PERSPECTIVES: NEUROSCIENCE

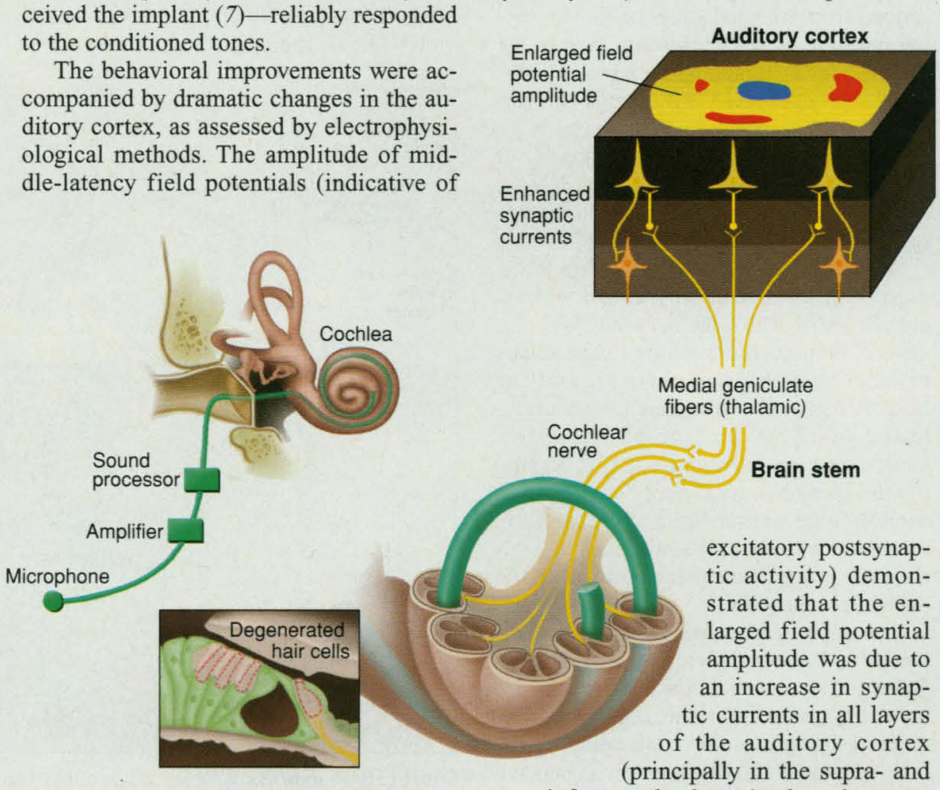
Making Brain Circuits Listen

Josef P. Rauschecker

It is well established that the cerebral cortex (and in particular the visual cortex) of young animals is plastic and able to respond to sensory experience with alterations in synaptic circuitry (*1*). Changes in the mapping of the body surface onto the brain's somatosensory cortex have been reported in response to peripheral injury or enhanced experience in both young and adult animals (*2*). There is relatively less direct evidence for such plastic changes in the auditory cortex (*3*, *4*). Now, on page 1729 of this issue, Klinke *et al.* (*5*) present convincing evidence that the functional auditory cortical map can be expanded in congenitally deaf kittens by electrical stimulation of their intact auditory nerves. The kittens are congenitally deaf due to degeneration of the organ of Corti (the part of the cochlea containing the sensory hair cells of the inner ear that ultimately transduce sound waves into electrical signals) before the onset of hearing. In these animals, the auditory nerves originating from the spiral ganglion cells of the cochlea remain largely intact (see the figure).

Klinke and colleagues implanted an electrical stimulation device (similar to some of the earliest cochlear implants designed for deaf humans) into the cochlea of 3- to 4-month-old kittens (*6*). The device, consisting of simple single-channel monopolar electrodes, electrically stimulates a large portion of the cochlea. Even though this cochlear implant permits only limited recognition of words in humans, it does enable deaf subjects to learn the significance of a variety of environmental sounds. The kittens' implants were connected to a microphone, which transmitted acoustic inputs from their environment (including their own vocalizations as well as those of other cats in the colony). A preamplifier and a sound processor converted the signal from the microphone into an analog time code of the environmental sounds and transmitted these electrical currents to the stimulating electrodes. Immediately after implant surgery, environmental sounds elicited reflexes of the kitten's outer ear (pinna) that are controlled by the brainstem. To make the sounds more behaviorally relevant and to reinforce the use of the auditory channel, the freely moving cats were conditioned to respond to sound stimulation by receiving a food reward with a particular tone burst. After a period of 1 to 3 weeks the kittens—completely deaf before they received the implant (*7*)—reliably responded to the conditioned tones.

The behavioral improvements were accompanied by dramatic changes in the auditory cortex, as assessed by electrophysiological methods. The amplitude of middle-latency field potentials (indicative of cortical activity) recorded on the surface and deep within the auditory cortex increased during the course of chronic electrical stimulation by the implant device. One month after implant surgery long-latency responses (cortical activation with a delay of >150 ms) appeared, which were not present in naïve kittens. The extent of middle-latency field potentials in the auditory cortex was mapped in 70 to 100 locations in each animal. The field potentials increased by a factor of 7 or more in deaf cats receiving electrical stimulation for several months compared with deaf kittens that did not receive implants. Single- and multi-unit recordings confirmed the presence of long-latency responses indicating higher order processing within the auditory cortex. Current-source density analysis (which reveals the pattern of excitatory postsynaptic activity) demonstrated that the enlarged field potential amplitude was due to an increase in synaptic currents in all layers of the auditory cortex (principally in the supra- and infragranular layers) where intracortical processing takes place.



Stimulating hearing. Auditory neural pathways from the cochlea of the inner ear to the auditory cortex in the brain. Hearing can be restored to congenitally deaf kittens with an electrode that stimulates the auditory nerves in response to environmental sound (relayed via a microphone and sound processor). Electrical discharges of neurons in the auditory pathway result in a strengthening of intracortical synapses and an enhancement of neuronal responses to sound. The area of the auditory cortex over which electrically evoked field potentials can be registered is enlarged in cats with early implants (red and yellow) compared to deaf cats (blue).

This dramatic awakening of the auditory cortex in congenitally deaf kittens after chronic electrical stimulation with a cochlear implant exceeds the positive changes found so far at other levels of the auditory pathway (*8*). Larger areas of the inferior colliculus (an auditory processing center in the brainstem) can be activated after intermittent chronic stimulation in cats neonatally deafened with the antibiotic neomycin, and survival of auditory nerve fibers is promoted in such cats. How the (physiologically determined) expansion of the auditory cortical map and the increased synaptic currents in the auditory cortex correlate with morphological changes in neurons is unknown. It was shown recently by staining with the fluorescent dye DiI that the number of dendrites and dendritic branches is greatly reduced in congenitally deaf cats (*9*). Whether electrical stimulation helps to promote the survival of dendrites, increase synaptic efficacy, or induce dendritic sprouting (*10*) needs to be clari-

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fied. New techniques—developed to visualize morphological changes in dendritic spines after long-term potentiation in vitro (*11*)—should provide answers to some of these questions.

Other notable areas that require clarification include the time course and the window of opportunity during which these changes in auditory cortical circuitry take place. Regarding the length of time for which sustained stimulation should be applied, Klinke and colleagues observed substantial changes in hearing capabilities after several weeks (but much shorter periods of stimulation may also prove beneficial). The rapidity of plastic changes under certain circumstances has been demonstrated in various parts of the cerebral cortex, even in adult animals (*12*). Klinke *et al.* and others believe that the most dramatic changes in cortical circuitry are possible if animals are given implants early enough due to the greater plasticity of the brain at a younger age (*4*).

The literature on cochlear implants in humans abounds with examples of failure, particularly for prelingually deaf adults. They never gain language competence and often request that the implant be removed. By contrast, in early-implanted prelingually deaf patients cochlear implants have recently proved quite successful (*13*, *14*). Cochlear implants are highly controversial in the deaf community, their opponents arguing that they violate the physical integrity of individuals who consider themselves different but not disabled (*14*). Visual communication by means of sign language and lip reading are considered good substitutes. This seems to be supported by neuroimaging studies demonstrating a reorganization of language systems in deaf humans capable of comprehending American Sign Language (*15*). Possibilities of compensatory plasticity and sensory substitution (*16*) notwithstanding, the tide is beginning to turn in the deaf community with the advent of a new generation of cochlear implants that combine multichannel technology with intelligent high-speed processors. These new devices permit word recognition rates of 80 to 100% (70% is sufficient to lead a phone conversation) and usually provide immediate success in adults who become deaf late in life. They are in demand by such individuals as well as by hearing parents of deaf children, and the costs of implant surgeries (about U.S.$40,000) are now covered by many U.S. health insurance companies and the British National Health Service.

In the case of early or congenitally deaf individuals, experience has shown that early implantation enhances later success. Even when cochlear implants do not provide a complete electrical code equivalent to that evoked during normal hearing, the brain is clever enough to figure out the rest. The Klinke study shows that the remarkable plasticity of the auditory cortex in young individuals is a major factor in this process, because it permits a representational adaptation to the new electrical code. Animal studies using multichannel devices to stimulate the central auditory system, combined with neuroimaging in humans (*17*), should help to further determine the temporal and spatial constraints of plastic reorganization of the auditory cortex after cochlear implant surgery.

References and Notes

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PERSPECTIVES: APPLIED PHYSICS

Playing Tricks with Light

John Pendry

The notion that altering the structure of a material can profoundly alter its electromagnetic properties has led to concepts such as the photonic insulator, enabling new technologies that offer control over light not previously thought possible. These new materials, often referred to somewhat imprecisely as "photonic materials," have in common the property of strong interaction with light.

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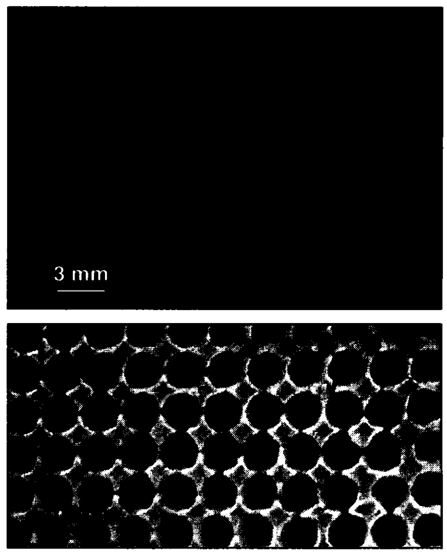
Yablonovitch (*1*) and John (*2*) first pointed out the importance of structure for electromagnetic properties by drawing analogies between light and electrons. Both have a wave-like nature and can therefore be diffracted. We are accustomed to electronic behavior being dictated by the diffraction of electrons from the periodic potential of an atomic lattice. In a normal metal, it is possible to excite the electrons by giving them a small amount of energy to set them in motion, whereas this is forbidden for insulators because of a gap in energy right above the occupied electronic levels. This gap arises from the diffractive interaction of the electron wave function with the atomic lattice, resulting in destructive interference at certain wavelengths.



Strong light diffraction. Assemblies of hollow graphitic spheres show brilliant opalescence. At higher resolution, the regularity of the assembly giving rise to this strong interaction with visible light can be seen (**bottom**). [From (*9*)].

What about light? The interaction of light with a material can be described by the material's refractive index or dielectric constant. Yablonovitch was the first to realize that setting up a periodic refractive index can result in a similar 'band theory' for

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