Mechanisms of Receptor Adaptation

Abstract. *Two determinants of adaptation in a mechanoreceptor (Pacinian corpuscle) are described. Both are filters of non-transients. One, a mechanical filter, prevents static components of the mechanical stimulus from reaching the transducer element (nerve ending). This filter is represented by the laminar capsule of the receptor. When the capsule is eliminated by dissection, the generator potential of the nerve ending in response to a sustained stimulus is markedly prolonged. Another filter is represented by an inactivation process of the mechanisms of nerve impulse initiation which prevents a steady outward current from producing repetitive impulses. Both filters cut the duration of the receptor response to a few milliseconds.*

When a stimulus is applied to a mechanoreceptor and its final intensity is maintained at a stable level, the receptor responds with a series of nerve impulses, the frequency of which is initially high and then declines. This is the common property of receptor adaptation. The rate of adaptation differs widely in receptors. Thus, in some, like the muscle spindle, adaptation takes minutes; while in others, like the Pacinian corpuscle, adaptation to zero frequency is complete within a few milliseconds. At the level of the precursor of the nerve impulse, the generator potential, adaptation manifests itself as a decline in potential, the time course of which resembles the decline in impulse frequency. The mechanisms of adaptation are not yet fully understood. A mechanical hypothesis of adaptation was proposed by one of us in 1956 (*1*). Briefly, according to this hypothesis, the rate of adaptation depends on the mechanical coupling between the external stimulus and the sensor element inside the receptor.

Support for the hypothesis was derived from work on certain touch receptors of the frog (*1*), and on stretch receptors of crustacea (*2*), in which differences in adaptation in generator potential seemed to reflect mechanical properties of the adventitious tissue rather than basic electrical ones of the sensor elements. Strong support for the mechanical hypothesis came later from the elegant experiments of Hubbard (*3*), who, in the Pacinian corpuscle, measured the radial displacement of the outer lamellae during steady compression. These experiments showed that the static component of lamella displacement attenuates markedly from periphery to center of the corpuscle; while the dynamic component, which has a time course resembling that of the generator potential, attenuates less. These results would have been quite conclusive in demonstrating the mechanical nature of generator potential adaptation had there been certainty as to whether the events at the outer lamellae reflect truly those at the inner core of the corpuscle; or, more generally, whether the lamella displacement indicates the mechanical energy field that excites the sensor element. But these are merely reasonable possibilities. Displacements were measured only at the periphery, not in the core where the sensor element is located; displacements within the core were not resolvable (*3*), and, as to the energy field, it is hard to make a prediction for a hydromechanical system which varies all the way from a fluid-filled laminar structure at the periphery to a relative solid one at the core.

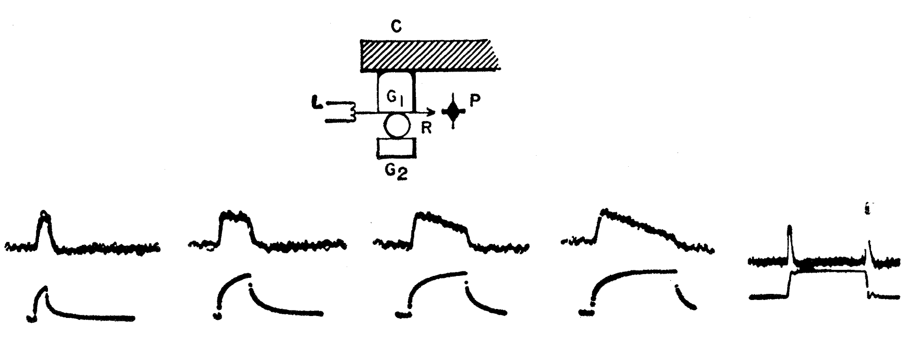

Fig. 1. Top. Diagram of set-up. The decapsulated ending (R) is compressed between a fixed (G_2) and a movable (G_1) plate; G_1 is driven by a Rochelle-salt crystal (C), and the resulting displacements monitored by a photoelectric system consisting of a miniature light source (L) and a phototransistor (P). Bottom. (*a* to *d*) generator potentials in response to mechanical stimuli of varying duration in a decapsulated ending (five to seven superimposed responses). (*e*) Response in an intact corpuscle. Upper beam, response; lower beam, photoelectric record of stimulus. Calibration line: 10 msec; 50 μv upper beam.

In the work reported here, we therefore took another approach. The laminar structure was, to a large extent, by-passed as a mechanical coupling, and the external stimulus applied rather directly onto the sensor element. After a substantial reduction in intermediary mechanical coupling, as represented by the laminar tissue, and in absence of other mechanical filters, one expects in the light of the mechanical hypothesis that the adaptation time of the generator current be prolonged. The experiments, indeed, showed that this is the case.

The lamellae of isolated Pacinian corpuscles (cat's mesentery) were eliminated by dissection. This left the nerve ending (the sensor element) surrounded by only a few core lamellae. As has been shown in previous work, such a preparation continues to be as good a mechanoreceptor as the intact organ (*4*). Stimuli, namely mechanical pulses from a piezoelectric crystal, were applied directly to the preparation (Fig. 1, top). The system was critically damped and monitored photoelectrically with an accuracy of 0.09 μ (*5*). This is particularly important in such experiments as these, which require that there be no repeated stimulation due to mechanical oscillations. Generator potentials were led off with external electrodes from the nerve fiber near its ending (*4*).

Figure 1*e* shows a generator response of an intact corpuscle. The generator potential falls to zero in about 6 milliseconds in the face of a sustained (single) mechanical pulse. This is the typical behavior of the normal generator potential which, in the intact corpuscle, decays with an exponential time course independent of stimulus duration (*6*). Figure 1, *a* to *d*, shows the generator response after removal of the lamellae. The duration of the generator potential becomes now continuously variable with the duration of the stimulus. The range over which the generator response could be made to follow the stimulus duration depended 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

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* Present address: Department of Physiology, New York University School of Medicine, New York.

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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-

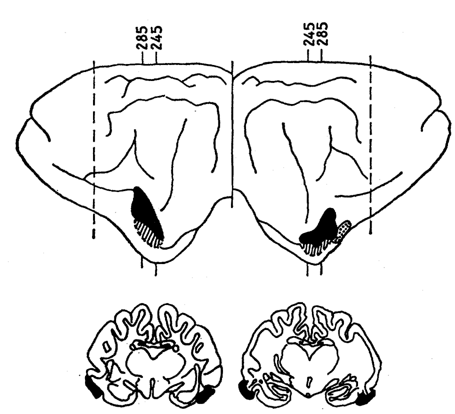

Fig. 1. Lateral reconstructions for cat C, with representative cross sections indicated. The posterior ends of each hemisphere are joined at the midline of the reconstruction. The dashed lines in each lateral view delineate ventral portions of insular-temporal cortex included in the ablation; the stippled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