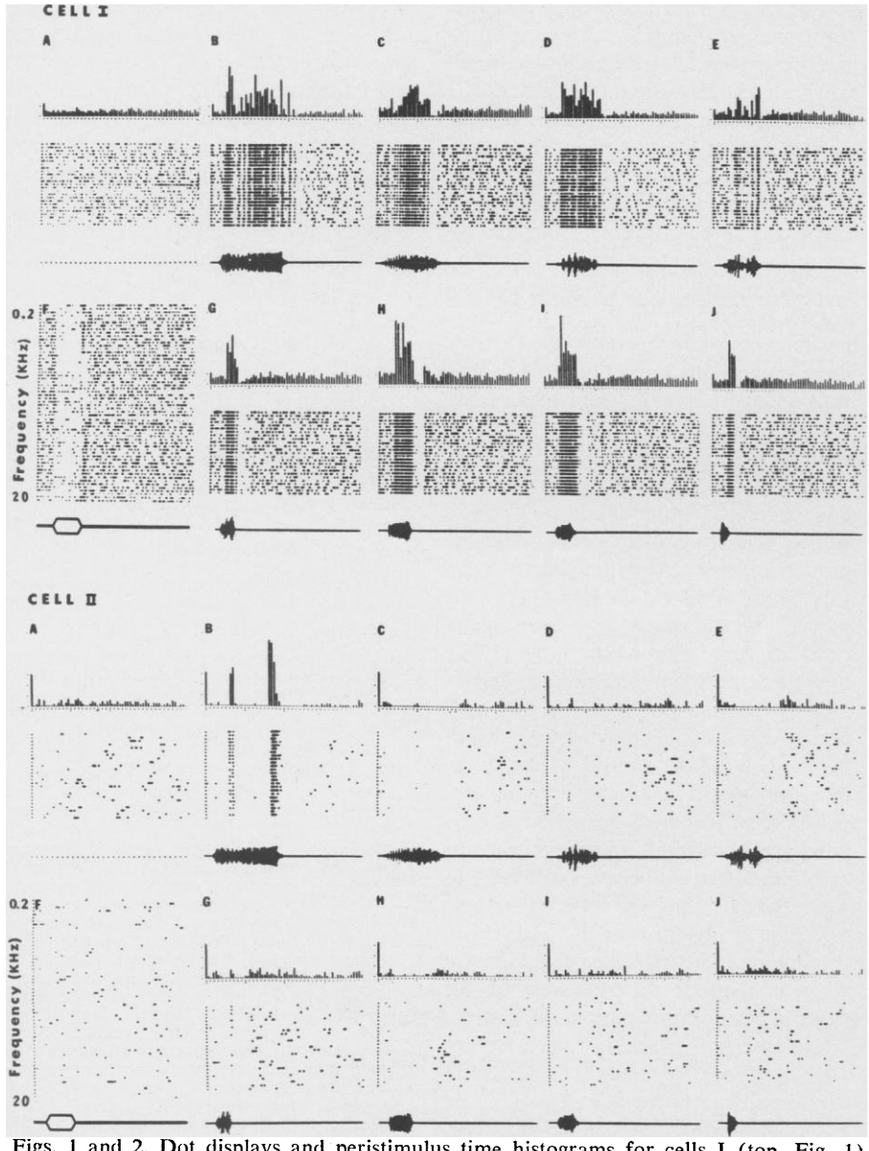
Auditory Cortex of Squirrel Monkey: Response Patterns of Single Cells to Species-Specific Vocalizations

Abstract. *Most of the neurons tested in the superior temporal cortex of awake squirrel monkeys responded to recorded species-specific vocalizations. Some cells responded with temporally complex patterns to many vocalizations. Other cells responded with simpler patterns to only one call. Most cells lay between these two extremes. On-line deletion of parts of a vocalization revealed the role of temporal interactions in determining the nature of some responses.*

Evidence suggests that the auditory cortex of mammals is involved in analysis of complex auditory signals (*1*). Hence it is reasonable to assume that this structure is also involved in analysis of complex sounds used in species-specific communication. The auditory cortex of primates is of special interest in view of the complex vocal repertoire which many primate species use in social communication (*2*). The vocalizations of the squirrel monkey (*Saimiri sciureus*) contain several groups of sounds whose acoustic properties and functional significance have been described (*3*). Neurons have been found in the auditory cortex (superior temporal gyrus) which respond to recorded samples of this species' vocalizations (*4*). We now describe some characteristics of these responses which suggest roles of the responding cells in the analysis and interpretation of vocalizations.



Figs. 1 and 2. Dot displays and peristimulus time histograms for cells I (top, Fig. 1) and II (bottom, Fig. 2). Stimuli: (A) Spontaneous activity; (B) Isolation Peep; (C) Err; (D) Twitter; (E) Err Chuck; (F) Tone bursts; (G) Rough Cackle; (H) Shriek; (I) Peep; (J) Vit. The stimulus is represented beneath each dot display. Vertical bars represent three times as many spikes in Fig. 1 as in Fig. 2. Left-most bar in each histogram and vertical row of dots in each dot display represent onset of sweep. Time scale (horizontal row of dots in A) is 60 msec between dots.

Extracellular unit discharges were recorded from 213 neurons in the superior temporal gyrus of awake squirrel monkeys during presentation of recorded vocalizations. Eleven calls, representing the major classes of this species' vocal repertoire, were used as acoustic stimuli. In addition, many neurons were tested with tone bursts covering the range from 0.2 to 20 khz, with bursts of white noise, and with clicks (*5*). Action potentials of a neuron were displayed as dots on the face of a storage oscilloscope (Tektronix 564). Changes in firing rate time-locked to the stimulus were revealed by changes in the distribution of dots. Peristimulus time histograms of unit responses were also plotted. Spontaneous activity of each cell was routinely recorded prior to the presentation of the stimuli.

More than 80 percent of the neurons tested responded to tape-recorded vocalizations. Response probabilities and patterns differed in different cells to the same vocalization, as well as in the same cell to different vocalizations. Cells with high rates of spontaneous activity tended to respond to many calls, with complex patterns. Cells with low rates of spontaneous activity tended to respond to only a few calls, with simple response patterns (*6*). Some cells responded with high probabilities to all calls, clicks, noise, and tone bursts. Other cells responded reliably to only one type of call. However, most of the cells lay between these two extremes, differing both in response probability and range of effective stimuli. Although in many instances response patterns to the same call were consistent in time, many cells showed changes in responsiveness as well as in pattern (*7*). Figures 1 and 2 show the discharge patterns of two cells, isolated in different penetrations in the same monkey, illustrating these two extremes. Cell I (*8*) had moderately fast spontaneous activity (mean rate of 23 spikes per second) (Fig. 1A), and responded with high probability to all stimuli used (Fig. 1, B–J). Tone bursts were effective over

the range from 0.2 to 20 khz (Fig. 1F). Cell II (*8*) had relatively slow spontaneous activity (mean rate of 3.3 spikes per second (Fig. 2A), did not respond to any tone, noise, or click, and responded with high probability to only one vocalization, the Isolation Peep (Fig. 2B). The other vocalizations elicited either weak excitation (Twitter, Rough Cackle; Fig. 2, D and G), suppression (Err, Err Chuck, Shriek, Vit; Fig. 2, C, E, H, and J), or had no observable effect (Peep; Fig. 2I).

Differences were also noted in the complexity of response patterns of these two cells. The response patterns of cell I were temporally complex, at least to calls of longer duration, and the structure of these responses differed for different calls. The most complex response was evoked by the Isolation Peep (Fig. 1B), which is also the longest call in this species' repertoire (*9*). That response consisted of several discrete components, which were highly time-locked to the stimulus. The responses to Err, Twitter, and Err Chuck were also complex (Fig. 1, C, D, and E), whereas the responses to Rough Cackle, Shriek, Peep, and Vit were simple, consisting of sustained discharges followed by suppression (Fig. 1, G–J). Responses to tone bursts, noise bursts, and clicks were also simple. Cell II, on the other hand, responded only with simple patterns. This is best seen in its response to the Isolation Peep (Fig. 2B), which consisted of three components, two of which are near the beginning of the call and one near the end.

The complex structure of most squirrel monkey vocalizations makes it difficult to deduce which acoustic features are necessary for a given neuron's response. A first step in solving this problem is to determine how different temporal segments of a vocalization affect the nature of neuronal response patterns. For this we used, in a number of instances, an electronic switch to delete, on-line, selected segments of a vocalization, and tested the effects of such manipulations on a cell's response. Using this method, we selectively removed parts of the Isolation Peep and tested the responsiveness of these same two cells to incomplete versions of this vocalization. Cell I was tested with a segment near the middle of the call. This produced a response coinciding in time with this part of the call. The cell was then tested with the middle section of the call missing (Fig. 3, B and C). The response again coincided

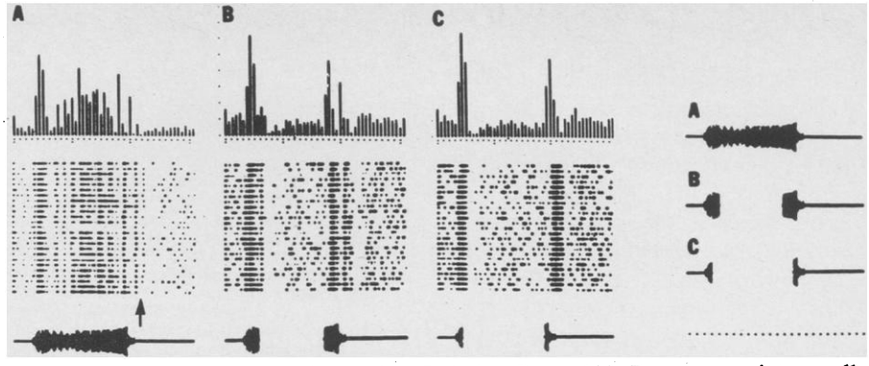


Fig. 3. Responses of cell I to incomplete Isolation Peep. (A) Response to intact call; (B) and (C), responses to incomplete versions of same cell. Right: oscillograms of Isolation Peep, comparing extent of deletions with intact call. Time scale is 60 msec between dots.

with the remaining parts of the call. The changed character of the response was also manifested in another way. The response to the intact Isolation Peep ended with two discrete components (arrow, Fig. 3A). With the middle of the call missing, however, the two components tended to merge together (Fig. 3B).

With a larger section of the call absent the two components disappeared and were replaced by a single component of longer duration (Fig. 3C). Thus, in addition to generating their own discrete response components, antecedent parts of this call interacted with later parts to determine the character of the later response components. The response of cell II, coinciding in time with two separate parts of the Isolation Peep, suggested that only limited parts of this call were necessary for this cell to respond. Yet, using the deletion technique, we revealed that the response of cell II is also a transformation involving temporal interactions of several parts of the call. In comparison with cell I, however, successive parts of the call were coded only by their effects on the late response component. Figure 4A shows the response of cell II to the intact Isolation Peep. Removing a small segment near the middle of the call had little effect on the response (Fig. 4B), but increasing the length of the missing segment (Fig. 4C) resulted in a weaker

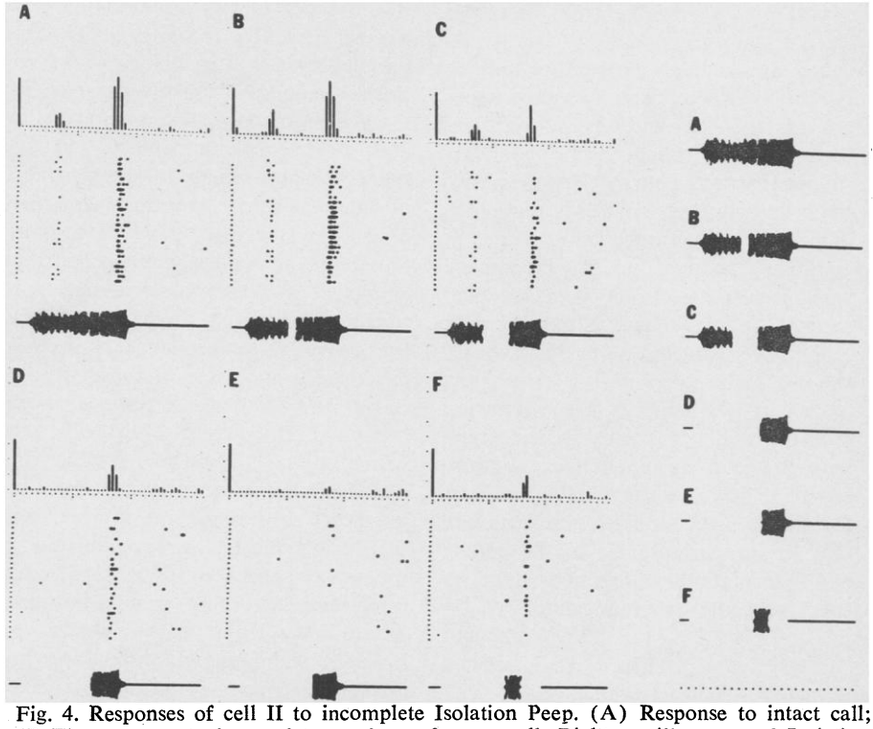


Fig. 4. Responses of cell II to incomplete Isolation Peep. (A) Response to intact call; (B–F) responses to incomplete versions of same call. Right, oscillograms of Isolation Peep, comparing extent of deletions with intact call. Time scale is 60 msec between dots.

late response component. Removing the front part of the call caused the early response component to drop out, without further affecting the late part of the response (Fig. 4D). When an additional small piece of the call (35 msec in duration) was deleted, the late response component also disappeared (Fig. 4E). Next, a 135-msec piece containing this 35-msec portion was replaced (Fig. 4-F). However, the late response component was only partially restored (compare Fig. 4, D–F). Thus, while a limited portion of this call was necessary for the production of the later response components, it was not sufficient to produce a full-strength response. It was only through interactions with other parts of the call, which did not produce separate response components in this cell, that a strong late response occurred.

The responses of cell I to vocalizations do not seem to be based on the analysis of simple acoustic cues but on analysis of the temporal structure of the calls. Neurons of this type permit the auditory cortex to code many different temporal patterns and are likely to be the elements underlying the cortex's demonstrated role in temporal pattern analysis (*1*). Conceivably, interpretation of specific vocalizations requires neurons with low noise and high response reliability to the total acoustic structure of a single call. Cell II comes close to meeting these criteria. It responded with high probability only to the Isolation Peep and had slow spontaneous activity, and several parts of the call were coded in the relatively simple response pattern. However, two factors imply that this cell is not at the highest level of specificity. First, it continued to respond to incomplete versions of the Isolation Peep, and second, it responded, although with much lower probability, to other vocalizations.

Our results support the suggestion that the auditory cortex is concerned with the analysis of complex auditory signals. They also suggest that, at least for the squirrel monkey, this structure plays an important role in the coding and interpretation of sounds used in species-specific communication.

ZVI WOLLBERG
JOHN D. NEWMAN
Behavioral Biology Branch, National Institute of Child Health and Human Development, Bethesda, Maryland 20014

References and Notes

1. Y. Katsuki, T. Watanabe, N. Maruyama, *J. Physiol.* **22**, 343 (1959); W. D. Neff, in *Sensory Communication*, W. A. Rosenblith, Ed. (M.I.T. Press, Cambridge, Mass., 1961), p. 259; E. F. Evans and I. C. Whitfield, *J. Physiol.* **172**, 52 (1964); N. Suga, *ibid.* **181**, 671 (1965); D. Symmes, *Exp. Neurol.* **16**, 201 (1966); J. H. Dewson, III, A. Cowey, L. Weisenkrantz, *ibid.* **28**, 529 (1970).
2. P. Marler, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart and Winston, 1965), p. 544; D. Ploog and T. Melnechuck, *Neurosci. Res. Prog. Bull.* **7** (1969).
3. P. Winter, D. Ploog, J. Latta, *Exp. Brain Res.* **1**, 359 (1966).
4. H. H. Funkenstein, P. Winter, P. G. Nelson, *Fed. Proc.* **29**, 394 (1970); P. Winter and H. H. Funkenstein, *Folia Primatol.*, in press.
5. A magnetic tape was made with each vocalization represented 25 times, 4.5 sec intervening between successive presentations. A pulse on the second channel of the tape preceded the onset of each vocalization; it triggered the instrumentation for data display and data analysis. The other stimuli were repeated at 2-sec intervals. The duration of tone and noise bursts was 300 msec. Clicks were produced by 0.3 msec rectangular pulses. Peak intensity for the vocalizations was 60 to 80 db relative to 0.0002 dyne/cm^2. Intensities of the tone and noise bursts were also within this range.
6. We define "response complexity" by subjective appraisal of the dot displays: a response is *simple* if it consists of up to three visibly separable columns of dots; *complex* when it has more than that.
7. J. D. Newman and Z. Wollberg, in preparation.
8. Our code numbers for cells I and II are, respectively: "CLG II-0.5,4" and "CRH I-1.5,1."
9. The Isolation Peep, although it is the longest call, has one of the simplest acoustic structures among calls we used (*3*).
10. We thank P. G. Nelson, D. Symmes, G. Fischbach, and H. Levitan for their comments.

13 August 1971

Human Taste Papilla Stimulation: Stability of Quality Judgments over Time

Abstract. *Human taste papillae are sensitive to two or more chemical stimuli. Individual papillae produce stable response patterns (quality and intensity) over a month's time. Hence, the response pattern does not appear to be affected by turnover of receptor cells.*

Studies of taste experience after chemical stimulation of human taste papillae have left a confusing picture of papillae response properties. Von Bekesy reported that each single taste papilla mediates only one taste quality (*1*). But, Harper *et al.* found that a taste papilla generally mediates more than one quality (*2*); they criticized the von Bekesy experiment on the grounds that there was no control for spread of stimulus to neighboring papillae and that there was no estimate of the reliability of data. To handle these problems they used a tiny suction ring which confined the stimuli to a given papilla, and they employed a double-blind design with statistical treatment of the data. However, their procedure appears to have produced a great loss of sensitivity because most of the taste responses were faint and ambiguous, even with very strong stimuli (*3*). Their suction ring may have produced enough tactile interference to diminish the subjects' sensitivity. We decided to reexamine the response properties of taste papillae by using less disturbing stimulation procedures. We employed essentially von Bekesy's technique of stimulation but included a control for stimulus spread, a double-blind design, and statistical estimates of data reliability.

In addition, we wanted to know if the response properties of a single papilla were stable over time. Beidler and Smallman (*4*) found that rat taste receptors have a life of about 250 hours; new receptors appear to be differentiated from surrounding cells. If human taste cells turn over at the same rate, then a taste papilla would have several new sets of receptors over a month's period (*5*). It is possible that a new set of receptors would mediate a different pattern of taste activity in the papilla.

Two subjects (1 male, 30 years; 1 female, 21 years) were given a preliminary test in making whole-mouth taste discriminations. This test consisted of recognition of sweet (0.04*M* sucrose), sour (0.001*M* citric acid), salty (0.04*M* sodium chloride), bitter ($3 \times 10^{-4}M$ quinine sulfate), and tap water. Each stimulus appeared five times in a randomly mixed order. After sampling 20 cm^3 of solution, the subjects reported the quality, rinsed their mouths with 20 cm^3 of water, and rested 1 minute until the next trial. As was expected with these concentrations, each taste report was the characteristic quality for that solution. Water yielded various weak taste sensations or none at all. All solutions were made with distilled water and were used at room temperature. Citric acid, sodium chloride, and quinine sulfate were reagent grade, and sucrose