associated with recognition are faithful accompaniments of perceptual processing; they are sufficiently robust to permit accurate electrophysiological prediction of recognition performance on individual trials.

Finally, these results have implications for neurophysiological theories of perceptual processing and for the interpretation of brain ERP components. The finding that the early N100 component of the ERP varies only with detection, whereas the late P300 component varies with both detection and recognition, parallels the differential involvement of these components with stimulus selection and target detection in selective information processing (*12*). The process of detecting a stimulus may thus begin before the process of recognition or identification, but at later stages detection and recognition seem to be concurrent processes. This view is in accord with recent theoretical elaborations of the SDT model (*13*) and with the hypothesis that detection and recognition proceed together as the nervous system develops probabilistic information of the sensory signal, which forms the basis for perceptual decisions of either type (*13, 14*). The finding that P300 amplitude indexes whether a stimulus will be recognized reliably suggests that P300 may reflect the quality of this information relative to some internal criterion. One interpretation of this finding is that the processes manifested in the P300 component directly influence stimulus recognition. An alternative interpretation is that this brain ERP component is a sign (*15*) of the interaction between more fundamental neurophysiological events and behavioral events. The direction of causality between brain events and behavioral events cannot be determined from these data, and is not presumed. Nonetheless, these results provide what we believe to be the first demonstration that the central electrophysiological events occurring during the perception of sensory stimuli are closely associated with the recognition of these stimuli by the nervous system.

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7. The single-trial EEG epochs were filtered with a minimum mean-square error digital filter. Filter coefficients were chosen individually for each subject to remove high-frequency EEG and EEG components uncorrelated with the ERP. A peak selection and detection routine modified from one developed by C. McGillem and J. Aunon [*IEEE Trans. Biomed. Eng.* **24**, 232 (1977)] searched for and obtained estimates of ERP components.
8. These data should be interpreted in conjunction with the data on the percentage of P300 peaks detected. For ratings 1 to 4, the percentages of peaks detected on single trials (at a 95 percent confidence level) were 85, 90, 86, and 75 percent (recognized targets) and 88, 85, 86, and 76 percent (unrecognized targets). There were no significant differences in the proportions of peaks detected between recognized and unrecognized targets. Thus, the P300 amplitude difference between recognized and unrecognized targets did not depend on the number of peaks reliably associated with these two categories of response.
9. The distance between target type and response in experiment 2 was given a value from 0 to 3, depending on the position of the cell relative to the diagonal in the confusion matrix (for example, correctly recognized targets = 0; 600-Hz target, 1700-Hz response = 2). The Spearman rank-order correlations between distance and P300 amplitude for subjects R.J., T.T., H.F., and A.C. were −.71, −.74, −.88, and −.81 (N = 16, $P < .01$ in each case).
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$$Pc_i(D + R/s) = Pc_i(D/s) - \left(\frac{M - 1}{M}\right)\int_0^{c_i} \frac{1 - Pc(D/s)}{1 - Pc(D/n)}\, dPc(D/n)$$

where M is the target set size, s and n refer to signal plus noise and noise alone, respectively, and $Pc(D/s)$ and $Pc(D/n)$ are the hit and false alarm probabilities, respectively, at the criterion c. The integral was estimated by an area measure

$$\sum_{j=1}^{i} \frac{1}{2}\left[\frac{1 - Pc_j(D/s)}{1 - Pc_j(D/n)} + \frac{1 - Pc_{j-1}(D/s)}{1 - Pc_{j-1}(D/n)}\right] \times [Pc_j(D/n) - Pc_{j-1}(D/n)]$$

where $[1 - Pc_j(D/s)]/[1 - Pc_j(D/n)] \rightarrow 1$ as $Pc_j(D/n) \rightarrow 0$.
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Acoustic Responses After Total Destruction of the Cochlear Receptor: Brainstem and Auditory Cortex

Abstract. *Acoustically evoked neural activity has been recorded from the brainstem and auditory cortex of guinea pigs after complete destruction of the organ of Corti by the aminoglycosidic antibiotic amikacin. These responses to sound differ in important respects from the evoked potentials normally recorded from the auditory pathways. At the brainstem level they resemble the potentials reported by others after stimulation of the vestibular nerve.*

Injury to the organ of Corti by aminoglycosidic antibiotics is a well-documented phenomenon (*1*). It results in a loss of sensitivity of the cochlea to acoustic stimulation beginning with the high frequencies; the functional loss increases as the destruction proceeds from the basal end toward the apex and is proportional to the amount of anatomical damage. Recently we reported examples of complete destruction of the organ of Corti in guinea pigs treated with massive doses of the antibiotic amikacin (*2*). In these animals, in which all sensory cells had disappeared except for a very few outer hair cells at the extreme apex, well-defined, short-latency responses to clicks could still be recorded. Such observations were later repeated in another group of animals, and a more detailed analysis of the characteristics of the responses strongly suggested that they were neural (*3*). On the basis of these data, the site of the acoustico-neural transduction remains unclear. The hypothesis of the stimulation of some nerve fibers still remaining within the cochlea is not easily tenable, whereas the implication of the vestibular system, whose structure and function were preserved, seems more likely. In particular, the possibility of electrical synapses (*4, 5*) in the vestibular neuroepithelia would explain the very short latency and the lack of adaptation of the responses.

This report is concerned with the structures of the central nervous system excited by this peripheral acoustico-neural transduction in the absence of the organ of Corti. It describes the results of far-field recordings of acoustically evoked brainstem potentials together with responses obtained with differential recordings from the auditory cortex in animals for which the peculiar round-window responses and the total cochlear hair cell destructions were also confirmed.

Adult tricolor guinea pigs were used in

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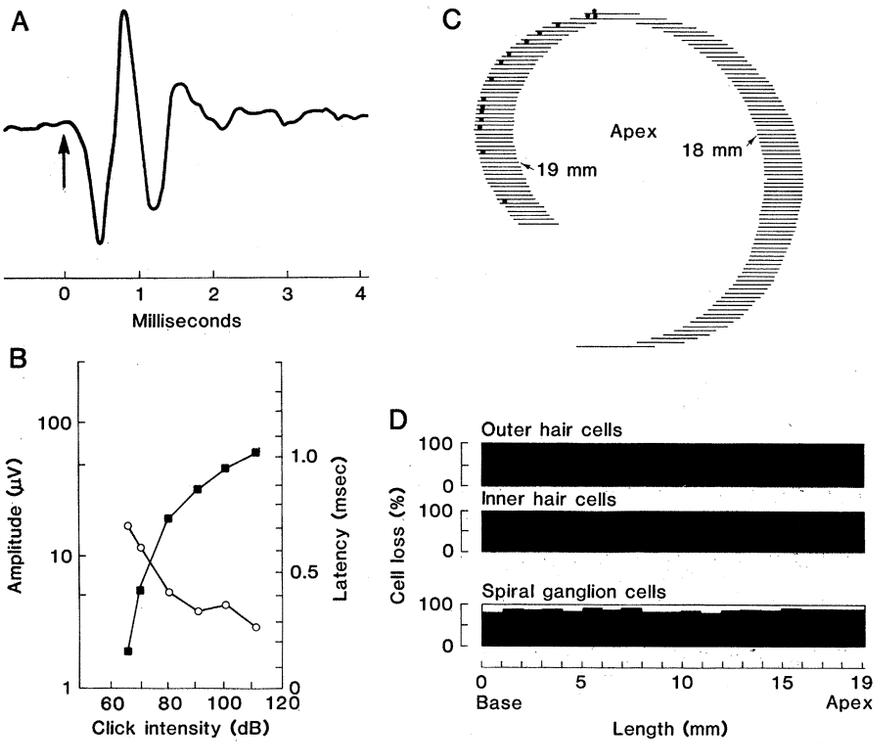
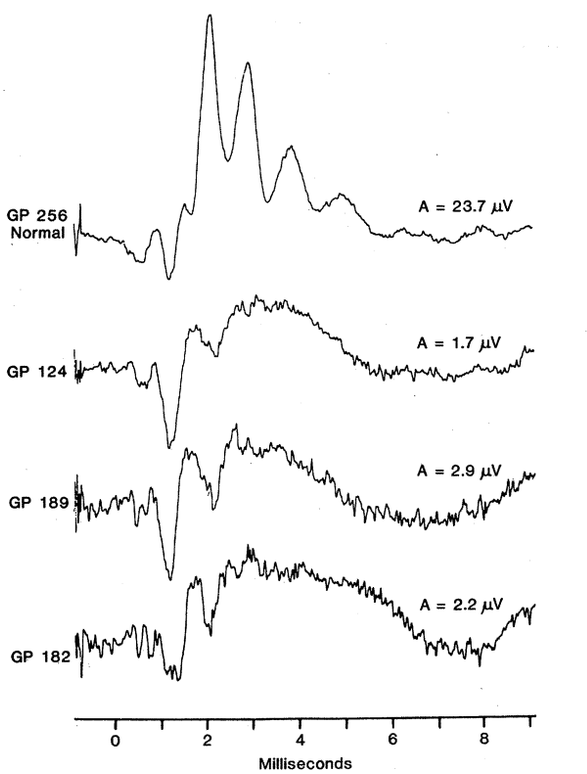


Fig. 1. Guinea pig 117. (A) Waveform of the round-window acoustic response to the unfiltered click at 80 dB NRL (above normal response level). In this and other figures, negativity at the active electrode is plotted downward. (B) Input-output functions for amplitude and latency of the response. (C) Location of remaining outer hair cells in the apical turn. (D) Histocochleograms showing losses (black areas) of outer and inner hair cells and of cells of the spiral ganglion.

these experiments. The animals, treated with high doses of amikacin, were taken from different experimental groups and had undergone the following drug treatment: 14 days of intramuscular injections of 450 mg per kilogram of body weight for guinea pig (GP) 189, 34 days at the same dose for GP's 117 and 124, and 67 days at 150 mg/kg for GP 182. Repeated electrophysiological tests were performed on GP's 117 and 124 for 5 months after the treatment and on GP's 189 and 182 for 12 months. The animals had permanent electrodes implanted at the round window, vertex, and auditory cortex; they were tested more than a week after implantation when they had completely recovered. We followed our routine procedure of implanting a permanent round-window electrode (*6*). In addition, two small stainless steel screws were fixed through the skull, 5 mm apart, touching the dura over the contralateral auditory cortex. A similar screw at the vertex, used as a reference for cochlear recordings, was taken as the active electrode to record brainstem-evoked responses in the far field, and a needle was inserted under the skin of the ipsilateral mastoid to serve as a reference. Round-window and auditory cortex responses



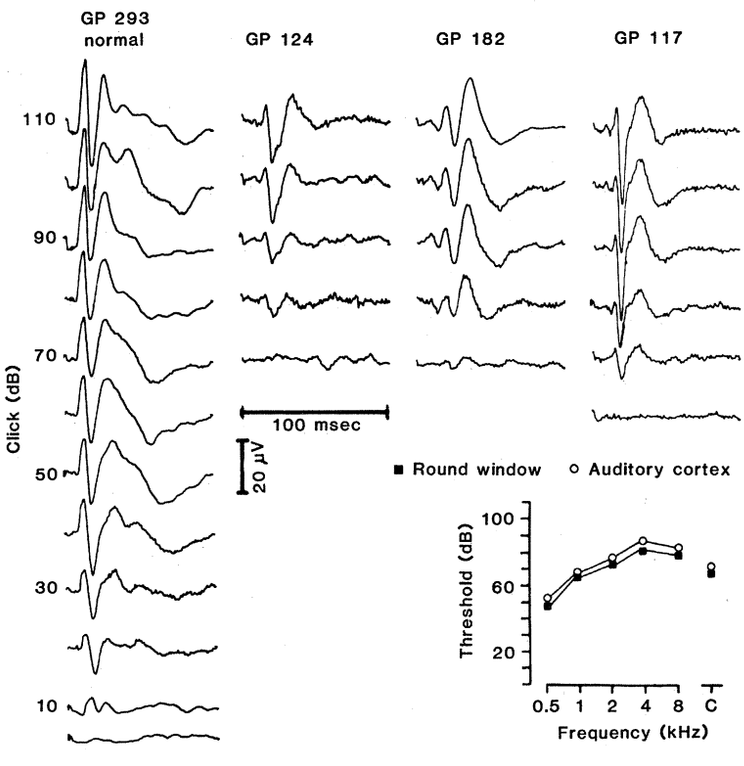


Fig. 2 (left). Far-field brainstem potentials in response to the unfiltered click at 90 dB NRL from normal and pathological animals. Note the reduced amplitude and the absence of late waves for the aminoglycoside-treated guinea pigs. Abbreviation: *A*, maximum peak-to-peak response amplitude. Fig. 3 (right). Click-evoked responses at the contralateral auditory cortex from threshold to 110 dB in 10-dB NRL steps, as observed in a control and three aminoglycoside-treated animals. The amplitudes are comparable, but the waveforms are altered. (Inset) Similarity of frequency thresholds measured with round-window and with cortical responses in GP 182.

were measured in waking, unrestrained animals; for brainstem recordings, however, the guinea pigs were sedated with an intramuscular injection of xylocaine (Rompun) at a dose of 3.75 mg/kg to improve the signal-to-noise ratio, which is poor due to far-field conditions. Acoustic stimuli consisted of an unfiltered click (generated by a 0.1-msec electrical pulse) and a series of third-octave filtered clicks delivered through an earphone (Telephonics TDH 39). Acoustic levels are referred to average thresholds for normal guinea pigs (that is, normal response level expressed as dB NRL). The methods of stimulus presentation and evoked response recordings have been described (*3*, *6*). Frequency threshold curves were determined for all animals, and suprathreshold responses to the broadband click were recorded in 10-dB steps. After these experiments the guinea pigs were killed, and their cochleas were examined with light and electron microscopy. Each cochlea was cut into 10-μm serial sections. For the lower turns, where no hair cells were to be found, every fifth section was examined. For the apical turn, where a few outer hair cells were still present, every section was examined to ensure that all remaining hair cells were counted. Ganglion cell degeneration was also evaluated by examining every fifth section.

For all treated animals, the histological findings as well as the round-window responses were identical to those observed in our previous experiments. Diphasic responses of very short latency could be recorded from the round window of guinea pig cochleas in which later histological examinations revealed a complete destruction of the organ of Corti except for a very few outer hair cells at the extreme apex (Fig. 1). The response, determined with filtered click stimuli, demonstrated greater sensitivity to low frequencies (inset in Fig. 3).

The far-field recording of acoustically evoked brainstem responses, first proposed by Jewett *et al.* (*7*), was later extensively studied in normal animals by Plantz *et al.* (*8*). The evoked response consists of a series of waves appearing within the first 5 msec after the stimulus, representing the activity of brainstem structures from the auditory nerve to the inferior colliculus (*9*) (Fig. 2). The responses from antibiotic-treated animals show a consistent pattern, but they differ from the responses of the control animal, particularly because of (i) their reduced amplitude and (ii) the absence of the normally predominant late waves. This result indicates that the propagation of acoustically evoked neural activity in the brainstem is drastically modified after total destruction of cochlear hair cells. The response pattern of treated animals resembles that evoked by vestibular nerve stimulation as described by Shimazu and Precht (*10*), which is also composed of two successive waves with similar latencies and amplitude ratio. Thus, the acoustic stimulus must excite the vestibular sense organ in these animals lacking a cochlear sense organ.

Differential recordings from the primary auditory cortex with electrodes situated on the guinea pig's temporal lobe area (*11*) were also made. Clear responses could thus be obtained from treated animals. These click-evoked potentials can be compared with those obtained in the same conditions from a normal guinea pig (Fig. 3). Auditory cortex responses from animals treated with the antibiotic are of the same order of magnitude and duration as those from the normal animal, but the first positive peak is reduced and the response is delayed—the negative peak occurs at about 20 msec instead of 15 msec. Thresholds of cortical responses to various filtered clicks were determined and compared with those defined with round-window responses; the frequency-threshold curves thus obtained were similar in all cases (Fig. 3). This result indicates that any recordable evoked activity at the periphery induces a response at the auditory cortex and also confirms the greater sensitivity of these treated animals to low frequencies.

These experiments demonstrate that in guinea pigs with completely destroyed cochlear hair cells, the acoustico-neural transduction we observed at the periphery (*2*, *3*) induces a neural activation of the central nervous system. This excitation propagates to the auditory cortex, although it does not seem to trigger the whole normal sequence of potentials from the auditory nuclei of the brainstem. At both brainstem and cortical levels, the patterns of electrophysiological responses obtained from such animals differ from those observed in normal animals and are therefore difficult to interpret. The resemblance of brainstem responses to the evoked potentials of the vestibular nuclei suggests that the vestibular system may be responding to sound. Such a sensitivity of the vestibular end organs to acoustic stimuli fits well with the evolutionary development of hearing in vertebrates (*12*) and also finds support from electrophysiological recordings of vestibular responses to sound in normal animals (*13*, *14*) and in humans (*15*). On the other hand, the activation of the auditory cortex does not support this hypothesis, since the cochlear and vestibular cortical projections are distinct (*11*, *16*). However, the distortions in the response waveform indicate that this auditory cortical excitation is not the same as in normal animals.

The nature of the sensation transmitted by this neural activity acoustically evoked without cochlear hair cells is unknown. Several observations in humans, generally referred to as the Tullio phenomenon, suggest that the vestibular organ can be activated by intense sound and can then give rise to a sensation of imbalance (*17*). A case of hearing without the organ of Corti has also been reported (*18*). Further studies are being conducted with separate recording from the cochlear and vestibular nerves; they should indicate which peripheral organ is actually responding. At the same time, behavioral methods (*19*) are being explored in an attempt to determine whether these impulses elicit any auditory sensation. The possible existence of similar responses in profoundly deaf human patients should be considered in interpreting the findings of evoked response audiometry.

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Canopy Orientation: A New Kind of Orientation in Ants

Abstract. *Celestial cues, such as the sun or patterns of polarized sky light, appear to have no detectable effect in the precise homing orientation of foragers of* Paltothyreus tarsatus. *Field and laboratory experiments reveal that canopy patterns are a major influence in the home range orientation of this ponerine ant, a common species in African forests. Canopy orientation appears to be well suited to the restrictive lighting conditions of tropical forests.*

Worker ants have one or more orientation mechanisms at their disposal during foraging and homing. Those of most species seem capable of a time-compensated sun orientation (sun compass orientation) (*1, 2*) and of orientation with respect to visual landmarks and to chemical cues (*1, 3*). However, the various orientation mechanisms are usually not in operation simultaneously, but alternatively, with the sequence being dependent on spatial situations (*2*) or on a hierarchical order of the orientation cues available (*4*). Most of our knowledge concerning orientation in ants stems from studies of the phylogenetically more advanced species. Very little is known about such behavior in the phylogenetically primitive ant species. A recent investigation of the African stink ant (*Paltothyreus tarsatus*) has revealed a new kind of visual orientation.

A member of the primitive subfamily Ponerinae, *P. tarsatus* is a scavenger and termite hunter, is widely distributed throughout Africa south of the Sahara, and lives primarily in forested areas (*5*). Its nest occupies a relatively large surface area (~ 10 to 25 m^2) and has multiple entrances. Individual ant workers depart from most of these exits for short foraging excursions on the ground (1 to 5 m). When homing, each returns precisely to the same exit from which it departed.

Celestial cues (sun or patterns of polarized sky light) have no significance in this precise response by *P. tarsatus* foragers. In the African forest (*6*) the view of the sun is restricted by trees most of the time, and even the sky is often completely covered with thick clouds. Despite these conditions, the ants achieve all but perfect orientation. Our experiments indicate that *P. tarsatus* workers are quite unable to use any sort of celestial orientation. When homing foragers were displaced about 20 m from their homing route, with the sun or blue sky (or both) visible above, they did not maintain the correct menotactical course, but rather moved randomly in searching loops. However, when they were placed back on their original path they immediately continued to home correctly. Possible chemical trail orientation was excluded by scraping off an approximately 0.5-cm layer of soil along the homing path before the ants started their return journey (*7*). These results suggest that visual landmarks may be the most important cues by which *P. tarsatus* workers are guided during foraging and homing.

The foraging area was subdivided by a grid (grid squares, 20 by 20 cm), so that it was possible to record the individual courses on a map with a similar grid system ten times reduced. The length of each course was then determined with a planimeter. When the length of an individual course exceeded approximately twice the distance between food source and nest entrance, the test was stopped before the ant reached the nest. As a food source, a portion of a termite nest with many termites exposed was offered at a distance of 200 cm from the nest. When a *P. tarsatus* forager discovered these insects it first killed all it could catch. Next it stacked three to five termites between its mandibles and returned directly to the nest entrance from which it had departed. Seconds after the forager had entered the nest it emerged again, returning directly to the food source. After the ant had traveled three to five times between food source and nest, I destroyed possible chemical orientation trails by scraping the soil along its line of travel.

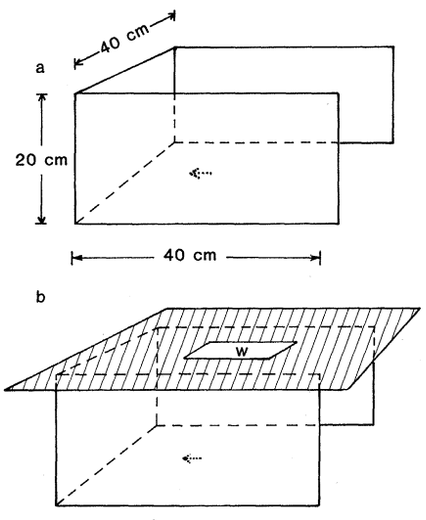

Fig. 1. (a) Blind which restricts the view of the ant (dotted arrow) to the front and to the sides. (b) The blind is covered by a cardboard, so that the ant's overhead view is blocked; *W*, red plexiglass window through which the ant can be observed.

Selected sections of the visual surroundings of the ant were then concealed in order to test their significance as homing cues. The homing ant was first surrounded by a horseshoe-shaped blind, which restricted the view of the ant to the front and to the sides (Fig. 1a). The blind was moved along the ants' course. Surprisingly, the ants still oriented toward home with great accuracy [length of course on map; experimental: $\bar{X}$ = 23.9 cm, standard deviation (S.D.) = 2.2, N = 20; control: $\bar{X}$ = 21.9 cm; S.D. = 1.5; N = 14]. Only when they were about 10 to 25 cm from the nest entrance did they experience difficulty in locating the entrance. When the overhead view was also blocked (Fig. 1b), the ants were unable to orient homeward and meandered randomly. The length of the course always exceeded twice the distance between food source and nest. When, however, only the overhead view was blocked by a piece of cardboard (40 by 40 cm) kept centered about 15 cm above the moving ant, the ant again oriented toward the nest entrance (length of course on map: $\bar{X}$ = 30.0 cm, S.D. = 6.4, N = 21), although its course was less straight than when homing with an unobstructed overhead view (t-test, $P < .001$).

These results suggested that the canopy pattern plays a major role in the home range orientation of *P. tarsatus*. Later, I was able to test this hypothesis in the laboratory under more rigorously controlled conditions. Fragments of a *P. tarsatus* colony consisting of approximately 100 workers were housed in a glass nest (14 by 14 by 1.5 cm) located at one end of a large foraging arena (75 by 150 cm). The ants had access to the arena through a small nest exit which could be closed

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