both on a psychological and neurological level. Accordingly, exposure to the distress and suffering of others can lead to two different emotional reactions. Empathic distress, on the one hand, results in negative feelings and is associated with withdrawal. When experienced chronically, empathic distress most likely gives rise to negative health outcomes. On the other hand, compassionate responses are based on positive, other-oriented feelings and the activation of prosocial motivation and behavior. Given the potentially detrimental effects of empathic distress, the finding of existing plasticity of adaptive social emotions is encouraging, especially as compassion training not only promotes prosocial behavior, but also augments positive affect and resilience, which in turn fosters better coping with stressful situations. This opens up many opportunities for the targeted development of adaptive social emotions and motivation, which can be particularly beneficial for persons working in helping professions or in stressful environments in general.

Future outlook

Despite these recent advances in the neuroscientific study of social phenomena such as empathy and compassion and their plasticity, many questions remain to be answered. Currently, researchers are investigating the longer-term effects of different types of such socio-affective training techniques, focusing not only on their effect on functional brain plasticity but also on changes in brain structure, health-related variables (stress hormones, immune parameters, neurogenetic markers) as well as ecologically valid everyday behavior and cognition (thoughts, prosocial actions, relationships to others).

Longitudinal follow-up studies will also have to determine how long such beneficial changes can be maintained and how these changes can be sustained. In addition, future research is needed to delineate in more detail the neurobiological mechanisms underlying the differential changes observed after empathy and compassion training. One such question relates to the neurotransmitters that are involved. And finally, future developmental neuroscience research may be able to determine critical periods throughout ontogeny which indicate when it is best to teach these socially relevant skills during development. Such knowledge could help to assure an effective education fostering subjective wellbeing, adaptive emotion-regulation, meaningful relationships and human prosociality.

Further reading

Batson, C.D. (2009). These things called empathy: eight related but distinct phenomena. In The Social Neuroscience of Empathy, J. Decety and W. Ickes, eds. (Cambridge: MIT Press), pp. 3–15.
de Vignemont, F., and Singer, T. (2006). The empathic brain: how, when and why? Trends Cogn. Sci. *10*, 435–441.
Eisenberg, N. (2000). Emotion, regulation, and moral development. Annu. Rev. Psychol. *51*, 665–697.
Fredrickson, B.L., Cohn, M.A., Coffey, K.A., Pek, J., and Finkel, S.M. (2008). Open hearts build lives: positive emotions, induced through loving-kindness meditation, build consequential personal resources. J. Pers. Soc. Psychol. *95*, 1045–1062.
Frith, C.D., and Frith, U. (2006). The neural basis of mentalizing. Neuron *50*, 531–534.
Hein, G., Silani, G., Preuschoff, K., Batson, C.D., and Singer, T. (2010). Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. Neuron *68*, 149–160.
Klimecki, O.M., Leiberg, S., Lamm, C., and Singer, T. (2013). Functional neural plasticity and associated changes in positive affect after compassion training. Cereb. Cortex *23*, 1552–1561.
Klimecki, O.M., Leiberg, S., Ricard, M., and Singer, T. (2014). Differential pattern of functional brain plasticity after compassion and empathy training. Soc. Cogn. Affect. Neurosci. *9*, 873–879.
Lamm, C., Decety, J., and Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. Neuroimage *54*, 2492–2502.
Leiberg, S., Klimecki, O., and Singer, T. (2011). Short-term compassion training increases prosocial behavior in a newly developed prosocial game. PLoS One *6*, e17798.
Lutz, A., Brefczynski-Lewis, J., Johnstone, T., and Davidson, R.J. (2008). Regulation of the neural circuitry of emotion by compassion meditation: Effects of meditative expertise. PLoS One *3*, e1897.
Singer, T. (2012). The past, present and future of social neuroscience: a European perspective. Neuroimage *61*, 437–449.
Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., and Frith, C.D. (2004). Empathy for pain involves the affective but not sensory components of pain. Science *303*, 1157–1162.

[1]Max Planck Institute for Human Cognitive and Brain Sciences, Department of Social Neuroscience, Leipzig, Germany. [2]Swiss Center for Affective Sciences, University of Geneva, Switzerland. [3]Laboratory for the Study of Emotion Elicitation and Expression, Department of Psychology, University of Geneva, Switzerland. [4]Laboratory for Behavioral Neurology and Imaging of Cognition, Department of Neuroscience, Medical School, University of Geneva, Switzerland.
*E-mail: singer@cbs.mpg.de

Cochlear implants

Olivier Macherey[1,*] and Robert P. Carlyon[2]

Cochlear implants are the first example of a neural prosthesis that can substitute a sensory organ: they bypass the malfunctioning auditory periphery of profoundly-deaf people to electrically stimulate their auditory nerve. The history of cochlear implants dates back to 1957, when Djourno and Eyriès managed, for the first time, to elicit sound sensations in a deaf listener using an electrode implanted in his inner ear. Since then, considerable technological and scientific advances have been made. Worldwide, more than 300,000 deaf people have been fitted with a cochlear implant; it has become a standard clinical procedure for born-deaf children and its success has led over the years to relaxed patient selection criteria; for example, it is now not uncommon to see people with significant residual hearing undergoing implantation. Although the ability to make sense of sounds varies widely among the implanted population, many cochlear implant listeners can use the telephone and follow auditory-only conversations in quiet environments.

The core functions of a cochlear implant are to convert the input sounds into meaningful electrical stimulation patterns, and then to deliver these patterns to the auditory nerve fibers. In this primer, we shall describe how these two steps are performed, show how the original information present in the sounds is degraded as a result of both device and sensory limitations, and discuss current research trends aiming to improve speech perception, particularly in challenging listening conditions.

Normal and impaired hearing

In normal hearing, sound pressure waves travel down the ear canal and cause the eardrum to vibrate. These vibrations are directly transmitted to the entrance of the cochlea by the small bones of the middle ear (Figure 1). The cochlea is responsible for transducing these mechanical vibrations into action potentials that will further propagate towards the brain and eventually elicit a sound percept. The cochlea is a tiny, fluid-filled, coiled structure divided along its length by a membrane that is large and flexible at one end (called the apex) and narrow and stiff at its other end (called the base). This longitudinal stiffness gradient makes the basilar membrane react differently depending on the frequency content of the incoming sounds.

For sounds with energy in the low-frequency range, vibrations are maximal at the apex of the cochlea, while for sounds with energy in the high-frequency range, vibrations are maximal at the base. This results in a *frequency-to-place* representation of the acoustic input. Attached to this membrane are thousands of sensory 'hair cells', the extremities ('hairs') of which bend back and forth in time with the vibration of the basilar membrane. The bending of the hair depolarizes the cell which then releases neurotransmitter onto the afferent nerve fibers. This finally triggers action potentials that travel to the central auditory system.

Hearing loss can arise from a malfunctioning of any of the anatomical structures involved in the transformation of sound signals by the auditory system. *Sensorineural hearing loss* is the most frequent type and usually arises from a defect at the level of the cochlea. Specifically, when hair cells are degenerated or missing, the transduction process from mechanical vibrations to action potentials is disrupted. If the hearing loss is not too severe, hearing aids, which amplify the sound, can help. In the case of severe to profound hearing loss, however, cochlear implants remain the only way to restore meaningful auditory sensations.

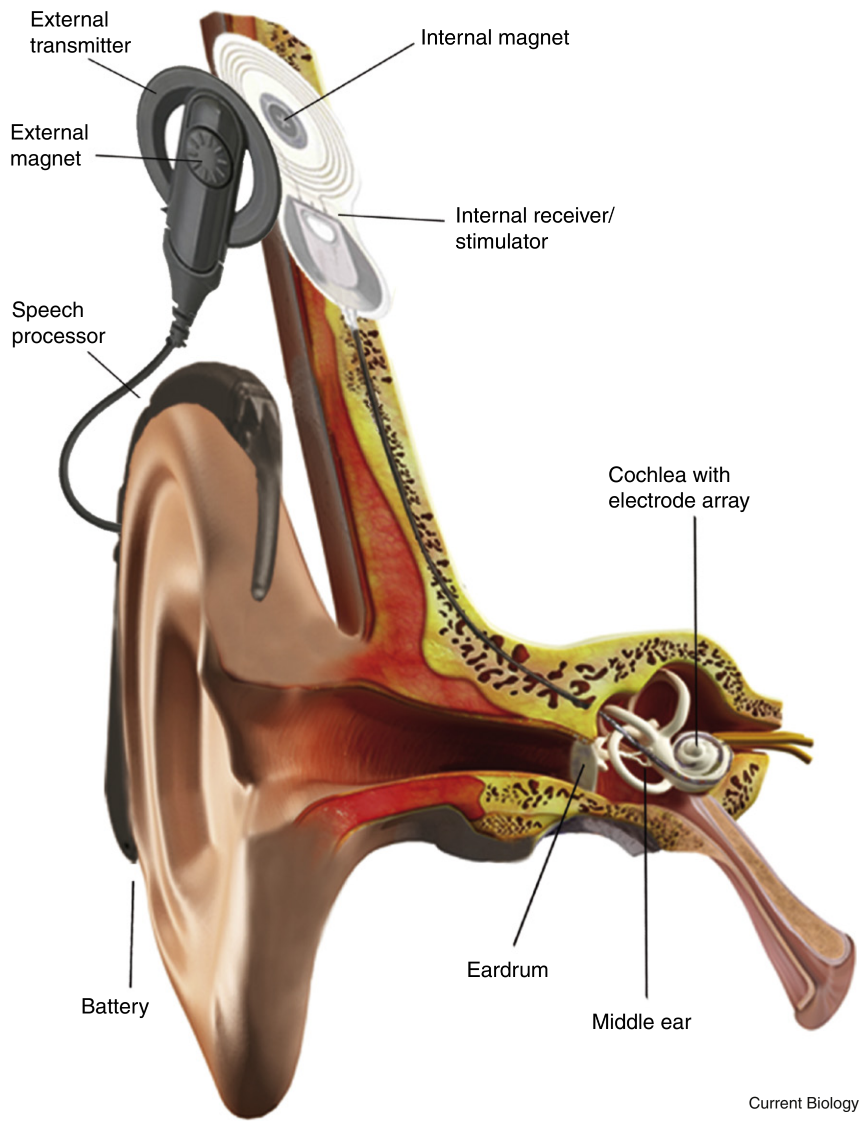

Figure 1. Sketch of a cochlear implant showing the external and internal parts of the device.

What does a cochlear implant do?

A cochlear implant consists of two parts: the first is internal and implanted by surgery; the second is external and worn behind the ear (Figure 1). The internal part of the device comprises an array of 12 to 22 electrodes surgically implanted along the cochlea (Figure 2A). The electrode array usually covers the first one-and-a-half turns of the cochlea and has a length of about 2 cm. The electrodes are connected to one or several internal current sources that are activated according to the instructions received from the external part of the device. Cochlear implants take advantage of the frequency-to-place representation of the cochlea: each electrode contact is located near auditory nerve fibers coding for different frequencies and usually elicits a percept consistent with its location (the electrode colored in red in Figure 2A sounds 'higher' or 'brighter' than the more apical electrode colored in blue).

The external part of the device captures the sound using one or several microphones and converts it into an electrical stimulation code via a battery-powered digital signal processing unit known as the speech processor. This stimulation code, as well as the power needed to activate the electrodes, is transmitted to the internal part via a radio-frequency link. The radio-frequency link consists of a pair of inductively-coupled coils referred to as the external 'transmitter' and the internal 'receiver' which are held in place across the skin by magnets. The receiver decodes the radio-frequency signal and sends stimulation currents to the electrodes according to the information present in the original sound. These currents depolarize the targeted nerve fibers, eventually producing action potentials.

The primary aim of the processing performed by a cochlear implant is to mimic the filtering normally performed by the bypassed portions of the auditory system. Many of

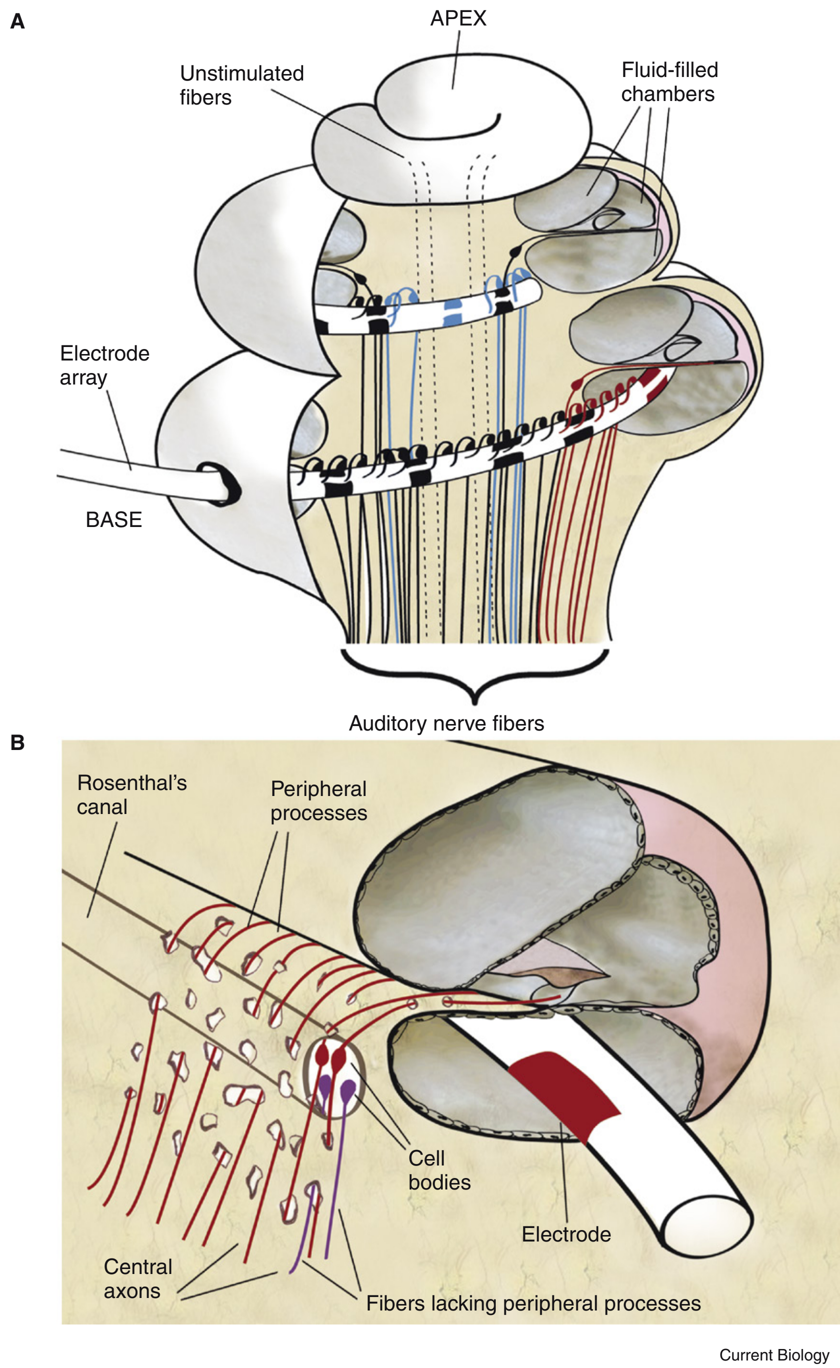

Figure 2. Sketch of an electrode array inserted in the cochlea.
(A) Schematic view of the electrode array positioned in the scala tympani (one of the fluid-filled chambers of the cochlea). For illustration purposes, only a limited number of nerve fibers is represented (in contrast, the normal cochlea comprises approximately 25 000 afferent fibers). In implanted patients, neural degeneration can be substantial and there may be parts of the cochlea where there is no fiber to excite. The apical electrode in blue lies in such a 'dead' region and will recruit fibers that are also activated by the neighboring electrodes, thereby creating cross-talk. Each electrode is meant to recruit auditory nerve fibers in its vicinity. The electrode in red excites fibers naturally coding for higher frequencies (also in red) than the more apical electrode in blue. (B) A cross-section of the cochlear canal. The core of the cochlea is made of bone with pores that allow the passage of the nerve fibers. The nerve fibers are bipolar cells consisting of a peripheral process, a cell body, and a central axon. The cell bodies of all fibers are located in a hollow canal within the bone called Rosenthal's canal. Some fibers may be partially degenerated and lack their peripheral processes (as shown in purple).

the speech-processing methods used in contemporary devices are based on the so-called 'Continuous Interleaved Sampling' (CIS) speech-processing algorithm. After digitizing the sound captured by the microphone, pre-emphasis is first applied: this boosts high frequencies slightly, which, for speech, has the effect of approximately equalizing energy across frequencies. The sound is then passed through a bank of filters that decomposes it into several frequency bands, much like the equalizer of a Hi-Fi audio system. There are usually as many filters as intracochlear electrodes. This processing step is a rough mimicking of the frequency-to-place mapping performed by the basilar membrane. The time-varying envelope of each filter's output is then extracted, somewhat mimicking the behavior of the hair cells. Finally, each envelope is used to modulate the amplitude of a train of electrical pulses that are directed to one of the electrodes.

Figure 3A shows the time-frequency representation of the utterance 'sound' and the corresponding electrical stimulation patterns generated by a hypothetical four-electrode cochlear implant, using the CIS algorithm. The consonant 's' contains high-frequency energy and therefore mostly activates the basal electrode, while the voiced segment 'oun' contains lower frequencies and activates the apical electrodes. Another type of algorithm, mostly used in the device manufactured by Cochlear Corporation, is similar, but, at any one time, only a subset of the available electrodes is stimulated. These 'n-of-m' algorithms select those frequency regions that contain the most energy for stimulation during each time frame.

How are sound features represented by a cochlear implant?

The information contained in the electrical stimulation patterns is used by cochlear implant listeners to extract important cues for sound perception. These cues may, however, not be correctly perceived, as a result of both device and sensory limitations. To disentangle these two sources of limitations, psychophysical studies have been performed using *direct stimulation* where the regular processing of the device is bypassed in order to precisely control the stimulation patterns delivered to the electrodes.

During everyday use of a cochlear implant, the frequency content of the sound is conveyed at any given time by the relative amplitudes of the pulses on the different electrodes. The time-evolution of this frequency content transmits all the important information that allows cochlear implant users to recognize sounds. This is clearly illustrated in Figure 3A, which shows that the electrodes are not similarly active across the whole sound duration. To deliver this frequency-content information accurately, however, the electrodes need to stimulate distinct portions of the auditory nerve array. Although contemporary cochlear implants all possess more than 12 intracochlear electrodes, direct stimulation experiments have shown that these electrodes do not stimulate independent neural populations. For example, some cochlear implant listeners cannot perceive a difference between stimulation of two neighbouring electrodes. It has been estimated that a cochlear implant usually does not convey more than about eight independent channels of information.

Second, the pitch of the sound is determined by the periodicity of the temporal modulations applied on the pulse trains of a given electrode. This is illustrated in Figure 3B, which shows that the electrical stimulation patterns during the voiced segment have modulations that repeat at the fundamental frequency of the speaker. The faster these modulations are, the higher the pitch. Although the envelopes extracted by the speech processor contain temporal modulations up to 400 Hz or more, direct stimulation experiments show that most cochlear implant listeners cannot distinguish between signals having different modulation frequencies when these are higher than 300 Hz. Hence, the limitation seems to be at least partly at the sensory level and imposes a limit on the range of pitches that can reliably be transmitted to the listener.

Third, the loudness of the sound depends on the amount of electrical charge delivered by the electrodes.

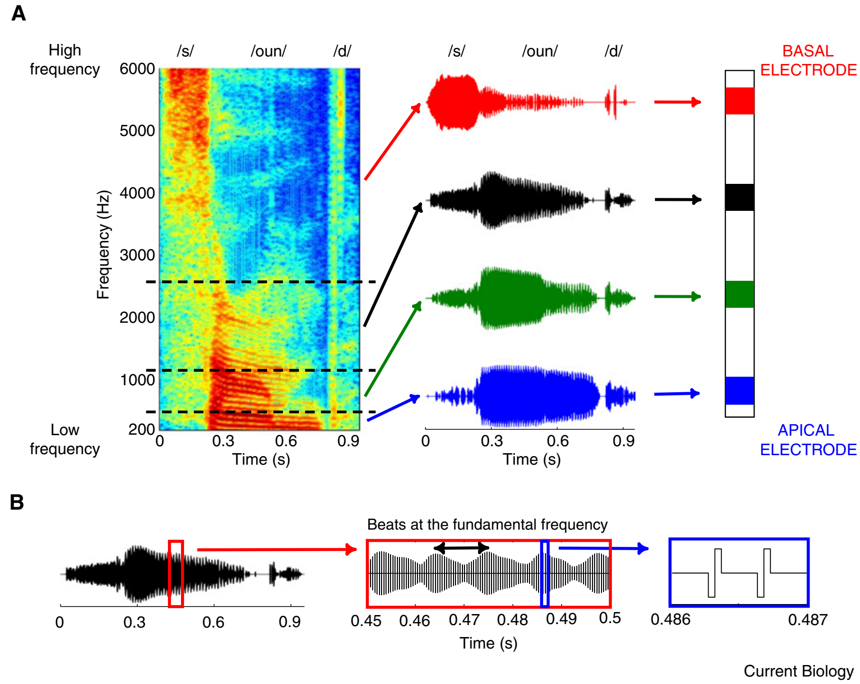

Figure 3. Example of the transformation of a sound into patterned electrical signals by a cochlear implant.
(A) The time-frequency representation (spectrogram) of the acoustic signal ‘sound’ pronounced by a male speaker and its conversion into electrical signals by a hypothetical four-electrode cochlear implant. The spectrogram shows that the different portions of the signal do not contain energy in the same frequency regions. The /s/ consonant contains energy mostly at high frequencies (above 3 kHz) while the /oun/ voiced segment contains energy in the low frequency range (below 2 kHz). Finally, the /d/ consonant contains energy across the whole range. The dashed lines decompose the frequency range in four bands which correspond to the analysis filters of our hypothetical cochlear implant. The time-varying envelope of each band is extracted and further used to modulate the amplitude of a train of electrical pulses. These modulated pulse trains are illustrated in four different colors. Consistent with the original sound, the electrical signal corresponding to the highest frequency band (in red) shows a higher amplitude during the /s/ than during the rest of the sound while the opposite is true for the signals corresponding to lower frequency bands. Each of these electrical signals is further directed to an electrode implanted in the cochlea. The electrical signal originating from the highest-frequency band (in red) is directed to the most basal electrode while that originating from the lowest-frequency band (in blue) is directed to the most apical electrode. (B) Electrical signal delivered on one electrode at different time scales during the voiced segment /oun/. The middle panel shows that the pulses are modulated at about 100 Hz, which corresponds to the pitch of the speaker’s voice. The right panel shows two individual pulses within the signal. These pulses are usually biphasic (they consist of two phases) and symmetric (the two phases have the same amplitude and duration and only differ in their polarity).

Making the sound louder is achieved by increasing the current level or, sometimes, the duration of the pulses. This manipulation increases the total amount of neural activity by recruiting the same fibers more effectively and/or by additionally recruiting more distant fibers. When measured on a single electrode, the ability of cochlear implant subjects to perceive a change in current level (or loudness) may, in some cases, approach that of normal-hearing listeners and be limited by the amplitude resolution of the device. However, this performance collapses when other electrodes are activated concurrently, as typically happens in real life.

These three observations show that the ability of cochlear implant users to extract information about sounds is limited in the frequency, temporal, and amplitude domains. The success of cochlear implants probably has a lot to do with the great faculty that our brain has to adapt to new inputs and with the way that speech can be understood even under greatly-distorted situations. This has been illustrated in several studies that attempted to *simulate* the amount of information transmitted by a cochlear implant device in normal-hearing listeners. It has been shown that, after training, speech in quiet can be understood using only four simulated electrodes, which is fortunately below the number of physical electrodes of all contemporary devices and below the estimated number of independent channels that a cochlear implant listener can perceive. Furthermore, the important modulations needed to understand speech have frequencies below 50 Hz, which is both below the highest modulations that pass through the speech processor and below the highest modulations that can reliably be perceived by cochlear implant listeners.

Listening in more complex situations: room for improvement

While both real and simulated cochlear implant listeners understand speech well in quiet conditions, speech sounds are rarely presented in isolation. The healthy auditory system uses many cues to extract a voice from a mixture of different sounds. These cues include the pitch of the signal, the fine spectral content, and the onset-time differences between the different sounds of the mixture. Similarly, the perception of music is highly related to the ability to distinguish different sound sources and, additionally, to correctly perceive melodies and harmonies.

To accurately perceive speech amidst noise or music, the amount of information needed by the auditory system is much larger than that needed for understanding speech in isolation. It has been shown that more independent electrodes, as well as perception of fast temporal information, are necessary. It is therefore not surprising that, compared to normal-hearing listeners, cochlear implant users struggle to understand speech in the presence of noise or to reliably recognize or even appreciate music. Possible causes for these limitations are detailed below.

Distortions in the frequency domain

Electrical stimulation requires current to flow from one electrode to another. This is usually achieved by stimulating each intracochlear contact with reference to a far-field ground located, for example, on the case of the internal receiver. However, the electrodes lie in a fluid-filled chamber and are separated from the neural elements they have to excite by a wall of porous bone with a much higher resistivity (Figure 2B); consequently, most of the current spreads longitudinally through the less resistive fluids. Electrical stimulation is, therefore, believed to produce a much broader spread of excitation across the auditory nerve array than that achieved in the normal ear.

As an illustration, the basilar membrane of the healthy human ear provides sharp frequency selectivity, equivalent to about 40 non-overlapping filters (i.e. 40 independent electrodes). The lack of spatial selectivity in cochlear implants inevitably creates cross-talk between the electrodes and distorts the internal representation of the frequency content of the sounds. This cross-talk likely explains why cochlear implant listeners cannot benefit from more than about eight electrodes. Hence it is unlikely that perception could be improved by increasing the number of physical electrodes present in contemporary devices, at least until the spatial selectivity is improved.

Distortions of frequency-content information are also inherent to the way the device is inserted. Although the cochlea contains slightly more than 2.5 turns, most electrode arrays are typically implanted only along the first one-and-a-half turns, to prevent mechanical damage to the tissue during surgery (Figure 2A). The cochlear implant may, therefore, not stimulate the apical nerve fibers that naturally code for low frequencies; however, it is important for information about these low frequencies to be transmitted by the electrodes, and so they are conveyed by electrodes that stimulate parts of the cochlea that would normally respond to higher frequencies. In other words, there is a mismatch such that sound information is not sent at the right place in the cochlea.

Finally, depending on the exact path taken by the current, a given electrode may excite neural elements remote from its location. Cases of cross-turn stimulation have been reported whereby a basal electrode excites fibers originating from a more apical turn. This has the effect of exciting off-frequency fibers and distorts the internal representation of the sound's frequency content. Furthermore, because of its close proximity to the auditory nerve, the facial nerve may sometimes be excited by some electrodes, thereby preventing their use for hearing.

Distortions in the temporal domain

On each electrode, the carrier signal used to transmit sound information to the nerve fibers is usually a train of symmetric biphasic pulses (Figure 3B). Each pulse has a very short duration of about 50 μs, which allows sound information to be sampled at a very high rate. Although the internal device is capable of stimulating at rates up to several thousands of pulses per second, no consistent advantage in speech perception tasks has yet been reported for rates higher than about 500 pulses per second. This lack of benefit may sound surprising given that high rates should better sample the fine temporal details of the input sounds. As previously mentioned, however, cochlear implant users cannot discriminate between stimuli differing in their temporal modulations when these are too fast. Four possible causes for this observation are listed below.

First, once a nerve fiber has fired, it enters a state of refractoriness lasting a few milliseconds during which it cannot fire again. Given that neural firings are highly synchronized to electrical stimulation, additional pulses presented during this refractory period may not produce action potentials and, therefore, not contribute to the coding of sounds.

Second, if they do not fire in response to a pulse, nerve fibers need time to return to their resting potential. If consecutive pulses are presented too closely, electrical pulses may not elicit discharges on their own but instead be integrated by the neural membrane and only fire at the time of the second pulse, thereby, once more, distorting the temporal representation of the sound.

Third, the pulses usually have a fixed rate and are only used as a carrier to transmit envelope information. Therefore, the exact timing of action potentials is discarded. This differs from the temporally-precise patterns of neural activity present in normal hearing.

Finally, the pulses have a symmetric shape and consist of two phases of opposite polarities (Figure 3B), both of which can produce action potentials with different latencies. This latency difference is presumably due to different polarities eliciting action potentials at different sites along the fibers (i.e. at the level of their peripheral processes and of their central axons, as shown in Figure 2B). This will have deleterious effects on the exact timing at which action potentials arrive in the cochlear nucleus (the next auditory center), and may therefore disrupt the temporal code transmitted to the central auditory system.

Distortions in the amplitude domain

It is often reported that the difference in level between a comfortably-loud and a just-audible sound is much smaller in cochlear implants than in normal hearing. This reduction in dynamic range may, however, not be a problem *per se* as long as the number of discriminable current steps remains the same.

There seems to be a great variability in the number of current steps that a user can perceive, ranging from a few steps (7) to near-normal (45). In normal hearing, auditory nerve fibers have different morphological properties and are not all excited at the same sound level. The thick fibers are recruited at low levels, whereas the thinner ones have higher thresholds and respond to higher levels. Interestingly, these two types of fiber project to different central structures, and it is possible that loudness information depends on how these structures are relatively excited. In contrast, the recruitment of these different nerve fibers is not controlled in cochlear implant stimulation and it is possible that the thinner ones, which are the most fragile, are partially missing.

Understanding the electro-neuron interface and adapting the stimulation

From the above, it is clear that the current limitations of sound coding in cochlear implants are not solely in the capabilities of the device, but mostly in the failure of the information to go through and correctly pass the electro-neuron interface. In recent years, researchers have tried to better understand this interface and novel speech-processing strategies have been developed.

Manipulating the electrical signals

The electrical signals delivered by the electrodes can be manipulated in two ways, spatially or temporally. It is possible in some devices to alter the spatial delivery of electrical charges. Instead of stimulating one electrode at a time with reference to an extracochlear ground, current can be delivered to several intra-cochlear electrodes simultaneously. Stimulating two electrodes with currents of the same polarity creates *constructive interferences* between the electrical fields and can elicit a percept intermediate to those produced by each electrode alone. These 'virtual electrode' techniques are currently used in the Fidelity 120 strategy of the device manufactured by Advanced Bionics and in the CIC (Channel Interaction Compensation) strategy of the device manufactured by Med-El.

Although such techniques can increase the number of discriminable percepts along the cochlea, they cannot solve the spatial selectivity problem and do not increase the number of independent information channels transmitted to the listener. In contrast, stimulating two or several electrodes with currents of opposite polarities creates *destructive interference* and can, therefore, restrict the current spread spatially. So far, these approaches have shown modest improvements in spatial selectivity but inconsistent effects on speech perception tasks.

Another application of destructive interference is to extend the range of percepts beyond the physical electrode array. Several research reports have shown that it is possible to create a percept equivalent to having an additional 'phantom' electrode implanted more apically. If implemented in a speech-processor, this technique could help recruit apical fibers that are usually not stimulated (Figure 2A). This would also reduce the mismatch between the frequencies extracted by the speech processor and the characteristic frequencies of the nerve fibers. Finally, although still at an experimental stage, two alternatives that may overcome the spatial selectivity problem in the future would be: (1) to insert an electrode array penetrating directly into the auditory nerve; or (2) to optically stimulate the nerve fibers using infrared radiations.

It is also possible to alter the temporal delivery of electrical charges. This can be done by modifying the shape of the electrical pulses and/or by varying their instantaneous rate. One requirement for safe electrical stimulation is that any injected charge should be compensated by the same amount of charge of opposite polarity — that is, the pulses must be charge-balanced. This is achieved in most contemporary cochlear implants by presenting symmetric biphasic pulses consisting of one phase of a given polarity shortly followed by the same opposite-polarity phase (c.f. Figure 3B). An exception is the device manufactured by Neurelec, which uses asymmetric pulses consisting of a first phase followed by a longer and lower-amplitude phase of opposite polarity, so that the pulses are still charge-balanced. Over the last ten years, research studies investigating different pulse waveforms have shed light on the basic mechanisms of auditory nerve excitation.

Using asymmetric pulses, our own work has shown that positive current is much more effective than negative current at stimulating the auditory nerves of cochlear implant patients. We have also used asymmetric pulses to selectively stimulate the apical region of the cochlea and found that these could better convey temporal cues to pitch, extending the upper limit at which pitch can be conveyed to cochlear implant subjects from 300–400 Hz to about 700 Hz. These data are consistent with animal studies showing that neural activity originating from the apex of the cochlea reaches neurons in the brainstem that may be specialized for high temporal acuity.

The FSP (Fine Structure Processing) strategy, implemented in the Med-El device, provides another way to activate this apical path. In this device, the most apical electrodes are inserted deep inside the cochlea and stimulate the fibers with a variable pulse rate time-locked to the original signal. This may have the advantage of reproducing the timing of action potentials present in normal hearing as well as of stimulating the apical path. This technique may allow some temporal coding of pitch, although there is no evidence yet that this form of apical stimulation extends the range of temporal pitch cues that subjects can use.

Improving hearing by less successful cochlear implant users

Variability in performance across cochlear implant patients is tremendous. Using the exact same device and stimulation parameters, one user may understand 100% of words correctly, while another may not get any sensible meaning from what s/he hears. Although part of this variability may have a central origin, it is clear that peripheral factors play a major role. One demonstration of this is that the ability of a given electrode to transmit sound information differs not only between patients but across electrodes for a given person. Some electrodes need less current to elicit a percept, some can transmit temporal modulations that are more easily detectable by the patient, some can produce more spatially-selective excitation, and some yield better pitch perception.

The reasons for this inter-electrode variability are probably two-fold. First, the exact location of each electrode is not controlled during surgery. The electrodes may be positioned at various distances from the nerve fibers. This will have an effect on the current needed to reach threshold and may also affect spatial selectivity. The challenge of modern electrode designs is to be able to position the electrode array close to the nerve fibers and insert it deeply enough to recruit apical fibers whilst avoiding trauma. Trauma can arise when the electrode array perforates the membranes separating the fluid chambers; a recent study has shown that this has a negative impact on speech perception scores.

Second, there is at present no direct way to infer the number of surviving neurons at a given location or their state of degeneration. Figure 2A illustrates schematically that neural survival may not be homogeneous across the cochlea. For example, the apical electrode colored in blue lies in a dead region and excites fibers (also in blue) that will be excited by the neighboring electrodes. Even if not completely degenerated, nerve fibers may lose their peripheral processes as shown in purple in Figure 2B. This may greatly change the way the nerve fibers are excited.

Understanding the causes of inter-subject and inter-electrode variability has become an important consideration. It is likely that future coding strategies will adapt the stimulation patterns on an individual and electrode basis. Furthermore, research is being carried out to find ways to prevent neural degeneration, to regenerate the nerve fibers and to promote the growth of the peripheral processes towards the electrodes.

Better mimicking normal hearing

Finally, the ability to best deliver sound information to cochlear implant listeners depends on a good knowledge of the neural code used by normal-hearing listeners to extract the important cues present in the sounds. Several features of sound coding in normal-hearing listeners are, however, not fully understood. The mechanism underlying our exquisite ability to discriminate tones of different frequencies, for example, still remains a matter of debate. As previously mentioned, pitch cues can only be conveyed to cochlear implant listeners via the temporal pattern of stimulation; however, this purely temporal code breaks down at rates above a few hundred Hertz, and gives poor pitch discrimination compared to that for pure tones in normal hearing.

Interestingly, similar limitations are observed with acoustic pulse trains, filtered so as to contain only temporal cues to pitch, in normal-hearing listeners. There are several possible reasons for this, including the facts that, as with cochlear implants, these stimuli: (i) contain no place-of-excitation cues; (ii) do not excite apical regions of the cochlea, that feed into brainstem neurons that may specialize in fine temporal coding; (iii) produce a 'mismatch' between the rate of stimulation and the range of frequencies to which auditory nerve fibers usually respond; and (iv) do not produce the reliable fine timing differences between the responses of different auditory nerve fibers, and which have been proposed as a mechanism for coding the pitch of low-frequency sounds in normal hearing. Clearly, an understanding of which, if any, of these factors limit pitch perception will have important implications for how to improve pitch perception by cochlear implant users.

Conclusion

Cochlear implants are at an exciting stage of their development. Contemporary devices have become increasingly flexible in terms of their stimulation parameters but most of these functionalities remain unused. The performance of cochlear implant listeners seems to be mainly limited by the electro-neuron interface, which points to a failure to reproduce the complex neural firings of the normal auditory system. Key questions addressed by researchers include: how to bring the stimulation as close as possible to the normal ear by proposing novel stimulation strategies; how to diagnose and take into account subject-specific properties such as the state of neural degeneration or the exact position of the electrode array; and how to regenerate the auditory nerve fibers.

Further reading

Bierer, J.A. (2010). Probing the electrode-neuron interface with focused cochlear implant stimulation. Trends Amplif. *14*, 84–95.
Bonham, B.H., and Litvak, L.M. (2008). Current focusing and steering: modeling, physiology, and psychophysics. Hear Res. *242*, 141–153.
Macherey, O., Deeks, J.M., and Carlyon, R.P. (2011). Extending the limits of place and temporal pitch perception in cochlear implant users. J. Assoc. Res. Otolaryngol. *12*, 233–251.
McDermott, H.J. (2004). Music perception with cochlear implants: a review. Trends Amplif. *8*, 49–82.
McKay, C.M. (2004). Psychophysics and electrical stimulation. In F.-G., Zeng, A.N., Popper, R.R. Fay, (eds), Cochlear Implants: Auditory Prostheses and Electric Hearing. New York: Springer, pp. 286–333.
Pfingst, B.E., Bowling, S.A., Colesa, D.J., Garadat, S.N., Raphael, Y., Shibata, S.B., Strahl, S.B., Su, G.L., and Zhou, N. (2011). Cochlear infrastructure for electrical hearing. Hear Res. *281*, 65–73.
van Wieringen, A., Macherey, O., Carlyon, R.P., Deeks, J.M., and Wouters, J. (2008). Alternative pulse shapes in electrical hearing. Hear Res. *242*, 154–163.
Zeng, F.G., Rebscher, S., Harrison, W., Sun, X., and Feng, H. (2008). Cochlear implants: system design, integration, and evaluation. IEEE Rev. Biomed. Eng. *1*, 115–142.

[1]LMA-CNRS, UPR 7051, Aix-Marseille Univ., Centrale Marseille, 31 Chemin Joseph Aiguier, F-13402 Marseille Cedex 20, France. [2]MRC Cognition & Brain Sciences Unit, 15 Chaucer Rd, Cambridge CB2 7EF, UK.
*E-mail: macherey@lma.cnrs-mrs.fr