig. 5-10). At higher intensities a complex pattern of activation and suppression occurs for tone burst frequencies in the range of 0.7-2 kHz (Fig. 5-10). If we compare the results from the stimulation with tone bursts to those of the stimulation with natural sounds some conclusions on the stimulus-response relation can be made. For those natural sound stimuli which have, at certain moments of time, considerable energy in the 0.7–2 kHz frequency range (Figs. 5-1, 5-2, 5-3, 5-5, 5-8) there is a high correlation between the time structure of the PSTH and the spectral density in this frequency range. Sometimes simple activation appears to occur (Fig. 5-1), sometimes both activation and suppression (Figs. 5-2, 5-3, 5-5). Note in Fig. 5-2 the differences in high frequency composition of both vocalizations and the similarity of the corresponding neural responses in the PSTH. The result in Fig. 5-3 appears to be consistent with these observations, however, at this level of analysis it remains unclear whether indeed the energy in the 0.7–2 kHz frequency band is responsible for the strong response between 1.0 and 1.3 s. In the remaining natural sound stimuli there is less energy in the 0.7–2 kHz frequency range and the stimulus-response relation is less clear. This is seen best in Fig. 5-4 where the sound evoked activity nearly equals the spontaneous level and in Fig. 5-6. It must be emphasized however that, although its nature is not immediately clear from Figs. 5-6, 5-7, 5-8, 5-9, a stimulus-response relation certainly exists, as concluded from the effectivity of all of these stimuli. The structure of the PSTH's in these cases is too complex to investigate the stimulus-response relation in a qualitative way only. The explanation or prediction of the responses to the natural sounds from the responses to tone bursts can be only partly successful since in the natural sounds complex spectro-temporal patterns are presented and in most cases the time envelopes are different from the 80 ms smooth envelope of the tone bursts. From the analysis with the tone bursts no information can be obtained on interactions of more frequency components with different intensities nor any information on the effect of envelopes other than the particular one used. This may be illustrated by the "sustained" response in PSTH 5-1 to the tonal harmonic vocalisation of the tomcat and the "suppression" response in PSTH 5-5 to the short tone "tweets" in the vocalisation of the coot. Intermediates can be seen in Figs. 5-2 and 5-3.

A more detailed and more elaborate evaluation of the data is necessary to gain more than the general impression outlined above (see Discussion).

3.2. Medial Geniculate Body

In Figure 6-1 the response of unit 90-3 from the medial geniculate body is presented. This unit is located at the border of the magnocellular and the principal nucleus of the MGB (Berman, 1968). The stimulus is the mewing sound of the tomcat which was presented to the contralateral ear. The PSTH clearly indicates that there is a stimulus-response relation, although its nature is not obvious. The peaks in the PSTH are larger where the energy in the spectrogram is lower and the bandwidth smaller, but no simple relation of the time courses exists. The analysis with tonal stimuli reveals that the unit responds to tones of frequencies between 1 and 4 kHz (Figs. 6-2, 6-3). There is an interaction of ipsilateral and contralateral stimuli, and there are differences in the response properties with only contralateral or ipsilateral stimulation (Figs. 6-4, 6-5, 6-6). The neuron is at least 20 dB more sensitive to contralateral than to bilateral stimulation, while the response type is completely different to both ways of stimulation (Figs. 6-2, 6-3). The unit was also investigated with long tone bursts (800 ms) (random FT-scans: Van Gisbergen et al., 1975). Although there is hardly any response to ipsilaterally presented tone bursts (Fig. 6-5), there is a clear influence of the ipsilateral stimulus (suppression) in the bilateral case (Figs. 6-4, 6-6). Additional information could be gained from other findings. The spontaneous discharge rate of the unit was 80 impulses/min. If stationary Gaussian wideband noise was presented to both ears the discharge rate fell to 3 impulses/min. Stimulation of only the ipsilateral ear appeared not to influence the discharge rate (75 impulses/min), whereas stimulation of the contralateral ear raised the discharge rate to 363 impulses/min. The unit responded better to frequency sweeps around 3 kHz in the upward than in the downward direction.

The responses to stimulation with the noise stimulus and with 800 ms tone bursts are somewhat puzzling. When noise stimulation is used, the lowest discharge rate is obtained upon bilateral stimulation, whereas with tonal stimuli ipsilateral stimulation yields the lowest discharge rate (Fig. 6-5). Apart from the obvious differences which exist between these stimuli, it should be noted that there is a time difference of about two hours between these recordings. It is clear that the response to the natural sound cannot be explained by the responses to tone bursts not even with the additional information gained. There is some similarity, however, between the nature of the responses to tone bursts of 800 ms and the response to the tonal mewing sound of the tomcat, both responses are burstlike (Fig. 6-1, 6-3).

The results for unit 94-1 are shown in Fig. 7. This unit was located in the medial geniculate body, as concluded from the electrode track, but could not be localised precisely.

The response to repeated bilateral presentation (256 times) of the call of the cuckoo is shown in Fig. 7-1. The PSTH shows a clear structure, with lowest event density at moments corresponding with high power spectral density in the stimulus. This structure clearly indicates that the neural activity is influenced by the stimulus. Results from the analysis with binaurally presented tone bursts are shown in Fig. 7-2. A comparison of the neural activity during binaural stimulation (Fig. 7-3) with the activity during monaural stimulation (Figs. 7-4, 7-5) was made with tone bursts of 80 ms duration presented at 250 ms intervals. There was no detectable influence of the tone burst stimuli on the neural activity. Evidently it is impossible in this case as well to explain the responses to the natural sound from the neural activity during tone burst stimulation, at least at this level of analysis.

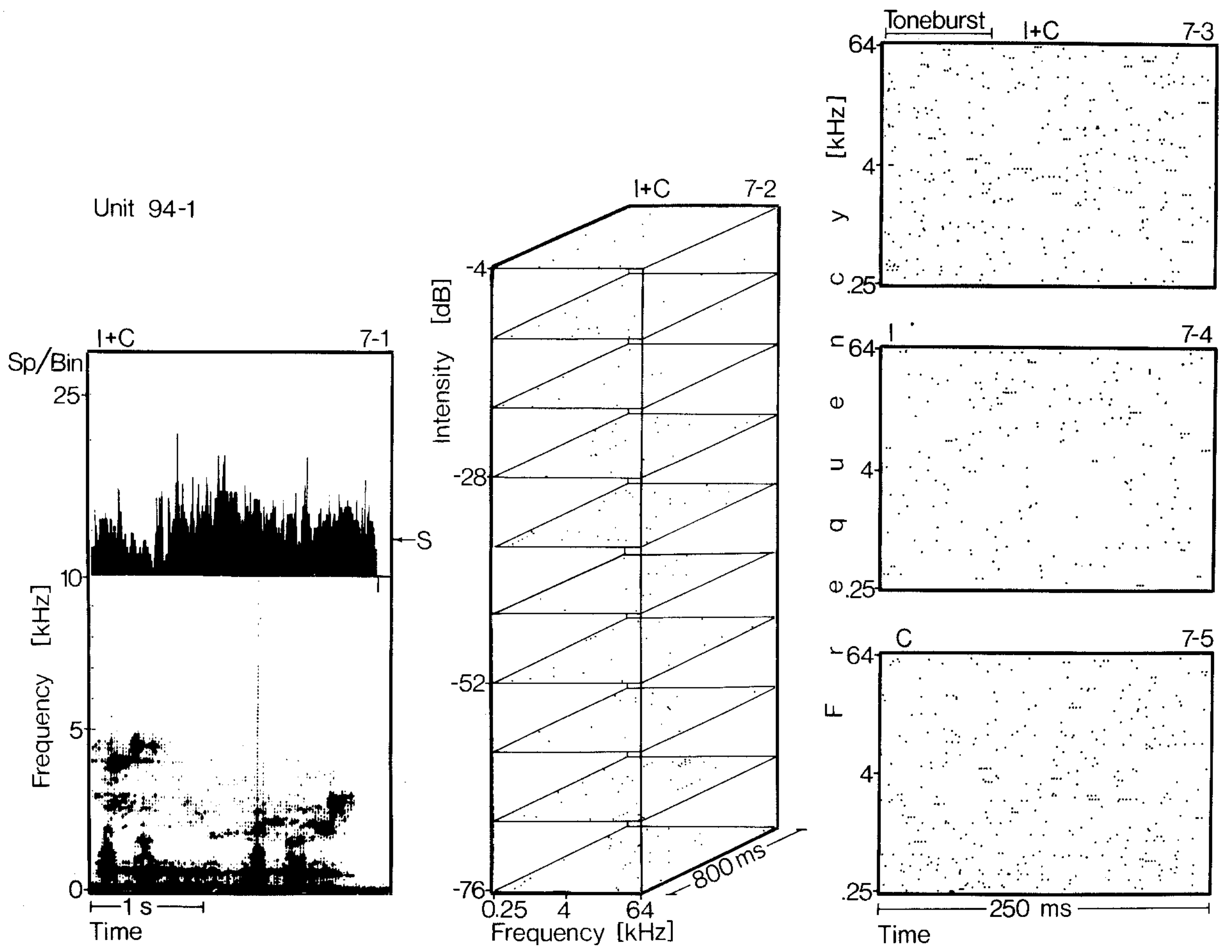

Fig. 7. Unit 94-1. Analysis of a medial geniculate body neuron with the vocalisation of the cuckoo and with tone bursts. The maximum peak intensity of the vocalisation was −20 dB relative sound level. **7-1** Sonogram of cuckoo vocalisation and PSTH of neural activity evoked by bilateral stimulation ($I+C$). Further details as in Fig. 4-1. **7-2** *IFT*-cube: neural activity as a function of tone burst maximum intensity I, tone burst frequency F and time T after tone burst onset. Explanation in the text. **7-3, 7-4, 7-5** Random *FT*-scans upon bilateral ($I+C$), ipsilateral (I) and contralateral (C) stimulation. Explanation in the text. Note the difference between the duration of the tone bursts (80 ms) and the time interval between tone bursts onsets (250 ms) in this case

4. Discussion

As reported in the methods section Nembutal anaesthesia was used in the surgical procedure, maintained in the CN-preparation and replaced by Flaxedil relaxation in the MGB-preparation. It is known that cats take a long time (up to 8 hours) to recover from Nembutal anaesthesia, which has been demonstrated to have a profound effect on neuronal responsiveness (Webster and Aitkin, 1971; Kallert, 1974): less activity and less suppression are to be found. This has been shown to occur already at the level of the dorsal cochlear nucleus (Evans and Nelson, 1973). All MGB-units, except for three of them, were recorded well beyond the period of 8 hours after Nembutal anaesthesia was stopped. In the case of unit 90-3 (Fig. 6) about 6 hours had expired. A comparison of results for the MGB-units does not give rise to the idea that neural responsiveness was strongly influenced by the anaesthesia.

From the present results it is clear that complex natural acoustic stimuli are effective in evoking single unit responses at low and higher levels in the cat's auditory system.

At the level of the cochlear nucleus the responses to natural sounds can be understood fairly well from the responses to tone bursts if the spectrotemporal properties of the natural sound stimuli are taken into account. At the level of the medial geniculate body the responses to different types of stimuli are much more complex. Responses to natural sounds do not appear to be simply predictable from responses to tonal stimuli. Apparently at this level new information can

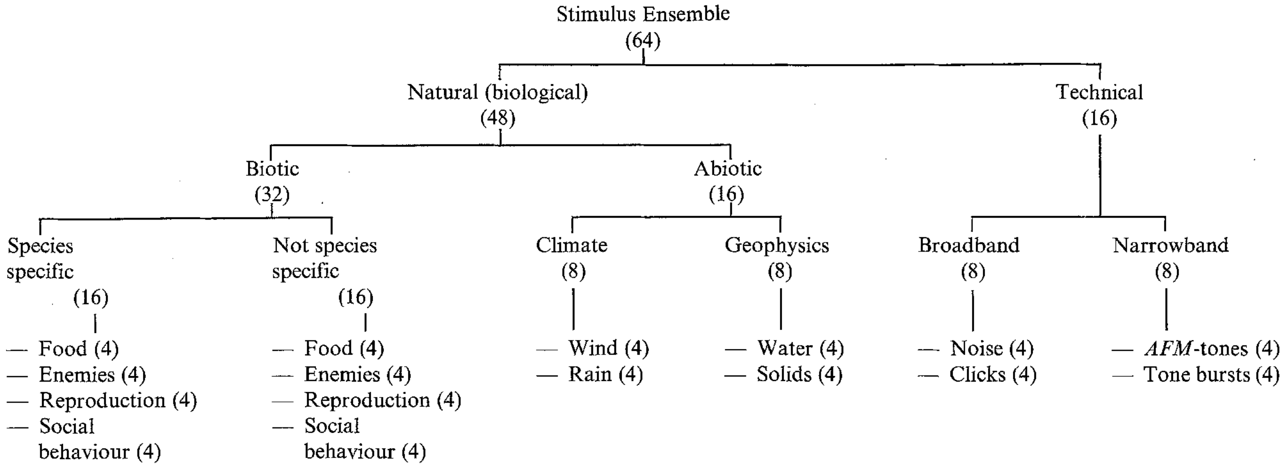

Diagram 1. Construction scheme for realisation of a stimulus ensemble inspired by the Acoustic Biotope of the cat

be gained by using natural stimuli, apart from technical stimuli.

One may wonder whether an experimental program, in which natural sounds with relatively short duration (in the present case about 2 s) are repetitively presented in order to compile PST-histograms, is the most optimal way to investigate neural responses to natural stimuli. Apart from the time consuming nature of such an approach when many different sounds are to be presented, several aspects of the stimulus, like novelty, context and the like, are strongly affected by it. Although, probably, in the present experiments the latter will not play a very important role, this might well be the case when recording from awake, behaving animals. A stimulus ensemble which takes into account these considerations as well as those mentioned in the introduction has been constructed and used: the *Acoustic Biotope* (Aertsen et al., 1979). A further elaboration of this ensemble can be found in the Appendix.

The analysis of data obtained with the Acoustic Biotope as a stimulus ensemble must be able to

1) decide whether any relation between the stimulus ensemble and the neural activity exists (Aertsen et al., 1979), and

2) if so, determine the characteristics of the stimulus response relation.

From 2) it follows that the analysis should comprise a detailed description of the stimulus ensemble. This description must involve the physical characteristics (spectro-temporal properties) as well as biological characteristics (ethological and ecological observations) of the sounds. This analysis thus bears much relation to the notions of "*information bearing elements*" (Suga, 1973) and "*bioacoustic dimensions*" (Scheich, 1977). The analysis of the stimulus-response relation can be performed according to methods inspired by nonlinear system theory (Johannesma, 1972; Grashuis, 1974). A report on the results from this analysis for an ethologically based stimulus ensemble, which takes into account both first and second order aspects of the stimulus-response relation, is in preparation (Aertsen et al., in prep.).

Appendix

The Acoustic Biotope as a Stimulus Ensemble

The natural environment in which an animal lives, as far as functionally related to the animal, is defined as its *biotope* or *habitat.* It encompasses both the biotic and abiotic components of this environment (Dahl, 1921; Odum, 1971). Important characteristics are: geographical location, geophysical properties, climate regime, variety and numbers of occurring plants and animals. The total of sensory aspects of the biotope forms the *Sensory Biotope*, which consists of different components, according to the different sensory modalities of the animal. The ensemble of sound signals from the biotope which can be perceived by the animal forms the *Acoustic Biotope*. It is clear that the Acoustic Biotope, and consequently the stimulus ensemble inspired by it, will vary for different animal species. Both the degree of complexity and the extent of the stimulus ensemble depend on the biotope of the animal as well as on its behavioural repertoire.

Elements from the Acoustic Biotope can be characterized according to different types of properties. Some of them are:

- ecological properties: sounds which have to do with geophysics, with animals, plants, with climate (wind, rain) etc.
- ethological properties: relation to behavioural context, for instance collection of food, avoidance of enemies, reproduction, social behaviour (Collias, 1959; Marler, 1961; Winter et al., 1966; Winter and Funkenstein, 1973).
- physical properties: spectro-temporal characteristics of the sound signals: frequency bandwidth, FM, AM etc.
- statistical properties: probability of occurrence of elements and combinations of elements.

A scheme for the composition of a wide ensemble of natural sound stimuli, inspired by the Acoustic Biotope of the cat, is shown in Diagram 1. This scheme takes into account the characteristics of sound signals as mentioned.

A stimulus ensemble based on this scheme has been constructed and used (Aertsen et al., 1979). The natural sounds used in the present investigation are a small selection from this ensemble. Note that technical sounds are included. The purpose of this is to be able to relate neural responses to natural stimuli and these commonly used technical stimuli.

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