80. Unit Responses of the Cat’s Auditory Cortex to Synthesized Formants

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It has been known since the early work by Katsuki et al.¹ that the auditory cortex units of anesthetized cats exhibited “on” and/or “off” responses to pure tone stimuli. Whitfield and Evans³ reported that many units of the primary auditory cortex respond periodically to the periodic stimuli in unanesthetized cats.

It is our common experience that the sensation to a sound continues during the stimulus. Therefore, the auditory cortex unit may exhibit a sustained response to a sound just adequate to the unit. The authors² have reported that about 25% of units of the auditory cortex AI exhibited sustained responses to pure tones and about 75% of the remaining units exhibited the sustained responses to bands of noise in cats paralyzed with flaxedil.

Since a considerable number of units had been unresponsive to both pure tones and bands of noise, in terms of sustained response, synthesized formants were applied to such unresponsive units in the present experiments.

We shall be concerned with the units which exhibit the sustained response only to the synthesized formant.

Materials and methods. Surgical operations were conducted under halothane anesthesia. Surgical wounds and pressure points were infiltrated with bupivacaine hydrochloride, long-acting local anesthetic, which was judged effective enough by the fact that no change in the corticogram was evoked by pinching the wound edge even at the end of the experiment. The animals were paralyzed with flaxedil.

The sounds used as stimuli and their abbreviations are explained in Fig. 1. In determining the modulation parameters, the spectrum of the sound was checked by using a Fourier analysis program of a PDP-11 computer.

In the synthesized formant, the distance between components will be called a “pitch” and the frequency at the peak of the envelope of the spectrum, a “formant frequency”. Since the phase of the sawtooth wave was locked by the carrier in generating the synthesized
Fig. 1. Schematic illustrations of wave forms and spectrums of sounds. Left column: Wave forms. Right column: Spectrums. A: Carrier, i.e., pure tone. B: Low-pass filtered white noise used to modulate the carrier (L-pass noise). C: Band of noise generated by using "L-pass noise" to modulate the amplitude of a carrier (AM band). D: Band of noise generated by using "L-pass noise" to modulate the frequency of a carrier (FM band). E: Saw-tooth wave used to modulate the carrier. F: Saw-toothedly amplitude-modulated tone (saw-tooth AM tone). G: Saw-toothedly frequency-modulated tone (saw-tooth FM tone). H: Synthesized formant generated by using "L-pass noise" to modulate the amplitude of the "saw-tooth FM tone". Pure tones, AM bands, FM bands, saw-tooth AM tones, saw-tooth FM tones and synthesized formants were used as stimuli.
formant, the pitch varied a little by changing the formant frequency, e.g., when the pitch was set at 200 Hz, the actual pitch measured varied between 190 Hz and 210 Hz.

Unit responses obtained from the auditory cortex AI by using glass micropipettes were represented with peristimulus time histograms by off-line analysis of a PDP-12 computer.

Results. The results in this paper are based on a study of 96 units. All units were first studied with pure tone stimuli and then with bands of noise. The synthesized formant was slightly effective to the units responsive to pure tones, but the pure tone was much more effective to these units. Most of the units responsive to bands of noise were also slightly responsive to the synthesized formants, but the bands of noise were much more effective to these units.

Out of 30 units which did not at all or hardly respond to both pure tones and bands of noise, 10 responded well to the synthesized formant with sustained discharges during the stimulus. An example of the units is shown in Fig. 2. Fig. 2A shows the responses to synthesized formants in which the pitch was 190–210 Hz and the bandwidth of components was 45 Hz. The unit responded well at 3261 Hz of the formant frequency, which was the best formant frequency. As the formant frequency was shifted away from the best formant frequency, the driven discharge decreased markedly; the unit hardly responded at 2957 Hz and did not at all at 3531 Hz. The unit was slightly respon-
sive to both FM bands and AM bands of 180 Hz width and of 710 Hz width, but the responses were of very low frequency (Fig. 2B). Then the unit was studied with variable bandwidth of components at the best formant frequency. The most dominant response was driven at infinitesimal width of components (Fig. 2C); a synthesized formant consisting of components of infinitesimal width was a “saw-tooth FM tone”. As shown in Fig. 2C, a “saw-tooth AM tone” was not effective to the unit, though the spectrum was almost the same as that of the “saw-tooth FM tone” which was the most effective stimulus.

In one case, the best formant frequency was first found at 3575 Hz. As the formant frequency of the stimulus was lowered to 3383 Hz, the discharge elicited decreased markedly, but, by lowering the formant frequency further, the unit again exhibited a marked response at 3275 Hz. This unit, therefore, had more than one local maximum equivalent to the best formant frequency.

The best formant frequencies of the 10 units ranged between 2000 Hz and 23000 Hz. The effective range of formant frequency in each unit was so restricted that about 10% deviation of the formant frequency made the stimulus ineffective.

Although a wide band of noise centered at the best formant frequency was slightly effective in some cases, it can be said that these units were responsive exclusively to the synthesized formant.

As for the bandwidth of components of the synthesized formant, the best bandwidth varied from 0 to 180 Hz wide with units. The “saw-tooth AM tone” was not effective to these units concerned.

![Graph](image)

Fig. 3. Spectrums of voices. Resolution bandwidth: 45 Hz. A: Human vowel “a”. B: Cat’s cry “miaow”.

Discussion. In the spectrum of the cry “miaowing” as well as
in that of a human vowel, we can distinguish several formants, each of which consists of discrete components ranging with an equal distance (Fig. 3). The spectrum of the synthesized formant also consists of discrete components and so it mimics one of the formants in the spectrum of the cat’s cry.

Since the units mentioned above were responsive exclusively to the synthesized formant, they would act as formant detector neurons in the auditory cortex. It is worthy to note that the “saw-tooth AM tone” was not effective. The most important difference between “saw-tooth FM tone” and “saw-tooth AM tone” was in phase relationship between the analyzed components. The phase of the component, therefore, is not negligible in the detection mechanism.

References