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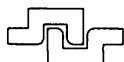
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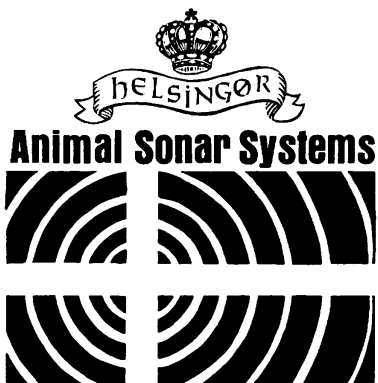
Paul E. Nachtigall and
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MIDBRAIN AREAS AS CANDIDATES FOR AUDIO-VOCAL INTERFACE IN
ECHOLOCATING BATS

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INTRODUCTION

In bats the auditory system and the vocalization system have a close functional relation to each other during acoustic communication as well as during echolocation. In many species the spectral parameters of the emitted echolocation sounds are adapted to the special echolocation tasks during a behavioral sequence. In order to control the parameters of the echolocation sounds appropriately the relevant information has to be transmitted from the auditory to the motor system.

The Doppler shift compensation behavior of CF-FM bats (Rhinolophus and Pteronotus) is a good model for the investigation of audio-vocal interaction. During this behavior, the bats vary only a single parameter of the emitted echolocation sounds, i.e. the emitted frequency, in order to cancel the Doppler-induced frequency shifts in the returning echoes.

Much data is available for the processing of the relevant frequencies (frequencies at and above the resting frequency of the bat) at different levels of the auditory system. The information on the efferent neuronal pathways controlling vocalization and on the neuronal connections mediating auditory information to the vocalization system are, in contrast, very scarce.

The efferent vocalization system has been studied recently at the level of the motor nucleus of the larynx, the NCl. ambiguus, by HRP injections into physiologically defined areas of this nucleus and the adjacent formatio reticularis (1). Following this study, many brain areas at different brain levels showed retrograde labeling, but their specific involvement in the control of vocalization remained unclear. In order to investigate their participation in the control of the echolocation calls, electrical microstimulation was used and tracer injections (HRP, WGA) yielded their connectional pattern within the efferent motor system. In addition, possible sources of auditory input into the motor system could be revealed.

MATERIAL AND METHODS

Eighteen rufous bats (*Rhinolophus rouxi*) from Sri Lanka were used in this study. The electrical stimulation experiments were conducted in a stereotaxic device allowing a reconstruction of stimulation sites with a precision of 100-200 μm in all three dimensions (2). The electrical stimuli consisted of 15 msec long trains of 15 pulses of negative polarity with a duration of 0.1 msec and were applied through insulated tungsten electrodes with tip diameters between 2 and 20 μm .

The elicited vocalizations were picked up with a condenser microphone, analyzed in frequency and intensity and stored on tape together with the electrical stimuli and the signal monitoring the respiration cycle. In parallel the animals were observed with a TV-camera and ear and facial movements were recorded on video tape.

Midbrain structures were systematically scanned between the level of the rostral superior colliculus and the caudal half of the inferior colliculus in a dense grid (100-200 μm) of stimulation coordinates. Only the very dorsolateral parts of the midbrain and the areas adjacent to the midsagittal plane have not been probed with the same density. Locations were termed "specific" for eliciting echolocation sounds under the conditions, that

- 1) the threshold for triggering vocalizations was smaller than 20 μA , lying typically even below 10 μA ;
- 2) the elicited vocalization corresponded to the natural echolocation sounds in respect to frequency, intensity and duration;
- 3) no other movements were elicited besides the vocalizations except ear or noseleaf movements which belong intimately to the pattern of sound emission;
- 4) the latency of vocalizations relative to the electrical stimulus was stable within 10 to 20 msec and smaller than 100 msec and
- 5) the vocalizations did not occur as a secondary reaction to stimulus induced general arousal.

Horseradish peroxidase (HRP) or wheat germ agglutinin (WGA) (3-4 μAmin and 4-5 $1\mu\text{Amin}$, respectively) was injected iontophoretically into the so defined "vocalization-specific" foci. The brains were histologically processed following the Mesulam TMB-protocol or a modified DAB-protocol (Adams) and every second section was counterstained with neutral red or the cytochrome oxidase reaction (Radtke-Schuller, in prep.). Data from stimulation experiments and anatomical information were reconstructed on a common data base.

RESULTS

Type of elicited vocalizations. When vocalizations could be elicited after the criteria (1,3,4,5) from above, in most cases the spectral pattern and duration were identical to those of natural echolocation sounds as uttered by the bat in the resting position. Only in pontine areas and the overlying fibers could vocalizations be elicited with extremely short duration and frequencies of the constant frequency portion lower than the resting frequency of the bat.

The latencies between electrical stimulation and onset of the vocalization ranged typically between 20 msec and 60 msec but in some locations it was consistently around 80 msec. With increasing stimulation intensity above threshold the latency

stabilized (variations below 10 to 20 msec) as long as there was no strong discrepancy between respiratory cycle and stimulation rate. The stimulation rate was found to be an important factor for consistently eliciting vocalization and most often was optimum at 7 Hz, which is about twice the spontaneous respiration rate.

Besides the amplitude of the emitted sound and in some locations the number of emitted vocalizations, no other parameter of the vocalization could be systematically influenced by changing the parameters of electrical stimulation. The resting frequency of the echolocation sounds could not be manipulated in the midbrain structures we have probed with electrical stimulation.

Correlation with ear and noseleaf movements. Stimulus induced ear movements could be elicited at many more brain locations than vocalizations. Movements of either one ear or coordinated movements of both ears occurred. At stimulation sites specific for triggering of vocalizations, the ear movements and vocalizations had very similar thresholds and were in strict temporal coordination to the emitted echolocation sounds. Nose leaf movements could be evoked either unilaterally or bilaterally and most often accompanied the vocalizations in close synchrony.

Correlation with respiration. The respiratory cycle was synchronized at many stimulation sites by stimulation currents smaller than the threshold currents needed to evoke vocalization. On the other hand, synchronized respiration could also occur as a secondary effect to the eliciting of vocalization as part of the entire pattern of sound emission.

Brain sites of specific triggering of vocalizations. Figure 1 indicates the areas of lowest thresholds for evoking species-specific vocalizations. The crosses indicate stimulation sites with thresholds below 10 μ A and the circles mark places where the thresholds lay between 10 and 20 μ A. In the shaded ranges the vocalizations were optimally elicited at lower or the same thresholds as the other constituents of the pattern of sound emission (respiration, ears, noseleaf). These loci specific for eliciting echolocation sounds are:

- 1) the deep and intermediate layers of the superior colliculus (SC) adjacent to the griseum centrale (CG) and dorsal to the Ncl. cuneiformis (CUN),
- 2) the Ncl. mesencephalicus profundus (NMP) in the dorso-lateral part of the reticular formation and
- 3) the Ncl. tegmentalis pedunculopontinus (NTPP), a cell aggregation medial and anteromedial to the rostral part of the Ncl. lemniscus lateralis dorsalis.

Injections of HRP and WGA. Figure 2 summarizes the interconnections of the superior colliculus (SC), Ncl. mesencephalicus profundus (NMP) and Ncl. tegmentalis pedunculopontinus (NTPP) within the efferent vocalization system and their inputs from auditory nuclei. None of these three areas showed a direct anatomical projection to the motor nucleus of the laryngeal nerves, the Ncl. ambiguus. The intermediate and deep layers of the SC have clear reciprocal connections with the NMP and with the CUN, where no vocalizations could be electrically elicited. The superior colliculus also receives inputs from the Ncl. tegmentalis pedunculopontinus (NTPP).

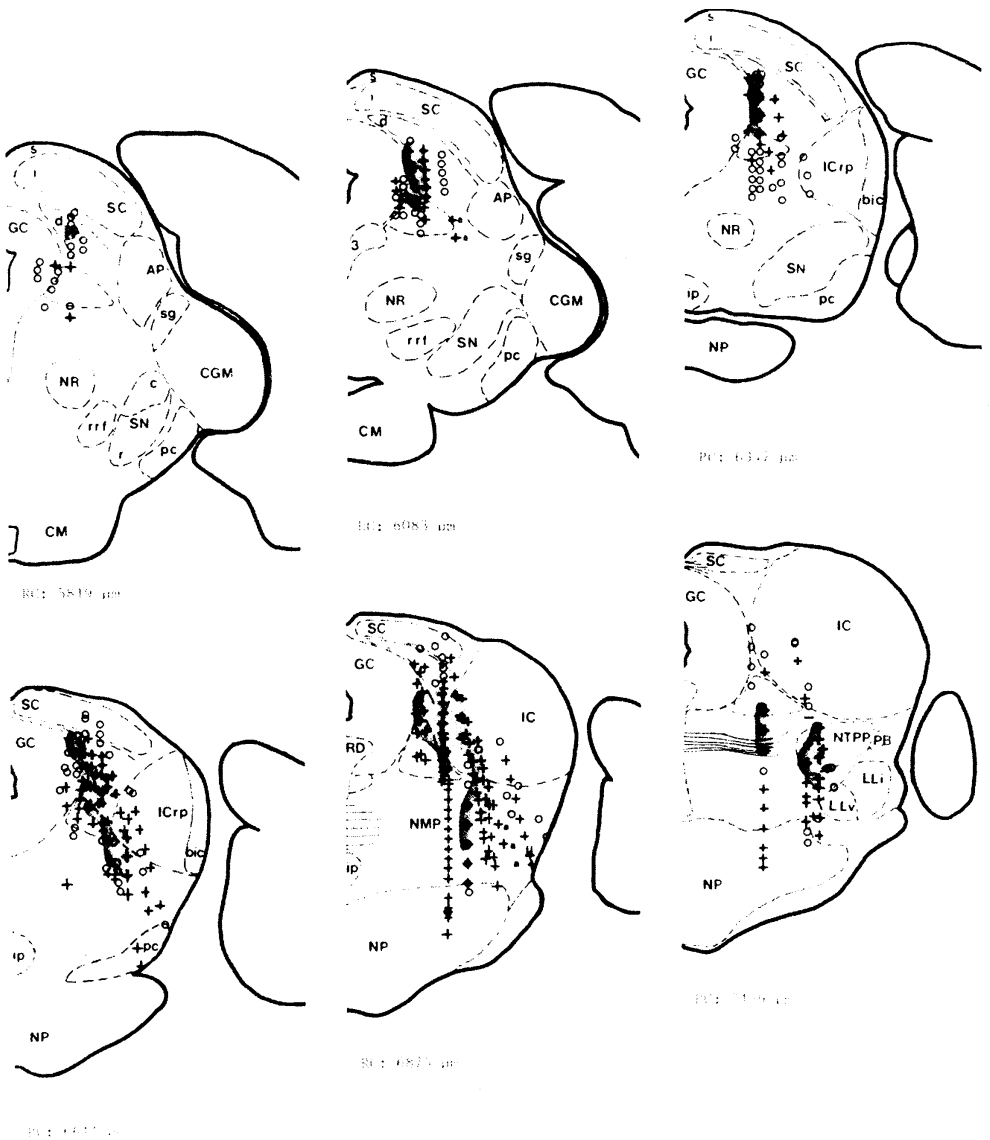


Fig. 1. Brain stimulation sites for species-specific vocalization in the bat, *Rhinolophus rouxi*. +: thresholds 10 μ A, o: thresholds 10-20 μ A, shaded: vocalization optimally evoked. GC: griseum centrale, SC: superior colliculus, AP: pretectal area, NR: Ncl. ruber, SN: subst. nigra, pc: cerebral peduncle, rrf: retrorubral field, IC: inferior colliculus, NMP: Ncl. mesencephalicus profundus, LL: lemniscus lateralis, PB: Ncl. parabigeminalis, bic: brachium of IC, CGM: corpus geniculatum mediale, NTPP: Ncl. tegmentalis pedunculo-pontinus (NTPP).

WGA-injections in the NMP provided evidence for an anterograde connection to the NTPP and for a reciprocal connection with the Ncl. cuneiformis, as well as of a projection to the Ncl. facialis. The link to the laryngeal motor nucleus was

demonstrated by tracer injections into the Ncl. cuneiformis which displayed strong anterograde transport to the Ncl. ambiguus, thus confirming the retrograde results of Rübbsamen and Schweizer (1). Besides the connections of SC, NMP, NTPP with the Ncl. ambiguus via the Ncl. cuneiformis there are at least 3 more indirect connections mediated by a) the reticular formation dorsolateral to the Ncl. facialis, b) the Ncl. retrofacialis immediately rostral to the Ncl. ambiguus and c) the dorsal portions of the Ncl. parabrachialis. Direct input from auditory brain areas (inferior colliculus, auditory cortex) reach the SC and the NTPP. In addition, indirect pathways to these nuclei and to the CUN may transmit auditory information to the efferent vocalization system via pontine and cerebellar nuclei.

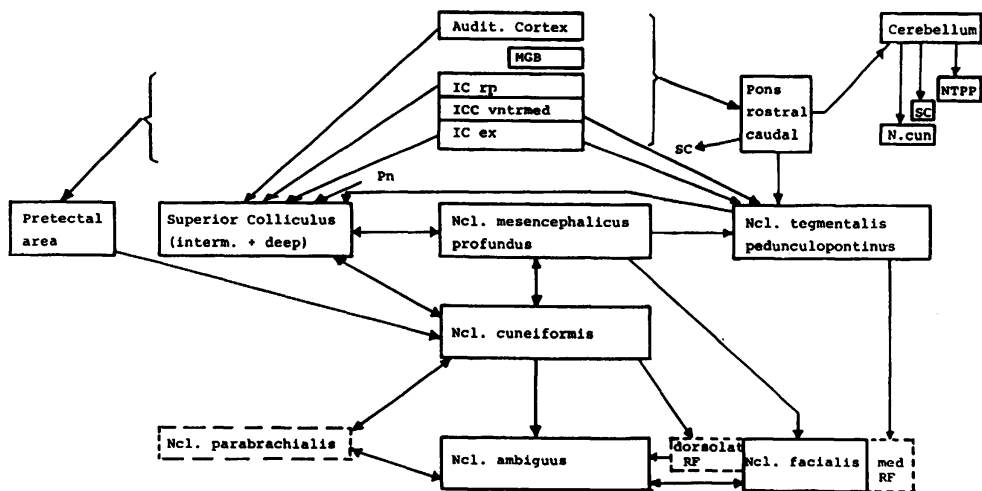


Fig. 2. Block diagram summarizing the projections of the "vocalization-specific" nuclei as revealed by HRP- and WGA-injections and connections to nuclei within the auditory system. Abbrev.: see Fig. 1 and rp: rostral pole, ex: external, RF: formatio reticularis, MGB: medial geniculate body.

CONCLUSIONS

Three foci for specific triggering of vocalization could be identified in the midbrain of the bat *Rhinolophus rouxi*. These areas are only indirectly coupled to the laryngeal motor nucleus. They are embedded in a complicated functional net coordinating the behavioral pattern of echolocation sound emission comprising the simultaneous control of respiration, the larynx and the facial movements. There also exists a number of direct and indirect connections of these premotor midbrain areas with auditory brain centers, which may convey auditory modulation of motor activity. Thus, the audio-vocal interface appears as a distributed, multipath connection between the hearing and the vocalization system, so that no unidirectional or hierarchical control of the vocal efferences can be expected.

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