pended on the amount of lamellae tissue left around the nerve ending. In the cleanest ending (which still had, of course, some core lamellae), the generator potential could be prolonged about 12-fold with respect to that of the intact corpuscle. The prolongation is clearly not due to effects of injury to the nerve ending. The prolonged potential retains all the salient characteristics of the generator potential in the normal corpuscle: The energy requirements for its production are of the same low order, it presents the same refractory-like behavior, and its amplitude is continuously variable with the intensity of the stimulus (*6*). However, aside from its duration, it differs in one other important way from the generator potential of the intact corpuscle. It cannot be elicited by "off-stimuli" (see Fig. 1). This is another property which may be expected, on the basis of the mechanical hypothesis, in the absence of an intermediary coupling acting as a high-pass filter (*7*).

Prolongation of generator potential, however, does not lead to an increase in the number of impulses discharged. At the level of the nerve impulse, the fast accommodation of the nerve fiber (*8*) sets another limit to receptor adaptation. Only one, or at best three impulses can be elicited with a continuously sustained current (at 20° to 24°C). This is so, regardless of whether the current source is a compound generator potential produced by high-frequency stimulation in the intact corpuscle, as shown before (*9*), or whether its source is an external nonbiological generator.

Thus, there appear to be at least two components in mechanoreceptor adaptation. One, a mechanical component, operates as a mechanical filter in the form of a laminar capsule at the level of the adventitious tissue preventing stationary components of the mechanical stimulus from being transmitted to the sensor element; and another one, an electrochemical component, acts at the level of impulse initiation precluding production of repetitive impulses. Both components represent filters of non-transients, and both tend to shorten severely the response of the receptor.

MARTIN MENDELSON*
WERNER R. LOEWENSTEIN
Department of Physiology,
College of Physicians and Surgeons,
Columbia University, New York

References and Notes

1. W. R. Loewenstein, *J. Physiol. London* **133**, 588 (1956).
2. C. Eyzaguirre and S. W. Kuffler, *J. Gen. Physiol.* **39**, 87 (1955); see also K. Krnjevic and N. M. van Gelder, *J. Physiol. London* **159**, 310 (1961); L. Wendler and D. Burkhardt, *Z. Naturforsch.* **16b**, 464 (1961).
3. S. J. Hubbard, *J. Physiol. London* **141**, 198 (1958).
4. W. R. Loewenstein and R. Rathkamp, *J. Gen. Physiol.* **41**, 1245 (1958).
5. M. Mendelson, *Med. Electron. Biol. Eng.*, in press.
6. R. Alvarez-Buylla and J. R. de Arellano, *Am. J. Physiol.* **172**, 237 (1953); J. A. B. Gray and M. Sato, *J. Physiol. London* **122**, 610 (1953); W. R. Loewenstein and R. Altamirano-Orrego, *J. Gen. Physiol.* **41**, 805 (1958).
7. The theoretical implications of this phenomenon will be considered in detail in another paper.
8. J. A. B. Gray and P. B. C. Matthews, *J. Physiol. London* **114**, 454 (1951).
9. W. R. Loewenstein, *J. Gen. Physiol.* **41**, 825 (1958); W. R. Loewenstein, *Ann. N.Y. Acad. Sci.* **94**, 510 (1961).
10. This work was aided by research grants from NSF and NIH.
* Present address: Department of Physiology, New York University School of Medicine, New York.

7 February 1964

Speech Sound Discrimination by Cats

Abstract. *Cats trained to discriminate between the speech sounds [u] and [i] do not retain and are unable to relearn this discrimination after bilateral ablation of the ventral insular-temporal cortex. In control animals, retention of this ability is not affected by bilateral removal of primary auditory receiving cortex.*

The ventral insular-temporal cortex has been implicated in the discrimination of tonal sequences by cats; bilateral ablation of this region disrupts the cat's ability to differentiate one tonal triad from another, but fails to alter its capacity of making simple frequency discriminations (*1*). In this report I show that after bilateral ablation of the insular-temporal cortex, cats are also unable to retain or relearn a discrimination between the speech sounds [u] and [i] if these sounds are presented for equal durations at equal overall intensities and fundamental frequencies.

The environment in which the cats were tested was a wire-mesh, cloth-draped cage located in a sound-insulated room. The back panel of the cage was solid and contained three levers and a food-well below the center lever. Stimuli of one-half second duration were repetitively presented from magnetic tape loops through a loudspeaker in the top of the cage.

Five adult cats were initially trained to press the right-hand lever in the presence of a 3700-cy/sec tone, and the left-hand lever in the presence of an 1100-cy/sec tone. A correct response served to terminate the test tone and introduce a second stimulus (the speech sound [a]) for 6 seconds. During this 6-second period, a press on the center lever allowed a food reward, after which another trial began. An inappropriate press of the right or left lever failed to activate the [a] sound or arm the center lever. After the animals had reached a criterion (on the side levers) of 80 percent correct responses over a block of 250 trials, the test stimuli were changed to [i] on the right-hand lever and [u] on the left-hand lever. The speech sound [a] was retained as the stimulus signaling activation of the center lever. The overall intensity of each of the stimuli was equal at 68-db sound-pressure level although a 20-db intensity difference between test stimuli was often given in the initial stages of training to facilitate discrimination. After a criterion of 70 percent correct responses on the side levers over a block of 250 trials was obtained, the fundamental frequency of the test stimuli was changed from 136 cy/sec to 219 cy/sec by changing from a male to a female speaker. Without excep-

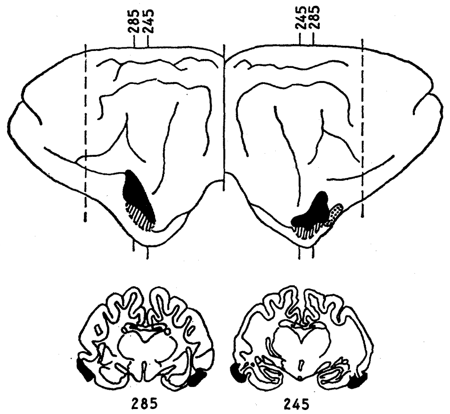

Fig. 1. Lateral reconstructions for cat C, with representative cross sections indicated. The posterior ends of each hemisphere are joined at the midline of the reconstruction. The dashed lines in each lateral view delineate ventral portions of insular-temporal cortex included in the ablation; the stippled area on the reconstruction of the right hemisphere indicates slight scarring of the pyriform cortex.

Table 1. Sessions required for criterion performance. The number of sessions required after ablation shown in parentheses. "Tone" or "Speech" refers to the nature of the stimuli; "Equal" or "Unequal" refers to their intensity.

Subject	Discrimination task: Unequal tones	Equal tones	Unequal speech	Equal speech
Experimental animals				
A	(7)*	4(1)	(10)*	40(>80)
C	15(1)	10(2)	(1)*	49(>98)
D	16(1)		7(2)	38(>76)
Control animals				
B	26(1)			42(1)
E		28(1)		46(1)

* No training prior to ablation.

tion, transfer took place within 50 trials (approximately 7 minutes' testing time) and was generally apparent after ten trials. Completion of the "female speech" control task was followed by a 2-week rest period, after which the animals were again tested with the "male speech" stimuli (all animals retained the discrimination within the first 50 trials). Bilateral subpial ablations were then made of: the insular-temporal cortex (three animals), the entire cortical auditory receiving areas, AI, AII, and Ep (posterior ectosylvian) (one animal), and portions of AII and Ep not bordering on the insular-temporal cortex (one animal). After a recovery period of at least 2 weeks, the animals were again tested, first on the tone discriminations and next on speech sounds.

Table 1 shows that all animals retained every discrimination except that of speech sounds of equal intensity. This particular task was retained by the two control subjects. The three experimental animals, although retaining their ability to discriminate between simple differences in frequency or intensity, or both, in the three-lever situation, did not retain and were unable to relearn the discrimination between speech sounds of equal intensity in twice as many sessions as had been given before they were operated on.

Operative lesions were confirmed by serial reconstructions; Fig. 1 shows the reconstructed cortical lesions of the experimental animal whose deficit on the critical discrimination was the most striking. For this animal (killed 3 months after surgery), no retrograde thalamic degeneration was evident anywhere in the medial geniculate body. It is generally thought (*2*) that the insular-temporal cortex receives only collaterals from axons projecting from medial geniculate to primary auditory cortex, hence a lesion restricted to this area need not necessarily result in retrograde thalamic degeneration. A recent report (*3*) suggests that the insular cortex receives direct input from AI. Since, in control animal E, all the primary auditory cortex was bilaterally ablated and no performance deficit resulted, transcortical connections from AI to the insular cortex appear unnecessary for the critical task.

Performance on the middle lever (the one through which primary reinforcement was received) reached 95 percent at an early stage in the training before the animals were operated on, and was sustained at this level by all five animals after ablation regardless of the discrimination task. This indicates that the experimental animals could still react appropriately to an immediate change from one speech stimulus to another. When, seemingly by chance, they chose the correct side lever, the [u] (or [i]) was replaced by [a]. The animals showed no deficit in detecting this change and responding to it correctly by pressing the middle lever.

The method described here thus yields data on two facets of discrimination: (i) differential response to one of a class of stimuli, and (ii) single response to stimulus change. The ability of the experimental animals to choose between two alternative responses to a single complex auditory stimulus is materially altered after bilateral ablation of the ventral insular-temporal cortex. This cortical area is thus shown to be implicated in the performance of differential responses to complex auditory signals but not in the performance of differential responses to simple differences in frequency or intensity. The central mechanisms through which this finding may be explained remain obscure.

JAMES H. DEWSON, III

Department of Psychiatry,
Stanford University School of Medicine,
Palo Alto, California

References and Notes

1. R. A. Butler, I. T. Diamond, W. D. Neff, *J. Neurophysiol.* **20**, 108 (1957); I. T. Diamond and W. D. Neff, *ibid.*, p. 300; J. M. Goldberg, I. T. Diamond, W. D. Neff, *Federation Proc.* **16**, 47 (1957); J. M. Goldberg and W. D. Neff, *J. Neurophysiol.* **24**, 119 (1961).
2. J. E. Rose and C. N. Woolsey, in *Biological and Biochemical Bases of Behavior*, H. Harlow and C. N. Woolsey, Eds. (Univ. of Wisconsin Press, Madison, 1958); I. T. Diamond, K. L. Chow, W. D. Neff, *J. Comp. Neurol.* **109**, 349 (1958).
3. Ya. A. Al'tman and A. S. Iontov, *Federation Proc.* **23**, T96 (Translation Suppl.) (1964).
4. Supported by a postdoctoral research fellowship, National Institutes of Health and U.S. Army contract MD-2328 to Karl H. Pribram. This work was reported at the 66th meeting of the Acoustical Society of America. I thank K. H. Pribram and H. H. Schaefer.

6 January 1964

The Plankton Community

The report on "Plankton: Optimum diversity structure of a summer community" [*Science* **140**, 894 (24 May 1963)] is open to several criticisms. B. C. Patten, the author, presents a linear programming model of a plankton community which requires that the available resources be allocated in a specific manner to give what he terms the optimum composition (diversity) of the community. From the solution of the author's model this optimum composition represents the standing crop at that point in time when at least one of the essential resources has been depleted.

As a consequence no materials will be available for further growth. This means that there can be no net community production. For this reason the model is not applicable to actively growing plankton populations or those undergoing species succession since only the final composition is specified and not the intermediate stages or the rates at which this optimum is attained. Since the York River plankton community had positive rates of net production, it is not really appropriate to discuss it in the context of the model presented.

The fact that some of the author's terms have one meaning in the model and another in the discussion of the York River is rather confusing to the reader. For example, in the model, *diversity* refers to both the qualitative and quantitative composition of the community. The numerical measure of diversity used for the York River plankton as expressed in bits per milliliter is a function of both the distribution of cells between the species present and the density of cells in the samples. One property of this function is that if the relative proportion of cells representing the various species in a sam-