

Vocalization Influences Auditory Processing in Collicular Neurons of the CF-FM-Bat, *Rhinolophus ferrumequinum**

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Summary. 1. In awake Greater Horseshoe bats (*Rhinolophus ferrumequinum*) the responses of 64 inferior colliculus neurons to electrically elicited vocalizations (VOC) and combinations of these with simulated echoes (AS: pure tones and AS(FM): sinusoidally frequency-modulated tones mimicking echoes from wing beating insects) were recorded.

2. The neurons responding to the species-specific echolocation sound elicited by electrical stimulation of the central grey matter had best frequencies between 76 and 86 kHz. The response patterns to the invariable echolocation sound varied from unit to unit (Fig. 1).

3. In 26 neurons the responses to vocalized echolocation sounds markedly differed from those to identical artificial ones copying the CF-portion of the vocalized sound (AS). These neurons reacted with a different response to the same pure tone whether it was presented artificially or vocalized by the bat (Fig. 2). In these neurons vocalization activities qualitatively alter the responsiveness to the stimulus parameters of the echoes.

4. A few neurons neither responded to vocalization nor to an identical pure tone but discharged when vocalization and pure tone were presented simultaneously.

5. In 2 neurons synchronized encoding of small frequency-modulations of the pure tone (mimicking an echo returning from a wing beating prey) occurred only during vocalization. Without vocalization the neurons did not respond to the identical stimulus set (Fig. 3). In these neurons vocalization activities

enhanced FM-encoding capabilities otherwise not present in these neurons.

6. FM-encoding depended on the timing between vocalization and frequency-modulated signal (echo). As soon as vocalization and FM-signal no more overlapped or at least 60–80 ms after onset of vocalization synchronized firing to the FM was lost (4 neurons) (Fig. 4).

7. 4 neurons weakly responded to playbacks of the bat's own vocalization 1 ms after onset of vocalization. But when the playback frequency was shifted to higher frequencies by more than 400 Hz the neurons changed firing patterns and the latency of the first response peak (Fig. 5). These neurons sensitive to frequency shifts in the echoes returning during vocalization may be relevant to the Doppler-shift compensation mechanism in Greater Horseshoe bats.

Introduction

Bats use ultrasonic echolocation signals for their orientation in space and for catching their prey. Emitting their echolocation pulses prior to the perception of the echoes, bats have to analyse the acoustical information of echoes during or immediately following a strong self-stimulation of their ear by the emitted sound.

There exists a wealth of data reporting the responses of auditory neurons to artificial stimuli that simulate echoes and echolocation sounds of bats. Many adaptations of audition to the requirements of echolocation have been described.

Grinnell (1963), for example, found neurons in the inferior colliculus of bats that preferentially responded to a second fainter tone pip in a pair of stimuli. This indicates that the preceding tone pip

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Abbreviations: AS, see Summary (1); AS(FM), see Summary (1); CF, constant frequency; FM, frequency modulated; VOC, electrically elicited vocalization

(echolocation sound) could enhance the response to the second fainter tone pip simulating an echo.

In *Rhinolophus ferrumequinum* the responses of collicular neurons to tone bursts at about 83 kHz, the frequency of the constant frequency portion (CF) of its natural echolocation sound, were enhanced if a tone burst of slightly lower frequency (78–83 kHz) preceded the stimulation (Möller, 1978). This specific stimulation mimicks the frequencies in the emitted echolocation pulse and in the returning echo of a hunting bat that compensates for the Doppler-shifts produced by its own flight speed (Schuller et al., 1974).

Behavioural experiments in the same bat have further demonstrated the necessity of interaction between the vocalized echolocation sound and the returning frequency-shifted echo for the functioning of the Doppler-shift compensation system (Schuller, 1977). This finding strengthened the hypothesis that vocalization by itself may influence the responsiveness of auditory neurons in some specific ways. The only experiment so far demonstrating a direct neural influence of the vocalization on auditory processing is that of Suga and Schlegel (1972). They reported that in the little brown bat (*Myotis grisescens*) evoked potentials of the lateral lemniscus to vocalized orientation sounds were attenuated compared to those to the playback of the echolocation sounds. They concluded that neural influxes preceding or accompanying vocalizations attenuate the responsiveness of lemniscal neurons to selfstimulation by vocalization.

Horseshoe bats are especially well suited for investigating the possible influences of vocalization on the processing of auditory stimuli. They emit a simple structured echolocation sound consisting of a long (10–80 ms) constant frequency portion (CF) terminated by a short frequency-modulated portion (1–3 ms, 16 kHz) (FM). The emitted frequencies of CF-portions range between 78 and 85 kHz. These species-specific echolocation signals can be consistently elicited by electrical stimulation in the central grey matter of the midbrain. On the other hand this CF-FM signal can easily be simulated electronically, be modified by behaviourally relevant modulations (frequency and amplitude modulations) and can be played back to the bat by an ultrasonic loudspeaker. By this approach changes in the neural auditory response to “echo-like” signals by neural activities due to vocalizations could be investigated.

Methods

Single neuron responses were recorded in 9 *Rhinolophus ferrumequinum*. Under ether anesthesia, the skull of the bats was exposed

and a screw was mounted with dental cement on its anterior part, small holes were drilled over the left inferior colliculus for the insertion of the recording electrodes and near the right colliculus (more medial and anterior to the center of the inferior colliculus) for the insertion of the stimulating electrode. After administration of neuroleptic (4 mg/1,000 g body weight, Droperidol) to reduce spontaneous body movements without inhibiting the capability to vocalize, the animals were put in an animal holder and the cemented screw was locked into a rigid metal bar to immobilize the head. The wound margins were continuously treated with local anesthetic agents (Novocain) during the experiment. The controlled emission of echolocation sounds was elicited by monopolar electrical stimulation in the region of the central grey matter with insulated stainless steel electrodes (80 µm diameter), where only the tip was exposed by cutting the wire. The electrical stimuli were produced by a Grass S-88 stimulator with an optical isolation unit (PSIU 6) and consisted of 3–10 ms long trains of pulses 0.1 ms wide and at a repetition rate of 1,000 Hz. The repetition rate of the trains was 3–6 Hz corresponding to the natural emission frequency of orientation pulses in a resting bat.

The electrical stimuli elicited orientation pulses with a latency of 20 to 60 ms. The elicited orientation sounds were undistinguishable in frequency pattern, intensity and duration from natural echolocation sounds. The stimulation site in the brain was adjusted to give a minimum of body movements or ear movements besides the emission of echolocation sounds.

The auditory stimulation setup and the ultrasonic loudspeaker characteristics were the same as described earlier (Schuller, 1979). The neurons recorded in the inferior colliculus were stimulated with different auditory stimulus sets:

a) Vocalizations (VOC). The neurons were stimulated by the electrically elicited echolocation sounds alone without any playback through the loudspeaker.

b) Vocalizations and Playback (VOC+PB). The neurons were stimulated by the electrically elicited vocalized echolocation sounds succeeded by a playback of the vocalization through the loudspeaker at a fixed delay of 1 ms. The echolocation sound could be frequency-shifted to higher frequencies thus mimicking Doppler-shifted echoes (see Schuller et al., 1974).

c) Vocalizations and Artificial Stimuli [VOC+AS, VOC+AS(FM)]. The electrically elicited vocalized echolocation sounds triggered an artificially produced tone pip (AS), that followed the echolocation sound after adjustable delay times. The tone could be sinusoidally frequency-modulated (AS(FM)) mimicking echoes returning from wing beating prey.

d) Pairs of Artificial Stimuli [AS+AS, AS+AS(FM)]. The first stimulus of the pair was a pure tone with the duration and the frequency of the CF portion of the echolocation sound but without final FM sweep so that the response of the neuron could be compared with that to the vocalized stimulation (see c). The second artificial stimulus was variably adapted to resemble the different echoes.

The echolocation sounds emitted by the bat were recorded with a Bruel & Kjaer microphone (type 4135) and the frequency of the constant frequency portion was measured with a frequency to voltage converter (Datel VFV-100 kHz). The frequency of the constant frequency portion of the electrically elicited orientation sounds showed the same typical 100–200 Hz standard deviation around the resting frequency of the bat as in the spontaneously emitted echolocation sounds. The sound pressure level of the emitted sounds was measured with an envelope detector.

The playback of the echolocation sounds or the artificial acoustical stimuli were delivered by a condenser loudspeaker to the contralateral ear of the bat under free field conditions, so that no direct reflections of the vocalizations could occur at the loud-

speaker. The experiments were performed in a room with sound absorbing wall covers to minimize echoes from the emitted sound. Single unit responses were recorded with conventional methods using 3 M KCl glass pipettes with an addition of alcian blue dye (Harnischfeger, 1978) for iontophoretic marking of the recording site. The nerve impulses were amplified and fed on-line to a PDP 11/40 laboratory computer. The computer was programmed by Hans Zöllner to accumulate post-stimulus-time histograms.

The stability of the recordings during vocalization constituted the most difficult methodical problem, as the movements of the brain during vocalization could only be reduced but not avoided.

Results

A. Responses to Electrically Elicited Echolocation Sounds or Similar Artificial Pure Tone Stimuli

The responses of 63 neurons have been recorded from the inferior colliculus to vocalizations, to artificial acoustical stimuli and combinations of both. Most of the neurons (52 or 80%) tested with vocalizations had best frequencies in the frequency range of the CF- and FM-portions of the echolocation sounds between 70 and 86 kHz. The response types and the tuning characteristics to pure tones corresponded to those commonly found in the inferior colliculus of the Greater Horseshoe bat (see f.e. Möller et al., 1978). With the exception of a few neurons (4) all neurons with best frequencies (BF) between 70 and 86 kHz responded to electrically elicited echolocation sounds.

The response patterns to stimulation by the emission of the echolocation sounds without any acoustical playback are shown in Fig. 1. The characteristic envelope of the sound and its frequency structure (CF-FM-pattern) are depicted schematically at the bottom of the figure. On-responses (18 neurons), pure off-responses or responses to the final FM-sweep of the sound (3 neurons), tonic responses (26 neurons) and on-off-responses (14 neurons) occur similar to the response patterns generally found with pure tone stimulation in collicular neurons. Due to the slightly varying duration of the vocalized echolocation sounds the responses to the final FM-sweep or the end of the sound are scattered in time and therefore the response peaks in the histograms are blurred. Within the limited sample of neurons no preferred response pattern was discernable, but the tonic response type was more frequently encountered as response to the vocalized sound than to artificial pure tone stimuli in collicular neurons.

In 25 neurons in the inferior colliculus the responses to vocalized echolocation sounds markedly differed from those to an artificial pure tone at the identical frequency of the CF-portion of the echolocation signal. Two examples are depicted in Fig. 2. Figure 2A shows the PST-histograms of a neuron to the

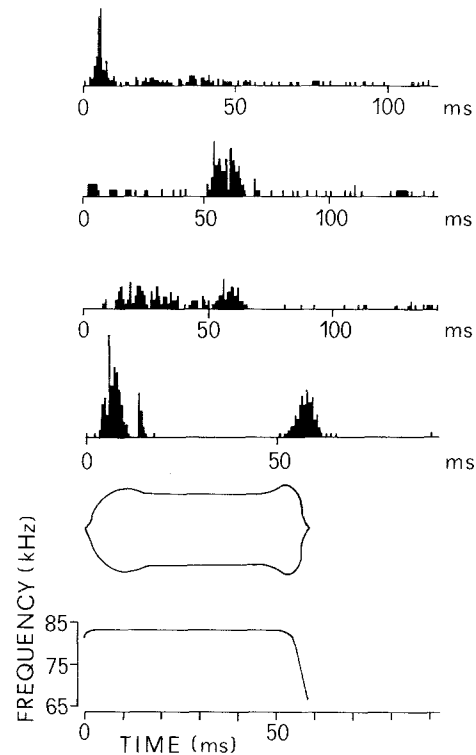


Fig. 1. Response patterns to electrically elicited vocalizations alone of 4 collicular neurons (upper 4 histograms). The two lower graphs show typical envelope (upper) and typical frequency pattern (lower) of vocalized echolocation sounds. Duration of echolocation sounds was different for each of the 4 neurons. Histograms summarize responses to 40 stimulus presentations

vocalization and to a pure tone at the CF-frequency with decreasing sound intensities. Whereas the vocalization provoked a weak tonic response without an off-response, the artificial pure tone clearly evoked on- and off-responses at all intensities.

The neuron in Fig. 2B has its characteristic frequency at 82.6 kHz and does not respond to an artificial stimulus frequency at 83.4 kHz as shown in the right half of the figure. However, the same frequency of 83.4 kHz vocalized by the bat as the constant frequency portion of its echolocation sound elicits a vigorous on-response (left column of the figure). The response to the end of the echolocation sound is probably due to the final FM-sweep. As may be seen in the PST-histograms of Fig. 2 the different response patterns and levels are not due to differences in intensity or frequency between vocalized and artificial tone. Thus the differences of the response can only be interpreted as caused by the vocalization itself. In this kind of neurons, susceptible to vocal activities, the responses to vocalized stimuli can not be deduced from their properties evaluated by conventional auditory stimulation.

In 32 of the 58 neurons the response patterns elicited by the vocalized echolocation sound did not

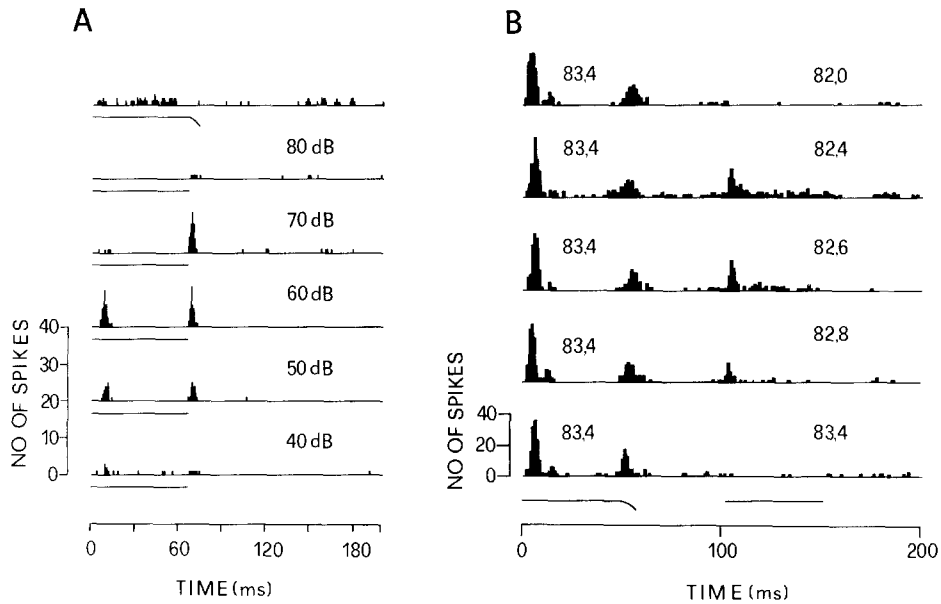


Fig. 2A and B. Responses of 2 collicular neurons to electrically elicited vocalizations and to artificial pure tones. **A** Response to vocalization alone (upper histogram). Lower 5 histograms: responses to artificial pure tones with the frequency of the CF-portion of the echolocation sound at different intensities as indicated on the right of each histogram. **B** Responses to vocalization and subsequent pure tone stimulation at different frequencies (intensity: 80 dB SPL). The CF-frequency of the echolocation sound lies at 83.4 kHz. Histograms were collected with 40 stimulus presentations

differ from that elicited by an artificial pure tone at the frequency of the CF-component of the echolocation sound. The off-responses showed some variations dependent on the type of stimulation. The responses to the end of the vocalizations were elicited either by the end of the constant frequency portion or by the final FM-component. In the latter case the end of an artificial pure tone elicited no spikes in the neuron tested. On the other hand some neurons showed off-responses to the artificial pure tone stimulus, that did not occur in the vocalized sound, i.e., when the CF-component was followed by the final FM-sweep. This finding corresponds to the results of Suga et al. (1974) showing in *Pteronotus p. parnellii* that a final FM-sweep suppressed the off-response to the end of a pure tone at the CF of the bat's echolocation sound.

B. Responses to Combinations of Vocalizations and Stimulated Echoes (VOC+AS)

In order to approximate natural stimulus patterns in echolocation the vocalizations were used as trigger for artificial tone pips that were delivered to the bat's ear by a loudspeaker at various delays to the beginning of the vocalizations between 0 ms and 200 ms. The frequency of the tone pips was variable and could be additionally modulated in frequency by a sinusoidal waveform thus mimicking in first approximation

the echo-reflections of a rhythmically moving target as f.e. beating wings of an insect.

In the majority of the recorded neurons prior or simultaneous vocalization had either no or an inhibitory effect on the response to the artificial stimulus (AS) simulating the echo. The vocalization usually reduced the discharge activity to the following stimulus but rarely completely inhibited the response. The inhibitory effect was strongest between 20 and 60 ms after the onset of the vocalization. In some neurons the vocalizations also deteriorated the response pattern to the sinusoidally frequency modulated [AS(FM)] stimuli. However, in other neurons the prior or concurrent vocalization changed the response pattern to the artificial echo in an enhancing way. In one neuron, for example, an artificial pure tone alone had an inhibitory effect on the spontaneous activity. When the pure tone was presented during the vocalization, however, the inhibitory effect of the pure tone was converted in an excitatory response, whereas the vocalization inhibited the spontaneous activity.

Two neurons were found that responded neither to vocalizations alone nor to a pure tone alone at the CF-frequency of the echolocation sound and at different intensities. However, the neurons discharged when vocalization and pure tone were presented simultaneously. Apparently the vocal activities gated these two neurons for the auditory processing of the pure tone stimulus. Under natural conditions these two neurons would therefore only respond to an echo

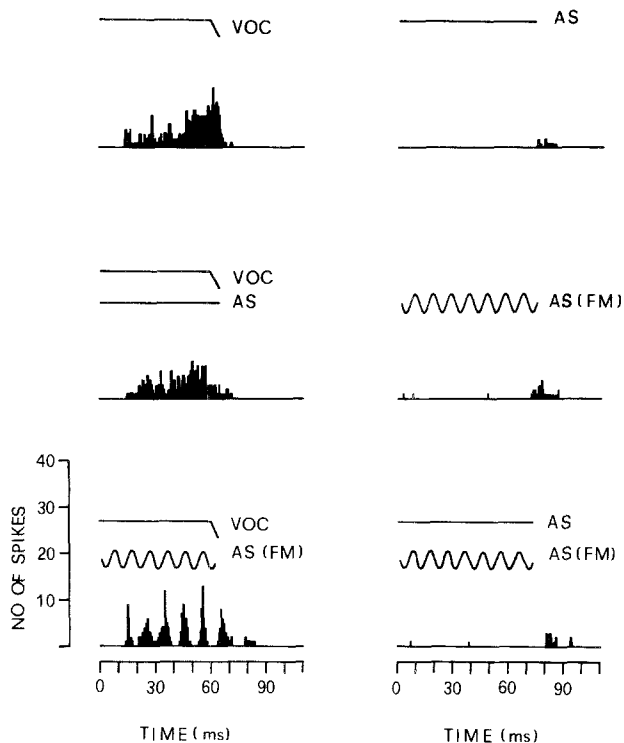


Fig. 3. Discharge patterns of a collicular neuron to (VOC) vocalization alone, (AS) to an artificial pure tone at the CF-frequency of the echolocation sound, (VOC+AS) to a combination of vocalization and the pure tone, [AS(FM)] to a sinusoidally frequency modulated tone (carrier frequency: CF-frequency, modulation depth: ± 500 Hz), [VOC+AS(FM)] to a combination of vocalization and the frequency modulated echo, and [AS+AS(FM)] to a combination of a pure tone at CF-frequency and frequency modulated echo. Intensity of artificial echoes 80 dB SPL throughout. Note especially different responses to the two acoustically identical stimulus situations in lower two graphs

if it stimulates the ear during the emission of the echolocation sound, thus providing the bat the information that it is with high probability dealing with its own echo.

Vocalizations not only gated the responsiveness of auditory neurons, but also enhanced the encoding capacities of neurons for artificial stimuli following the electrically elicited vocalized orientation sounds. The neuron shown in Fig. 3 responded to vocalized orientation sounds with a CF-frequency of 83 kHz with a slow built-up pattern (VOC). The same pure tone frequency presented as an auditory stimulus without vocalization (AS) only elicited a very weak off-response. When a vocalized echolocation sound simultaneously triggered a pure tone of the same frequency (VOC+AS) thus mimicking a CF-echo, the response pattern was rather the same as to vocalization alone and the total spike number slightly decreased. When the vocalized echolocation sound triggered a frequency-modulated artificial stimulus [VOC+AS(FM)] [AS(FM): center frequency 83 kHz,

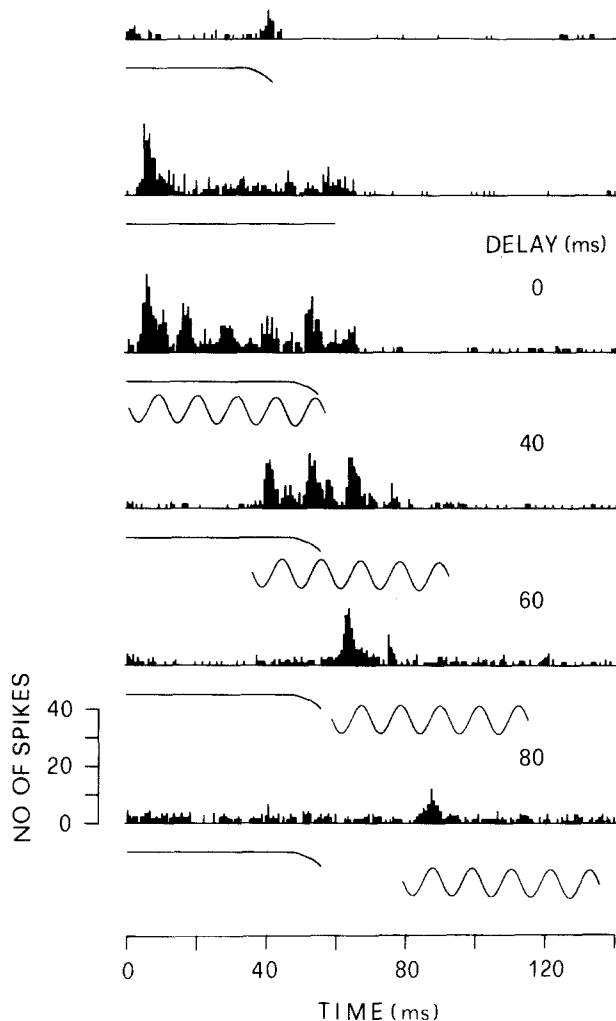


Fig. 4. Responses of a collicular neuron to vocalization followed by a sinusoidally frequency modulated artificial stimulus (carrier frequency 1 kHz higher than CF-frequency, modulation depth ± 500 Hz) at different time delays to the onset of vocalization. Histograms sampled with 40 stimulus presentations

modulation depth ± 500 Hz, modulating frequency 100 Hz], simulating an echo returning from a wing-beating insect, the neuron vigorously discharged in strict synchrony to the modulation cycle of the frequency modulated signal. However, when a similar stimulus configuration consisting of a pure tone at 83 kHz simulating the CF-portion of the vocalization together with the frequency-modulated artificial echo was presented to the bat's ear [AS+AS(FM)] the neuron kept silent and only discharged with a small off-response as in all the other stimulations without concurrent vocalization. In fact, no artificial auditory stimulus could substitute the vocalization in this neuron to evoke the modulation encoding response to the frequency-modulated CF-part of an "echo".

This example shows that the behavioural state of vocalization may enhance auditory neurons in their

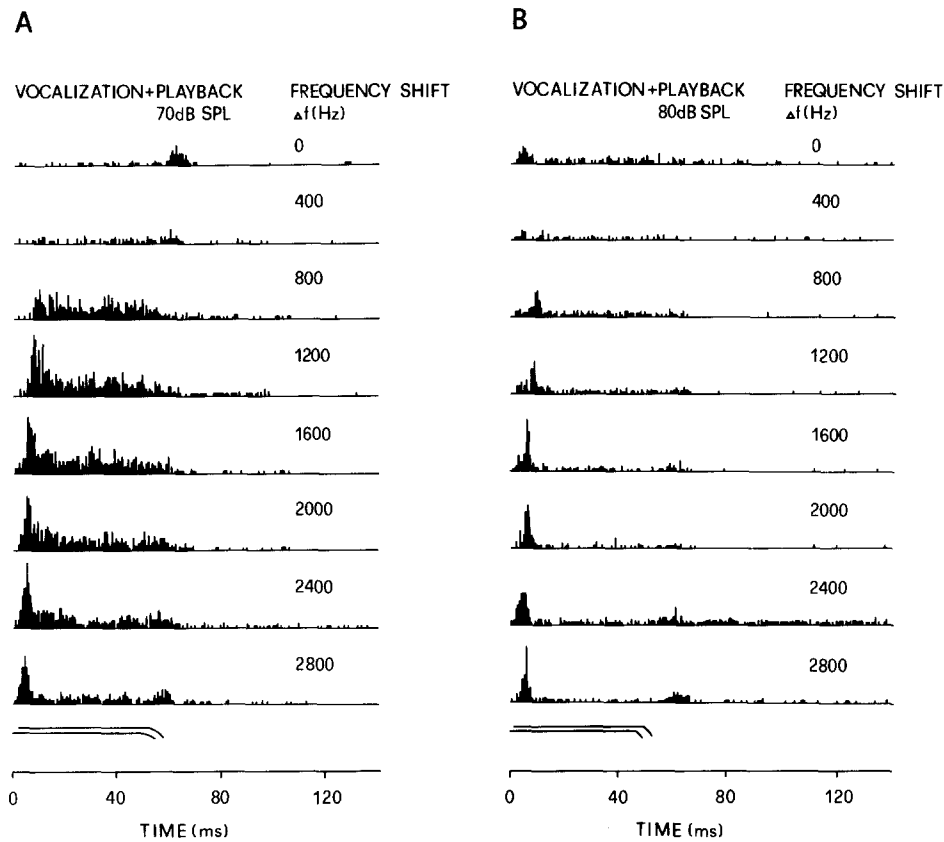


Fig. 5. Responses of 2 collicular neurons to vocalizations presented together with frequency-shifted playback echoes. Echoes were played back with a delay of 1 ms to onset of vocalization and frequency shifts are indicated to the right of each histogram. Histograms are responses to 40 stimulus presentations

response to behaviourally relevant stimulus parameters. On the other hand it has to be emphasized that among 63 neurons only 2 showed these specific properties.

Enhanced encoding of frequency modulations [AS(FM)] triggered by vocalization activity is also dependent on the temporal relationship between the vocalization and the artificial echo. This was found in 4 neurons and one example is illustrated in Fig. 4. The vocalized echolocation sound elicited a weak tonic activity followed by a small off-response to the end of the sound. An artificial pure tone at 84.3 kHz, that is 1 kHz higher than the frequency in the CF-portion of the emitted orientation sound, is responded by this neuron with a clear on-response and a small tonic response during the stimulation. When the bat emitted orientation pulses and artificial frequency modulated signals [VOC+AS(FM)] were presented at the same time the neuron fired synchronously to the downward half-cycle of the frequency modulation. However, the synchronized firing was more and more lost when the AS(FM) stimulus was delayed relative to the onset of the vocalization. In fact when the vocalization and the AS(FM) stimulus no more over-

lapped the encoding of the SFM-cycles disappeared. As the duration of the vocalization could not be manipulated it is an open question whether the acoustical overlap between the vocalization and the artificial echo or a temporal gating effect starting with the onset of the vocalization and lasting some 10 ms is responsible for the encoding of the frequency modulations.

C. Responses to Vocalizations and "Doppler-Shifted Echoes"

In a flying echolocating horseshoe bat the frequency of the returning echo is shifted to a higher frequency due to the bat's flight speed. To simulate this situation neurons were stimulated with the vocalized echolocation sound and the frequency-shifted "echoes" played back 1 ms after beginning of the vocalization. The frequency-shifted echo is the frequency-shifted identical replica of the echolocation sound. The shifts ranged between 0 and +4,000 Hz. Whereas most neurons did not change their discharge characteristics due to different frequency-shifts, four neurons showed specific responses to frequency shifted playback

(Fig. 5). Both neurons demonstrated in Fig. 5 fired vaguely to a playback of the original orientation sound ($df=0$ Hz). When, however, the frequency shift of the playback signal was increased to more than 400 Hz a distinct on-response (B) or tonic response (A) pattern appeared. Such clear response pattern changes always appeared, if at all, at frequency shifts between 400 and 800 Hz. Interestingly the latency of the response in these neurons was correlated with the amount of frequency shift in the playback signal. In both neurons the latency jumped from a short latency of about 6 ms at $df=0$ Hz to a latency of about 12 ms at $df=+400$ Hz or $+800$ Hz frequency shift. With increasing frequency shift above 800 Hz the latency of the response decreased again and reached its original value of about 6 ms at about $+2,000$ Hz. During the recordings of these neurons the bats were not compensating for the frequency shifts, that is the CF-frequency of the vocalized echolocation sound was not altered with changing frequency shifts. In a fully compensating bat no controlled recordings have been made yet.

Discussion

The most interesting result of this study is the fact that from 63 recorded collicular neurons 26 responded differently to a vocalized pure tone echolocation sound than to an artificial identical auditory stimulus. In a few neurons vocalization induced encoding capacities were not seen when stimulating with artificial echo alone: two neurons encoded frequency modulations of an artificial echo only during ongoing vocalization, some neurons responded to artificial tones only after onset of vocalization and in a few neurons vocal activities enhanced the response to pure tones with Doppler-shifted frequencies. All these vocally induced specific effects are behaviourally relevant in an echolocating horseshoe bat.

In interpreting these results the central question arises how the bat's vocalization exerts the influences on the auditory processing in collicular neurons. One may first think of the middle ear muscle reflex invariably elicited by vocalization of the echolocation sounds in bats (e.g. Suga and Jen, 1975).

In horseshoe bats middle ear muscle contraction has only a minor attenuating effect which is frequency dependent and yields only 2–3 dB attenuation in the frequency range around 80 kHz (Oswald, 1976). No other auditory effects of middle ear muscle contraction within the frequency range of echolocation signals in horseshoe bats have been recorded. It is therefore most unlikely that the vocal influence onto auditory neurons is mediated via the middle ear muscle reflex.

Vocalization may in fact have two other ways of interference with auditory echo processing.

First, the vocalized signal has a purely acoustical effect comparable to the first stimulus of a two-tone stimulation with artificial signals. In all 26 neurons this possibility was carefully checked by presenting a range of acoustical stimulus sets mimicking as closely as possible the stimulus situation during vocalization. Especially in the two neurons in which vocal activity evoked a specific FM encoding capacity (Fig. 3) one may think of an acoustical interference of emitted and artificial signal. But mimicking the vocalization by an artificial stimulus could not substitute vocalization in producing the specific auditory responses (see Figs. 2, 3).

Secondly, vocalization exerts some neural effects onto the neurons of the inferior colliculus or its inputs. Since middle ear muscle effects and purely acoustical phenomena can be most likely excluded, direct neural influences of vocal activity are the most reasonable interpretation left. This hypothesis is corroborated by the fact that the vocal influence onto these auditory neurons is limited in time (Fig. 4). Since the duration of the electrically elicited echolocation sound could not be manipulated it can not be decided whether the vocalization triggers a fixed time gate of specific enhancement or if the influences on auditory neurons last as long as the vocalization endures.

Suga and Schlegel (1972) have already shown that a direct neuronal influence of vocal activity onto auditory neurons is possible. Whereas they describe a general attenuating effect of vocalization reducing self-stimulation the results reported here indicate more sophisticated enhancing and behaviourally relevant influences of vocal activity on some collicular neurons.

It would be most interesting to know which neural centers are involved in these conditioning effects of vocalization on auditory neurons. To answer this question combined neurophysiological and neuroanatomical studies with modern tracer methods are under way. The neural influences of the vocalization process on the analysis of the echo information during a certain time after the onset of the pulse emission would help the bat to recognize the echoes that are produced by its own echolocation sound and screen out to a certain extent spurious echoes from, for example, other individuals.

These results coincide favourably with behavioural data, that indicate that horseshoe bats compensate Doppler-shifts in echoes only when the signal arrives within a certain time after the onset of the echolocation sound emission (Schuller, 1977). The encoding of Doppler-shift information has been tested in collic-

ular neurons by stimulation with the vocalized echolocation sound and its frequency-shifted version arriving with a time delay of 1 ms at the bat's ear (Fig. 5). Two features may be stressed and compared with behaviourally found data. First, the neurons showed in many cases distinct discharge pattern changes at frequency shifts of 400 to 800 Hz. This amount of frequency shift is in the order of magnitude of the minimum frequency-shift to which the bat behaviourally reacts with a lowering of the emitted frequency.

The pattern change around 400 Hz goes together with a sudden jump of latency of the onset peak of the response, and with increasing frequency-shifts the latency gradually decreases until it reaches its original value again at a frequency-shift of about 2,000 Hz. These latency shifts (about 0.5 ms/100 Hz) are not found if a pure tone is presented mimicking the CF-portion of the playback echoes at the different frequencies.

These neurons fulfill two requirements of the Doppler-shift compensation system, as found in behavioural experiments. First, they indicate when a minimum frequency-shift in the returning echo of about 400 Hz is reached and second, they encode the deviation of the frequency in the echo from the reference frequency or the emitted frequency of the bat.

The bat therefore has collicular neurons that specifically respond to Doppler-shifted echoes while it is emitting echolocation sounds. The information encoded in the response of these neurons is relevant for the task to detect and to compensate Doppler-shifts in the echo and thus to keep the echo frequency in the range of the reference frequency around 83 kHz, where the bat disposes of its optimum resolving power for biologically meaningful modulations of the echo (Schuller, 1979).

Finally one may ask if the electrical stimulation of the grey matter for evoking vocalization may have also influenced the auditory neurons and provoked the response changes reported here. Although this can not be excluded completely such an artifact is most unlikely for several reasons. The most important

ones are 1) the long latency between electrical stimulation and the onset of vocalization (30–60 ms) and 2) the fact that the majority of all neurons tested under these conditions showed responses as neurons in conditions without electrical stimulation do. Therefore we are left with the conclusion that in horseshoe bats auditory neurons exist which are specifically conditioned by neural influences of vocalization to behaviourally relevant signals.

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