

Auditory Sensitivity of the Diencephalon of the Leopard Frog *Rana p. pipiens*

Karen M. Mudry, Martha Constantine-Paton*, and Robert R. Capranica

Section of Neurobiology and Behavior and School of Electrical Engineering,
Cornell University, Ithaca, New York 14853, USA

Received October 11, 1976

Summary. Evoked potentials were recorded from the posterocentral nucleus in the dorsal diencephalon of leopard frogs (*Rana p. pipiens*) in response to acoustic stimulation. This electrophysiological study confirms the anatomical study by Neary (1974) of the existence of an auditory area within this nucleus.

The response of the auditory thalamic area showed a selectivity for stimuli that simultaneously excited both the amphibian and the basilar papillae in the inner ear. The magnitude of the evoked potential to the combination of either low (300 Hz) and high (1700 Hz) or mid (600 Hz) and high (1700 Hz) frequency tones was much greater than the sum of the responses to the component tones individually (Fig. 5). This selective convergence is not seen in the torus semicircularis: in this midbrain center the sum of the responses to the individual tones is approximately equal to the magnitude of the response to the combination tone (Fig. 7).

The selectivity of the thalamic center for stimuli with patterned energy distributions is compared to the spectral combinations occurring within several of this species' vocal signals. This comparison indicates that the extraction of spectral patterns involves a hierarchical organization within the anuran's auditory system which probably plays a major role in processing complex sounds.

Introduction

Anuran amphibians are well suited for investigations of signal processing in the auditory nervous system because their vocal repertoire is small, highly stereotyped and tends to occur in well defined behavioral contexts, suggesting that these signals are of primary significance for sound communication. Furthermore,

* Present address: Princeton University, Biology Department, Guyot Hall, Princeton, New Jersey 08540

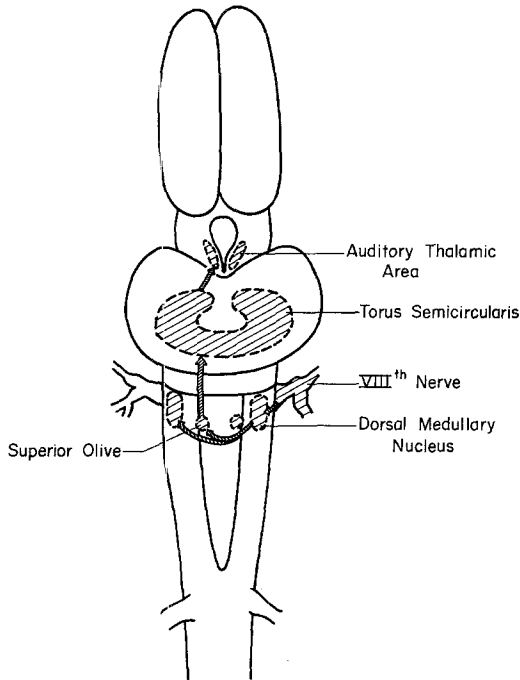


Fig. 1. Schematic diagram of the anuran's ascending auditory pathway illustrating the location and the major connections between the known auditory nuclei. The auditory portion of the VIIIth nerve projects to the dorsal medullary nucleus (Larsell, 1934; Gregory, 1972; Fuller and Ebbesson, 1973). From this nucleus the main projections are to the contralateral superior olivary nucleus and to the contralateral dorsal medullary nucleus (Grofova and Corvaja, 1972; Fuller and Ebbesson, 1973). The torus semicircularis in the midbrain receives its primary input from the ipsilateral superior olive (Rubinson and Skiles, 1975); cells within the torus project to the auditory thalamic area (Neary, 1974)

electrophysiological studies in the eighth nerve (Frishkopf and Goldstein, 1963; Frishkopf et al., 1968; Liff, 1969; Moffat and Capranica, 1974; Capranica and Moffat, 1975; Narins and Capranica, 1976) and central auditory pathway (Potter, 1965; Frishkopf and Capranica, 1966; Loftus-Hills, 1971; Capranica et al., 1973; Feng, 1975) have demonstrated that the anuran's auditory system is closely tuned to the spectral and temporal features of species-specific vocal signals.

A diagram summarizing the major ascending connections within the frog's auditory system is presented in Figure 1. Previously the highest known center in this pathway was the torus semicircularis which receives its input from the medullary nuclei. However, recently an ascending projection from the torus to the medial region of the posteroventral nucleus in the dorsal thalamus has been demonstrated using anterograde degeneration techniques (Neary, 1974). The evoked potential study described in this paper was undertaken to physiologically confirm the existence of this auditory nucleus in the anuran diencephalon and to conduct a preliminary investigation of the acoustic stimuli to which this area is most responsive.

The anuran labyrinth contains two sensory organs—the amphibian and the basilar papillae—which are sensitive to acoustic stimuli. The two organs are innervated by separate groups of primary VIIIth nerve fibers (Boord et al., 1971) and microelectrode recordings from these fibers reveal that each organ is driven by a separate range of frequencies (Feng et al., 1975). Across the several anuran genera now examined, the amphibian papilla is tuned to lower frequencies (approximately 100 to 1000 Hz) while the basilar papilla responds to higher frequencies. Units arising from the amphibian papilla can be further subdivided into two populations depending upon whether or not they exhibit tone-on-tone suppression (i.e., the response to an excitatory tone can be suppressed by the addition of a second, inhibitory tone; Liff and Goldstein, 1970).

The separation of frequency sensitivity provided by the anuran labyrinth is maintained in the auditory pathway up to the torus semicircularis. That is, primary auditory nerve fibers and cells in the nuclei in the medulla all show simple “V” shaped tuning curves with only one “best” excitatory frequency that falls either in the range of the amphibian papilla or the basilar papilla (Frishkopf and Capranica, 1966; Capranica et al., 1973; Feng, 1975). Convergence of this dual frequency projection is first seen at the level of the torus semicircularis. Here a small proportion of cells have bimodal or “W” shaped tuning curves with two separate best frequencies, one of which corresponds to input derived from the amphibian papilla and the other to input from the basilar papilla (Potter, 1965; Ewert and Borchers, 1971; Loftus-Hills, 1971). These cells respond when *either* auditory receptor organ is stimulated *or* when both organs are stimulated simultaneously. In this paper we report that an auditory center within the anuran’s dorsal thalamus may perform one further step in the integration of frequency information from the two labyrinth organs. We present evidence that this center in the leopard frog’s auditory system is selective for certain combination tones, responding maximally when spectral energy is present *simultaneously* in the sensitivity ranges of the amphibian and basilar papillae.

Our major emphasis in this study has been on the potentials evoked in the dorsal thalamus of the leopard frog *Rana pipiens pipiens* by controlled acoustic stimulation. However, in order to compare the processing of frequency information at multiple levels in this species’ auditory nervous system, we also present an analysis of the frequency sensitivity of single fibers in the VIIIth nerve and of the types of evoked potentials recorded with our procedures in the torus semicircularis.

Methods

Adult *Rana p. pipiens* of both sexes were obtained from Hazen and Co., Alburg, Vermont. The animals were immobilized by an intramuscular injection of d-tubocurarine chloride (6 µg/g); subsequent doses were given when necessary to maintain this state. Moist gauze placed over the animal’s body enabled cutaneous respiration.

The surgical and recording procedures used in our laboratory for studying single auditory fiber responses in the VIIIth nerve have been described previously (Capranica and Moffat, 1975).

Very briefly, the nerve was exposed through the roof of the mouth and single fibers were isolated with 3 M-KCl filled micropipettes (40 to 80 megohms). Action potentials were passed through a high-impedance, unity-gain follower, amplified by a low-noise pre-amplifier and then simultaneously displayed on an oscilloscope and broadcast over a loudspeaker.

For the evoked potential study, the dorsal surfaces of the midbrain and the diencephalon were exposed by drilling a small hole through the skull and retracting the dural membrane. The recording electrodes consisted of finely sharpened tungsten wire insulated with glass according to the method of Merrill and Ainsworth (1972). After plating with gold and then platinum black, the tip diameters were 6 to 10 microns. Evoked potentials were recorded from the side of the brain opposite to the ear receiving acoustic stimulation (i.e., the contralateral side). A low-noise amplifier (Lansing Corp.) with a gain for 10,000 and a passband from 1 Hz to 3 kHz was used to amplify the electrical signals from the recording electrode. A pin inserted into the hind leg served as the indifferent (ground) electrode. The evoked potentials were viewed on a storage oscilloscope and also averaged using a DEC Lab-8E computer. The averaged response was used for all quantitative measurements of the amplitudes of the various peaks in the evoked potential waveform. After a recording session the position of the electrode tip was marked by passing a current of 6 μ amps through the electrode (electrode negative) for 10 s by means of a constant-current generator (French and Capranica, 1968). The animals were then perfused through the heart with amphibian Ringer's solution containing amyl nitrate as a vasodilator, followed by 10% buffered formalin (Lillie, 1954). The brain was later dissected out, dehydrated, embedded in paraffin and sectioned at 15 microns. These serial sections were stained with cresyl violet and the position of the electrode was then verified by locating the lesion (Hubel, 1959).

In both the single unit and the evoked potential studies, the animals were isolated in a darkened audiometric room (Industrial Acoustics Corporation model 1204A) and the room temperature was maintained between 23 °C to 25 °C. Acoustic stimuli were delivered through a PDR-10 earphone (Permoflux Corp.) enclosed in a special housing. The sound intensity at the animal's eardrum was monitored with a Bruel and Kjaer 4134 condenser microphone positioned at one end of a symmetrical "T" shaped coupler attached to the earphone housing. The other end of the coupler was sealed around the animal's eardrum with silicone grease, forming a closed acoustic stimulation system. The frequency response of the stimulus system was flat within ± 5 dB over the frequency range of interest (50 to 5000 Hz).

Tone bursts consisting of either a single tone or a combination of two or three tones were used as acoustic stimuli. The relative amplitude of each tonal component could be controlled independently. This complex of tones was generated by means of audio oscillators (Hewlett-Packard 200CD), audio attenuators (Hewlett-Packard 350D) and a resistive adder. The resultant bursts had a duration of 75 ms, a rise-fall time of 10 ms and they could be presented at various interstimulus intervals under control of a series of Grason-Stadler 1216 timers and a 1287 electronic switch.

Results

Peripheral Tuning – VIIIth Nerve Recordings

Frequency sensitivity and threshold were determined for 273 single auditory nerve fibers in seventeen *Rana p. pipiens*. Figure 2 shows a histogram of the distribution of the best excitatory frequencies. Our histogram is trimodal and reflects the presence of three distinct populations of fibers in contrast to Liff's (1969) earlier finding of only two types. Based on a comparison with the study by Feng et al. (1975), the low-frequency sensitive population centered between 200 to 300 Hz and the mid-frequency population centered around 600 to 700 Hz likely originate from the amphibian papilla. Besides the difference in the best excitatory frequencies, these two populations can also be separated on the basis that only the low-frequency population exhibits tone-on-tone suppression. That is, units with best excitatory frequencies below about 500 Hz can be inhib-

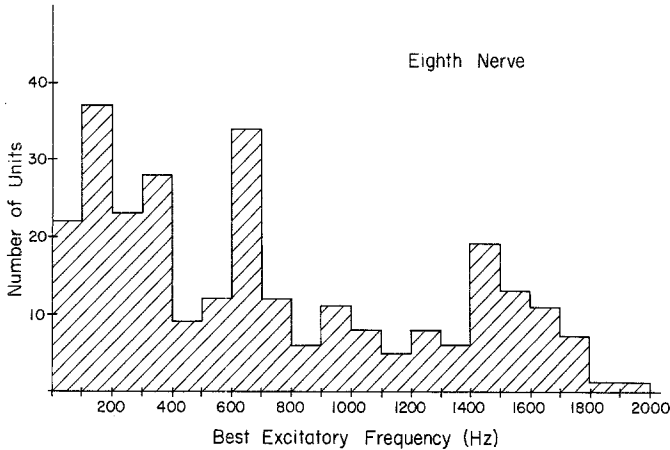


Fig. 2. Histogram of the best excitatory frequencies of 273 single units from the VIIIth nerve of *Rana p. pipiens*. The best excitatory frequency is defined as that tone to which the fiber has the lowest threshold. Bin width is 100 Hz

ited by tones of higher frequencies (approximately 500 to 1000 Hz). The third population in this histogram, the high-frequency population concentrated between 1400 to 1800 Hz, is probably derived from the basilar papilla. This population does not show tone-on-tone inhibition nor can frequencies within this range inhibit the other two populations.

Thalamus and Midbrain Recordings

Twenty adult *Rana p. pipiens* were used in this phase of our study. When tonal stimuli and presentation rates were optimal, auditory evoked potentials could be detected throughout most of the dorsal thalamus. However multiunit activity and a correspondingly large evoked potential were restricted to a relatively discrete region in the posterior thalamus extending slightly rostral from the posterior commissure. Figure 3 is a photomicrograph of a Nissl-stained transverse section through this region. The lesion (arrow) marks the location where these auditory responses were recorded.

Figure 4 shows an oscilloscope trace of the evoked potential and multiunit activity recorded in the posterior dorsal thalamus in response to a combination tone of 300 Hz and 1700 Hz. The evoked potential is biphasic with an initial sharp negative phase and a longer duration positive phase. The amplitude of this response varied from trial to trial even when stimuli were presented in random order and at slow repetition rates. Consequently, while a single evoked potential was readily seen without further processing, an average of at least 16 repetitions was used in making all quantitative comparisons.

A pronounced refractory period was observed in the thalamic evoked auditory response. When the same stimuli were presented at intervals of less than ten seconds, the activity rapidly disappeared. This degree of refractoriness is not seen in lower auditory centers. In the torus semicircularis, for instance,

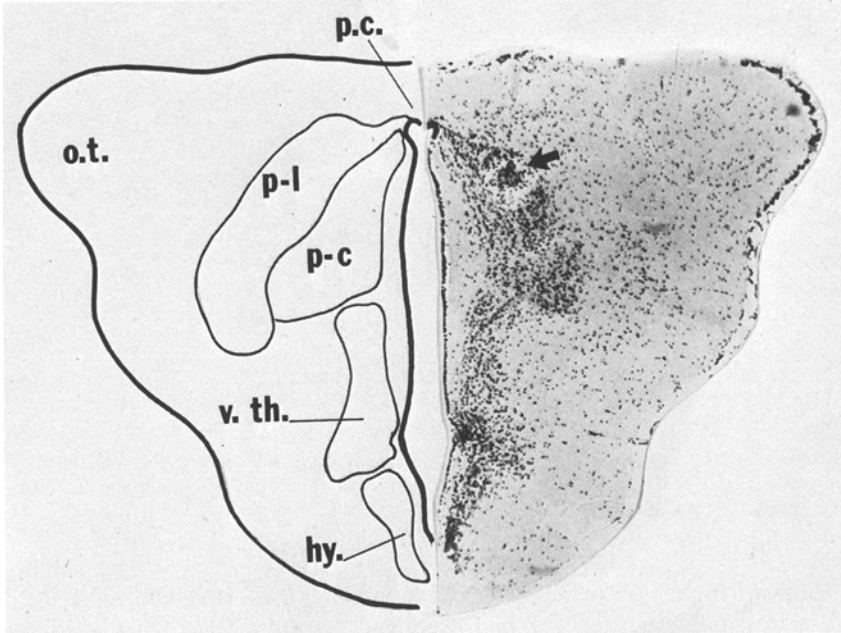


Fig. 3. The posterior diencephalon of *Rana p. pipiens*. *Right side:* Nissl stained transverse section containing a lesion (arrow) in the auditory thalamic area. *Left side:* A schematic outline of this region as defined by Frontera (1952). *p.c.*, posterior commissure, *o.t.*, optic tectum, *p-l*, posterolateral nucleus, *p-c*, posteroventral nucleus, *v.th.*, ventral thalamic mass, *hy.*, hypothalamus

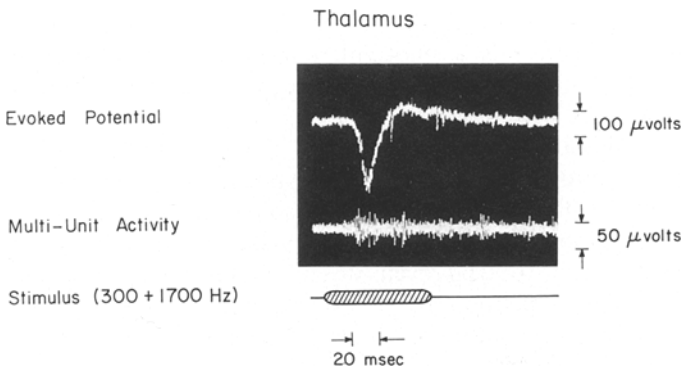


Fig. 4. An oscilloscope photograph of a representative evoked potential and multiunit response recorded from the same location in the auditory thalamus. The evoked potential was band-passed filtered from 1 Hz to 3 kHz and the multiunit activity was filtered between 200 Hz and 3 kHz. The stimulus was a combination tone of 300 and 1700 Hz and its envelope is indicated below the photograph

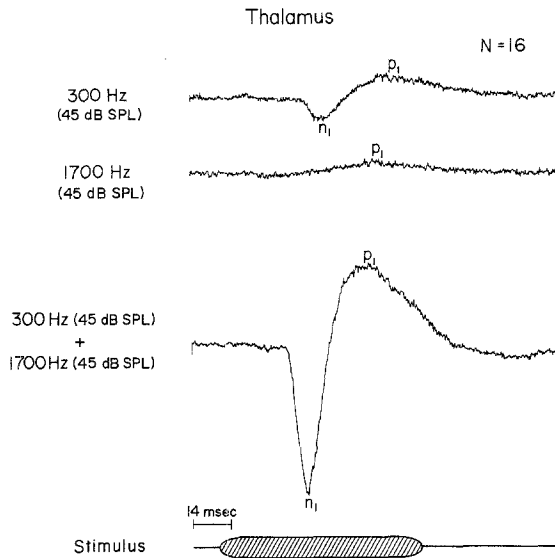


Fig. 5. Average evoked responses recorded from the auditory thalamus. Each trace represents the average response to 16 presentations of the stimulus. The vertical scale is in arbitrary units but is identical in all three cases. The stimulus envelope is indicated at the bottom of the figure

single units continue to respond to stimulus repetition rates of one every two seconds (Potter, 1965) and evoked potentials can be elicited with stimulus rates as rapid as two per second (Loftus-Hills and Johnstone, 1970).

It was found that good evoked potentials could be recorded in response to combinations of two tones as long as the stimulus contained a component within the range of 100 to 900 Hz and a component between 1000 to 1900 Hz. This corresponded to stimuli that simultaneously excited both the amphibian and basilar papillae. When a stimulus contained energy that excited only one of the two organs, there was either no response or a minimal response. In order to routinely test for this convergence, we used three standard frequencies. A 300 Hz tone and a 600 Hz tone were used to stimulate respectively the low- and the mid-frequency populations of fibers from the amphibian papilla. A tone of 1700 Hz was chosen to stimulate high-frequency fibers from the basilar papilla even though it did not fall in the center of the high-frequency range. Since the tuning curves of the mid-frequency fibers are fairly broad and overlap, we chose the 1700 Hz tone on the upper end of the high-frequency range in order to minimize the simultaneous stimulation of the mid-frequency population.

The averaged evoked potential recorded in response to low- and high-frequency tones alone and in combination is shown in Figure 5. The first trace is the averaged response to a 300 Hz tone at 45 dB SPL. The second trace is the averaged response to a 1700 Hz tone at the same sound level and the third trace is the averaged response to a combination tone composed of 300 Hz and 1700 Hz. The amplitude of the negative peak n_1 for each tone presented separately does not add up to the amplitude of n_1 for the combination tone. The same conclusion applies to the positive peak p_1 . This type of response was

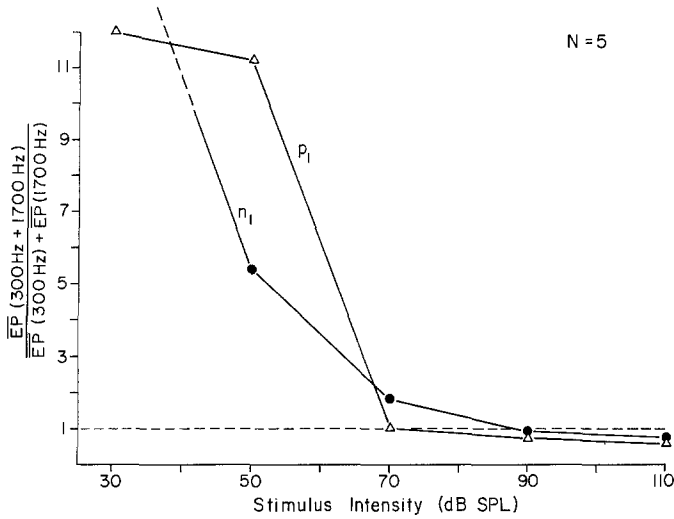


Fig. 6. The effects of stimulus intensity on the facilitated response. \bar{EP} is the magnitude of the first positive peak (p_1) or negative peak (n_1) in the evoked potential averaged over 5 stimulus presentations. At 30 dB SPL the magnitude of the negative peak to each tone alone was very much smaller than that to the combination tone, making the ratio very large

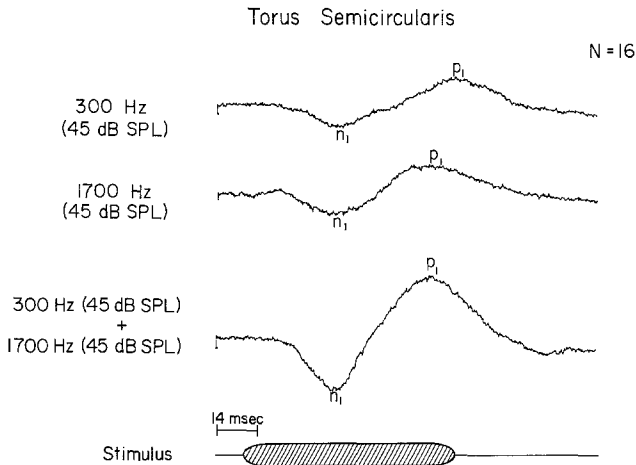


Fig. 7. Average evoked responses recorded from the torus semicircularis. Format as in Figure 5

obtained over a normal physiological range of sound intensities, that is, from about 30 dB SPL to 80 dB SPL. Figure 6 compares the evoked potential amplitude in response to the combination tone with the sum of the evoked potential amplitudes to the two tones presented individually. A linear response, namely a response involving simple summation, would yield a ratio of one. However this ratio is considerably greater than one at lower stimulus levels, indicating a nonlinear convergence.

The evoked potential to the combination tone was largest when the relative intensities of the two individual tones were within 10 dB of each other. When

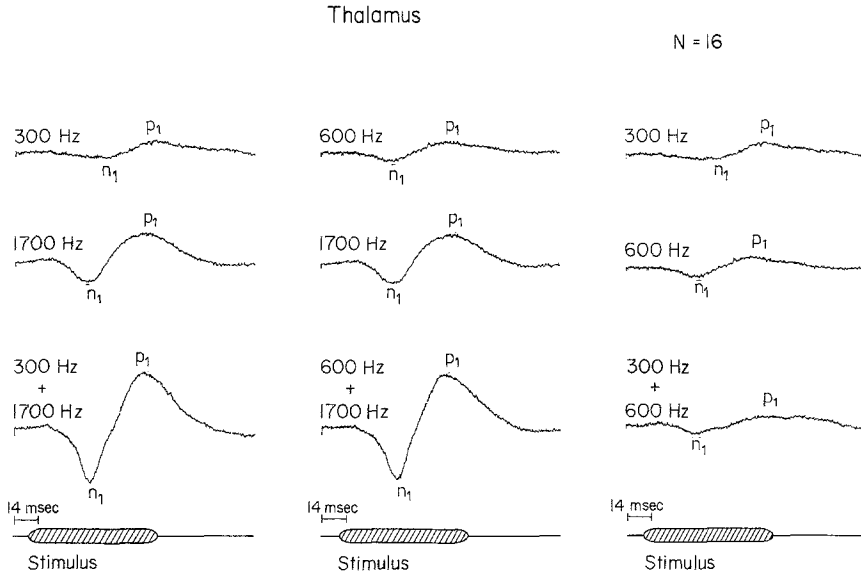


Fig. 8. Frequency dependence of the facilitated effect. When a single tone was used as the stimulus the intensity of the tone was 55 dB SPL. When a combination tone was used, the intensity of each component was also 55 dB SPL resulting in an overall intensity of 61 dB SPL. Each trace is the average of 16 stimulus presentations. The vertical scale is in arbitrary units but is identical in all cases. The stimulus envelope is shown at the bottom of each column

the combination tone was used as the stimulus, the intensity of the 300 Hz component was 45 dB SPL and that of the 1700 Hz component was 45 dB SPL, giving an overall stimulus intensity of 51 dB SPL. However, the greater response to the combination tone was not simply a result of increased stimulus energy since either tone alone presented at this higher level failed to produce a potential equivalent in amplitude to the combination tone response.

This selectivity for the simultaneous presence of low- and high-frequency tones does not occur in the midbrain auditory center. Figure 7 shows the average evoked responses recorded in the torus semicircularis to the same set of stimuli. These recordings were made in the same animal as those shown in Figure 5. In this nucleus the amplitudes of n_1 for each tone presented separately approximately add up to the height of n_1 for the combination tone. This also applies to the positive peak p_1 . Whereas in the torus semicircularis the effects of a combination tone can be explained by simple summation, in the thalamus the effect is nonlinear.

Figure 8 illustrates typical potentials evoked by the three pairwise combinations of our test frequencies. Facilitated thalamic responses were recorded when a low- and a high-frequency tone were presented simultaneously and when a combination of a mid- and a high-frequency tone was used (columns 1 and 2 of Figure 8). However, this selective response was never seen when a low- and a mid-frequency tone were presented together (column 3, Fig. 8).

Discussion

The results presented in this paper confirm the existence of an auditory nucleus in the anuran's dorsal thalamus. Multiunit activity and large evoked potentials could only be recorded from restricted regions of the posterocentral nucleus, approximately at the level of the posterior commissure. Neary (1974), in his degeneration studies on *Rana catesbeiana*, found that the torus semicircularis projected to a more anterior portion of the posterocentral nucleus. This discrepancy is probably due to a species difference; studies of *Rana catesbeiana* in our laboratory verify that the thalamic auditory area in this species occupies a more anterior position.

A principal motivation for studying auditory processing in anurans stems from the close correlation between behaviorally meaningful features of their species-specific vocalizations and the tuning in lower centers. Consequently, it is of interest to consider our electrophysiological findings in relation to detection of the spectral and temporal characteristics of these calls. In *Rana p. pipiens* the vocal repertoire has not been well documented. However our spectral analysis of a few of their vocalizations (Fig. 9) shows that these calls have energy distributions which will stimulate some combination of fibers from both the amphibian and the basilar papillae. Therefore it is reasonable to ask whether higher centers in the auditory system of *Rana p. pipiens* respond to this influx of spectral information in a manner that could account for recognition of particular calls.

Previous studies (Potter, 1965; Ewert and Borchers, 1971; Loftus-Hills, 1971) in the torus semicircularis have shown that a small proportion of cells in this midbrain center have "W" shaped tuning curves with two best frequencies, one of which falls within the range of the amphibian papilla and the other within the range of the basilar papilla. These cells can be termed "OR" gates because they will fire when a stimulus contains energy in either one *or* the other of their two ranges of sensitivity. "OR" units will also fire when energy is present simultaneously in *both* ranges. However, in order to recognize (i.e., be selective for) this simultaneity, a population of "OR" units would have to dramatically increase its spike output in response to this combination of spectral energy. This could be accomplished by increasing the firing frequency of single units within the population. Alternatively, or in addition, the threshold of a significant proportion of the population could be lowered so that a particular spectral pattern would activate more cells than a stimulus with a more limited spectral distribution of the same amount of energy. Neither of these effects has been reported in any of the single unit studies that are presently available on the anuran torus. Furthermore, this absence at the midbrain level of combination tone selectivity is substantiated by our evoked potential results. In the torus semicircularis all of the potentials driven by a combination tone are less than or equal to the sum of the potentials produced in this region when it responds to each tone alone.

This situation is dramatically different, however, for the potentials which we have recorded from the auditory thalamus. In this center, combination tones that simultaneously excite either the low- or mid-frequency fibers from

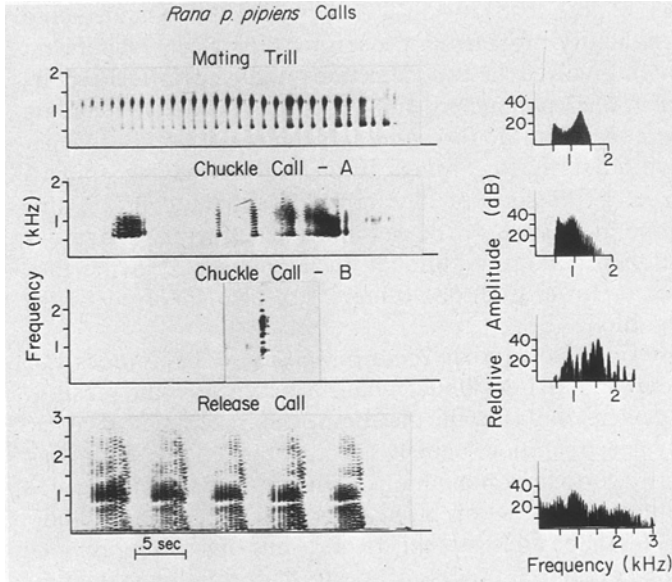


Fig. 9. Sonograms (left) and spectrographic sections (right) of several vocalizations of *Rana p. pipiens*. The mating trill and chuckle calls were obtained from the record *Voices of the Night* by P.P. Kellogg and A.A. Allen (Library of Natural Sounds, Laboratory of Ornithology, Cornell University, Ithaca, New York). The classification of these three calls is based on the discussion of the signal characteristics of the vocal signals within the *Rana pipiens* complex by Schmidt (1968) and Mecham (1971). The release call, evoked by tactile stimulation, was recorded in the laboratory

the amphibian papilla *and* the high-frequency fibers from the basilar papilla result in a response which is greater than the simple sum of the potentials produced by the presentation of either of the component frequencies. Furthermore, such a large evoked response cannot be achieved by increasing the intensity of individual tones regardless of their level.

Since the evoked potential reflects the overall activities of cell populations, we do not yet know how this selectivity is achieved in terms of the response of single units. One possibility is that the thalamus contains at least two populations of highly specialized neurons which function as "AND" gates. One population would fire when only low *and* high frequencies are present in the stimulus and a second population would fire when only mid *and* high frequencies are present. Alternatively the nonlinear thalamic response to a combination tone could reflect facilitation of "OR" unit responses in one or both of the ways discussed above (i.e., by lowering thresholds or increasing firing rates). Single unit studies in this center should help to distinguish between these possibilities.

It seems clear from our results that the thalamic area of *Rana p. pipiens* is in some way selective for the spectral combinations found in several of the species' vocalizations. However since *Rana p. pipiens* calls are pulsed at frequencies greater than one every one half minute, a perplexing feature of this selective thalamic response is its extremely rapid decrement when stimuli

are presented at intervals of less than 20 to 30 s. It is difficult to understand the role played by this refractory property in processing biologically significant sounds. Certainly a center involved in call detection might be influenced by a large number of motivational parameters and probably by the surrounding environment, so that the animal on the recording table may not be in a proper physiological and behavioral state. Recordings from awake behaving animals may help clarify this issue. If the state of the animal is not the cause of this discrepancy between temporal features of the call and the refractory properties of the thalamic response then perhaps additional nuclei, elsewhere in the thalamus or in other higher or lower auditory centers, are also involved in the task of anuran call recognition.

In summary, the posterior thalamus of *Rana p. pipiens* probably does not perform the conclusive step underlying call detection. Nevertheless, the sensitivity of this diencephalic nucleus builds upon the tuning characteristics of lower centers and adds a totally new operation, namely selectivity for the simultaneous presentation of particular two-tone combinations. This nonlinear convergence seems similar to the facilitatory interaction mechanism seen in the central auditory pathway of cats by Watanabe and Katsuki (1974). Thus our study provides evidence for a hierarchically organized process of spectral information extraction within the ascending auditory pathway in anurans and suggests that these relatively simple vertebrates will provide a useful model for the neural decoding of complex sounds.

This research was supported by the U.S. Public Health Service (NIH Research Grant NS-09244).

We would like to thank Anne Moffat for her assistance in collecting data on the tuning characteristics of the VIIIth nerve units.

References

- Boord, R.L., Grochow, L.B., Frishkopf, L.S.: Organization of the posterior ramus and ganglion of the VIIIth cranial nerve of the bullfrog *Rana catesbeiana*. M.I.T. Res. Lab. Electron. Quart. Prog. Rept. **99**, 180–182 (1971)
- Capranica, R.R., Frishkopf, L.S., Nevo, E.: Encoding of geographic dialects in the auditory system of the cricket frog. *Science* **182**, 1272–1275 (1973)
- Capranica, R.R., Moffat, A.J.M.: Excitation, inhibition and “disinhibition” in the inner ear of the toad (*Bufo*). *J. acoust. Soc. Amer.* **55**, 480 (1974)
- Capranica, R.R., Moffat, A.J.M.: Selectivity of the peripheral auditory system of spadefoot toads (*Scaphiopus couchi*) for sounds of biological significance. *J. comp. Physiol.* **100**, 231–249 (1975)
- Ewert, J.P., Borchers, H.W.: Reaktionscharakteristik von Neuronen aus dem Tectum Opticum und Subtectum der Erdkröte *Bufo bufo* (L.). *Z. vergl. Physiol.* **71**, 165–189 (1971)
- Feng, A.S.: Sound localization in anurans: an electrophysiological and behavioral study. Ph. D. Thesis, Cornell University, Ithaca, New York (1975)
- Feng, A.S., Narins, P.M., Capranica, R.R.: Three populations of primary auditory fibers in the bullfrog (*Rana catesbeiana*): their peripheral origins and frequency sensitivities. *J. comp. Physiol.* **100**, 221–229 (1975)
- French, J.C., Capranica, R.R.: A low-noise source follower incorporating an electrode marking circuit. *IEEE Trans. on Biomed. Engin.* **BME 15**, 62–63 (1968)
- Frishkopf, L.S., Capranica, R.R.: Auditory responses in the medulla of the bullfrog: comparison with eighth-nerve responses. *J. acoust. Soc. Amer.* **40**, 1262–1263 (1966)
- Frishkopf, L.S., Capranica, R.R., Goldstein, M.H., Jr.: Neural coding in the bullfrog’s auditory system—a teleological approach. *Proc. IEEE* **56**, 969–980 (1968)

- Frishkopf, L.S., Goldstein, M.H., Jr.: Responses to acoustic stimuli from single units in the eighth nerve of the bullfrog. *J. acoust. Soc. Amer.* **35**, 1219–1228 (1963)
- Frontera, J.G.: A study of the anuran diencephalon. *J. comp. Neurol.* **96**, 1–69 (1952)
- Fuller, P.M., Ebbesson, S.O.E.: Projections of the primary and secondary auditory fibers in the bullfrog (*Rana catesbeiana*). *Proc. Third Ann. Meeting. Soc. Neurosci.* **1973**, 333 (1973)
- Gregory, K.M.: Central projections of the eighth nerve in frogs. *Brain Behav. Evol.* **5**, 70–88 (1972)
- Grofova, I., Corvaja, N.: Commissural projection from the nuclei of termination of the VIIIth cranial nerve in the toad. *Brain Res.* **42**, 189–195 (1972)
- Hubel, D.H.: Single unit activity in striate cortex of unrestrained cats. *J. Physiol. (Lond.)* **147**, 226–238 (1959)
- Larsell, O.: The differentiation of the peripheral and central acoustic apparatus in the frog. *J. comp. Neurol.* **60**, 473–527 (1934)
- Liff, H.: Responses from single auditory units in the eighth nerve of the leopard frog. *J. acoust. Soc. Amer.* **45**, 512–513 (1969)
- Liff, H.J., Goldstein, M.H., Jr.: Peripheral inhibition in auditory fibers in the frog. *J. acoust. Soc. Amer.* **47**, 1538–1547 (1970)
- Lillie, R.D.: *Histopathologic technic and practical histochemistry*, p. 34. New York: McGraw-Hill 1954
- Loftus-Hills, J.J.: Neural correlates of acoustic behavior in the Australian bullfrog *Limnodynastes dorsalis* (Anura: Leptodactylidae). *Z. vergl. Physiol.* **74**, 140–152 (1971)
- Loftus-Hills, J.J., Johnstone, B.M.: Auditory function, communication, and the brain-evoked responses in anuran amphibians. *J. acoust. Soc. Amer.* **47**, 1131–1138 (1970)
- Mecham, J.S.: Vocalizations of the leopard frog, *Rana pipiens*, and three related Mexican species. *Copeia* **1971**, 505–516 (1971)
- Merrill, E.G., Ainsworth, A.: Glass coated platinum-plated tungsten microelectrodes. *Med. Biol. Eng.* **10**, 662–672 (1972)
- Moffat, A.J.M., Capranica, R.R.: Sensory processing in the peripheral auditory system of treefrogs (*Hyla*). *J. acoust. Soc. Amer.* **55**, 480 (1974)
- Narins, P.M., Capranica, R.R.: Sexual differences in the auditory system of the treefrog, *Eleutherodactylus coqui*. *Science* **192**, 378–380 (1976)
- Neary, T.J.: Diencephalic efferents of the torus semicircularis in the bullfrog, *Rana catesbeiana*. *Anat. Rec.* **178**, 425 (1974)
- Potter, H.D.: Patterns of acoustically evoked discharges of neurons in the mesencephalon of the bullfrog. *J. Neurophysiol.* **28**, 1155–1184 (1965)
- Rubinson, K., Skiles, M.P.: Efferent projections of the superior olivary nucleus in the frog *Rana catesbeiana*. *Brain Behav. Evol.* **12**, 151–160 (1975)
- Schmidt, R.S.: Chuckle calls of the leopard frog (*Rana pipiens*). *Copeia* **1968**, 561–569 (1968)
- Watanabe, T., Katsuki, Y.: Response patterns of single auditory neurons of the cat to species-specific vocalization. *Jap. J. Physiol.* **24**, 135–155 (1974)