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On the Mechanisms of Call Coding Through Auditory Neurons in the Squirrel Monkey

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Summary. The main goal of the study was to investigate the neural processing of those acoustic signals through auditory neurons whose relevance for communication is either obvious or has been tested by psychoacoustic or behavioral experiments. Thus the activity of cortical, thalamic (MGB) and midbrain (IC) neurons of the auditory pathway were studied with periodically amplitude-modulated (AM) sounds, species-specific AM vocalizations and self-produced vocalizations. With regard to the processing of AM stimuli, there is evidence of a neural correlate to the psychoacoustic phenomenon "fluctuation strength": maximum of the Best Modulation Frequency (BMF) for the cortex was registered at 4 Hz. Furthermore, a relatively large number of units within the IC and the MGB can encode such amplitude changes which have been shown to be of communicative function; here too a neural correlate to the encoding processes of species-specific calls was indicated. Self-produced vocalizations do not seem to underlie a specific processing except that in higher auditory structures, they evoke quantitatively lower responses. In the midbrain, such less active areas are rare and were localized in regions belonging more to secondary auditory structures than primary ones.

Key words: Auditory system – Vocalizations – Neural processing – Squirrel monkey

Introduction

As regards the acoustic expression of emotions, it is generally assumed that man and monkey, as well as other mammals, share many elements in their repertoires of acoustic signals. Language, however, is a prominent property which clearly distinguishes man from his closest evolutionary neighbors, the nonhuman primates. That the differences in the acoustic behavior of man and monkey may not be as great as originally thought or wished has been suggested by recent behavioral experiments. It has been demonstrated that monkeys also produce and perceive acoustic signals in a manner which makes it possible for them to deliver information to the conspecific containing more than an indication of their emotional state (Seyfarth et al. 1980; Marler 1985).

Thus monkeys might be suitable subjects not only for studying the basic anatomical and physiological properties of the systems underlying the performance of primate acoustic behavior, but also in the search for correlates which may help explain the processes of more complex acoustic communicative functions. The research dealing with these anatomical and physiological properties has been given great attention and served as a basis for numerous studies carried out with the aid of neuroanatomical and neurophysiological methods. On the other side, many behavioral experiments were centered on the evaluation of those rules controlling the more complex relations of acoustic communication. Information about the connection between the two research directions is extremely limited: what is the neuronal correlate of a specific acoustic behavioral element?

The aim of this paper is to report, in a more comprehensive way, the results of several different experimental approaches all designed for collecting information on the neural processing of those acoustic signals which have been established, by behavioral or psychoacoustic tests, to be of biological relevance or to have a communicative function.

Methods

Preparation. Experiments were performed on adult squirrel monkeys (Saimiri sciureus) whose outer ears showed no sign of damage or infection. Preparation for, and the technique of the extracellular recording of single cell activity have been described elsewhere (Müller-Preuss and Ploog 1981) and will be mentioned here only briefly. Recordings were carried out in a sound-attenuated chamber. The animals were awake and undrugged and were partially restrained in a small chair which allowed both head fixation and small body movements. The action potentials of single neurons from the auditory pathway (cortex, thalamus, and midbrain) were recorded with tungsten microelectrodes (2–10 MOhms), amplified for computer analysis and prepared using traditional methods.

Acoustic Stimulation. Acoustic stimuli were presented via a loudspeaker mounted 1.5 m in front of the animal's head. Artificial (AM) stimuli were generated with a Wavetek 146 Multifunction generator (tones) and a Grason-Stadler noise generator (noise) whose intensity was varied sinusoidally. Frequency of modulation was selected in octave steps from 1 Hz to 128 Hz. An electronic switch (Grason General-Radio 1396 B) determined stimulus length. The sound pressure level was controlled by an attenuator (HP 350). The data obtained from 15 stimulus presentations were used for calculating one peri stimulus time histogram (PSTH) which in turn served for further data analysis.

Natural AM Stimuli. As natural stimuli showing modulations in amplitude so-called "cackle" vocalizations were used. These cackle vocalizations were recorded from behavioral experiments which had revealed that definite amplitude changes within these calls were of communicative relevance (Maurus et al. 1984). The vocalizations were digitized (20 kHz) and stored in a computer. For stimulation, the calls were randomized by computer control and presented at intensities varying between 80 and 30 dB. Each call was presented eight times and the data obtained used for PSTH calculation.

Self-produced vocalizations were recorded either during spontaneous utterances or after electrical brain stimulation of the central grey matter. To avoid consequences to the neuronal recordings due to stimulus artifacts, only those vocalizations which occurred some 100 ms after the stimulation were used. The evoked calls were recorded together with the cell activity and stored on analog tape as well as in the computer. The uttered calls were also recorded on an endless-loop tape and played back for comparison at different intensities immediately after the self-produced vocalizations.

Data Analysis. Those PSTHs obtained from AM stimulation were analyzed by a fast fourier transformation for the purpose of defining the best modulation frequency (BMF). The rate of digitization was 448 or 896 c/s. Remaining PSTHs (natural AM calls, self-produced, and playback calls) were analyzed by inspection.

Histology. Several electrode tracks within the particular structures studied were marked by electrolytic lesions (5–20 μA/5–20 s). The remaining tracks were reconstructed on the basis of stereotactic data and the lesion-verified tracks. For histological preparation, the animals were perfused under deep anesthesia with physiological saline and 4% formaldehyde. Paraffin sections of 10 μm were stained for Nissl preparations with cresyl violet.

Results

Sounds with Periodic Amplitude Modulations

The records of the action potentials of 59 cortical cells and 72 midbrain (inferior colliculus) cells during stimulation with white noise and tones were analyzed. The intensity of the stimuli was modulated sinusoidally. The frequency of the tones corresponded with the neurons' characteristic frequency. Units which did not display a characteristic frequency were always tested with white noise. In some cases, neurons were tested with both tones at CF and white noise. Only in a few instances was a difference in BMF responses to tone and noise detected. Therefore, the responses to tones and white noise were considered together in the analysis presented here.

Response Properties of Cortical Neurons

The penetrations were directed vertically to the surface of the superior temporal gyrus between anterior posterior coordinates 11–4 (Gergen and MacLean 1962) with the Sylvian fissure as the upper and the superior temporal sulcus as the lower border. Thus the primary auditory area as well as the secondary auditory areas yielded electrode penetrations. However, most units described here came from the primary auditory cortex (AI), some were from regions posterior and lateral to AI. Since the responses of such units differed only in a small amount from those of the AI region, they were analyzed together. As can be seen in Fig. 1, cortical neurons did not follow modulation frequencies higher than 64 Hz. Most of the units responded best between 1 and 32 Hz (90%), with the BMF maximum being registered at 4 Hz.

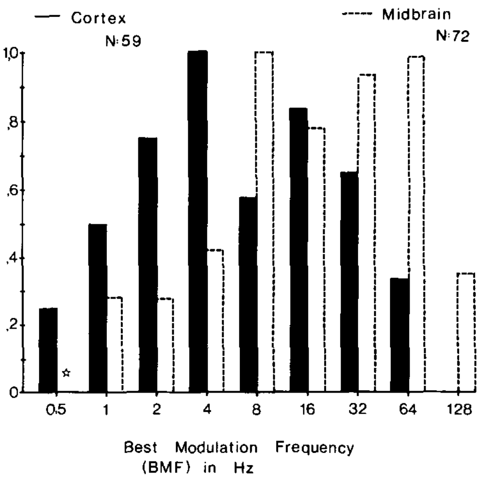

Fig. 1. Responses to BMF of cortical and midbrain (inferior colliculus) cells. For comparison the number of cells are normalized to those BMF to which most cells of the particular structure responded. *Black columns:* cortical cells; *white columns:* cells from the colliculus inferior. Note that midbrain cells were not tested at 0.5 Hz (white star)

Response Properties of Midbrain Neurons

All neurons were recorded in the inferior colliculus, most of them in its central nucleus. In contrast to the cortex, relatively few neurons displayed BMFs lower than 8 Hz. Most of the collicular neurons responded between 8 Hz and 64 Hz (72%); a maximum BMF appeared at 8 Hz as well as at 64 Hz. The modulation frequency of 0.5 Hz was not tested in the colliculus.

In Fig. 1 the results for both structures are outlined together for comparison. As can be seen, the BMF responses of both areas showed a bandpass characteristic: only a few cells responded at low modulation frequencies and at high modulation frequencies. The maximum of the bandpass was for the cortex between 4 and 16, for the colliculus between 8 and 64 Hz. Thus collicular neurons can on average code higher modulation frequencies.

Amplitude-modulated Species-specific Vocalizations

To investigate the processing of amplitude changes in a closer relationship to species-specific acoustic behavior, eight examples of squirrel monkey vocalizations with no frequency modulations were used as stimuli. These vocalizations had their spectral energy between 100 and 3000 Hz. Similarly, the response properties of 82 collicular and 32 thalamic (medial geniculate body) neurons were studied. For all units such general response properties as tuning areas or rate level functions were evaluated in addition. Many collicular as well as thalamic neurons did not differentiate between the particular vocalizations. If there was a difference in response, often it could be explained by the frequency response characteristic (tuning) of the unit or by its simple rate/level relationship. Nevertheless, a relatively large number (15%–20%) of units whose response

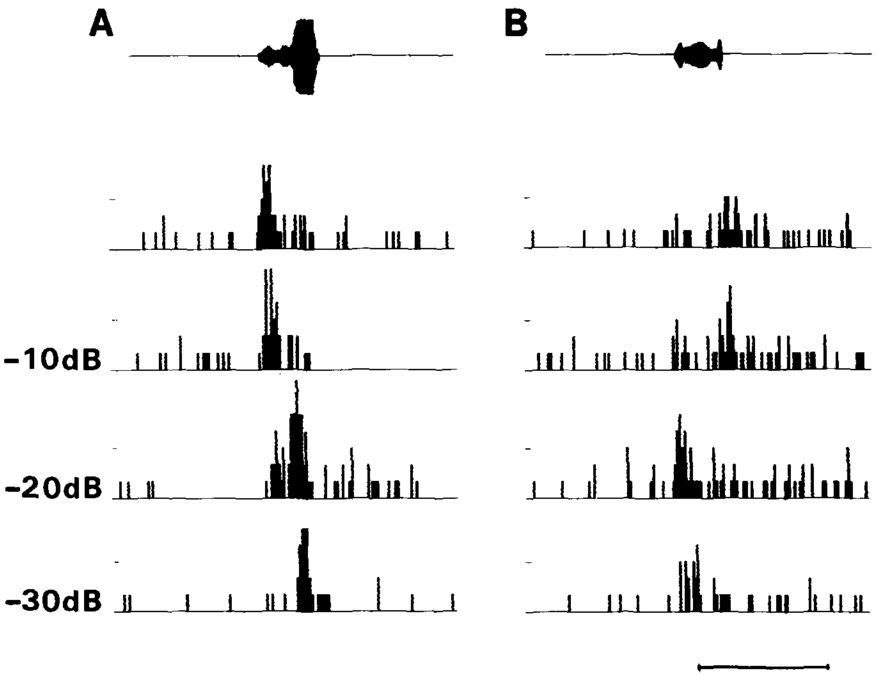

Fig. 2. Responses of two midbrain cells during stimulation with AM Kakel calls at four intensities are outlined in PSTHs. Greatest average intensity was 65–75 dB. Bar = 100 ms; bin width of PSTH is 2 ms. For better comparison of particular call components with neuronal activity, latency is compensated for in the figure. Above the PSTH's, the amplitude course of the calls is outlined

Fig. 3. *Left:* The particular structures of the auditory pathway of the squirrel monkey are summarized in one plane with the aid of several frontal Nissl sections. *Right:* In a corresponding outline drawing, the responses during the utterance of vocalizations and to playback calls of midbrain neurons are summarized: *cross-hatching* indicates those regions where almost no differences in the responses to self-produced vocalisations and their playbacks were registered. *Hatching* from the upper right to the lower left indicates areas where some neurons were found which displayed no response during the utterance of vocalizations. *Abbreviation: CN,* cochlear nucleus; *Ctx*, cortex; *GM*, medial geniculate body; *IC*, inferior colliculus; *LL*, dorsal nucleus of lateral lemniscus; *OS*, superior olive; *I*, primary auditory cortex; *II*, secondary auditory cortex

patterns gave evidence of a specific processing of specific amplitude changes within a call were found. Two examples of such cells are given in Fig. 2. In part A the responses of a collicular cell to a call with three distinct amplitude leaps are shown: one leap at the beginning, one in the middle, and the relatively largest at the beginning of the last third. With regard to general response properties, this neuron responded monotonically to increasing white noise and showed a broad tuning characteristic. To the call, however, the neuron reacted in a very specific manner: at highest intensity (the uppermost PSTH) a response was seen at the first amplitude change. Lowering the intensity by about 10 dB evoked no change. But with the next 10 dB step the activity of the neurons suddenly shifted to the third amplitude leap. This activity also remained for the next 10 dB step (lowest PSTH). Thus the cell can encode, indepedently from the absolute level of the call, definite amplitude leaps within a call. The second example shown in part B of Fig. 2 represents a similar situation. Here the call can also be divided in three parts along the amplitude course. In contrast to the first example, there was no difference in the absolute amplitude level between the three parts: all had a similar height of amplitude. When comparing the four PSTHs, a very specific coding of the particular amplitude leaps, independent from the level, can be seen: at the highest intensity, the third change evoked a response which remained at the next weaker level. With the next step (third PSTH) a shift from the third amplitude leap to the first occurred which again remained by lowering the amplitude about 10 dB. It is of interest to note that the second leap, despite being on the same level as the first and the third, evoked no reaction. Some 15% (colliculus) and 20% (thalamus) of the neurons sampled displayed such responses. No histological correlation to different substructures of the inferior colliculus or the medial geniculate has been established so far.

Self-produced Vocalizations

A further approach to investigating the processing of biologically relevant sounds was the recording of the activity of auditory neurons during the utterance of vocalizations. The data presented here came from 350 auditory neurons whose activity was recorded from structures within the midbrain: the inferior colliculus, the dorsal nucleus of the lateral lemniscus, and parts of the reticular formation. The largest number of cells responded to the self-produced vocalizations. The kind of response was thereby very similar to those reactions which were evoked by the most comparable stimuli, the playback of self-produced vocalizations. However, some of the cells (less than 10% of the sample) showed no or only a very weak response during the self-produced calls, even when there was a clear response to the playback calls of comparable intensity. The existence of different amplitude levels between self-produced vocalizations and their playbacks were compensated by the presentation of the latter at different intensities. Such differentiating neurons are found only in specific regions of the midbrain. The histological verification of the electrode tracts leads to the assumption that such neurons are restricted to marginal regions of the inferior colliculus and to an area in the reticular formation. Figure 3 shows the situation in the midbrain from a structural point of view: areas within the central nucleus of the inferior colliculus and the dorsal nucleus of the lateral lemniscus contained almost exclusively neurons which responded to self-produced vocalizations (cross-hatching). Areas which contained differentiating neurons are indicated by hatching from the upper right to the lower left.

Discussion

The results presented here came from studies concerned with the evaluation of neuronal mechanisms of call coding within the auditory pathway of primates, with the squirrel monkey being the experimental model. Species-specific calls of squirrel monkey are mostly of a complex structure consisting of many parameters. Theoretically, therefore, many of these parameters, or call substructures, could be responsible for causing a neuronal response. Using simple artificial sounds as stimuli, the processing of particular parameters of calls, such as frequency, intensity, location, and their various combinations, has been investigated in numerous neurophysiological studies (for a review see Pickles 1982). It has been shown that up to the cortical level, even simple stimuli often evoke complex responses. These findings make the interpretation of neuronal responses to species-specific calls very difficult for, without parallel behavioral indicators, it is impossible to differentiate between reactions caused purely by the existence of a distinct parameter set within a call and reactions evoked by the biological relevance of the call. To partially circumvent such interpretatory restrictions, conditioning experiments can be applied where the sensation-evoked response can be correlated with a behavioral reaction. Unfortunately, however, such studies are often limited by the experimental setup required for electrophysiological recordings. Another approach is the use of only such stimuli whose relevance is either obvious or has been clarified by experimental testing. Three out of a number of thinkable calls or stimulus types have been chosen for investigation of the neuronal activity of higher auditory centers.

(1) In the search for a neuronal correlate of the psychoacoustic phenomenon "fluctuation strength", sinusoidally modulated tones have been selected, for in psychoacoustic experiments, it has been shown that periodically changing amplitudes of noise and tone stimuli evoke the sensations of roughness and fluctuation strength (Fastl 1982, 1983). Whereas roughness is evoked by modulation frequencies between 50 and 150 Hz, fluctuation strength reaches its maximum at 4 Hz. Analysis of the BMF of cortical responses revealed a maximum at 4 Hz, analysis of collicular neurons one from 8 to 64 Hz. So there seems to be a decrease in value of the BMF when transferred from lower to higher auditory centers, an assumption supported by reports from Møller (1972), Rees and Møller (1983) and Schreiner et al. (1983). In other words, the higher a neuron is located within the auditory pathway, the lower is the AM frequency encoded. As regards human acoustic communication, 4 Hz also seems to be the best frequency, so the results for cortical cells may be considered an indication that a neuronal correlate to the described psychoacoustic phenomenon exists. These considerations are somewhat weakened by the fact that squirrel monkey calls, if they contain periodical AM parts, do not show frequencies lower than 12 Hz. The question arises why the auditory cortex of squirrel monkeys should be tuned to a BMF which is not of species-specific relevance. Frequencies higher than 12 Hz could be better encoded by midbrain than by cortical neurons.

Future studies are required to clarify in which way these findings are related to species-specific communication and whether they can be interpreted as an indication of a neuronal prerequisite for the coding of acoustic cues relevant in human communication.

(2) Several studies have been conducted dealing with the response properties of auditory neurons to species-specific calls in primates (Winter and Funkenstein 1973; Newman and Wollberg 1973; Glass and Wollberg 1983). In general, the stimulus sets were chosen as a representative sample of the animals' vocal repertoire. Contrary to exceptations, no high selectivity of auditory cells was found: most of the cells responded to most of the calls presented. These findings indicate that the processing of vocalizations is not organized by coding one call type through one neuron type. Since the response patterns were often highly complex, it may be assumed that distinct parameter sets were responsible for the reaction. As mentioned before, this would require the testing of numerous parameter constellations with numerous neurons. The results reported here, however, have been obtained by an approach concentrating on those calls or call parts which had been shown to have a communicative function. More explicitly, the availability of behavioral data reduces the number of response interpretations. Based on behavioral experiments, it has been shown that the frequency of production of distinct amplitude changes (leaps) within nonfrequency modulated calls (cackles) and their position within a call can be correlated with distinct behavioral situations (Maurus et al. 1984). Using such calls as acoustic stimuli, it has been shown that a relatively large number of auditory neurons of the midbrain and the thalamus can encode specifically the position of such amplitude leaps. There is also evidence of a neuronal correlate of a mechanism processing acoustic signals with a communicative function. Although these experiments are at their very beginning, the results obtained so far let experimenters hope that by following this concept, they may gain a closer insight into the neuronal processing mechanism of biologically relevant signals.

(3) Auditory neurons are stimulated in a relatively natural way (i.e., not via a loudspeaker) by an individual's vocal activity. During the utterance of vocalizations not only information on the sensory processing of an individual's acoustic activity is obtained but also data on possible relationships of the auditory system with structures involved in sound production. According to earlier studies, a relatively large number of neurons of the auditory cortex and thalamus did not respond to self-produced vocalizations, results which were not obtained in the inferior colliculus (Müller-Preuss and Ploog 1981; Müller-Preuss 1983). So it seems that higher stations of the auditory pathway display less activity during an animal's vocal activity than lower ones. The findings presented here confirm these observations: very few neurons in the auditory midbrain did not respond to self-produced vocalizations even though they reacted to playback calls. It is interesting to note that such neurons are found in marginal regions of the inferior colliculus, regions which also receive projections from nonauditory structures (Aitkin et al. 1975). The situation is similar in the region of the reticular formation. On account of these connections to nonauditory areas, the "unresponsiveness" may possible be explained as follows: structures active during vocalization can influence parts of the auditory pathway, gradually increasing this influence the higher the auditory stations are. Such neural processing may represent a mechanism monitoring an individual's acoustic activity perhaps required for learning or controlling vocal performance. Another explanation may be that the role an individual's vocal activity plays in his own sensory system gradually lessens the higher the auditory station is. Self-produced vocalizations may not be of as much communicative value to the producer as to a possible companion to which the activity is directed. The auditory system of the producer will, of course, receive his vocal activity but, inasmuch as the weight a signal is given depends on the situation, not necessarily perceive it. In the midbrain, most of the neurons do respond to self-produced vocalizations. A comparison of the responses to self-produced vocalizations with those obtained by stimulation via playback calls revealed many similarities. Consequently, from a qualitative point of view (response patterns), there seems to be no special processing of self-produced vocalizations.

On the occasion of this special issue, a survey of results of recent experiment conducted by our laboratory has been given here: three different approaches based on one methodological concept were used to find out more about the neural processing of signals relevant to the acoustic behavior of primates. The results once more demonstrate the usefulness of a combined application of neurophysiological and behavioral methods: unburdened by the multitude of mostly meaningless acoustic signals, investigations can be concentrated on those which are of importance in intraspecific communication.

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